Estimates of the Homoeology of Wheat Chromosomes by Measurements of Differential Affinity at Meiosis

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ESTIMATES OF THE HOMOEOLOGY OF WHEAT CHROMOSOMES BY MEASUREMENTS OF DIFFERENTIAL AFFINITY AT MEIOSIS

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1. INTRODUCTION

THE chromosome complement of the hexaploid wheat of commerce, *Triticum aestivum* (2n = 6x = 42), can be classified into seven homoeologous groups, each of three pairs, or into three genomes, each of seven pairs. The genomes represent the sets of chromosomes combined together—from three distinct diploid species—during the allopolyploid evolution of wheat. The 14-chromosome, diploid, ancestors of *T. aestivum* were *Triticum monococcum*, *Aegilops speltoides* and *Aegilops squarrosa*, or their close relatives—the contributors of the A, B and D genomes respectively (McFadden and Sears, 1944; Riley, Unrau and Chapman, 1958).

The three pairs of chromosomes in each homoeologous group perform similar genetic functions. Thus, although all the 21 different nullisomics of *T. aestivum* are phenotypically abnormal, plants that are simultaneously nullisomic for one and tetrasomic for another chromosome are of more or less normal phenotype, provided that the chromosomes in altered dosage are homoeologous. By contrast there is no compensation for the defects caused by nullisomy when the tetrasomic and nullisomic chromosomes are in different homoeologous groups (Sears, 1954, 1965).

Of the three homoeologous chromosomes in each group, one is in each genome. Consequently the correspondence in the genetic activities of homoeologues implies that they represent equivalent chromosomes derived from the different diploid parents of the hexaploid. Their equivalence may be presumed, therefore, to be due to their origin from the same chromosome of a remote common progenitor of all three ancestral diploid species.

Only bivalents are formed at meiosis in *T. aestivum* and there is disomic inheritance. Each chromosome therefore pairs only with its single fully homologous partner and there is normally no meiotic association between homoeologues. The absence of homoeologous pairing has been shown to be due to a genetic activity of a single chromosome—number 5B (Riley and Chapman, 1958; Riley, 1960; Riley and Kempanna, 1963). Homoeologous pairing occurs in plants deficient for this chromosome, although the deficiency of no other chromosome causes similar changes in the course of meiosis. The prevention of homoeologous pairing in the presence, and its occurrence

in the absence, of chromosome 5B takes place in polyhaploid forms of *T. aestivum* as well as in normal hexaploid plants.

There is little pairing at meiosis in 28-chromosome hybrids between *T. aestivum* and a range of diploid species in the genus *Aegilops* because homoeologous synapsis is inhibited. This results from the continued activity of chromosome 5B, in the hybrids, and from the extension of its influence to the inhibition of the synapsis of *Aegilops* with wheat chromosomes (Riley, 1965; Riley and Law, 1965). By contrast there is a high level of meiotic pairing in hybrids between *T. aestivum* and the two diploid species, *Ae. speltoides* and *Ae. mutica*. Bivalents, trivalents and quadrivalents are common, although higher configurations are very rare, and there are some cells in which all 28 chromosomes have undergone synapsis (Riley, Kimber and Chapman, 1961; Riley, 1965). From behaviour of this type the hypothesis was formulated that the pairing is homoeologous and that consequently the normal inhibitory activity of chromosome 5B is suppressed in the presence of the genotype of either *Ae. speltoides* (Riley, Unrau and Chapman, 1958; Riley, Kimber and Chapman, 1961) or *Ae. mutica* (Riley, 1965).

The present work was initiated to test this hypothesis by the determination of the relationships of the chromosomes that paired in *T. aestivum* × *Ae. speltoides* hybrids. In the event, not only was the hypothesis shown to be correct, as has been indicated in a preliminary publication (Riley and Chapman, 1964*a*), but new detail was revealed about homoeologous relationships, and meiotic differential affinity was estimated quantitatively from cytological observations for the first time.

2. MATERIAL AND METHODS

The wheat plants used in the present work were all derivatives of *Triticum aestivum* L. emend. Thell. ssp. *vulgare* Mac Key variety Chinese Spring ($2n = 6x = 42$). All the lines employed were ditelocentric, having 20 pairs of normal chromosomes, with median or sub-median centromeres, and one pair of telocentric chromosomes. One arm of the chromosome marked by the telocentric condition was present in the normal double dose, while the other arm was completely deficient. The advantage of such material is that the marked chromosome is readily recognisable, by its distinctive morphology in both mitotic and meiotic metaphase preparations.

The chromosomes of *T. aestivum* are designated in a manner that indicates the homoeologous group and the genome to which they belong. The chromosomes of homoeologous group 1 are thus 1A, 1B and 1D, while those of the A genome are 1A, 2A . . . 7A. In the present paper a plant carrying a pair of telocentrics for one arm of a chromosome, for example 1A, and deficient for the other arm, will be designated *ditelocentric 1A*.

The other species used in the present study was *Aegilops speltoides* Tausch ($2n = 14$), in which the entire chromosome complement has median or sub-median centromeres. The taxonomic and evolutionary status of this species has most recently been considered by Zohary and Imber (1963).

Anthers from the plants studied were fixed in acetic-alcohol and stained by the Feulgen procedure, supplemented by the addition of propionic orcein. Analyses of chromosome pairing were made on permanent squashes of pollen mother cells at first metaphase of meiosis.

3. EXPERIMENTAL PROCEDURE

To determine the relationships of the chromosomes that pair in *T. aestivum* × *Ae. speltoides* hybrids it was necessary to introduce two structural markers simultaneously, since wheat chromosomes are indistinguishable from each other at meiosis. This was achieved by crossing together plants from lines in which different chromosomes were ditelocentric. The products of the cross had two pairs of chromosomes in which one member of the pair was a normal chromosome and the other was telocentric. These derivatives were pollinated by *Ae. speltoides* to produce 28-chromosome hybrids which were selected for the presence of two telocentric chromosomes. Such *T. aestivum* × *Ae. speltoides* hybrids carried the telocentrics of two different, but identified, chromosomes.

Hybrids were produced in which two chromosomes were simultaneously marked by a telocentric condition for all three combinations of chromosomes of homoeologous group 5. The marked chromosomes in these within-group combinations were thus 5A-5B, 5A-5D and 5B-5D. In order that the pairing behaviour of non-homoeologous chromosomes could be compared with that of homoeologues, an attempt was made to produce hybrids in which every chromosome of group 5 was telocentric in combination with every chromosome of groups 3 and 6. The eleven, out of sixteen possible, combinations of this type obtained are indicated below:—

	5A	5B	5D
3A	+	+	
3B	+	+	
3D	+	+	+
6A			
6B	+	+	
6D		+	+

It should be mentioned that the telocentric of chromosome 5B, used in this work, was for the arm responsible for the profound genetic effect on meiotic pairing. Consequently the wheat components of the genotypes of the hybrids were in no instance responsible for homoeologous conjugation.

4. CONFIGURATIONS INVOLVING MARKED CHROMOSOMES

(i) *Non-homoeologues*

In the *T. aestivum* × *Ae. speltoides* hybrids in which eleven different combinations of two non-homoeologous telocentrics were separately present the marked chromosomes were never observed in the same configuration. The telocentrics participated in bivalents, trivalents and quadrivalents, but always in different figures (plate I, fig. 1). Although very many meiotic cells with marked non-homoeologues were examined,

the failure to detect non-homoeologous pairing, like all negative observations, is of course not conclusive. It cannot be asserted categorically that the non-homoeologous chromosomes concerned never pair; but it can be accepted without question that, if such pairing occurs, it does so with extreme rarity.

(ii) *Homoeologues*

The meiotic behaviour of the marked chromosomes relative to each other was quite different in the three types of *T. aestivum* × *Ae. speltoides* hybrids with two homoeologous chromosomes telocentric. The chromosomes marked by telocentric conditions in these hybrids were either 5A and 5B, 5A and 5D, or 5B and 5D; and in every instance, in some first metaphase cells, these marked homoeologues participated in the same configuration.

Some cells had both telocentrics unpaired, while in others both paired with a complete chromosome in separate bivalents. In other cases only one telocentric had paired and it was involved in either a bivalent or a trivalent. These types of pairing were of course uninstructive in terms of the relationships of the telocentrics concerned, since they were also to be found in hybrids with non-homoeologues marked.

The categories that were unique to hybrids with homoeologues marked were those in which the two telocentrics were associated in the same configuration. In the most commonly observed figure the two telocentrics were paired together directly to form a rod-shaped bivalent (plate I, figs. 2 and 3). This was the most direct and unequivocal distinction separating the meiotic behaviour of marked homoeologues from that of non-homoeologues. However, there were also two other patterns of pairing, found only when the telocentrics were homoeologous. The two telocentrics were sometimes associated with a single complete chromosome to form a triradial trivalent (plate I, fig. 4), or with two complete chromosomes to form a chain-of-four quadrivalent with the telocentrics at opposite ends. No matter which of the three combinations of two chromosomes of group 5 were telocentric, the same configurations were formed.

Since non-homoeologous telocentrics were never observed to pair, the involvement of group 5 chromosomes in common configurations provides clear confirmation of the hypothesis that meiotic pairing in *T. aestivum* × *Ae. speltoides* hybrids is homoeologous. Furthermore, because such pairing in haploids and hybrids is normally prevented by the activity of the long arm of chromosome 5B (Riley, 1960; Riley and Chapman, 1964*b*), which was present in all the hybrids, this activity must be suppressed in the presence of the genotype of *Ae. speltoides*.

The capacity of the telocentrics of 5A, 5B and 5D to pair, under the present experimental conditions, provides cytological evidence that

reinforces the genetical criteria used by Sears (1954, 1965) in assigning these chromosomes to the same homoeologous group. In addition, it is apparent that the technique employed—using marked chromosomes and the suppression of the 5B effect—permits the unequivocal recognition of cytological homoeology. However, as will be seen later, while the overall pattern of genetical and cytological homoeology may be the same, there may be differences in detail.

(iii) *Arm relationships of homoeologues*

The nature of the figures in which the telocentrics of 5A, 5B and 5D participated together also provided evidence on the relationships of the arms of the chromosomes concerned. In every instance the telocentrics used in the present work paired together directly (table 1). That is, chiasma formation was possible between the arms that were telocentric, under conditions permitting homoeologous synapsis (plate I, figs. 2 and 3). Thus all three telocentrics represent corresponding arms of the homoeologues. This might indeed have been expected, since in all three cases the telocentric for the longer arm of a heterobrachial chromosome was employed. Nevertheless the present evidence is the first available on the arm relationships of homoeologues; and it shows that the arms with the following genes, or effects, are equivalent:

5A—Q (speltoid suppression), b_1 (recessive to dominant awn inhibitor).
5B—p_{5B} (inhibitor of homoeologous pairing).
5D—spring/winter growth habit.

5. DIFFERENTIAL AFFINITY OF HOMOEOLOGUES

There were striking contrasts in the frequencies with which the marked homoeologous chromosomes participated in different pairing configurations, depending upon the particular telocentrics present in the *T. aestivum* × *Ae. speltoides* hybrids (table 1). Thus, when 5A and 5B or 5A and 5D were telocentric, the direct pairing of the marked homoeologues—either in a bivalent or in a trivalent—was comparatively rare, occurring in only eight cells in one hundred in both combinations. By contrast, when 5B and 5D were marked the telocentrics

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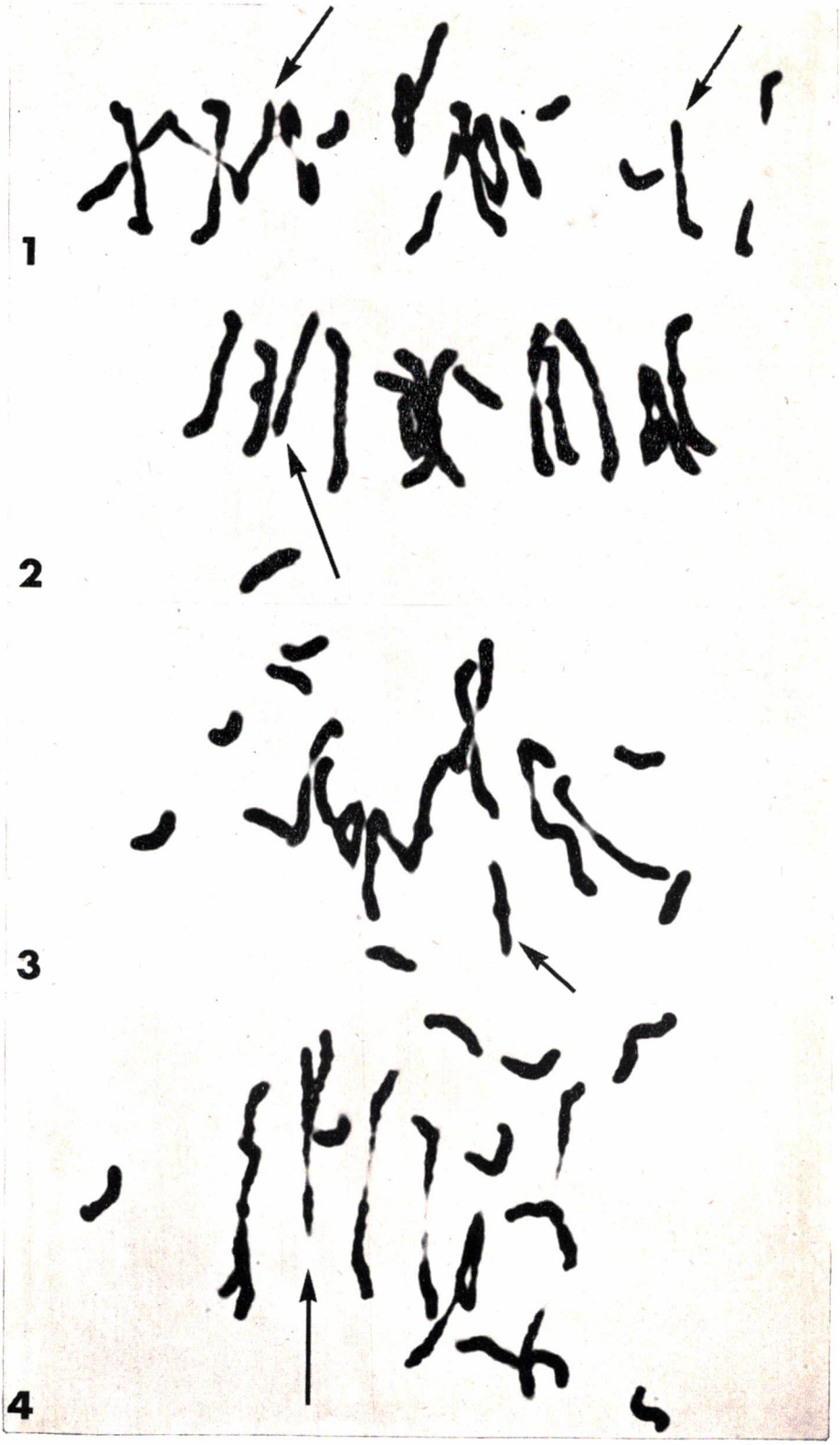
PLATE I (*opposite*). First metaphase of meiosis in pollen mother cells of *T. aestivum* × *A. speltoides* hybrids in which two chromosomes of *T. aestivum* are marked by a telocentric condition.

FIG. 1. There are two quadrivalents, one trivalent, seven bivalents and three univalents. The telocentrics are 3D, which is in a quadrivalent (arrowed), and 5D, which is in a bivalent (arrowed).

FIG. 2. One trivalent, 11 bivalents and three univalents; chromosomes 5B and 5D, which are telocentric, are paired together to form a bivalent (arrowed).

FIG. 3. One quadrivalent, one trivalent, six bivalents and nine univalents; chromosomes 5B and 5D are telocentric and paired together in a bivalent (arrowed).

FIG. 4. Two trivalents, five bivalents and 12 univalents; chromosomes 5B and 5D are telocentric and participate with a complete chromosome in a triradial trivalent (arrowed).



to face p. 50

paired together directly in more than half the cells scored (table 1). In conditions permitting homoeologous pairing there was, therefore, pronounced meiotic differential affinity between the long arms of chromosomes 5A, 5B and 5D—5B and 5D displaying much closer affinity to each other than either did to 5A.

TABLE 1

Pairing behaviour of two telocentric chromosomes of homoeologous group 5 at M1 of meiosis in T. aestivum × Ae. speltoides *hybrids*

Telocentric chrom.	No telo pairs	Telos together			One telo/complete				Two telo/complete			Total cells
				sum				sum			sum	
5A-5B	21	7	1	8	48	4	2	54	17	—	17	100
5A-5D	24	7	1	8	50	5	1	56	11	1	12	100
5B-5D	14	44	8	52	30	—	—	30	3	1	4	100
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)

= telocentric chromosome

= complete chromosome

However, there were four chromosomes in each group capable of homoeologous pairing in the present hybrids, as is displayed by the occasional occurrence of quadrivalents (plate I, figs. 1 and 3) (table 1). Pairing may be presumed to be possible between the three chromosomes of group 5 derived from *T. aestivum* and between the corresponding chromosome of *Ae. speltoides*, which may be called 5S. In the largest configurations—quadrivalents—chromosomes 5A, 5B, 5D and 5S must all participate, and similar quadrivalents must be visualised involving the four chromosomes of every other group.

The relative affinities of each of the group 5 chromosomes derived from *T. aestivum* have already been discussed, but the recognition that four, not three, chromosomes were capable of homoeologous conjugation means that the relative affinities of each chromosome for three others can be separately estimated. It is thus possible to consider meiotic affinities in six two-by-two combinations of the group 5 chromosomes. These may be expressed as follows with the letters a, b, c, x, y and z representing the frequency with which two particular chromosomes paired at first metaphase:—

$5A-5B = a$ $\qquad$ $5A-5S = x$

$5A-5D = b$ $\qquad$ $5B-5S = y$

$5B-5D = c$ $\qquad$ $5D-5S = z$

Values for *a*, *b* and *c* were observed and can be taken from column (4) of table 1. These values may be accepted as the frequencies with which chiasma formation occurred between the long arms of the stipulated chromosomes. The only ambiguity in these observations stems from the inclusion of occurrences of triradial trivalents, recorded in column (3), since these involve a minimum of two chiasmata which might be distributed:—(i) one between the telocentrics and one between a telocentric and a complete chromosome or (ii) both between a telocentric and the complete chromosome. In the latter instance there would have been no direct association between the telocentrics. However, the absolute frequency of these trivalents was so low that little error is introduced by accepting all as due to distributions involving direct chiasma formation between the telocentrics. With this proviso, however, the relative affinities of chromosomes 5A, 5B and 5D may be taken from table 1 column (4), where they are expressed as the percentages of cells in which the telocentrics paired, so that:—

$$a = 8$$
$$b = 8$$
$$c = 52.$$

These results are the first direct cytological observations—apparently in any organism—that have permitted an expression of differential affinity in quantitative terms.

The values for *x*, *y* and *z* cannot be obtained from direct observation since it was not possible to mark chromosome 5S of *Ae. speltoides*. However, the values can be estimated using the observed frequency with which a marked telocentric chromosome paired with an unmarked chromosome in the three types of hybrid with two group 5 chromosomes marked. Thus, for example, where chromosomes 5A and 5B were marked, the pairing of a marked with an unmarked chromosome could be of four types—5A with 5D, 5A with 5S, 5B with 5D, or 5B with 5S. Therefore, if the frequency of pairing between marked and unmarked chromosomes is called T, then

$$T_{(5A/5B)} = b+x+c+y.$$
$$\text{Similarly, } T_{(5A/5D)} = a+x+c+z,$$
$$\text{and } T_{(5B/5D)} = a+y+b+z.$$

The value for T in each formula can be obtained from table 1 by the summation of the frequencies of marked and unmarked pairing, recorded in columns (3), (8) and (11) × 2. The frequencies for column (11) are doubled since each cell recorded had two instances of chiasma formation between marked and unmarked chromosomes. Thus,

$$T = \text{columns } (3)+(8)+(11)\times 2,$$
$$\text{and } T_{(5A/5B)} = 89$$
$$T_{(5A/5D)} = 81$$
$$T_{(5B/5B)} = 46.$$

Since values for a, b and c were derived by direct observation, they can be substituted in the above formulae, as can the values for T. When this is done,

$$89 = 8+x+52+y$$
$$81 = 8+x+52+z$$
$$46 = 8+y+8+z$$

and

$$x+y = 29$$
$$x+z = 21$$
$$y+z = 30.$$

Solving for x, y and z shows that,

$$x = 10$$
$$y = 19$$
$$z = 11.$$

Although these estimates are likely to be subject to some error, it is probably not large; and the overall determinations of affinities must at least indicate their order, and in general terms, the degree of expression. Consequently it can be unquestionably asserted that there are pronounced differences between the relative affinities of the four chromosomes for each other, which from the present evidence can be expressed as follows:—

$$5A-5B = 8$$
$$5A-5D = 8$$
$$5B-5D = 52$$
$$5A-5S = 10$$
$$5B-5S = 19$$
$$5D-5S = 11.$$

This result may be interpreted as representing the relative similarity or difference of the chromosomes of homoeologous group 5 in structure and gene content. However, this is not the only interpretation, and the meaning of these observations will be considered more extensively later.

Nevertheless, it seemed useful to attempt to compare the affinity of homoeologues with that of fully homoeologous chromosome, under comparable genetic conditions. Unfortunately such a comparison could not be made on a group 5 chromosome because appropriate parental material was not available. Instead use was made of a parental stock of *T. aestivum* Chinese Spring that had 20 normal pairs of chromosomes but in which chromosome 6B was represented by a telocentric for one arm only, in the trisomic condition. A plant of this type was pollinated by *Ae. speltoides* and 29-chromosome hybrids produced, in which the telocentric of 6B was present in double dose. The pairing at first metaphase of meiosis of these two fully homologous telocentrics was scored in the same way as that already described for homoeologous telocentrics (table 2).

The two 6B telocentrics paired together and formed a bivalent in the majority of cells, and only rarely did they pair with an unmarked chromosome—presumably a homoeologue. Applying the same system of measurement as to the group 5 homoeologues, the numerical estimate of the affinity of the homologous 6B telocentrics for each other is 86. In these terms, therefore, chromosomes 5B and 5D have 60

TABLE 2

Pairing behaviour of two homologous 6B telocentric chromosomes at MI of meiosis in T. aestivum × Ae. speltoides *hybrids*

No telo pairs	Telos together			One telo/complete				Two telo/complete			Total cells
			sum				sum			sum	
12	82	4	86	1	—	—	1	1	—	1	100

 = telocentric chromosome

 = complete chromosome

per cent. of the affinity for each other displayed by the 6B telocentrics. Yet in normal euploid individuals of *T. aestivum* the 6B homologues almost always pair at meiosis, while the 5B and 5D homoeologues never do so. This nicely demonstrates the narrow margin of distinction between homologues and homoeologues upon which the discriminatory pairing imposed by the 5B system normally operates.

6. THE INTERPRETATION OF DIFFERENTIAL AFFINITY

The present observations, which uniquely demonstrate the validity of the concept of differential affinity originally proposed by Darlington (1928, 1937), permit the phenomenon to be described numerically. In so doing they force the acknowledgment of a problem which, though long recognised (Darlington, 1937; Dobzhansky, 1941), has been largely ignored; namely, the extent to which the capacity of chromosomes to pair at meiosis measures similarities in their overall structures and in the totality of their genetic equivalence. That the extent of meiotic pairing is not a strict measure of such similarity is shown by the effect of chromosome 5B on the meiosis of *T. aestivum*. Judgments made from the meiosis of material displaying this effect would ascribe no equivalence to homoeologues, despite the cytological similarities revealed in its absence and the genetic similarities displayed by nullisomic-tetrasomic compensation tests. It seems unlikely that further

genetic restrictions of pairing specificity, applying to the entire chromosome complement, occurred in the present hybrid situations. Nevertheless, other processes may have influenced the pairing of particular chromosomes in a way that rendered the frequency of pairing a distorted measure of gross genic and structural correspondence.

However, disregarding these possibilities in the first instance, if the group 5 pairing is assumed to measure total genetic congruence, then the closest relationship exists between chromosomes 5B and 5D, followed at a considerable distance by that between 5B and 5S. Indeed, using the evidence of the behaviour of the 6B telocentrics, about 60 per cent. of the genetic equivalence of completely homozygous homologues could be ascribed to the 5B and 5D homoeologues. An interpretation of this type, accepting the assumption of a common origin of homoeologues, implies that the differential affinity of chromosomes is an expression of their relative evolutionary proximities. Consequently chromosome 5A must be considered to have diverged from 5B and 5D to a much greater extent than 5B and 5D have from each other. If true, this presents to our view a new facet of the cytogenetic structure of *T. aestivum*, indicating that chromosomes in the A and B genomes—that have been together longest, first in tetraploid then in hexaploid wheat—have diverged from each other widely. This is in accord with other evidence, primarily from the study of mutagenesis at different levels of polyploidy, showing that the tetraploid species of *Triticum*, with only the A and B genomes, have much less duplication of genetic material than the hexaploid. On the present evidence, the divergence must, so far as group 5 is concerned, have resulted principally from changes in chromosome 5A, since the original similarity, which may be presumed for all homoeologues, is still retained to any considerable extent only by 5B and 5D. Whether the proposals, derived from the study of the group 5 situation, are of general application to the majority of chromosomes in each genome can only be determined by similar work on other homoeologous groups. However, if the same patterns of relationships are usual, then their interpretation in terms of genomic divergence and the overall genetic distinctions of chromosomes must be valid.

There are at present, however, certain anomalies that qualify the acceptance of determinations of differential affinity solely as measurements of gross genetic equivalence. First, although the B genome of *T. aestivum* was almost certainly derived from *Ae. speltoides*, or a close relative (Sarkar and Stebbins, 1956; Sears, 1956; Riley, Unrau and Chapman, 1958), chromosomes 5B and 5S—while displaying the second-highest affinity—paired considerably less frequently than 5B and 5D. Since the acceptance of an interpretation of the results in terms of gross similarities requires the assumption that 5B is little changed, this must imply that 5S has undergone marked changes since it gave rise to 5B. While this is possible, it contrasts with the conditions of the chromosomes of the A and D genomes of the hexaploid

species relative to those of the corresponding genomes of the diploid species, from which they were derived. Corresponding chromosomes of these diploids and the hexaploid can still be described as homologous, since they are able to pair at meiosis even when the restriction imposed by 5B is operative. The present evidence seems to indicate that, even if *Ae. speltoides* is the B genome donor, its hybrid with *T. aestivum* would show little or no meiotic pairing were the 5B activity not suppressed. For, by analogy with the behaviour of chromosomes of the A and D genomes, chromosomes 5B and 5S should be regarded as homologous, yet they have less affinity than some homoeologues. Some doubt must remain, therefore, that the frequency of 5B-5S pairing is even an approximate indication of their overall genetic relationship.

Similar doubt arises from the high pairing between chromosomes 5B and 5D since this result leads to the expectation that there would be good compensation in nullisomic-tetrasomic combinations in which these chromosomes were in altered dosage. By contrast less satisfactory compensation would be expected when chromosome 5A was in altered dosage in the same nullisomic-tetrasomic genotypes as either of the other two group 5 chromosomes. However, such expectations were not realised in Sears' (1965) studies, since although there was a slight superiority of the nullisomic 5D tetrasomic 5B condition over all other group 5 combinations, this was not repeated in nullisomic 5B tetrasomic 5D. While it may be that differential affinity is simply a more sensitive measure of overall genetic correspondence than is compensatory capacity in nullisomic-tetrasomic conditions, the alternative possibility must also be recognised that different properties may be measured by the two methods. If different aspects of chromosomal relationships are indeed involved, then the compensation test—which depends upon the occurrence of similar genetic activities in homoeologues—is more likely to measure gross genetic correspondence.

By what alternative conditions therefore might the differential affinity of homoeologues be determined? It is only possible to speculate upon other conditions but, for example, synapsis might be visualised as dependent upon contacts made between particular regions of chromosomes that are of limited extent and number. If this were so, differential affinity might measure not the overall similarities of chromosomes but the relative structural and genetic congruence of the contact regions. Homoeologues with contact regions that had undergone evolutionary divergence would then pair infrequently despite an occurrence of general correspondence in their genetic activities.

An alternative to this notion of limited but autonomously functioning contact points is the postulate that the pairing specificity of each chromosome is independently determined by gene activity. Pairing would thus result in part from the structural equivalence of the potential pairing partners but it would also be subject to variation caused by the presence of particular gene products. In terms of the expression of differential affinity there would be no detectable difference between

the outcome of the operation of either specific pairing genes or limited contact regions. However, in the investigation of homoeologous pairing between the chromosomes of *T. aestivum*, it will probably be easier to test the ideas concerning restricted contact regions. This arises from the largely distal chiasma formation, indicating that pairing is initiated distally and that the hypothetical contact regions may be supposed to be located towards the ends of wheat chromosomes. Consequently homoeologues with structural modifications confined to their terminal regions could be used to test whether differential affinity is determined by particular regions of the potential partners.

Despite the scepticism expressed regarding the interpretation of differential affinity in terms of gross genetic equivalence, the possibility nevertheless remains that its measurement for the chromosomes of group 5 may provide a true estimate of the strength of genetic homoeology. In any event, these observations certainly indicate the direction in which the study of the genetic structure of wheat should progress. Whether obtained by cytological or by genetical procedures, quantitative expressions of the relationships of homoeologous chromosomes to each other will illuminate the contemporary genetic status of *T. aestivum* as well as reveal its evolutionary history and some of its future potentialities in greater detail.

7. SUMMARY

1. Hybrids between common wheat, *Triticum aestivum* ($2n = 6x = 42$), and *Aegilops speltoides* ($2n = 14$) have high levels of chromosome pairing at meiosis, with numerous multivalents. The assumption that this pairing was between homoeologous chromosomes was tested by producing *T. aestivum* × *Ae. speltoides* hybrids in which two wheat chromosomes were marked by a telocentric condition. When the marked chromosomes were not homoeologous they never participated in the same configuration. By contrast, when the marked chromosomes were homoeologues, belonging to group 5, they were frequently involved in the same configurations as bivalents, trivalents or quadrivalents. Thus pairing in these hybrids was shown to be homoeologous, and the genotype of *Ae. speltoides* must therefore suppress the activity of chromosome 5B of wheat by which homoeologous pairing is normally inhibited.

2. Since the telocentric of only one arm of chromosomes 5A, 5B and 5D was used, and yet each was capable of pairing with either of the others *directly as a bivalent*, the chromosome arms represented are shown to correspond.

3. Comparisons of the relative frequencies with which the four chromosomes—5A, 5B and 5D from *T. aestivum* and 5S from *Ae. speltoides*—paired together showed pronounced differential affinities of these chromosomes for each other. The association of 5B with 5D was much more frequent than any of the other five possible two-by-two

associations. The next most common pairing was between chromosomes 5B and 5S. A quantitative estimate of the differential affinity of particular chromosomes at meiosis was thus made, apparently for the first time in any organism. The interpretation of this differential affinity is discussed in relation to its possible indication of the gross genetic equivalence of the participating chromosomes.

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