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THE ANEUPLOIDS OF COMMON WHEAT[1]

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For several years there has been available for each of the 21 chromosomes of the common-wheat variety Chinese Spring the complete series of aneuploids, nullisomic through tetrasomic. The origin and characteristics of these aneuploids have been described previously in some detail (Sears, 1939, 1944, 1954) and presumably need be reviewed only briefly here.

Almost every one of the 21 different nullisomics, each with only 20 pairs of chromosomes, differs greatly from normal. The nullisomics have been placed in groups of three within which the resemblances are in some cases striking. Nullisomics are derived from monosomics in the way indicated in table 1. On the

TABLE 1—*Breeding behavior of a typical monosomic plant.*

Female	Male	
	21-Chromosome Pollen 96%	20-Chromosome Pollen 4%
21-Chromosome Eggs 25%	21II Plants 24%	20II+1I Plants 1%
20-Chromosome Eggs 75%	20II+1I Plants 72%	20II Plants 3%

Totals		
Disomics	(21II)	24%
Monosomics	(20II+1I)	73%
Nullisomics	(20II)	3%

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female side there is apparently no selection against 20-chromosome eggs, which therefore constitute about 75 per cent of those fertilized. (The monosome, always a univalent at meiosis, is lost about 50 per cent of the time.) The frequency of functioning 20-chromosome pollen then determines the number of nullisomics obtained, and this varies from about 1 per cent to more than 5 per cent, depending on the chromosome concerned. About half of the nullisomics are either male-sterile or female-sterile and thus cannot be maintained as nullisomic lines. Even those that are fertile are not entirely stable as lines, for they tend to acquire compensating trisomes.

Most of the monosomics differ little or not at all from normal in appearance. They have been obtained from haploids, from partially asynaptic nullisomic III, from X-rayed pollen, and occasionally spontaneously from more or less normal material.

Trisomics, which are also generally normal in phenotype, have originated from haploids, nullisomic III, other nullisomics, and triploids. They give rise to tetrasomics in frequencies comparable with those of nullisomics from monosomics.

The tetrasomics are less nearly normal than monosomics or trisomics, but nearly all are less abnormal than the corresponding nullisomics. All can be maintained as lines, although these lines require cytological checking to assure against loss of the extra chromosomes.

In addition to the simple aneuploids mentioned, there are some of a secondary nature, of which the most important are the monotelo- and monoisosomics and the ditelosomics. The monoisosomics which are monosomic for an isochromosome for one or the other arm of a particular chromosome, are chiefly of value because the isochromosome is cytologically recognizable. In a few cases the monoisosomic plant is more nearly normal than the simple monosomic, and usually it segregates a higher proportion of nullisomic offspring. The telocentric chromosomes, which consist of a single arm, are also recognizable cytologically, and the ditelosomic forms a reasonably stable line particularly suitable for use in the identification of unknown chromosomes. Both isochromosomes and telocentrics are the result of misdivision of univalents, which occurs frequently in the variety Chinese Spring.

The nullisomics and particularly the monosomics are being used fairly widely now in genetic experiments and to a lesser extent in breeding work. Tetrasomics can be very useful, too, for the determination of gene dosage effects and especially for the analysis of genetic relationships between chromosomes. It is easily possible to combine any tetrasome with any nullisome, provided the combination is viable, and to observe whether the tetrasome tends to exaggerate the deleterious effects of the nullisome or whether it may tend to cancel these effects. In the latter case we may assume that the two chromosomes concerned are genetically related; that is, that they have genes in common.

GENETIC HOMOEOLOGIES

On the basis of resemblances between different nullisomics, and from study of nullisomic-tetrasomic combinations, the 21 chromosomes have been placed

in 7 homoeologous groups of 3 (Sears, 1952). Within these groups each tetrasome shows the ability to compensate to some degree for either of the other two nullisomes. All 42 possible nullisomic-tetrasomic combinations within groups have been synthesized, and each shows some superiority over the simple nullisomic. In many cases the compensation has been almost complete, and has been strikingly good in all but a few combinations.

Within groups 1 (chromosomes I, XIV, XVII), 3 (III, XII, XVI), and 7 (VII, XI, XXI), all the nullisomic-tetrasomics are reasonably normal plants, indicating that the three chromosomes in each of these groups are very closely related genetically. In groups 2, 4, and 6 there is one chromosome (II, IV, and X, respectively) which seems to contain important genes that the others do not carry. As a tetrasome this chromosome compensates well for the other two nullisomes, but as a nullisome it is poorly compensated for by the other two tetrasomes. In the remaining group, 5, there are some complications because of the extreme effect of the speltoid-suppressing gene Q, which lies on chromosome IX, and of a gene for earliness on chromosome XVIII. But all combinations in group 5 show some degree of compensation.

It is not enough, of course, just to synthesize nullisomic-tetrasomic combinations within the homoeologous groups, for it is conceivable that the compensation effect can be a general phenomenon not dependent on specific close relationship of the chromosomes concerned. Therefore, some 50 nullisomic-tetrasomics involving chromosomes from different groups were synthesized. In not a single case was there any evidence of compensation. In every one the nullisomic-tetrasomic, if obtainable, was inferior to the simple nullisomic. In many cases even the monosomic-tetrasomic was distinctly abnormal, to the extent of being completely or nearly sterile.

The fact that no nullisomic-tetrasomic combination between groups has shown compensation does not necessarily mean that no genetic relationship exists between chromosomes other than those in the same homoeologous group. The test is not likely to reveal a small degree of relationship, for it only shows whether the restoration of the dosage of genes common to the two chromosomes has a beneficial effect great enough to outweigh the deleterious effect of the accumulation in extra dosage of genes present on the tetrasome but not on the nullisome. It seems likely that 2 chromosomes may have 10 or perhaps 20 per cent of their genes in common without any relationship being detected by this method. Evidence will be presented which suggests that certain chromosomes in different homoeologous groups are to some extent related. Unfortunately, most of these apparently related chromosomes have not yet been subjected to the nullisomic-tetrasomic test.

ANALYSIS OF PAIRING IN HAPLOID

It has long been known that some non-homologous chromosomes of hexaploid wheat can pair, particularly in haploids, where up to four pairs may occur. If this pairing is due to certain non-homologues having a segment in common, as is generally supposed, then we may suspect that the pairing chromosomes are genetically as well as cytologically related and should therefore belong to the same homoeologous group. Fortunately we are now able to determine which chromosomes are responsible for at least part of the pairing in the haploid.

Since 1939 it has been known that many of the functional female gametes of haploids carry translocations (Sears, 1939). Since these are presumably the result of crossing-over in the paired, essentially non-homologous chromosomes, it is only necessary to identify the chromosomes involved in a particular translocation to know that these two chromosomes have paired in the haploid.

Thirteen translocations from haploids have now been analyzed (Okamoto and Sears, in manuscript), and all but four of these involve homoeologous chromosomes (table 2). Chromosomes VI and XIX were involved in 4 of the 13 translocations, II and XX in 2, and XI and XXI in 2. It is obvious that most of the pairing is between chromosomes belonging to the same homoeologous group, but that some chromosomes from different groups are also able to pair. Furthermore,

TABLE 2—*Identification of the chromosomes involved in translocations obtained from haploids. (From Okamoto and Sears, in manuscript.)*

Chromosomes Involved in Translocations	Number of Occurrences
Homoeologous:	
VI, XIX	4
II, XX	2
XI, XXI	2
XII, XVI	1
Non-Homoeologous:	
II, VIII	1
IV, XII	1
VI, XVIII	1
IX, XI	1

it is clear that certain homoeologous chromosomes tend to pair much more frequently than do others. Of 21 possible different homoeologous pairings, only 4 were represented among the 9 cases analyzed. Although the sample was small, it is noteworthy that no pairing was discovered involving chromosomes so closely related genetically as XIV and XVII, III and XII or XVI, and VII and XXI. It must be pointed out, however, that pairing between chromosomes having only a terminal segment in common would not be detected by this method.

ASYNAPTIC EFFECT OF CHROMOSOME V

There remains the anomaly that with very close genetic relationship of chromosomes within the homoeologous groups, such that up to seven trivalents per cell ought to occur in the haploids, very little pairing can actually be found. How can such closely related chromosomes fail to pair when given such an excellent opportunity as they have in the haploid? A reasonable answer to this question has presented itself in some findings of M. Okamoto at the University of Missouri and R. Riley at Cambridge, England. Their results confirm and complement each other in a rather remarkable way.

When Okamoto (1957a) crossed *Triticum aestivum* (genome formula AABBDD) with the amphidiploid *T. aegilopoides* x *Aegilops squarrosa* (AADD), he expected to find 14 bivalents and 7 univalents at meiosis in the F_1, which

was of the constitution AABDD. This expectation was not realized, 13 pairs being the maximum found, and the average being only about 6 pairs. When he used monosomic-V *T. aestivum*, however, the hybrids which were deficient for chromosome V frequently showed 15 bivalents and averaged over 12 bivalents per cell.

Okamoto then made hybrids of mono-V with *T. aegilopoides*. It has been shown by a number of investigators (see Kihara, 1937) that this hybrid (constitution AABD) has three to seven pairs, with an average of five or perhaps six. In the absence of chromosome V, 5 to 13 pairs were found in the F_1, with an average of about 10 (Sears and Okamoto, 1958). One cell was found with all the chromosomes paired. In addition to pairing of *A.* einkorn with *A. aestivum*, there obviously was pairing of chromosomes of the B genome with those of D, and presumably also of B and D with A, for there were frequent trivalents.

The results of Riley (1958) agree in indicating that in one of the chromosomes of wheat, presumably V, there exists a gene that reduces pairing of chromosomes which are not fully homologous. Thus homoeologues are largely prevented from pairing, while homologues can still pair regularly. The effect of the gene can be seen in the reduced frequency with which a ring of four is formed in hexaploid vs. diploid plants heterozygous for a reciprocal translocation. The ring is regularly formed in diploid wheat but often gives way to a chain of four or of two bivalents in hexaploid wheat. It thus appears that polyploid wheat, which originally must have been somewhat unstable because of chromosome irregularities resulting from multivalent formation, has achieved diploid pairing and stability by the simple acquisition of a mutation which reduces the intensity of pairing.

IDENTIFICATION OF A-GENOME CHROMOSOMES

For a full exposition of the origin and relationships of the chromosomes of wheat, it is necessary to know which belong to genome A, which to B, and which to D. For genome D this determination is easily made, for it involves only crossing each monosome with a tetraploid wheat and observing whether the F_1 has $14^{II}\ 6^{I}$ or $13^{II}\ 8^{I}$. The chromosomes of the D genome were therefore early identified, and were numbered XV to XXI. Information is less easily obtained for the other 14 chromosomes, now numbered I to XIV without regard to their affiliation with a particular genome.

Crosses of *T. aestivum* with diploid wheat are difficult to make, and pairing in the hybrid is sufficiently irregular that erroneous conclusions might easily be drawn from simple determinations of the amount of pairing. The problem of crossability can be solved by using the above-mentioned AADD amphidiploid instead of AA; but the difficulty of irregular and reduced pairing remains or is somewhat intensified. Now Okamoto (1957b) has overcome this difficulty by introducing telocentrics of particular A- and B-genome chromosomes into the cross. Then when the chromosome concerned happens to pair with another, the result can be detected with certainty by the occurrence of a heteromorphic bivalent.

Using the telocentric method, Okamoto (1957b and unpublished) has been able to determine the ability of 10 different chromosomes to pair with A-genome chromosomes (table 3). These 10 chromosomes belong to 6 different homoeo-

TABLE 3—*Results of cytological analysis of hybrids between AADD and Chinese Spring wheat having known telocentric chromosomes.*
(From Okamoto and Sears, in manuscript.)

Homoeologous Group	Chromosome Telocentric	No. Microsporocytes Observed	Percent with Heteromorphic Bivalent		Genome Assignment
			Certain	Doubtful	
1	I	150	0.00	0.67	B
3	III	260	0.00	0.38	B
3	XII	141	7.09	0.00	A
4	VIII	760	0.00	0.13	B
5	V	2,185	1.74	0.05	B
5	IX	1,450	9.72	0.00	A
6	VI	478	10.88	5.23	A
6	X	332	0.00	1.51	B
7	VII	500	0.00	0.00	B
7	XI	416	2.64	0.48	A

logous groups, with only group 2 not being represented. In three of the four cases where two chromosomes from one group were tested, the results showed conclusively that one belongs to the A genome and one to the B, for one telocentric paired in appreciable frequency while the other showed no pairing at all that could be identified with certainty. In the other case, involving chromosomes V and IX, there can be little doubt that V belongs to the B genome and IX to A, even though a few heteromorphic bivalents were observed involving telocentric-V. More than five times as many heteromorphics occurred with IX as with V. It may be assumed that the pairing involving telocentric V is homoeologous pairing with either IX or XVIII.

In group 1, chromosome I obviously belongs to the B genome, and chromosome XIV can safely be placed in the A genome, for it carries a gene (or two very closely linked genes) for pubescence and black coloration of glumes. The same gene or tight linkage is evidently present in diploid wheat (Smith, 1939).

With five homoeologous groups thus shown to contain both an A- and a B-genome chromosome, it is presumably safe to assume that the untested chromosome IV belongs to the A genome, for VIII quite clearly is in the B genome.

This leaves untested only group 2, consisting of chromosomes II and XIII. Although telocentric chromosomes have only recently become available for these two chromosomes, it has been possible to obtain evidence indicating that chromosome XIII is in the B genome. From a cross of monosomic XIII x AADD there was obtained a plant deficient not only for chromosome XIII but also for another chromosome, evidently V. Chromosome pairing in this plant was very much better than in sister plants deficient only for chromosome XIII. When comparison was

made of pairing in this plant with pairing in ordinary V-deficient plants, it was found that the only significant difference was in the frequency of univalents. This is what would be expected if chromosome XIII is in the B genome. It seems best, however, to leave II and XIII in the doubtful category until crosses which have now been made involving telocentrics can be grown and analyzed.

NEW NUMBERS FOR THE CHROMOSOMES

It is now possible to assign each chromosome except possibly II and XIII to its respective genome (table 4). With this assignment made, there arises the

TABLE 4—*Assignment of the chromosomes of hexaploid wheat to their respective genomes and homoeologous groups.*

Homoeologous Group	Genome A	Genome B	Genome D
1	XIV	I	XVII
2	II?	XIII?	XX
3	XII	III	XVI
4	IV	VIII	XV
5	IX	V	XVIII
6	VI	X	XIX
7	XI	VII	XXI

question of the desirability of renumbering the chromosomes to conform to some logical system. It would appear that the advantages of changing the numbers would in the long run far outweigh the disadvantages, particularly if the change can be made before much additional literature has accumulated. At the same time it would be highly desirable to abandon the use of the rather clumsy Roman numerals.

Whatever system is adopted for renumbering the chromosomes, each chromosome's number should presumably indicate to which genome and to which homoeologous group it belongs. Another important consideration is to make the new system such that the transition from the old numbers to the new will be as easy as possible.

Any system which simply renumbered the chromosomes from 1 to 21, placing them in logical sequence with respect to the three genomes and the seven homoeologous groups, would have two distinct disadvantages. First, most of the old numbers would be re-used for different chromosomes. To be sure, the new numbers would be Arabic rather than Roman, but this is only obvious when they are written, not when they are spoken. During the period of transition there would surely be confusion on this account. Second, the fact that chromosomes 1, 8, and 15, etc., are homoeologous would not be sufficiently apparent. People are not accustomed to using numerical systems based on seven. Until the different combinations had been memorized, it would be necessary to make arithmetic calculations to know whether a particular two chromosomes were homoeologous.

In view of the foregoing considerations, the following system is proposed. It is essentially the one proposed by Winge (1924) more than 30 years ago. By this

system the number of each of the present homoeologous groups is used for all three chromosomes of the group, with the letters A, B, and D being added to distinguish the three (table 5).

TABLE 5—*Recommended new numbers for the chromosomes of hexaploid wheat.*

Homoeologous Group	Genome A		Genome B		Genome D	
	New	Old	New	Old	New	Old
1.....	1A	XIV	1B	I	1D	XVII
2.....	2A	II?	2B	XIII?	2D	XX
3.....	3A	XII	3B	III	3D	XVI
4.....	4A	IV	4B	VIII	4D	XV
5.....	5A	IX	5B	V	5D	XVIII
6.....	6A	VI	6B	X	6D	XIX
7.....	7A	XI	7B	VII	7D	XXI

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