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# The genetic regulation of meiotic behaviour in wheat and its relatives

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The study of the genetic regulation of meiotic behaviour in *Triticum aestivum* is necessary for a number of reasons, both theoretical and practical. From the practical standpoint, the course of meiosis is of fundamental importance to the reproductive processes upon which yield depends. Moreover, the success or failure of many breeding procedures depends upon the outcome of meiotic events, and it has now been established that the genotype can be adjusted to increase the probability of certain of these. In addition, without a grasp of the genetic regulation of meiosis, it would be difficult to comprehend the cytogenetic structure of wheat in the manner demanded by the application of certain modern breeding techniques.

The course of evolution of any polyploid species is closely related to changes in its organisation of meiosis. A unique opportunity is offered by *T. aestivum* for the study of the outcome of the evolution of the organisation of meiosis, and inferences can be drawn of the means by which the present organisation was attained. This permits a wider understanding of the polyploid evolution of the genus and makes *Triticum* an example that must be considered by all interested in the evolution of plants.

Further, the cytogenetic techniques available in *T. aestivum* make it possible to provide detailed information on the genetic regulation of meiosis that is unattainable in other species. It is, therefore, of the utmost importance that those of us who have the opportunity to work with wheat should exploit its peculiar potentialities to the full.

The present paper is an attempt to summarize and collate the present state of our knowledge of the genetic regulation of meiosis in wheat. In the space available there has not been much opportunity for the inclusion of original results but the detailed evidence for all the work quoted is already, or will be shortly, available elsewhere.

## The meiotic diploidizing system

A hint that chromosome 5B of *Triticum aestivum* (2n=6x=42) performed some function in the regulation of meiotic behaviour was provided by OKAMOTO (1957) who proposed that it carried an asynaptic gene or genes. Subsequently RILEY and CHAPMAN (1958) and SEARS and OKAMOTO (1958) were able to suggest that the activity of 5B resulted in an alteration in the meiotic affinities of chromosomes rather than in a change in the amount of pairing. The evidence for this came from the large increase in non-homologous meiotic pairing in nulli-5B haploids, relative to euhaploids, and in *T. aestivum*×einkorn hybrids deficient for 5B.

Because of the frequency of trivalents and the rarity of quadrivalents in nulli-5B haploids, RILEY and CHAPMAN (1958) suggested that an activity of the chromosome might normally preclude meiotic conjugation between homoeologues. Moreover they were able to demonstrate that multivalent formation, resulting from non-homologous as well as homologous pairing, takes place in 40-chromosome plants nullisomic for 5B.

Non-homologous pairing and recombination result in the production of translocations relative to the original chromosome structure. RILEY and KEMPANNA (1963) used translocations originating in this way to determine the relationships between the chromosomes that had paired non-homologously. The chromosomes were identified that participated in nine distinct translocations extracted from a parent nullisomic for 5B and tetrasomic for 5D. This genotype was employed because tetrasomy for 5D compensates for the sterility normally caused by nullisomy for 5B, without preventing non-homologous meiotic pairing. All the translocations were between homoeologous chromosomes so vindicating the original hypothesis that the activity of chromosome 5B resulted in the meiotic diploidization of hexaploid wheat. The regular disomic inheritance, and classical allopolyploid behaviour, of *T. aestivum* therefore depends upon this activity. Removal of chromosome 5B leads to a breakdown in the meiotic isolation of the genomes, and wheat is revealed to be a segmental allopolyploid.

RILEY, CHAPMAN and KIMBER (1960) using wheat-rye hybrids, deficient for each wheat chromosome in turn, demonstrated that only 5B performs this diploidizing function. Moreover, RILEY (1960 a) used hybrids between *T. aestivum* and *Aegilops cylindrica*, deficient for the complete 5B chromosome or for each arm in turn, to show that the effect on meiotic pairing was confined to the long arm of the chromosome. More recently RILEY and CHAPMAN (unpublished) have confirmed this by the demonstration that 42-chromosome plants ditelo-

centric for the short arm were multivalent forming whereas those ditelocentric for the long arm were not. OKAMOTO's (1962) demonstration of the possibility of removing the diploidizing effect by mutation suggests that a relatively restricted region of 5B is responsible. A more precise determination of the effective region of the long arm of 5B is unlikely until such mutants can be fixed and analysed genetically. However, there seems to be no reason, in principle, why this should not be possible.

The restriction of meiotic pairing to full homologues in the presence of 5B cannot depend upon a reduction in the numbers of chiasmata since the breakdown of the restriction is accompanied by lower chiasma frequencies in the absence of 5B from nullisomics and amphiploids (RILEY 1960 a, KIMBER 1962, RILEY and CHAPMAN 1963). Changes in the processes that initiate synapsis must therefore be responsible for the changes in pairing specificity. It may be postulated that the effect of the chromosome 5B mechanism is so to shift the degree of genetic and structural similarity that is needed for synapsis to occur that homologues, but not homoeologues, can pair. It should be appreciated that the critical region of 5B is responsible for the suppression of the effects of other components of the genotype that would otherwise have led to homoeologous conjugation. Thus, speculating about the process involved, if the 5B effect results from an outcome of the blockage, or diversion, of a synthetic pathway it may offer a first access to the biochemistry of meiotic pairing specificity.

## The evolution of the diploidizing system

The present activity of chromosome 5B of *T. aestivum* could simply be the continuation of a precisely similar activity that it performed in the diploid species, probably *A. speltoides*, from which it was derived. Although, of course, at the diploid level the effect on meiotic behaviour would not have been the same as that produced in polyploid wheat. Alternatively the present activity might have resulted from a change in function subsequent to the inclusion of 5B in the polyploid. RILEY, KIMBER and CHAPMAN (1961) tested these alternatives using hybrids between *T. aestivum*, with and without chromosome 5B, and two possible B genome donors, *A. speltoides* and *A. longissima*.

In hybrids between *T. aestivum* and *A. longissima* the suppression of homoeologous pairing was still effective in the presence of 5B, but not in its absence. Moreover the meiotic behaviour of hybrids involving *T. aestivum* with most other diploid species of *Aegilops* conforms to this pattern (Table 2). This implies that the genotypes of *A. longissima* and

most other diploids do not remove the 5B-effect, nor in the absence of 5B can they take over its functions. These diploids in their present forms could not, therefore, have provided directly a chromosome functioning like 5B.

There is homoeologous pairing in hybrids between *T. aestivum* and *A. speltoides* in the presence of chromosome 5B. Consequently the genotype of *A. speltoides* can inhibit the effect of 5B, and it can be concluded that this species also could not have contributed a chromosome that without modification performed the function of 5B of *T. aestivum*. Indeed there is no diploid with a genetic regulation of meiotic pairing like that performed by chromosome 5B, and it can be concluded that the present activity results from a change of function subsequent to the inclusion of the chromosome in polyploid wheat. Since all polyploid wheat species apparently have alleles on chromosome 5B similar in effect to that of *T. aestivum*, the mutation must have occurred early in the polyploid history of the genus. The likely course of evolution of the diploidizing system has been discussed by RILEY (1965 a).

Knowledge of the nature of the change of 5B, in polyploid wheat, might be provided by an understanding of the genetics of the different effects produced by *A. speltoides* and, for example, *A. longissima* on chromosome pairing in hybrids with wheat. For this purpose $F_1$ hybrids of *A. longissima*×*A. speltoides* have been pollinated with polyploid wheat, but without success. However, in a very small progeny derived from the cross (*T. aegilopoides*×*A. speltoides*) (2n=28)×(*T. aegilopoides*×*A. bicornis*) (2n=28) $F_1$)×*T. aestivum*, in which *A. bicornis* substituted for *A. longissima* as the non-suppressor of the 5B-effect, there were big differences between plants in the levels of meiotic pairing. This suggests segregation for the *A. speltoides*—*A. bicornis* difference and that the difference is relatively simple genetically.

## The 5B effect and the origin of the B genome

On the grounds of gross plant morphology SARKAR and STEBBINS (1956) proposed that the B genome of polyploid wheat was contributed by *A. speltoides*. RILEY, UNRAU and CHAPMAN (1958) agreed with this conclusion using additional evidence derived from karyotypic studies and from the investigation of the genetic control of diploidization. They pointed out that, since both the satellited chromosomes—1B and 6B—of *T. aestivum* were in the B genome, the diploid contributor of the genome must also have two pairs of satellited chromosomes—like *A. speltoides*. Moreover they concluded that, if the diploidizing system of the polyploids had arisen by mutation this was more likely to have taken place from

TABLE 1. Mean chromosome pairing at $M_1$ of meiosis in $F_1$ hybrids between *A. mutica* ♂ and various other species (ranges of configuration in brackets).

| Alternative ♀ parents | Chrom. no. | Cells | Univ. | Biv. | Triv. | Quad. | Chiasmata |
|---|---|---|---|---|---|---|---|
| *T. monococcum* | 14 | 50 | 2.52 (0—6) | 4.96 (3—7) | 0.28 (0—1) | 0.18 (0—1) | 8.26±0.27 |
| *T. aegilopoides* | 14 | 50 | 3.70 (0—8) | 4.88 (3—7) | 0.10 (0—1) | 0.06 (0—1) | 6.78±0.24 |
| *A. speltoides* | 14 | 50 | 2.84 (0—10) | 5.58 (2—7) | — | — | 7.68±0.27 |
| *A. longissima* | 14 | 50 | 3.52 (0—10) | 5.06 (2—7) | 0.12 (0—1) | — | 6.26±0.26 |
| *A. caudata* | 14 | 30 | 3.53 (1—6) | 3.33 (2—6) | 1.27 (0—2) | — | 6.10±0.26 |
| *T. dicoccoides* | 21 | 50 | 6.52 (2—13) | 4.30 (1—7) | 1.88 (0—5) | 0.06 (0—1) | 9.42±0.10 |
| *T. durum* | 21 | 50 | 6.38 (3—11) | 4.68 (2—7) | 1.70 (0—4) | 0.04 (0—1) | 10.26±0.18 |
| *T. persicum* | 21 | 50 | 6.86 (0—13) | 4.60 (2—7) | 1.50 (0—5) | 0.08* (0—1) | 9.04±0.24 |
| *T. aestivum* | 28 | 50 | 5.32 (2—11) | 5.14 (1—10) | 2.06 (1—4) | 1.52 (0—4) | 17.10±0.45 |
| *T. aestivum*-5B | 27 | 50 | 5.96 (1—9) | 5.24 (1—10) | 1.54 (0—4) | 1.56 (0—3) | 16.20±0.25 |

* sexavalents=0.02

the 'dominant' condition of *A. speltoides* than from the 'recessive' condition of the other species.

However, it was pointed out by CHENNEVEERAIAH (1960) that *A. mutica* also has two pairs of satellited chromosomes, like *A. speltoides*, so on karyotypic ground was equally likely to have been the B genome contributor. To investigate *A. mutica* further it was used at Cambridge as a parent in a series of hybrids that have been studied meiotically (Table 1). There is high pairing at meiosis in hybrids with both tetraploid wheat, as was originally reported by KIHARA and LILIENFELD (1935), and hexaploid wheat. This high pairing is presumably due to the occurrence of homoeologous conjugation through the suppression of the activity of 5B. Consequently, there is no distinction between *A. mutica* and *A. speltoides* on the grounds either of karyotype or of the genetic control of pairing specificity. These two attributes are of no value, therefore, in distinguishing which of the species was the B genome donor. However, from studies of DNA content (REES personal

communication) and on morphological evidence, *A. speltoides* still seems more likely to have filled this role.

It should be pointed out that the absence of any translocation difference between *A. speltoides* and *A. mutica* confirms the phylogenetic proximity of the two species that is indicated by their similarities in karyotype and pairing control (Table 1). However, pairing in the *A. speltoides*×*A. mutica* hybrids is not so high as that in hybrids between *A. speltoides* and other members of the *Sitopsis* section of *Aegilops* (KIMBER 1961). Unfortunately a full treatment of the significance of *A. mutica* must be deferred through lack of space, but will be published elsewhere.

## Effect of the removal of chromosome 5B on meiosis in interspecific hybrids

Data on the meiotic behaviour of hybrids, between *T. aestivum* and various other species, with and without chromosome 5B of wheat, are shown in Table 2. In every instance there is a pronounced increase in the amount of pairing in the absence of 5B. This presumably results in part from the occurrence of homoeologous conjugation between wheat chromosomes. However, as was originally pointed out by RILEY, CHAPMAN and KIMBER (1959), the formation of higher multivalents in the 27-chromosome 5B-deficient hybrids than occur in nulli-5B haploids indicates allosyndetic pairing, although this is rare or absent when 5B is present. Presumably the relationships between the chromosomes of wheat and those of the alternative parents with which they pair are similar to the relationships between homoeologous wheat chromosomes.

There is an increase of between 0.50 and 0.61 in the mean proportion of the chromosome complement that pairs in hybrids involving diploid *Aegilops* species following the absence of 5B (Table 2). By contrast the increase is only between 0.20 and 0.41 on the removal of 5B from hybrids involving polyploid *Aegilops* species. The two possible explanations for this difference are that it results either from increased synaptic competition due to the greater chromosome number, or that it arises from the presence of genetic diploidizing systems, in the *Aegilops* polyploids, that counteract the effects of the 5B deficiency. It should shortly be possible to distinguish between these hypotheses, but if the second proves to be correct it will imply that the diploidization of polyploid *Aegilops* species and the diploidization of polyploid wheat result from somewhat different processes.

The behaviour of rye is quite anomalous in that it gives rise to hybrids with wheat in which the absence of 5B causes a relatively small

TABLE 2. Mean chromosome pairing at $M_1$ of meiosis in $F_1$ hybrids, with and without chromosome 5B, from crosses between *T. aestivum* monosomic 5B ♀ and various other species.

| Alternative ♂ parent | Chrom. no. | 5B | Cells | Mean pairing | | | | | | Proportion complement paired | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Univ. | Biv. | Triv. | Quad. | Quin. | Sex. | Mean | Mean increase in 5B deficiency |
| *A. comosa* | 28 | present | 50 | 22.44 | 2.46 | 0.06 | — | — | — | 0.20 ± 0.005 | 0.50 ± 0.013 |
| *A. comosa* | 27 | absent | 50 | 8.20 | 5.10 | 2.04 | 0.62 | — | — | 0.70 ± 0.012 | |
| *A. longissima* | 28 | present | 100 | 24.04 | 1.96 | 0.01 | — | — | — | 0.14 ± 0.010 | 0.58 ± 0.016 |
| *A. longissima* | 27 | absent | 100 | 7.50 | 7.58 | 0.70 | 0.56 | — | — | 0.72 ± 0.013 | |
| *A. umbellulata* | 28 | present | 30 | 24.50 | 1.60 | 0.10 | — | — | — | 0.13 ± 0.015 | 0.52 ± 0.021 |
| *A. umbellulata* | 27 | absent | 50 | 9.44 | 4.98 | 1.76 | 0.50 | 0.06 | — | 0.65 ± 0.014 | |
| *A. caudata* | 28 | present | 100 | 24.12 | 1.82 | 0.08 | — | — | — | 0.14 ± 0.008 | 0.61 ± 0.027 |
| *A. caudata* | 27 | absent | 100 | 6.77 | 5.77 | 2.09 | 0.55 | 0.02 | 0.02 | 0.75 ± 0.026 | |
| *S. cereale* | 28 | present | 100 | 25.26 | 1.37 | — | — | — | — | 0.10 ± 0.004 | 0.20 ± 0.011 |
| *S. cereale* | 27 | absent | 100 | 18.00 | 3.18 | 0.70 | 0.11 | 0.02 | — | 0.30 ± 0.010 | |
| *A. ovata* | 35 | present | 70 | 29.67 | 2.62 | 0.03 | — | — | — | 0.15 ± 0.004 | 0.40 ± 0.010 |
| *A. ovata* | 34 | absent | 100 | 15.40 | 5.60 | 1.90 | 0.36 | 0.09 | — | 0.55 ± 0.009 | |
| *A. triuncialis* | 35 | present | 30 | 26.97 | 3.77 | 0.17 | — | — | — | 0.23 ± 0.017 | 0.41 ± 0.027 |
| *A. triuncialis* | 34 | absent | 30 | 12.33 | 6.27 | 2.33 | 0.50 | — | — | 0.64 ± 0.021 | |
| *A. cylindrica* | 35 | present | 50 | 20.82 | 6.74 | 0.18 | 0.02 | — | — | 0.41 ± 0.012 | 0.20 ± 0.022 |
| *A. cylindrica* | 34 | absent | 50 | 13.20 | 6.92 | 1.56 | 0.56 | — | — | 0.61 ± 0.018 | |
| *A. turcomanica* | 42 | present | 50 | 29.02 | 4.38 | 0.98 | 0.32 | — | — | 0.30 ± 0.010 | 0.24 ± 0.016 |
| *A. turcomanica* | 41 | absent | 50 | 19.00 | 4.28 | 2.12 | 0.80 | 0.52 | 0.14* | 0.54 ± 0.012 | |

* 0.04 = VII  0.02 = VIII

TABLE 3. Mean pairing at $M_1$ of meiosis in amphiploids, with and without chromosome 5B, from the cross *T. aestivum*×*A. longissima*.

| Chrom. no. | Chrom. 5 B | Mean pairing | | | | | | | | Chiasmata per cell | Chiasmata per paired chrom. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Univ. | Biv. | Triv. | Quad. | Quid. | Sex. | Sept. | Oct. | | |
| 56 | present | 1.25 | 27.13 | 0.03 | 0.10 | — | — | — | — | 50.93±0.89 | 0.923±0.015 |
| 54 | absent | 4.10 | 18.83 | 1.27 | 1.67 | 0.20 | 0.10 | — | 0.03 | 41.67±0.72 | 0.834±0.069 |

increase in pairing. Indeed the gross pairing in a wheat-rye hybrid, deficient for 5B, is less than that in a nulli-5B haploid of *T. aestivum*. This may indicate that the rye genotype inhibits pairing to produce an effect that is similar, at least in part, to that of 5B.

## The 5B effect and the introduction of alien genetic variation

Clearly the comparative freedom of allosyndetic pairing in interspecific hybrids involving wheat lacking chromosome 5B offers greatly improved opportunities for the incorporation in wheat chromosomes of genes from other species. In attempting to exploit this situation use can be made of the initial hybrids, although they are very infertile, to obtain backcross derivatives. Alternatively the chromosome numbers of hybrids can be doubled to produce amphiploids lacking 5B. As RILEY and CHAPMAN (1963) have shown such amphiploids are multivalent forming and there is pairing between the chromosomes of the different parents (Table 3).

*T. aestivum* types with potentially useful modifications of the phenotype of the original parent have been obtained from the 27-chromosome hybrid, *T. aestivum* Holdfast monosomic 5B×*A. bicornis*, after two backcrosses to Holdfast followed by two generations of selfing. The use of the first hybrid, in the way described, probably gives the best chance of allosyndetic recombination since allosyndetic pairing must be relatively less in amphiploids due to homologous competition.

Amphiploids deficient for 5B have reasonable seed fertility, so that the products of allosyndetic recombination can be allowed to accumulate over several generations. At any stage the amphiploid can be backcrossed to *T. aestivum*, to return to the hexaploid state, and this system of handling can be accompanied by appropriate selection procedures.

One aspect of the meiotic behaviour of 5B-deficient amphiploids is of particular academic interest. This is the lower frequencies of chiasmata per cell, and per paired chromosome, relative to the 5B-present situation (Table 3). RILEY and CHAPMAN (1963) have ascribed this to synaptic competition.

An alternative method for the production of allosyndetic recombination, being used at Cambridge, primarily by my colleague GORDON KIMBER, involves the suppression of the 5B activity by the incorporation of the *A. speltoides* genotype. Situations are created in which all the chromosomes of, for example, wheat and rye and *A. speltoides* are present, so that the activity of the *speltoides* genotype promotes crossing over between wheat and rye chromosomes. In a variant of this situation, also being used in our laboratory, alien chromosome addition lines, in which a beneficial character is contributed by the alien chromosome, are crossed with *A. speltoides* to produce addition line—*A. speltoides* hybrids, for backcrossing. Of course it may be assumed that suppression of the 5B effect by the *A. mutica* genotype would also be effective in inducing allosyndetic recombination.

## A cytological check of intra- and interspecific homoelogy

SEARS' (1954) homoeologous classification of the chromosomes of *T. aestivum* was based on a genetic test. The suppression of the 5B effect by *A. speltoides* will permit a cytological test of homoeology to be conducted, and work with this purpose is now well advanced at Cambridge. Plants of *T. aestivum* with two different bivalents marked by being telocentric/complete are obtained by crossing together plants ditelocentric for different chromosomes. The plants with two different telocentrics are pollinated with *A. speltoides* and interspecific hybrids that again have two telocentrics are selected and examined at meiosis. The occurrence of two telocentrics in the same configuration will demonstrate their cytological homoeology, their participation in different quadrivalents will demonstrate non-homoeology.

A similar technique is also being applied to the determination of the relationships between rye and wheat chromosomes. In this case plants with a single known wheat and a single known rye telocentric have been pollinated with *A. speltoides* and the hybrids will be examined at meiosis to determine the relative cytological homoeologies of the marked wheat and rye chromosomes.

## Chromosome 3B effect

The presence of chromosome 3B was demonstrated by SEARS (1944) to be necessary for the maintenance of normal levels of chiasma formation in *T. aestivum*. Nullisomic 3B plants are partially asynaptic and KEMPANNA and RILEY (1962) have suggested that this is due to the failure of chiasma formation rather than to the absence of pairing.

RILEY and KEMPANNA also showed, from wheat-rye hybrids lacking both 3B and 5B simultaneously, that there was a form of interaction of the effects of the two deficiencies that might imply an evolutionary relationship between the two systems. Consequently hybrids with and without 3B were developed from crosses between *T. aestivum* monosomic 3B and either *A. longissima* or one of three different *A. speltoides* parents. Two diploid parents, *A. longissima* and *A. speltoides* (G), had pronounced reductions in pairing in the absence of 3B, but another—*A. speltoides* (M)—showed the reverse effect. The analysis of variance of chiasma frequencies in the *A. speltoides* crosses shows that this experiment was too limited for an effect to be attributed with certainty to the absence of 3B (Table 4). There is indeed a suggestion that forms of *A. speltoides* might differ in their response to the 3B situation. Nevertheless, if it could be confirmed that the B genome contributor was unable to compensate for the absence of 3B in hybrids—like *A. speltoides*

TABLE 4. Mean chromosome pairing at $M_1$ of meiosis in $F_1$ hybrids, with and without chromosome 3B, from crosses between *T. aestivum* monosomic 3B ♀ and *A. longissima* or *A. speltoides* (50 cells per plant).

| Alternative ♂ parents | Chrom no. | Chrom. 3B | Mean | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Univ. | Biv. | Triv. | Quad. | Quin. | Sex. | Chiasmata |
| *A. longissima* | 28 | present | 24.52 | 1.68 | 0.04 | — | — | — | 1.74±0.20 |
| *A. longissima* | 27 | absent | 26.64 | 0.18 | — | — | — | — | 0.18 |
| *A. speltoides* (G) | 28 | present | 8.44 | 6.22 | 1.38 | 0.74 | — | — | 13.66±0.38 |
| *A. speltoides* (G) | 27 | absent | 11.38 | 6.06 | 0.84 | 0.24 | — | 0.02 | 9.78±0.45 |
| *A. speltoides* (E) | 28 | present | 6.60 | 6.60 | 1.44 | 0.92 | 0.04 | — | 15.22±0.32 |
| *A. speltoides* (E) | 27 | absent | 6.88 | 5.62 | 1.64 | 0.94 | 0.04 | — | 15.14±0.30 |
| *A. speltoides* (M) | 28 | present | 9.82 | 6.02 | 1.38 | 0.50 | — | — | 11.80±0.46 |
| *A. speltoides* (M) | 27 | absent | 8.14 | 5.84 | 1.76 | 0.44 | 0.02 | — | 13.12±0.35 |

Analysis of variance in the *A. speltoides* crosses for chiasma frequencies.

| Item | d. f. | Sums of squares | Mean squares | Variance ratio | P |
|---|---|---|---|---|---|
| 3B presence/absence | 1 | 58.08 | 58.08 | 8.01 | $<0.001$ |
| *A. speltoides* parents | 2 | 663.92 | 331.86 | 45.77 | $<0.001$ |
| 3B presence/absence — *A. speltoides* parents | 2 | 360.68 | 180.34 | 24.87 | $<0.001$ |
| Error | 294 | 2131.00 | 7.25 | | |
| Total | 299 | 3213.68 | | | |

(G) or *A. longissima*—this would suggest that the present effect of 3B resulted from a mutation subsequent to the inclusion of the chromosome in polyploid wheat. The increased chiasma frequency arising from such a mutant might have restored, to some degree, the reduction that can be postulated to have followed the restriction of synapsis to homologues by the 5B mutant.

## Polygenic effects

In a study of chiasma frequencies in the full series of monosomics, nullisomics and monotelosomics, KEMPANNA (1963) was able to demonstrate that genes on several chromosomes influence the character. There was marked evidence of the duplication of the 3B effect—although with reduced expressions—on the homoeologous chromosomes 3A and 3D. Indeed three of the five nullisomics that departed significantly from euploid were in group 3—the others being 2B and 5D. This confirms the observation of SEARS (1954) that 2B has an influence on chiasma frequency. The summation of all the differences, from euploid, of each of the 21 nullisomics greatly exceeded the euploid value, so that there must be considerable interaction between genes on different chromosomes in the expression of chiasma frequency.

In addition, KEMPANNA demonstrated that there were exceptional differences between the monosomics of group 2 and euploid in that the relevant genes on these chromosomes are apparently hemizygous ineffective. By contrast the monosomics for chromosomes of group 3 were close to euploid, so there was no evidence of the additivity of effects of genes on these homologues.

The incorporation in the analysis of data from the monotelocentric lines allowed an assessment of the distribution of effects between arms. The effects were generally asymmetrically distributed between arms, for example the three monotelocentrics of group 3 chromosomes showed that the pronounced activities of 3A, 3B and 3D were each respectively confined to one arm.

Although a picture of some complexity is revealed by this work it is nevertheless clear that a coherent view of the regulation of chiasma frequency can be discerned. There is, for example, clear evidence of the consistency of effect within certain homoeologous groups and of constant patterns in the distribution of effects between arms in homoeologues.

## The overall control of meosis

In the contemporary genetic regulation of the meiotic behaviour of *T. aestivum* we can thus recognise major effects such as those produced by chromosome 3B and 5B, minor effects like those associated with 3A and 3D and a range of very small effects. The control of meiosis is, therefore, extremely complex and the complexity is further increased by the occurrence of secondary pairing between bivalents at first metaphase (RILEY 1960 b, KEMPANNA 1963). Moreover, we are just beginning to obtain evidence of interactions in the determination of chiasma frequency as well as hints of inter-relationships between the processes in which 3B and 5B are involved. From these investigations the evolutionary integration of the overall system may ultimately be discerned.

Our attempts to comprehend the organisation and evolution of the regulation of meiosis in *T. aestivum* have directed our interest to similar processes in other species, and already information has begun to accumulate about various *Aegilops* species. As yet this is not particularly coherent but one early objective is clear, namely the need to explain the diploidizing systems of the polyploid *Aegilops* species.

The exploitation of our knowledge of genetic diploidization has already begun in attempts to introduce alien variation into *T. aestivum*. In addition examinations are being made of the practical potentialities of the intergenomic recombinations that can be produced by the removal of the 5B control (RILEY 1965 b). This is therefore a field of activity that provides in an unusual way for the simultaneous investigation of applied as well as of fundamental problems.

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## SUMMARY

A description is given of the genetic regulation of meiotic chromosome pairing in wheat and its relatives. The system is of some complexity involving major genes and polygenic components. Separate control is probably exercised over the synapsis of chromosomes and over chiasma formation. The specificity of pairing is genetically controlled as well as the extent of pairing.

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## Discussion

MÜNTZING: Does the absence of chromosome 5B induce a homologous or non-homologous pairing? The former alternative would seem more probable in the light of the genetical control of chromosome pairing in *Phleum pratense.*

RILEY: The situation in *Phleum pratense* is not, as I understand it, quite like that in wheat. *P. pratense* has meiotic pairing in bivalents but polysomic inheritance, consequently pairing is not restricted to precise homologues but occurs at random between the six homologues of each members of the complement. This contrasts with the situation in *T. aestivum*, in which there is bivalent pairing accompanied by disomic inheritance, so that each chromosome pairs only with its single fully homologous partner.

Regarding the effect of *Ae. speltoides*; the genotype of this species suppresses the 5B-effect. So that if we visualize the situation in terms of variation at a single locus then the alleles are $P_s$ in *Ae. speltoides* and *Ae. mutica*, $p_{5B}$ in the polyploid wheat and $p_1$ in *Ae. longissima* and all the other diploids. Thus, *Ae. speltoides* and *Ae. mutica* carry the dominant allele, and the other diploids a recessive of null-effect in terms of our present test. This is the simplest hypothesis that can be used to describe the situation and ultimately it may prove to be too simple.

OKAMOTO: To the question of Dr. MÜNTZING, Dr. RILEY answered that *Ae. mutica* has the same effect as *Ae. speltoides*. Dr. MOCHIZUKI of Hyogo Agriculture University has found the same in many crosses involving *Ae. mutica.*

I would like to ask whether it should not be worth while to start from tetra-5B-nulli-5D in testing the nonhomologous pairing, because there may be confusion due to repeated crossing over and translocation.

RILEY: I agree with Dr. OKAMOTO's comment about the difficulty of using the cross nulli-5B tetra-5D×euploid in determining the chromosomes involved in non-homologous recombination. Aneuploidy for chromosomes 5B and 5D was a nuisance to Dr. KEMPANNA and myself in this work.

If we were to start again I would use instead the cross nulli-5B tetra-5D×nulli-5D tetra-5B. This would mean, as we have recently demonstrated, that the $F_1$ would be euploid but would be heterozygous for translocation differences that had arisen by homoeologous recombination on the nulli-5B tetra-5D side of the parentage.

GERSTEL: Are the quadrivalents formed in the absence of chromosome 5B behaving at anaphase as quadrivalents in wheat usually do, *i.e.* do they disjoin in a balanced and directed way?

RILEY: I am afraid that we have no data on the frequencies of different orientations of the multivalents due to heterozygosity for homoeologous translocation differences. However, general observation leads one to suspect that they are largely disjunctionally orientated.