1961

M. Feldman

1961

ORIGIN OF GENETIC CONTROL OF DIPLOID-LIKE BEHAVIOR OF POLYPLOID WHEAT

RALPH RILEY, GORDON KIMBER AND VICTOR CHAPMAN*

WORK with 20-chromosome nulli-V haploids and 40-chromosome V-nullisomics has demonstrated that the purely bivalent-forming meiotic organization of common wheat, *Triticum aestivum* ($2n = 6x = 42$), is controlled by one or more genes on chromosome 5 [1,2]. Simultaneous confirmation of this was provided by work on hybrids deficient for chromosome 5 [7], and subsequent investigation has shown that this chromosome alone is concerned in the diploidization of wheat[2]. When chromosome 5 is absent, corresponding homoeologous chromosomes from the three different genomes can pair at meiosis; in its presence this does not normally occur. The effective gene, or genes, on chromosome 5 thus provide the potentiality of high fertility and the genetic stability which have made *T. aestivum* a successful polyploid and have allowed it to develop into one of the major crop plants of the world.

It is immediately pertinent to ask, therefore, whether the control exercised by chromosome 5 was developed subsequent to the origin of the polyploid state, or whether it occurred as a fortuitous result of the incorporation of an unaltered chromosome from a diploid ancestor Chromosome 5 is in the B genome[6] and so was brought with that genome into the tetraploid wheat species, and from the tetraploids into the hexaploids. The B genome was probably provided by a diploid species in the Sitopsis section of the genus *Aegilops*[4, 5]. It is therefore relevant to examine the Sitopsis section for indications of genetic effects on chromosome pairing similar to those caused by chromosome 5.

The Sitopsis section contains only diploid species. They are *A. speltoides, A. bicornis, A. longissima* and *A. sharonensis,* although the last two species are extremely closely related, forming fertile hybrids, and probably constitute a single genetic species. As pointed out by Riley *et al.*[3], there are important differences between the Sitopsis species in the influence they have, in hybrids with tetraploid wheat, on the pairing of wheat chromosomes. Triploid hybrids, involving *A. longissima, A. bicornis* or *A. sharonensis* and tetraploid wheat, have very little meiotic chromosome pairing. The *Aegilops* chromosomes rarely pair with the wheat chromosomes and the wheat chromosomes rarely pair with each other.

By contrast, when *A. speltoides* is crossed with a tetraploid wheat there are completely different pairing relationships in the triploid hybrid. Not only do the *A. speltoides* chromosomes pair with wheat chromosomes but wheat chromosomes pair with each other. Trivalents are common, and these must arise from the conjugation of structurally corresponding chromosomes in the two wheat genomes together with the related *Aegilops* chromosome.

The *A. speltoides* genotype thus breaks down the meiotic isolation of homoeologous chromosomes in tetraploid wheat, just as the removal of chromosome 5 does in hexaploid wheat. However, the chromosome 5 condition of the hexaploids is also repeated in tetraploid wheat since no segregants with homoeologous pairing are produced in tetraploid-hexaploid crosses. Thus, some component of the *A. speltoides* genotype suppresses the effect of the chromosome 5 gene. It appears, therefore, that the

*Plant Breeding Institute, Cambridge, England.

other Sitopsis species, which do not alter the normal meiotic affinities, are similar to the present condition of wheat in the genetic control of chromosome pairing. Consequently, *A. speltoides* seems less likely to be the B genome donor, despite the favorable evidence of karyotype and external plant morphology[3, 4].

To clarify this situation the genetic relationships have been investigated between the pairing control exercised by chromosome 5 of hexaploid wheat and the influence of two different species in the Sitopsis section of *Aegilops*. The aim of this work was to study meiotic pairing in hybrids, between wheat and the *Aegilops* species, with and without chromosome 5 of wheat.

Materials

To obtain hybrids deficient for chromosome 5, crosses were made using plants of *T. aestivum* monosomic for chromosome 5 as female parents. These were pollinated by the *Aegilops* parent, so that the same cross could give rise to hybrids with and without chromosome 5.

The monosomic 5 parents were in *Triticum aestivum* L. variety Chinese Spring, and were kindly supplied by Dr. E. R. Sears. However, in the case of crosses between monosomic 5 and *A. speltoides,* only 27-chromosome hybrids, deficient for 5, were produced. Consequently, the 28-chromosome class was completed using hybrids of which the female wheat parent was *T. aestivum* L. variety Holdfast ($2n = 42$). The change of variety is not likely to have affected pairing significantly since Chinese Spring and Holdfast are essentially similar in chromosome structure, differing only in a reciprocal translocation involving chromosomes 3 and 17.

The two *Aegilops* species of the Sitopsis section involved in hybrids with *T. aestivum* were *A. longissima* Schweinf. and Muschl. ($2n = 14$) and *Aegilops speltoides* Tausch *ligustica* Savign. ($2n = 14$).

Meiosis was studied in Feulgen-orcein stained squashes of pollen-mother-cells from anthers fixed in acetic alcohol.

Results

First of all it should be indicated (Table I) that the two Sitopsis species *A. speltoides* and *A. longissima* were very similar in chromosome structure. Pairing was very good in hybrids between them, apart from the interference caused by heterozygosity for a reciprocal translocation. Thus, the differences in pairing between their hybrids and polyploid wheat species are not related to structural divergence.

The genetic differences between *A. speltoides* and *A. longissima,* which show in hybrids with tetraploid wheats, were also apparent in 28-chromosome hybrids with *T. aestivum* (Table II). The 28-chromosome hybrids with *A. speltoides* had very high pairing with many trivalents and quadrivalents. In a few cells every chromosome was conjugated; for example, one had five bivalents, two trivalents and three quadrivalents. Homoeologous chromosomes from all three wheat genomes, as well as the matching *A. speltoides* chromosome, must have participated in the quadrivalents. By contrast the 28-chromosome hybrid with *A. longissima* had very little pairing—hardly more than might be expected in a euhaploid of wheat. There were never more than 12 chromosomes paired in any cell. Clearly the *A. speltoides* genotype removes the inhibition of homoeologous pairing caused by chromosome 5 of wheat, but the *A. longissima* genotype does not.

However, there were no major differences between the 27- and 28-chromosome hybrids with *A. speltoides*. Re-

TABLE I. Mean chromosome pairing at metaphase I of meiosis in an *A. longissima* × *A. speltoides* F_1 hybrid

Cells	univ.	Bivalents			triv.	quad.
		rod	ring	total		
50	0.54	2.32	2.86	5.18	0.34	0.52

moval of wheat chromosome 5 produced no modification of pairing, presumably because its influence was already suppressed by the *A. speltoides* genotype. By contrast the 27-chromosome hybrids with *A. longissima* had much higher pairing than the normal 28-chromosome hybrids. There were numerous trivalents and quadrivalents and there were occasional cells without any univalents. Apparently, as in nulli-V haploids, homoeologous pairing could then take place.

Discussion

The effect of the *A. longissima* genotype is like that of wheat chromosome 5 in that neither breaks down the meiotic isolation of homoeologous chromosomes. There is a distinction, nevertheless, in that chromosome 5 produces a positive effect — homoeologous pairing only occurring in its absence. When chromosome 5 is absent, however, the *A. longissima* genome cannot prevent homoeologous pairing in hybrids. Thus, there is nothing in the *A. longissima* genotype which can compensate for the absence of chromosome 5. Consequently, whatever the fundamental effect of chromosome 5 may be, it is not produced by *A. longissima.* The *A. speltoides* and *A. longissima* genotypes, and chromosome 5 of wheat, all operate differently in their influence on chromosome pairing.

A. bicornis is like *A. longissima* in lacking the capacity to compensate for the absence of chromosome 5 (Riley unpublished). Unless there are intraspecific differences, therefore, no Sitopsis species has a genotype which matches the activity of chromosome 5. Consequently, the control exercised by this chromosome probably developed after the inclusion of the B genome in polyploid wheat. If, as this suggests, the genetic regulation of the diploid-like behavior of wheat had a mutational origin, a number of hypotheses can be advanced concerning the nature of the change involved. It should be indicated, however, that a mutational origin of the system is most readily conceived if changes at a single locus are involved. Therefore, the succeeding hypotheses are founded on such a notion, although a more complex organization cannot be excluded.

The significance attached to the different meiotic patterns produced by *A. speltoides* and the other Sitopsis species, in hybrids with wheat, is critical in every evaluation of the problem. For example, it may be that the distinctive behavior of *A. speltoides* depends upon a gene in the chromosome homologous, or homoeologous, to chromosome 5 of wheat. Then the different effects on pairing produced by *A. speltoides, A. longissima* and chromosome 5 might depend upon different alleles at the same locus. Of these the *A. speltoides* allele would be dominant to the other two, and in terms of the others the *A. longissima* allele would be an amorph. On this hypothesis the chromosome 5 allele could have arisen from either of the others by mutation. However, a recessive mutation from the dominant is more probable, and this would fit with other evidence favoring the derivation of the B genome from *A. speltoides.*

Alternatively, *A. longissima* and *A. speltoides* may carry the same allele, at the locus

TABLE II. Mean chromosome pairing at metaphase I of meiosis in hybrids with and without wheat chromosome 5

Hybrid	Chrom. No.	cells	univ.	Bivalents rod	ring	total	triv.	quad.
T. aestivum × *A. speltoides*	28	50	6.04	4.60	2.04	6.64	1.88	0.76
T. aestivum × *A. speltoides*	28	50	3.40	4.14	2.00	6.14	2.20	1.38*
T. aestivum × *A. speltoides*	27	30	6.13	2.63	2.50	5.23	1.76	1.23†
T. aestivum × *A. speltoides*	27	30	6.90	3.37	2.73	6.10	1.33	0.93†
T. aestivum × *A. longissima*	28	100	23.90	1.96	-----	1.96	-----	-----
T. aestivum × *A. longissima*	27	100	7.50	5.97	1.61	7.58	0.70	0.56
T. aestivum × *A. longissima*	27	100	9.80	5.54	0.87	6.45	0.87	0.41

*Associations of five, 0.04 per cell.
†Associations of five, 0.03 per cell.

concerned with meiotic pairing, on their chromosomes which correspond to chromosome 5 of wheat. Then the gene-differences, causing different meiotic pairing in hybrids, would reside elsewhere in their genotypes. If this were so, mutation on chromosome 5 might have caused it to assume control of intergenome pairing in the polyploid. This would presumably require no other alteration to a genotype like that of *A. longissima*. However, if the *A. speltoides* genotype were involved, the alteration of the epistatic genes, which suppress the chromosome 5 effect, would also be necessary.

Then again it might be that *A. speltoides* and *A. longissima* are indeed different at the significant locus of the chromosomes corresponding to wheat chromosome 5. On this hypothesis *A. speltoides* might already carry the same allele as wheat chromosome 5, but epistatic genes elsewhere in the genotype suppress its effects and cause the breakdown of homoeologous isolation in hybrids. Under these circumstances, if *A. speltoides* had contributed the B genome, mutation of the epistatic suppressors could have unmasked the chromosome 5 condition. It would then be left in control, exercising its restrictive influence on homoeologous pairing.

Synthetic tetraploids, derived from diploid wheat and either *A. speltoides, A. bicornis* or *A. longissima,* all form multivalents at meiosis, behaving more like segmental allopolyploids than true allopolyploids[3,5,9]. Presumably the first tetraploid wheat also behaved in this way, although all contemporary polyploids are bivalent formers. Consequently, there would be considerable selective advantage in favor of a change which reduced or eliminated homoeologous pairing, and restricted conjugation to homologous partners only. Selection would favor the purely bivalent formers because of their genetically balanced gametes and improved fertility. It seems likely that a mutation producing this result occurred either on chromosome 5 or elsewhere in the B genome, and subsequently the mutant was selected to fixation.

Since the pairing control exercised by the B genome of the polyploid wheats could have originated either from the *A. speltoides*- or from the *A. longissima*-type of organization, the present results give little assistance as to the source of that genome. However, it should be noticed that two of the three hypotheses proposed somewhat favor an origin from *A. speltoides*. As indicated earlier, the karyotype and gross morphology of this species also suggest it as the most likely source of the B genome.

Summary

Chromosome 5 of hexaploid common wheat, *Triticum aestivum,* carries one or more genes which prevent homoeologous chromosomes from pairing at meiosis. This chromosome is in the B genome and was probably derived from a species in the Sitopsis section of *Aegilops*. Consequently, the Sitopsis species may be examined to determine whether any have a genetic influence on meiotic pairing similar to that of chromosome 5. Chromosome pairing has been compared in hybrids between common wheat, with and without chromosome 5, and two Sitopsis species, *A. speltoides* and *A. longissima*.

Homoeologous pairing occurred in the hybrids involving *A. speltoides* irrespective of the presence or absence of chromosome 5. Therefore, this genotype removes the inhibition of wheat chromosome 5 on intergenome pairing.

There was no abnormal intergenome pairing in hybrids involving *A. longissima* when chromosome 5 of wheat was present. In its absence, however, the isolation between the genomes broke down. Thus, the *A. longissima* genotype is unable to compensate for the deficiency of chromosome 5 and cannot operate in the same way.

Apparently none of the possible B genome donors has a genotype which functions like the critical wheat chromosome. Therefore, a number of alternative hypotheses are proposed to account for the origin by mutation of the diploidizing influence exercised by chromosome 5.

Literature Cited

1. Riley, R. and V. Chapman. Genetic control of the cytologically diploid behaviour of hexaploid wheat. *Nature* 182: 713-715. 1958.

2. ————, V. Chapman and G. Kimber. Position of the gene determining the diploid-like meiotic behaviour of wheat. *Nature* 186: 259-260. 1960.

3. ————, J. Unrau and V. Chapman. Evidence on the origin of the B genome of wheat. *Jour. Hered.* 49: 91-98. 1958.

4. Sarkar, P. and G. L. Stebbins. Morphological evidence concerning the origin of the B genome in wheat. *Amer. Jour. Bot.* 43: 297-304. 1956.

5. Sears, E. R. The B genome of *Triticum. Wheat Inf. Service* 6: 8-10. 1956.

6. ————. The aneuploids of common wheat. *Proc. First Int. Wheat Genet. Symp.* 221-2238. 1958.

7. ———— and M. Okamoto. Intergenomic chromosome relationships in hexaploid wheat. *Proc. Tenth Int. Cong. Genet.* 2: 258-259. 1958.

8. Tanaka, M. Chromosome pairing in hybrids between *Aegilops sharonensis* and some species of *Aegilops* and *Triticum. Wheat Inf. Service* 2: 7-8. 1955.

9. ————. Chromosome pairing and fertility in the hybrid between the new amphidiploid S^1S^1AA and emmer wheat. *Wheat Inf. Service* 3: 21-22. 1956.