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The Basic and Applied Genetics of Chromosome Pairing

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INTRODUCTION

Ten years ago at the First International Wheat Genetics Symposium in Winnipeg I reported our work which showed that a genetic activity of a particular chromosome of the complement of *Triticum aestivum* is apparently responsible for the prevention of meiotic synapsis between homoeologous chromosomes (Riley and Chapman 1958, Riley and Bell 1959). During much of the intervening period my colleagues and I at Cambridge have worked to confirm and elaborate our knowledge of this system and it is probably not necessary to discuss the earlier results in detail since they will be familiar to many of you. It will be sufficient to remind you that only chromosome 5B performs this activity, that the activity is performed by the long arm (Riley 1960, Riley and Chapman 1964a), that it was confirmed that the abnormal pairing in the deficiency of 5B is indeed between homoeologues (Riley and Kempanna 1963) and that the $5B^L$ activity is suppressed by the genotypes of *Ae. speltoides* (Riley and Chapman 1964b, 1966) and *Ae. mutica* (Riley 1966a) but not by those of other related diploids (Riley and Law 1965). We were able to conclude that chromosome $5B^L$ causes the failure of homoeologous pairing because of a direct effect on synapsis and not through an effect on chiasma formation (Riley 1960, Riley and Chapman 1963). In addition it was shown that in the absence of 5B, wheat chromosomes will synapse with alien homoeologues from related species although this does not occur in its presence (Riley 1960, Riley and Law 1965).

In the present discussion I shall attempt to outline some of the more recent results of Victor Chapman, Roy Johnson, Angela M. Belfield, Anthony M. Hayter and myself. In addition I will attempt to indicate the directions in which some of our thoughts are currently turning.

COMPAIR

First of all I shall discuss the introduction into wheat of the stripe (yellow) rust resistance of *Ae. comosa* ($2n = 14$) by interference with the $5B^L$ system.

From the very outset of our work with this system it was predicted that disruption of the activity could be exploited to enable useful homoeologous recombination to take place between wheat and alien chromosomes (RILEY and CHAPMAN 1958). The extraction of the breeder's variety Compair with the stripe rust resistance of *Ae. comosa* is, I think, an instructive example of the application of this notion.

The preliminary part of the pedigree of Compair involved a backcrossing programme, initiated from *T. aestivum* Chinese Spring x *Ae. comosa* hybrids, which was accompanied by selection for rust resistance (Fig. 1). The programme resulted in the isolation of an addition line in which chromosome 2M of *Ae. comosa,* determining rust resistance, was added to the full complement of Chinese Spring. The homoeology of chromosome 2M, in a separately isolated disomic addition line, was determined by entire-chromosome substitution procedures which illustrated that it would substitute and compensate for chromosomes 2A (II), 2B (XIII) and 2D only (RILEY, CHAPMAN and MACER 1966). Incidentally, a useful byproduct of this test of homoeology was the development of 42-chromosome disomic substitution lines in which 2M replaces each of these three wheat chromosomes in turn.

During the extraction of the addition line, chromosome 2M passed through several meiotic divisions in the presence of its homoeologues without recombining and presumably without synapsing with them. In order to induce homoeologous recombination use was made of *Ae. speltoides* which carries a dominant allele that suppresses the $5B^L$ activity (RILEY and CHAPMAN 1964a, KIMBER 1966). The 2M monosomic addition line was crossed with *Ae. speltoides* to produce hybrids with the haploid complements of Chinese Spring and of *Ae. speltoides* in addition to chromosome 2M. Since there was homoeologous pairing, chromosome 2M was able to synapse and recombine with its wheat homoeologues.

The hybrids were crossed with Chinese Spring and a backcrossing programme instituted using Chinese Spring as the recurrent parent (Fig. 1). Selection was practised for rust resistance and the outcome of the programme, in the part of the pedigree under consideration, was the isolation of a 21 bivalent-forming plant with the rust resistance of *Ae. comosa.* This plant was heterozygous for a dominant rust resistance condition and from its derivatives homozygotes were established by progeny testing (RILEY, CHAPMAN and JOHNSON 1968, 1969). The resulting lines, which together constitute the foundation of Compair, have the rust resistance of *Ae. comosa* and when crossed with Chinese Spring, or any standard wheat variety, give hybrids with full chromosome pairing at meiosis. Moreover the F_2 generations from such crosses segregate to give simple 3 resistant : 1 susceptible ratios. Thus Compair can be used by breeders to incorporate the resistance of *Ae. comosa* in agronomic forms without regard to meiotic chromosome behaviour.

Compair is homozygous for a recombinant condition affecting chromosomes 2M and 2D. The recombinant chromosome, which is designated 2M/D, has

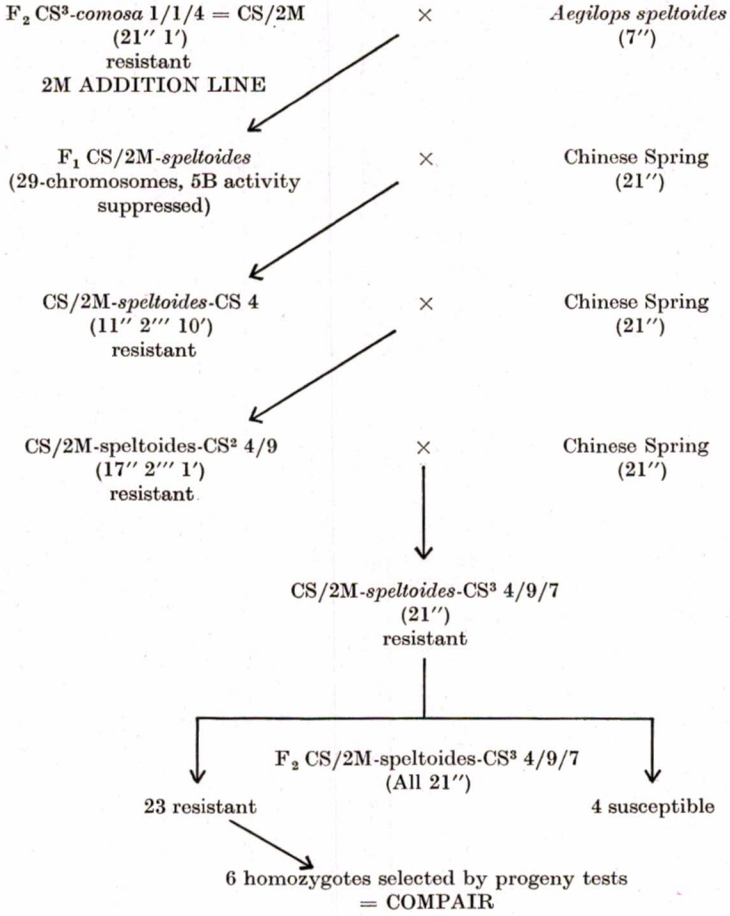

Fig. 1. Pedigree of Compair.

the short arm, the centromere and a proximal segment of the long arm of chromosome 2M: it also has a distal segment of the right arm of chromosome 2D. The evidence for this conclusion is as follows:—

i. Monosomic analysis shows the segregation of stripe rust resistance to be disturbed from the usual 3:1 ratio in the F_2 generation of the cross Chinese Spring monosomic 2D x Compair.

ii. In 43-chromosome F_1's of the cross, 2M addition line x Compair, 20 bivalents and one trivalent are usually formed at meiosis, so 2M material is present in Compair.

iii. At meiosis in F_1's from the crosses of 2M/2A or 2M/2B substitution lines x Compair, 19 bivalents, one trivalent and one univalent are usually formed, so chromosomes 2A and 2B are not implicated.

iv. By contrast, in F_1's from the cross, 2M/2D substitution line x Compair, 21 bivalents are regularly formed. This demonstrates the involvement of chromosome 2D with 2M.

v. At meiosis in hybrids from the cross of the $2M^S$ telocentric addition line x Compair, 20 bivalents and a trivalent, which includes the short telocentric, are commonly present. Thus $2M^S$ material is present in Compair.

vi. The susceptibility of the $2M^S$ addition line to stripe rust demonstrates that the resistance is determined by the long arm. Consequently, in addition to $2M^S$ a segment of the long arm must also be present.

vii. Finally, at meiosis in hybrids from the cross, $2D^R$ ditelocentric line x Compair, 21 bivalents are formed in one of which the $2D^R$ telocentric participates. This shows that a segment of $2D^R$ is present in 2M/D.

The suggested structure of 2M/D is the simplest that will meet the requirements of this evidence.

The segregation of the *Ae. comosa* resistance from crosses between Compair and susceptible varieties is explicable on the assumption that resistance is determined by the dominant allele at a single locus. The resistance gene has been designated Yr_8, but it should be emphasised that its simple segregational definition may conceal a more complex structure. So far as wheat improvement is concerned, the significance of Yr_8 is that it gives 00-0 hypersensitive fleck reactions to all the European races of *Puccinia striiformis* to which it has been exposed.

Numbers of operational procedures have been considered by which homoeologous recombination between wheat and alien chromosomes might be induced (Riley 1960, Riley and Kimber 1966, Sears 1967). These include backcrossing from *T. aestivum* x alien species hybrids deficient for 5B, or backcrossing from *T. aestivum*—alien species amphiploids lacking 5B, or the use of nullisomic-5B tetrasomic-5D wheat parents in interspecific crosses. The use of *Ae. speltoides* to suppress the 5B activity, as in the Compair work, has the disadvantage that the initial hybrids involving *Ae. speltoides* are very infertile. Consequently large scale and painstaking pollination is necessary for the production of the first backcross generation. The *Ae. speltoides* system has, however, one important advantage, namely that since there is dominant suppression of the 5B activity this may be retained through several backcross generations so extending the period during which homoeologous recombination is possible. By contrast, when euploid wheat is used as the recurrent parent in backcrossing with 5B-deficient hybrids, there is an immediate restoration of the 5B restriction of pairing to full homologues so that homoeologous recombination can only occur in the F_1 generation. Which ever method is employed, however, our experience confirms that manipulation of the 5B system has a beneficial rôle in the introgression of useful alien variation into wheat.

MUTATION IN THE 5B SYSTEM

A major restriction of several aspects of the study of the 5B system of *T. aestivum* has been the absence of allelic variation—genetic differences can only be created by the manipulation of chromosome constitutions. Allelic variation is necessary for the completion of the formal genetic analysis of the system, for the simplification of practical breeding work and for the provision of material to be used in the study of gene action in a causal analysis of synapsis. Consequently ANGELA BELFIELD, VICTOR CHAPMAN and I have induced mutations in which homoeologous pairing occurs and one of these mutants is under detailed investigation.

All the mutants were induced using ethyl methanesulphonate (EMS) as a mutagen. In order to mark the potentially mutant chromosome 5B, the stock treated was always Chinese Spring ditelocentric $5B^L$, seeds of this genotype being soaked in 0.5 or 1.0 per cent aqueous solution for 16 or 24 h. In the first experiment the treated plants were crossed with rye because the occurrence of homoeologous pairing is easily recognised in wheat-rye hybrids. Three mutants occurred among 206 hybrids, giving a mutation rate of 1.5 per cent (RILEY, CHAPMAN and BELFIELD 1966).

In a second experiment the treated Chinese Spring $5B^L$ ditelocentric plants were crossed with euploid Chinese Spring to make any potential mutants heterozygous. These potential heterozygotes, which also had chromosome 5B telocentric and complete, were pollinated with rye. The resulting wheat-rye hybrid families were examined for the occurrence of homoeologous pairing. Four of the resulting 444 hybrid families contained mutants, giving a mutation rate of about one per cent. It seems clear that this is about the rate of mutation in the 5B system under our experimental conditions and it is not too different from the rate of 3.4 per cent reported by OKAMOTO (1966) for X-ray induced mutation.

In order to have a control with which to compare this frequency, meiosis was examined in more than 1000 wheat-rye hybrids from crosses with 230 untreated euploid plants of Chinese Spring. There was one hybrid in which homoeologous pairing occurred but no other mutant could be recovered in the progeny of the Chinese Spring plant from which it was derived. Although there were 28 chromosomes in the hybrid with homoeologous pairing the presence of 5B could not be confirmed so there is no certainty that it carried a mutant allele. In any case, it is apparent that EMS treatment greatly enhances the mutation rate in pairing control systems.

It is not yet certain that the mutants induced in our work are at loci on chromosome 5B since the evidence does not discriminate between this and the mutation of suppressor loci elsewhere in the genotype or even of the pairing loci known to be present on 5D, 5A and on the group 3 chromosomes. To check this we are currently undertaking detailed study of one mutant line, designated Mutant 10/13, which has now been isolated in the homozygous condition in a

line of Chinese Spring ditelocentric for $5B^L$. An examination of the effect of Mutant 10/13 on the meiosis of wheat-rye hybrids shows that the level of pairing is close to that of hybrids deficient for 5B and much higher than that of non-mutant hybrids (TABLE 1).

TABLE 1. Mean chromosome pairing at first metaphase of meiosis in Chinese Spring wheat-rye hybrids carrying $5B^L$ or deficient for 5B and from crosses with Chinese Spring Mutant 10/13.

Wheat genotype	Plants	Cells per plant	Univ.	Biv.	Triv.	Quad.	Xta/cell
Non-mutant	5	20	27.64	0.18	—	—	0.18
Mutant 10/13	4	20	19.00	3.60	0.43	0.13	4.95
Deficient 5B	3	20	17.41	3.35	0.93	0.03	5.85

The Mutant 10/13 line was crossed with euploid Chinese Spring, and the resulting heterozygotes, which were also heteromorphic in the 5B pair, were crossed with rye and the meiotic behaviours of the resulting hybrids are illustrated in Table 2. There was no deviation from a 1 : 1 segregation of high : low pairing ($\chi^2_{(1)} = 1.31$ P = 0.2 — 0.3), so that the mutant condition probably derives from change at a single locus. However, a contingency test shows that the alternative meiotic pairing conditions segregated independently of the alternative states of chromosomes 5B. Consequently the mutant locus is either not on $5B^L$ or is so distal that it segregated independently of the centromere.

TABLE 2. Segregation of meiotic pairing behaviour and 5B chromosomal condition from the cross (Mutant 10/13 $5B^L$ ditelocentric × euploid Chinese Spring) × rye.

Pairing / 5B constitution	$5B^L$ telocentric	5B complete	Total
High	16	18	34
Low	24	17	41
Total	40	35	75

Current work is aimed at the determination of the precise chromosomal location of the mutant locus in Mutant 10/13. However, even before the location has been determined a number of useful points have been established. We know, for example, that genes controlling homoeologous pairing can be mutated and the mutant alleles fixed in the homozygous condition and used in simple breeding experiments. In addition, since Mutant 10/13 is apparently as effective in causing homoeologous pairing as is the deficiency of $5B^L$, induced mutants are likely to form useful tools in breeding work.

INTERACTION OF 5A AND 5D ACTIVITIES WITH TEMPERATURE

At the Oxford Chromosome Conference in 1964, I reported that the deficiency of chromosome 5D from Chinese Spring results in asynapsis at low temperatures (15°C or lower) (RILEY, 1966b). Subsequently it was recognised that nullisomic-5D tetrasomic-5A plants have almost normal pairing, although the deficiency of 5A caused no abnormality (RILEY, CHAPMAN, YOUNG and BELFIELD, 1966). Consequently it could be concluded that 5D performs an activity that promotes synapsis at low temperatures and that 5A performs a similar activity but less effectively. At the same time it was pointed out that AABB tetraploid forms of *Triticum* have normal meiotic pairing over the temperature range 12-28°C although obviously 5D is not present.

In order to ascertain the nature of the genetic difference between Chinese Spring and *T. dicoccum*, the segregation of meiotic pairing at 15°C was studied in F_2's from 34- and 36-chromosome hybrids, between the species, that were either nullisomic or disomic for 5D. The distribution of chiasma frequency was unimodal in the F_2 generation in which 5D was disomic but was bimodal in the 5D-deficient F_2 (HAYTER and RILEY 1967). In this F_2, 14 plants had fewer than 0.17 chiasmata per chromosome while 44 had more than 0.75 chiasmata per chromosome. All 82 plants in the disomic-5D F_2 had more than 0.75 chiasmata per chromosome.

The behaviour of the 5D-deficient F_2 was consistent with the segregation of alleles at a single locus. The locus has been designated *Low temperature pairing* (*Ltp*) and the genotype of *T. dicoccum* is assumed to be *Ltp Ltp* while Chinese Spring is *ltp ltp*. The dominant allele in *T. dicoccum* apparently performs an activity very like that of 5D of Chinese Spring and our present hypothesis, as yet unconfirmed, is that *Ltp* is located on 5A and that the recessive allele in Chinese Spring is not totally ineffective. This would imply that *Ltp* is the duplicate of a locus on 5D and that we are dealing with homoeologous loci.

$5B^S$ ACTIVITY

RILEY, CHAPMAN, YOUNG and BELFIELD (1966) directed attention to the contrast between the low chiasma frequencies in plants with four doses of $5B^L$ as two isochromosomes and the much higher frequencies in plants tetrasomic for the complete 5B chromosome. It was postulated that $5B^S$ affects synapsis genetically in the opposite manner to $5B^L$. This was confirmed by RILEY and CHAPMAN (1967) who showed, for example, that at 15°C in plants tetrasomic for the $5B^L$ telocentric there was a mean of 0.42 ± 0.03 chiasmata per chromosome compared with 1.05 ± 0.01 in tetrasomics for 5B complete. By contrast ditelocentrics for $5B^L$ and euploids disomic for 5B had 0.97 ± 0.01 and 1.14 ± 0.02 chiasmata respectively. Similar distinctions occurred at 20°C, so clearly the presence of $5B^S$ increases the level of synapsis and greatly diminishes the effects of increased dosage of $5B^L$.

It seems reasonable to assume that the $5B^S$ activity is mediated through its influence on the same process affected by $5B^L$. Moreover, since we are aware that 5D and 5A affect pairing it may be that they also have separate long and short arm effects. This may imply that the synaptic phenotype of euploid wheat is the product of a balance between these separate individual activities and that we are therefore dealing with a classical polymeric system.

From the point of view of the practical exploitation of this information in breeding work, apparently the probability of homoeologous synapsis and recombination will be maximised when the $5B^L$ activity is removed but the $5B^S$ activity retained.

FUNCTION OF PAIRING CONTROLS

The fundamental interest of the genetic systems that are known in *T. aestivum* and its relatives to be implicated in the regulation of synapsis is the insight that they offer into the general nature of this crucial phenomenon. Ultimately it seems likely that the genetic variation with which we are familiar will afford points of experimental access in the causal analysis of synapsis. In the meantime the distinctive patterns of synapsis, that characterise different genetic and temperature regimes in wheat, provide a framework around which we can erect various hypotheses. In the present discussion I will consider three hypotheses.

DNA-histone

One of the concerns of A. M. Hayter and myself has been to assess the relevance, for genetic and temperature distinctions in synapsis in *Triticum,* of the one clue that is available concerning a possible biochemical change that is correlated with synapsis. The clue was provided by the work of Ansley (1958), on *Loxa flavicolis* and *Scutigera forceps,* which showed that the nuclear contents of histone relative to DNA were less in meiotic cells destined to undergo synapsis than in cells due to have asynaptic meiosis. Clearly a model can be built around these observations that relates the recognition of pairing sites of partner chromosomes to the dissociation of DNA from its masking histones.

In testing this hypothesis we have made cytophotometric comparisons of the DNA : histone ratios of early meiotic pollen mother cells of plants with different patterns of synapsis. Nuclei, specifically stained for DNA by the Feulgen procedure and for histone by high pH fast green FCF, were measured on an integrating microdensitometer to estimate the relative contents of the two substances in arbitrary units.

Comparisons were made of genotypes of *T. aestivum* with and without chromosome 5B, of nullisomic-5D tetrasomic-5B plants at temperatures causing either asynapsis or normal pairing and of asynaptic mutants and normal genotypes of *T. durum* isolated by Martini and Bozzini (1966). The results of all the comparisons made showed no significant differences in DNA : histone ratios to

be associated with synaptic differences. Thus a gross distinction in DNA : histone ratios is not an essential prerequisite for the development of differences in chromosome synapsis. So far as the variation in *Triticum* is concerned the validity of the histone hypothesis has not been confirmed.

Spatial

The imaginative hypothesis of FELDMAN (1966) asserts that the whole of the genetic variation in synapsis known to occur in *T. aestivum* is explicable in terms of the relative co-orientation and spatial proximity of potential pairing partners at the time that synapsis is initiated. This notion fits the very clear effects of $5B^L$ in doses from zero to six. At the bottom of the dose series homologues and homoeologues are assumed to be adjacent and co-orientated, while at the top of the series even homologues are assumed to be inadequately co-orientated and spatially too separate for synapsis to be regular.

The spatial hypothesis is difficult to test but some help in evaluating its validity is given by the behaviour of chromosome 2M/D in Compair. As I said earlier, 2M/D arose by homoeologous recombination so that different segments of homoeologues are linked. Of course 2M/D can be made heterozygous with either 2M or 2D in the crosses, 2M/2D substitution line x Compair or Chinese Spring euploid x Compair. Under these conditions—since partner chromosomes have homologous as well as homoeologous regions—it might be expected that the homoeologous segments would synapse, if synapsis is a function of spatial order, since their relative positions would be determined by the homologous segments to which they are linked. However this does not appear to happen, instead synapsis is apparently confined to the completely homologous regions, if it is accepted that the failure of chiasma formation in homoeologous segments is adequate evidence of the failure of synapsis.

Further evidence of this kind must be evaluated before the spatial hypothesis is either accepted or discarded, but qualification must be introduced immediately. First the centromere can have no rôle in determining the relations of potential partners since when 2M/D is heterozygous with 2M and the centromeres are homologous, homoeologous synapsis does not occur. Consequently, if positioning is important it must be determined by chromosome ends—possibly by the relationships between telomeres and the membrane—or by numbers of sites along each chromosome, which seems unlikely. The behaviour of chromosome 2M/D, therefore, limits the spatial hypothesis but leaves open the question of its validity.

Timing

A third hypothesis which can be advanced to account for the present evidence in wheat and other organisms depends upon the notion that chromosome pairing is a two stage process as was originally suggested by FABERGÉ (1942). The first stage is conceived to involve the attraction together of potential partners while the second stage involves their detailed synapsis. As elaborated in our

thinking at Cambridge the attraction phase may be variable in time, and ultimately attraction is terminated by the independently initiated phase of detailed site-for-site synapsis. Under these circumstances the following conditions would apply:—

i. In the deficiency of $5B^L$ the attraction phase is long, thus permitting the association of homologues and homoeologues.
ii. With increased dosage of $5B^L$ the attraction phase is progressively shortened such that with low doses it is long enough only for homologues to associate. At higher doses detailed synapsis terminates the attraction phase so early that there is greatly reduced pairing and bivalent interlocking occurs because attraction has lasted for too short a period for chromosomal entanglements to be completely unsnarled.
iii. On this hypothesis the $5B^L$ activity reduces the time of the attraction phase, while $5B^S$, 5D and 5A increase the time of the attraction phase.
iv. Asynaptic mutants, like those in *T. durum,* can be visualised as diminishing the length of the attraction phase.
v. In addition the length of the attraction phase can be depicted as being temperature dependent but the initiation of detailed synapsis is independent of temperature. This would account for the reduced synapsis at low temperatures in *T. aestivum* deficient for 5D.

The timing hypothesis has the virtue of being amenable to experimental testing and Victor Chapman and I are currently engaged in determining the duration of meiosis in wheat genotypes with different patterns of meiotic pairing.

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