

# THE INHERITANCE OF GLUME SHAPE IN *TRITICUM*

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(With Three Text-figures)

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## 1. INTRODUCTION

THE shape and thickness of the empty glume, and the brittleness or toughness of the rachis, are among the most important characters that define the different species of *Triticum*. The genetical relationship between the different types was discussed in an earlier paper (Watkins, 1928), when it was suggested that the factorial relationship between the different types could be represented as follows:

Hexaploids:

<i>vulgare</i>	round, loose glumes and tough rachis	kk.K'K'
<i>speltoid</i>	keeled, thick glumes and tough rachis	KK.K'K'
<i>Spelta</i>	keeled, very thick glumes and brittle rachis	K <sup>s</sup> K <sup>s</sup> .K'K'

Tetraploids:

<i>durum</i>	} keeled, loose glumes and tough rachis	KK
<i>turgidum</i>		
<i>dicoccum</i>	keeled, thick glumes and brittle rachis	K <sup>s</sup> K <sup>s</sup>

k, K and K<sup>s</sup> are allelomorphs to each other, but probably represent groups of completely linked factors rather than single allelomorphs. K' is a similar group carried by one of the additional chromosomes of the hexaploids that remain unpaired when hexaploids and tetraploids are crossed; it affects the same characters and is responsible for the difference in appearance between hexaploids and tetraploids that are otherwise of

the same generic constitution. The morphology of the different types of glume and rachis is fully described in the earlier paper. The linkage group therein described as  $K_2$  is here denoted  $K^s$  in accordance with the report given by Tammes & de Haan (1937); and the factor pair  $B$  and  $b$  (Watkins, 1928; Watkins & Cory, 1931) is denoted  $B_1, b_1$ .

Morphological and genetic evidence was given to support the suggestion that *Spelta* and *dicoccum* both owed their characteristic features to the group  $K^s$ ; but the suggestion was not finally proved, and complete proof was especially needed since the hypothesis, if correct, meant that  $K^s$  had rather different morphological effects in the two groups. In order not to prejudge the question, the group from *dicoccum* will here be denoted  $K^d$ ; we shall then have to consider whether as  $K^d$  and  $K^s$  are identical.

Owing largely to the pressure of other work it has not been possible to present earlier the results obtained by further analysis, which have confirmed and extended the conclusions already reached.

## 2. *T. VULGARE* $\times$ *T. DICOCCUM*

This cross is critical for testing the relationship suggested. In *vulgare*  $\times$  *Spelta*,  $k$  and  $K^s$  segregate normally giving a simple 1 : 2 : 1 ratio, and about 30% of crossing-over with  $b_1$  and  $B_1$  the factors for bearded and tip-awned; in crosses between hexaploids and tetraploids the cross-over percentage of  $k$  and  $B_1$ , in recombination with  $K$  and  $b_1$ , is about 40. The reason for the difference in value found in these two crosses is not definitely known. In *dicoccum*  $\times$  *vulgare*, if  $K^s$  and  $K^d$  are identical, we should be able to show that  $K^d$  and  $b_1$  give a similar cross-over value; and that hexaploid segregates  $K^dK^d, K'K'$ , that is, synthetic *Spelta*, are found as well as the original *vulgare* type,  $kk, K'K'$ .

This expectation was borne out. In the cross *T. vulgare* var. Swedish Iron  $\times$  *T. dicoccum* var. Emmer, the  $F_1 B_1 b_1 K^d k$  was back-crossed to the tetraploid Emmer,  $b_1 b_1 K^d K^d$ , and in a few cases to the tetraploid *turgidum* var. Cambridge Rivet,  $b_1 b_1 KK$ . Classification of the resulting plants as tip-awned,  $B_1 b_1$ , or bearded,  $b_1 b_1$ , was easily effected; and in nearly all cases the keeled plants,  $K^d K^d$ , could be separated at once from the heterozygous rounds,  $K^d k$ , only very few needing to be grown on for confirmation. The results were as follows:

$\varnothing$ gametes	$b_1 K^d$	$B_1 K^d$	$B_1 k$	$b_1 k$	Total
$F_1 \times$ Emmer	53	41	41	61	196
$F_1 \times$ Rivet	10	2	11	14	37
	63	43	52	75	233

Recombinations =  $\frac{75}{233} = 40.8\%$ ; s.e. = 3.2%.

This agrees well with the linkage value found, 39.7%, for the factors  $B_1$  and  $k$  in the cross *vulgare*  $\times$  *turgidum* (Watkins & Cory, 1931), and with the 41.3% given by the rather larger numbers now available, as follows:

♀ gametes	bK	BK	bk	Bk	Total
$M_1 \times$ Rivet	104	75	79	110	368
$F_1 \times$ Iron	37	23	18	24	92
Iron $\times F_1$	35	23	24	33	115
Rivet $\times F_1$	30	17	16	27	90
	196	138	137	194	665

Recombinations =  $\frac{277}{665} = 41.3\%$ ; s.e. = 1.9%.

It seems clear that the factor group  $K^d$  from *dicoccum* segregates with and occupies the same region in the chromosome as  $K$  from *turgidum*, which was already shown to be allelomorphous with  $K^s$  from *Spelta*. To prove how far these two groups  $K^d$  and  $K^s$  are the same we have to compare the synthetic *Spelta* derived from the cross *vulgare*  $\times$  *dicoccum* with the true *Spelta*. From Fig. 1 it can be seen that the two are probably not quite identical. Their general similarity is clear, the synthetic *Spelta* having very tough glumes and a brittle rachis that breaks like *Spelta*, not like *dicoccum*; but the true *Spelta* ear seems to have thicker glumes, especially at the base, than synthetic *Spelta*. For a strict comparison it would be necessary to isolate several true breeding lines of synthetic *Spelta* with 42 chromosomes; and this has not been done, most of the plants examined, including probably the plant illustrated, having less than 42 chromosomes; but in general the impression is that the *Spelta* characters are more highly developed in the true *Spelta* than in the synthetic *Spelta*. Thus, two representative  $F_1$  families homozygous for  $K^d$  were rubbed out, and most ears proved to be less brittle and the grains less tightly enclosed by the glumes than in true *Spelta*; all gave *Spelta*-like breaks except for one ear in which some *dicoccum*-like breaks also occurred. This shows that the factor group  $K^d$  from *dicoccum* may have small differences from the factor group  $K^s$  from *Spelta*, but the conclusion cannot be drawn with certainty since the difference may be due to the modifying influence of other factors.

A general confirmation of the similarity between  $K^d$  from *dicoccum* and  $K^s$  from *Spelta* is given by the cross *Spelta*  $\times$  *dicoccum* which behaves as if the difference between the two species is associated entirely with the extra chromosomes of *Spelta*.  $F_1$  from this cross is intermediate in appearance but resembles *Spelta* rather than *dicoccum*. The rachis usually breaks like that of *Spelta* but a few *dicoccum* breaks were found; on the whole it was less brittle than either parent, an effect that may, however, have been associated with the partial sterility of the ear. The  $F_1$  was

backcrossed to both parents. Nineteen plants from the backcross to *dicoccum* had rachides that broke either like *dicoccum* or with both kinds of break; in  $F_3$ , obtained by self fertilizing these backcross plants, some families bred true to having *dicoccum*-like breaks, others contained plants



Fig. 1. *a*, synthetic *Spelta* from the cross *vulgare*  $\times$  *dicoccum*. *b*, true *Spelta*. *c*, *dicoccum*-like, sterile segregate, descended from the cross (*Spelta*  $\times$  *dicoccum*) back-crossed to *Spelta*; all other segregates were *Spelta*-like, but occasional sterile *dicoccum*-like segregates, lacking both  $K'$  chromosomes were expected. ( $\times \frac{2}{3}$ .)

that gave both kinds of break; this would be expected if the extra *Spelta* chromosomes determined the *Spelta* break. Twenty-four plants from the backcross  $F_1 \times Spelta$  all had *Spelta*-like breaks, and all the  $F_3$  plants examined were the same with one exception. This plant was poorly developed and sterile and resembled *dicoccum* rather than *Spelta*; the rachis was not very brittle but where breaks occurred they were like *dicoccum*

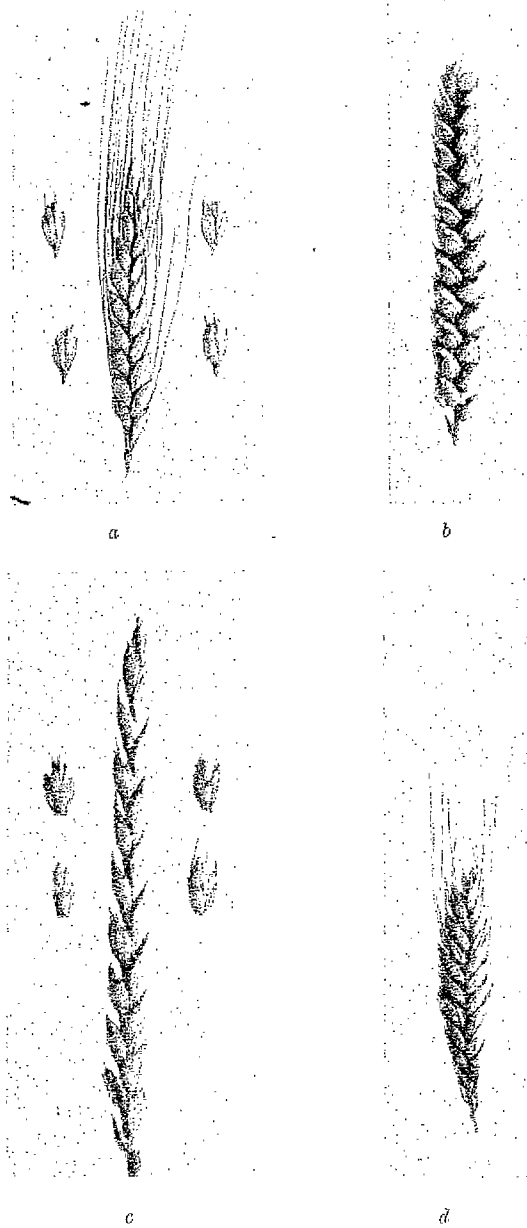


Fig. 2. *a*, *T. dicoccum* var. Emmer. *b*, *T. vulgare* var. Swedish Iron. *c*, Spelt-like segregate extracted from the cross, showing the effect the *dicoccum* group,  $K^2$ , has when transferred from that species to *vulgare*. *d*, round glumed *dicoccum* extracted from the cross. ( $\times \frac{2}{3}$ .)

and not like *Spelta* (see Fig. 1); from its appearance this plant was almost certainly a "sterile combination", lacking both the extra chromosomes determining the *Spelta* break, and therefore provides confirmation of the theory put forward, since such plants would occasionally be expected.

### 3. *T. TURGIDUM* × *T. DICOCIMUM*

The results described show a single difference between *turgidum*,  $\mathbf{KK}$ , and *dicoccum*,  $\mathbf{K}^d\mathbf{K}^d$ . Crosses between these two species might therefore be expected to show unifactorial segregation for  $\mathbf{K}$  and  $\mathbf{K}^d$ , but this expectation was not fulfilled. In the cross *T. dicoccum* var. Ajar, an Indian variety, × *T. turgidum* var. Rivet the  $F_1$  is intermediate, but resembles Ajar rather than Rivet, the glumes being rather thick and adhering closely to the rachis, which breaks up like Ajar when the ear is rubbed out, though less easily. In a large  $F_2$  of some 2000 plants little or no segregation for these characters was observed, all plants being approximately like the  $F_1$ . In this respect the plants show a striking uniformity, and the same appeared in a large  $F_3$  population consisting of 700 families of about twenty plants each. The two parents differ in a number of characters besides those we are dealing with, such as rough and smooth chaff, early (Ajar) and late (Rivet), short (Ajar) and tall (Rivet), colour of chaff, which is grey on red in Rivet, and yellowish white in Ajar with a tendency to form black pigment in some seasons. Some of these characters appeared to give Mendelian segregation. Rough and smooth chaff gave a ratio of 239 rough: 75 smooth; colour was difficult to classify owing to seasonal effects but suggested simple segregation; early and late certainly showed segregation. On the other hand, in the case of tall and short, it is doubtful whether forms as short as the short parent were recovered. The uniformity in glume shape and toughness is readily visible to the eye, but is not easily illustrated. It can be fairly well seen, however, in Fig. 3 which shows a series of glumes in transverse section. In comparison with *turgidum*, the  $F_2$  glumes all have a thickened keel which tends to form a straight line with the face of the glume. A difference in keel thickness can be seen between the two glumes at the left and right hand ends respectively of the uppermost row of the  $F_2$  but these probably represent the extreme difference that would be found in a sample of any size.

Only 700 ears were rubbed out to test brittleness of rachis but all these were uniformly brittle like the  $F_1$  with no evidence of segregation, and the general appearance of the other plants examined, with their thick, tough glumes, suggested that the rachides of all were equally brittle.

The most probable explanation of this behaviour—normal segregation for some characters, and a constant intermediate condition for the

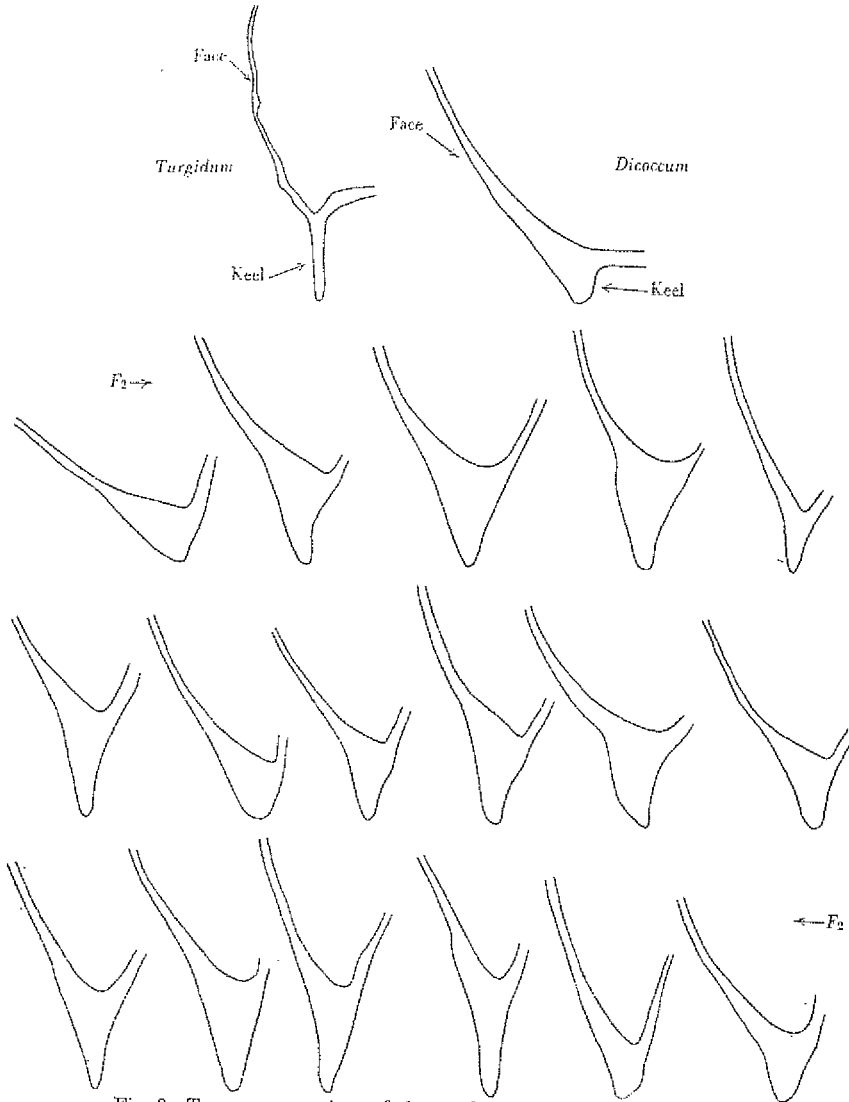


Fig. 3. Transverse sections of glumes drawn in outline with the aid of a camera lucida. ( $\times 20$ .)

tough glumes and brittle rachis—is that the tetraploid species *turgidum* and *dicoccum* each contain two pairs of the factor groups  $K$  and  $K^d$  and that autosyndesis occurs. The gametes of *turgidum* and *dicoccum* carry

KK and  $K^dK^d$  respectively so that the  $F_1$  has the formula

$$K^dK.K^dK,$$

but instead of giving a bifactorial ratio the two chromosomes of *dicoccum* carrying  $K^d$  pair with one another and the two *turgidum* chromosomes carrying K thus

$$K^dK^d.KK.$$

All  $F_1$  gametes will then be  $K^dK$  and all  $F_2$  plants will have the formula  $K^dK.K^dK$  like the  $F_1$ , and like the  $F_1$  will continue to breed true.

The existence of autosyndesis in tetraploid wheat hybrids was first suggested by Darlington (1927) to explain the "shift" in glume length investigated by Engledow (1930) in the cross *durum*  $\times$  *polonicum*, but the occurrence of an  $F_1$  that is a constant intermediate for some characters has not previously been reported.

#### 4. THE RELATIONSHIP BETWEEN *DICOCCUM*, *TURGIDUM*, *VULGARE*, *SPELTA* AND SPELTOID

From the two lines of evidence described we can formulate a more comprehensive scheme for the relationship between the wheat species dealt with, so far as the glume and rachis characters are concerned. The tetraploids, with two series of factors, have the genetic formulae

$$\begin{array}{l} \text{dicoccum } K^dK^d.K^dK^d \\ \text{turgidum } KK.KK \end{array}$$

Both species were found to differ from *vulgare* by only a single linkage group in the segregating chromosomes; so that from the cross with *dicoccum* the formula deduced for *vulgare* would be  $kk.K^dK^d$  plus a third group carried by the unpaired chromosomes, and from the cross with *turgidum* it would be  $kk.KK$  plus a third group carried by the unpaired chromosomes. It must be supposed, therefore, that *vulgare* has the formula  $kk.KK.K^dK^d$ , and that  $K^d$  remains unpaired when it is crossed with *turgidum* and K when it is crossed with *dicoccum* thus:

$$\text{vulgare} \times \text{turgidum } kk.KK.K^dK^d \times KK.KK \quad F_1 (Kk) (KK) K^d$$

$$\text{vulgare} \times \text{dicoccum } kk.KK.K^dK^d \times K^dK^d.K^dK^d \quad F_1 (K^dk) (K^dK^d) K$$

That a different chromosome should remain unpaired in the two crosses is not unexpected, since it would follow of necessity if the two chromosomes carrying K and  $K^d$  do not normally pair, and this was already concluded to be the case in the *turgidum*  $\times$  *dicoccum* cross.

We should then have for the three chief hexaploid types:

$$\begin{array}{ll} \text{vulgare} & kk.KK.K^dK^d \\ \text{speltoid} & KK.KK.K^dK^d \\ \text{Spelta} & K^sK^s.KK.K^dK^d \end{array}$$



where the factor formerly denoted  $K'$  is now identified with  $K^d$ , and  $K^s$  is similar to or identical with  $K^d$ .

These formulae agree with all the evidence given formerly (1928) and in the present paper, though it should be pointed out that a final conclusion is made more difficult by the manifold pairing possibilities that must, it seems, be considered in dealing with these crosses and further confirmation is to be desired. In the meantime it will be pointed out that three further facts, though not in themselves conclusive, are in agreement with the scheme proposed.

The first of these is the origin of speltoids as "mutants" in lines of *T. vulgare*. The gametic formula of *T. vulgare* is  $kkK^d$ . Speltoid mutants would then arise by an internal segregation that substitutes  $K$  for  $k$ , giving  $KKK^d$ , the formula already deduced for speltoid.

The second comes from the cross speltoid by *Spelta*. It is known that both these differ from *vulgare* by a single difference (Watkins, 1928) but this alone is compatible with formulae of the type *Spelta* =  $AB$ , *vulgare* =  $Ab$  and speltoid =  $ab$ , speltoid differing from *vulgare* by two factors and giving *vulgare* segregates, among others, when crossed with *Spelta*. This did not occur however; classification was difficult, and no accurate separation into classes was possible, but no plants fell outside the range of the two parents and segregation was consistent with the formulae suggested, *Spelta* =  $KK.K^sK^s.K^dK^d$  and speltoid =  $KK.KK.K^dK^d$ , and an  $F_1$  ( $KK$ ) ( $K^sK$ ) ( $K^dK^d$ ) that segregated for a single difference. Though this simple segregation could not be proved, the parental types are sufficiently alike that this is not surprising.

Thirdly, Love & Craig (1919) reported the appearance of forms resembling *dicoccoides* from the cross *durum*  $\times$  *vulgare*. The features distinguishing *dicoccoides* are a tuft of hairs at the base of the spikelet and along the sides of the rachis, tough glumes and brittle rachis. No evidence is available for the appearance of the hairs, but the possibility of forms with tough glumes and brittle rachis appearing from a cross between two forms with loose glumes and tough rachis is explicable on the formulae proposed. The formula of *durum* is uncertain, and is considered in more detail below, but it may be assumed, like *turgidum*, to carry the  $K$  group four times. Then in *durum*  $KK.KK \times$  *vulgare*  $kk.KK.K^dK^d$ , if  $K^d$  occasionally pairs with  $K$  from *durum*, instead of remaining unpaired as it does in crosses with *turgidum*, occasional tetraploid segregates having the gametic formulae  $KK.K^dK^d$  would be found, and these would have tough glumes and brittle rachis like the *turgidum*  $\times$  *dicoccum*  $F_1$  described above.

5. *T. DURUM* AND OTHER WHEATS

Typical *durum* and *turgidum* differ from each other by a flinty instead of mealy grain and a number of vegetative characters; but transition forms, the result probably of intercrossing, are not uncommon in regions like Greece where both species are found. The glumes of the two species, though usually recognizable if one is familiar with them, are not markedly different; both are keeled, and it would be expected that they have the same formula, **KK.KK**. This is confirmed by a cross between a beardless round Emmer, **kk**, and a beardless Indian Runner (extracted from *vulgare* × *durum* var. Indian Runner), which gave clear 1 : 2 : 1 segregation for the characters keeled and round. In crosses between *durum* and *vulgare* however, instead of the simple segregation of 1K : 1k found for *vulgare* × *turgidum*, considerable difficulties are met with. The evidence does not permit a final interpretation, but it may be suspected that as a result of translocations, inversions or other changes, the arrangement in the chromosomes of the factors constituting the **K** group is different in *durum* from that found in *turgidum*. The nature of the evidence will be briefly considered.

The *vulgare* parents used were either Swedish Iron or a variety from Croatia (Yugoslavia); the *durum* parents were Indian Runner and a variety from Morocco numbered D 27/2. Other crosses for which exact data are not available behaved in a like manner. The most striking feature is the difficulty of isolating round glumed *durum*. In the *turgidum* cross,  $F_1$  × *turgidum* gives a ratio of 1 **KK** : 1 **Kk**; the **Kk** forms are easily separated from the **KK**, and true breeding round, **kk**, are easily obtained in the following generation. In the *vulgare* × *durum* crosses this does not happen;  $F_1$  × *durum* gives plants in few of which is it possible to detect any roundness. This presumably means that keeled is dominant; but it is further found that round is uncommon in the following generation and true breeding rounds are difficult to extract. The rarity of the round plants and difficulties in classification have made analysis difficult, but the principles seem clear from the evidence given below and a more detailed analysis will be made later.

In the first place, segregation for **B**<sub>1</sub> and **b**<sub>1</sub> approaches normal.

CROSS	<b>B</b> <sub>1</sub>	<b>b</b> <sub>1</sub>	Ratio found in families descended from heterozygotes, expect 3 : 1
(Iron × D 27/2) × D 27/2	13	9	90 : 12
" " × Iron	5	4	—
(Iron × Indian Runner) × Indian Runner	3	9	90 : 25
" " × Iron	3	9	45 : 21
(Croatian <i>vulgare</i> × D 27/2) × Moroccan <i>durum</i>	7	5	111 : 35
" " × D 27/2	6	4	43 : 19
	37	40	239 : 100 (omitting 90 : 12)

The ratio for  $B_1 : b_1$  approaches 1 : 1; good 3 : 1 ratios are obtained in the following generation, and beardless 28 chromosome segregates have been extracted. The ratio 90 : 12 found in one case differs significantly from 3 : 1 so that irregularities may sometimes be found; but in general it is clear that, as in *vulgare* × *turgidum* crosses,  $B_1$  and  $b_1$  are carried by chromosomes that pair and segregate normally.

$K$  is linked to  $b_1$ ; so whatever the irregularities in the inheritance of  $K$  may be we must assume that it also is carried by a chromosome that segregates normally. It should, therefore be present in half the plants obtained by backcrossing, and if the data are examined from this point of view a number of significant facts emerge. The classification beyond  $F_2$  was carried out by Dr S. Ellerton and in many cases was checked by the writer, substantial agreement between the two being recorded. Those classed as intermediate were sometimes separated from keeled with difficulty.

The most extensive data were obtained from the cross (Iron × D 27/2) × D 27/2, which was carried to  $F_4$ .

*Segregation in vulgare × durum (Iron × D 27/2) × D 27/2*

$F_2$ no.	$F_2$ classification	$F_3$ segregation for keeled and round
1	Bearded keeled	13 keeled plants
2	"	6-7 keeled : 3-2 intermediate
3	"	4 keeled
4	"	13 keeled
5	"	12 keeled
6	"	11 keeled : 4 intermediate
7	"	10 keeled
8	"	5 keeled
9	Bearded intermediate	2 keeled : 7 intermediate : 9 round
10	Beardless keeled	2 keeled : 3 intermediate
11	"	10 keeled : 5 intermediate : 2 round
12	"	4 keeled
13	"	1 keeled : 6 intermediate : 1 round
14	"	14 keeled
15	"	1 keeled : 4 intermediate : 1 round
16	"	5 keeled
17	"	6 keeled
18	Beardless intermediate	0 keeled : 4 intermediate : 4 round*
19	Beardless keeled	2 keeled : 4 intermediate : 1 round
20	"	3 keeled : 4 intermediate : 1 round
21	Beardless intermediate	1 keeled : 3 intermediate : 4 round†
22	"	2 keeled : 3 intermediate : 2 round

\* From  $F_4$  data.

† Confirmed in  $F_4$ .

Some families are small; but if we disregard this we have 10 families breeding true to keeled: 12 families segregating for keeled and round or intermediate. This suggests the 1 : 1 ratio expected for a backcross, and that keeled was generally more or less dominant to round. The segregating families do not all give the same ratio; that there are at least two different

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ratios is shown if we separate families descended from intermediate  $F_2$  plants from those descended from keeled  $F_2$  plants.

	Keeled	Inter	Round
From intermediate $F_2$ plants	2 0 1 2	7 4 3 3	9 4 4 2
Total	5	17	19
From keeled $F_2$ plants	6-7 11 2 10 1 1 2 3	3-2 4 3 5 6 4-5 4 4-5	0 0 0 2 1 ?1 1 ?1
	36-7	32-5	4-6

The two series deviate in opposite directions from the expected 1 : 2 : 1.

If all the crosses available are classified on the same assumption—that a backcross ( $F_2$ ) plant with only keeled progeny was  $KK$ , and one that gave any number of round in its progeny was  $Kk$ —we obtained the following result for the  $F_1$  gametes:

Cross	$b_1K$	$b_1k$	$B_1K$	$B_1k$
(Iron × Indian Runner) × Indian Runner	5	4	0	3*
(Iron × Indian Runner) × Iron	4	3	2	1
(Croatian <i>vulgare</i> × D 27/2) × D 27/2	4	1	3	2 + ?1
(Croatian <i>vulgare</i> × D 27/2) × Croatian	3	1	4	2
(Iron × D 27/2) × D 27/2	6	3	3	9
(Iron × D 27/2) × Iron	0	3	3	2 ? since numbers within the families were small
	22	14	15	19 + ?1 total = 71

\* 1 large  $F_3$  family was

Keeled	Inter	Round
12	8	1 beardless
23	34	8 beardless
35	42	9

Recombination =  $\frac{7}{35} = 41\%$ , s.e. = 6%.

The numbers are small but the recombination value is the same as in the *vulgare* × *turgidum* cross and is therefore consistent with the previous conclusion that the chromosome carrying  $b_1$  and  $K$  pairs and segregates normally in  $F_1$ .

The seven families from (Iron × Indian Runner) × Indian Runner that segregated for keeled and round gave a total ratio of 77 keeled : 69 intermediate : 16 round, a significant deficiency of round and heterozygous plants, and not very different from the ratio 36 : 32 : 4 found for the eight

families from (Iron  $\times$  D 27/2)  $\times$  D 27/2. There were no families corresponding to the four families of the latter cross that gave 5 : 17 : 19 excess of round.

The six families from (Iron  $\times$  Indian Runner)  $\times$  Iron that segregated for keeled gave a total of 10 keeled : 30 intermediate : 29 round, a significant deficiency of keeled and heterozygous plants. Backcrossing to the hexaploid therefore gives plants segregating too few keeled, while backcrossing to the tetraploid gives plants segregating too few round.

From these results the following conclusions are suggested:

- (1) As a general rule the chromosome carrying **K** and **b<sub>1</sub>** segregates normally, with normal crossing-over, in the  $F_1$  between *durum* and *vulgare*.
- (2) **B<sub>1</sub>** and **b<sub>1</sub>** often, but not always, give normal 3 : 1 ratios.
- (3) When tetraploid heterozygotes, **Kk**, are selfed there are too few round tetraploid segregates. This is not the effect of irregular segregation but of elimination of zygotes or pollen-carrying **k**. In a few families instead of too few round segregates there are too few keeled and excess of round. These results would follow if, for example, **k** were linked to a deficiency and crossing-over occurred between **k** and the deficiency.
- (4) In hexaploid heterozygotes, **Kk**, there is excess of round segregates and defect of keeled. This means that the extra chromosomes of *vulgare* are responsible for modifying the ratio, as they would for example if they carried the sector for which the **k** chromosome was deficient.
- (5) The deficiency linked to **k**, or whatever else is responsible for the aberrations, comes from the **k** chromosome of *vulgare*. It is effective in tetraploid segregates from crosses with *durum* but not in tetraploid segregates in crosses with *turgidum*.

These results suggest that the **K** chromosomes in *durum* and *turgidum* are structurally different. The exact nature of the changes can best be considered after further study. The results here presented suggest certain conclusions, but the small size of many families and the difficulties of classification make it possible that there may be other irregularities besides those summarized above.

#### CONCLUSION

The results described show that the differences in glume shape, and in brittleness or toughness of rachis, that characterize the different wheat species are largely controlled by a group of completely linked factors carried by a chromosome pair that is present twice in the tetraploids and three times in the hexaploids. An extensive survey of the world's wheats

confirms the view that the formulae proposed—*dicoccum* =  $K^dK^d.K^dK^d$ , *turgidum* =  $KK.KK$ , *vulgare* =  $kk.KK.K^dK^d$ , *Spelta* =  $K^sK^s.KK.K^dK^d$ —are diagnostic for the species: e.g. all *vulgare* wheats, judging by inspection, contain the group  $k$ , with the exception of the occasional speltoids,  $KK.KK.K^dK^d$ , that arise from them by internal segregation. It is, of course, possible that  $k$  is not identical in all *vulgare* wheats but it is clear that any differences that occur within the species are small compared with the difference between  $k$  and  $K$  or any of the other groups found in other species.

The two forms of *durum* used as parents contain  $KK.KK$ , like *turgidum*, but the chromosomes concerned are structurally different from those in *turgidum*. It is suspected that this difference is characteristic of the species *durum* but no other forms of this species have yet been tested. The difference occurred in crosses with *vulgare* forms from China and Australia, as well as the two from N.W. Europe and Yugoslavia referred to in this paper. An Abyssinian tetraploid, which in the writer's view is not readily to be classified either as *durum* or as *turgidum*, behaved like *turgidum* in this respect. The data do not allow us to specify exactly the nature of the structural changes involved.

$K^s$  and  $K^d$  are closely similar but may not be identical.

Among the hexaploid wheats, *Spelta* shows little variation either in vegetative or ear characters. The known forms suggest the possibility that a change in the  $K$  group alone differentiates them from *vulgare*; indeed, if  $K^d$  and  $K^s$  are actually identical, *Spelta* could have originated from *vulgare* simply by internal segregation,  $kk.KK.K^dK^d$ , giving  $K^dK^d.KK.K^dK^d$ , which would be identical with  $K^sK^s.KK.K^sK^s$ . This would agree with Flaksberger's conclusion, on linguistic, cultural and other evidence (1930), that *Spelta* arose from *vulgare* north-west of the Alps at some time since the Stone Age; but it needs first to be tested by a more exact analysis.

Among the tetraploids, *durum* and *turgidum* differ by several characters, such as grain texture and presence of hairs on the leaves, which there is no reason to suppose are linked to the  $K$  group; but it is interesting that changes in the chromosome carrying  $K$  seem to be associated with the specific difference. Modern *dicoccum* is undoubtedly a relic of greater diversity, and we cannot say without a separate investigation whether it differs from other tetraploid species, such as *durum*, only by the differences between  $K^d$  and  $K$ . In general, however, the comparative simplicity of the results here described suggest that when fully worked out they should enable us to obtain more exact evidence on the origin

and relationship between the wheat species than has hitherto been possible.

## SUMMARY

1. The most important characters diagnosing different wheat species are the shape of the empty glume and brittleness or toughness of the rachis. It was shown earlier that hexaploid *vulgare* and tetraploid *turgidum* differ by allelomorphous units  $k$  and  $K$  that affect a number of characters and probably represent groups of completely linked genes.  $K$  and  $k$  are linked to  $B_1$  and  $b_1$ , genes for tip awns and bearded, with a crossover value of about 41%. A third group,  $K^s$ , present in the hexaploid *Spelta* is allelomorphous to  $k$  and  $K$ , and gives about 30% crossing over in crosses between *Spelta* and *vulgare*.

2. The group  $K^d$ , present in the tetraploid *dicoccum*, is allelomorphous to  $k$  and gives a cross-over percentage of about 41 with  $B_1$  and  $b_1$  in crosses between *dicoccum* and *vulgare*. Transferred to *vulgare*,  $K^d$  gives forms resembling but not necessarily identical with true *Spelta*.  $K^d$  is therefore similar to or identical with  $K^s$ .

3. The effect of  $K^d$  in the tetraploid species is rather different from its effect in the hexaploid species, as suggested earlier.

4. Crosses between the two tetraploid species *turgidum* and *dicoccum* give an intermediate  $F_1$  that breeds true for the characters considered. This is explicable on the assumption that *turgidum* is  $KK.KK$  and *dicoccum*  $K^dK^d.K^dK^d$ , and that autosyndesis occurs in  $F_1$  and later generations.

5. These results all agree with the following formulae:

<i>dicoccum</i>	$K^dK^d.K^dK^d$
<i>turgidum</i>	$KK.KK$
<i>vulgare</i>	$kk.KK.K^dK^d$
speltoid	$KK.KK.K^dK^d$
<i>Spelta</i>	$K^sK^s.KK.K^dK^d$

where  $k$ ,  $K$ ,  $K^d$  and  $K^s$  are allelomorphous groups of completely linked genes and  $K^s$  is similar to or identical with  $K^d$ .

6. Like *turgidum*, *durum* probably has the formula  $KK.KK$ , but with a different gene arrangement within the groups concerned.

7. If these conclusions are correct the most conspicuous features differentiating the five wheat species considered are caused by variation in a single chromosome present four times in the tetraploids and six times in the hexaploids.

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