NULLISOMIC-TETRASOMIC COMBINATIONS IN HEXAPLOID WHEAT*

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1. INTRODUCTION

THE discovery that the 21 different chromosomes of common wheat (*Triticum aestivum* L.) fall into seven homoeologous groups of three (Sears, 1952, 1954) was based primarily on the ability of each tetrasome to compensate for the nullisome of each of the other two chromosomes of the same group. Supporting evidence has come from the finding of Okamoto and Sears (1962) that the pairing in haploids is largely between chromosomes belonging to the same homoeologous group, and from the work of Riley and Kempanna (1963), who found only pairing of homoeologues when increased pairing was induced by the absence of chromosome 5B.

Some brief general observations were made by Sears and Okamoto (1956) concerning the 40 within-group (compensating) and 47 between-group (non-compensating) combinations then in existence. Those observations will be extended in the present paper to include the additional two compensating and 14 non-compensating combinations now available. Detailed data on origins will also be presented, along with figures on fertility and information on morphological characters.

The system of numbering developed by Sears (1958) and Okamoto (1962) will be employed. These numbers correspond as follows to those previously used: 1A = XIV, 1B = I, 1D = XVII, 2A = XIII, 2B = II, 2D = XX, 3A = XII, 3B = III, 3D = XVI, 4A = IV, 4B = VIII, 4D = XV, 5A = IX, 5B = V, 5D = XVIII, 6A = VI, 6B = X, 6D = XIX, 7A = XI, 7B = VII, 7D = XXI.

The terms nullisomic, monosomic, etc., will usually be shortened to nulli, mono, etc. Where a pair of chromosome designations (as 1A-1B) are given, the chromosomes concerned are of reduced and increased dosage, respectively. A single designation (as tetra-3D) implies that the other 20 chromosomes are disomic.

One of the nulli-tetras (5D-5B) was kindly provided by Dr. Ralph Riley of the Plant Breeding Institute, Cambridge. All the materials belonged to the variety Chinese Spring.

* Co-operative investigations of the Crops Research Division, Agricultural Research Service, U.S. Department of Agriculture, and the Field Crops Department, Missouri Agricultural Experiment Station. Journal Series No. 2796 of the Missouri Station. Approved by the Director.

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2. COMPENSATING COMBINATIONS

(i) *Origin*

Of the 42 nullisomic-tetrasomics involving chromosomes of the same homoeologous group, 25 were synthesised by pollinating a monosomic by a tetrasomic, backcrossing the resulting mono-tri by the tetrasomic, and selfing the resulting mono-tetra. The other 17 combinations arose in various ways (fig. 1), five spontaneously (without crossing).

In order to obtain the mono-tetras from mono-tri × tetra, from eight to 16 (average 13·5) plants were grown, and from one to 12 (average 3·9) from each cross were examined cytologically. The frequency of mono-tetras was thus in reasonable accordance with expectation on the basis of about three-fourths of the gametes of a monosomic plant being nullisomic and about one-third of the gametes of a trisomic carrying an extra chromosome.

The number of nulli-tetras recovered from selfed mono-tetra depends primarily upon the degree to which the extra chromosome compensates in the pollen for the missing one. Approximately three-fourths of the gametes are expected to be deficient for one chromosome

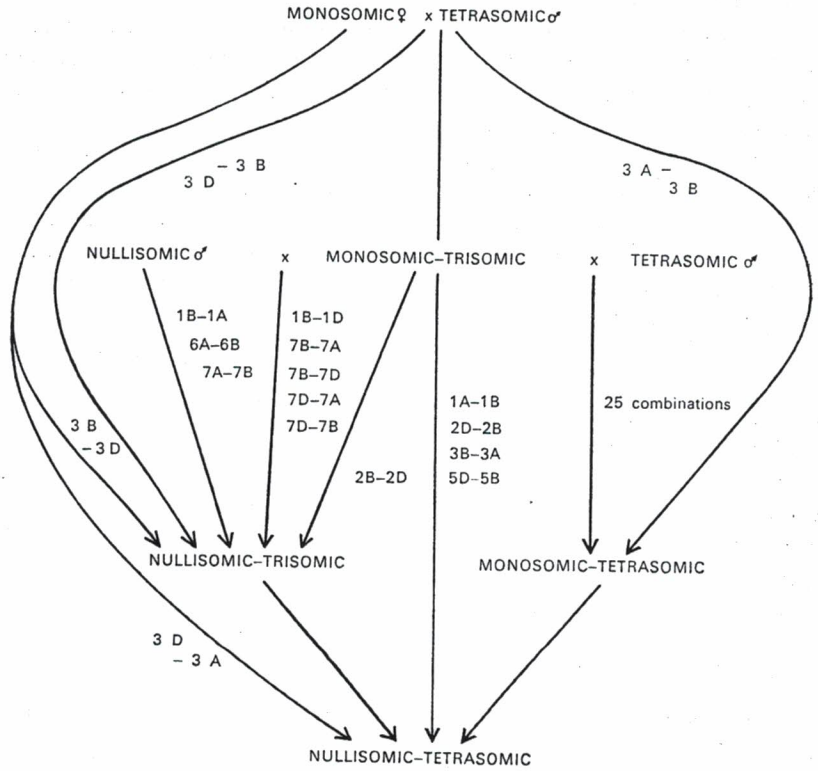


FIG. 1. Manner of origin of nullisomic-tetrasomics involving homoeologous chromosomes.

and duplicated for the homoeologue, assuming regular 2:2 distribution of the members of the tetrasome at meiosis, an assumption not realised with certain tetrasomes, notably those of group 3 (Sears, 1954). With no selection on the male side, this would result in about 9/16 nulli-tetra offspring. Because homoeologous chromosomes were involved, selection in favour of nulli-di pollen (n−1+1) could be expected in some cases. Since the offspring analysed cytologically (table 1) were usually not a random sample, no general conclusion can be drawn as

TABLE 1

Chromosome constitution of offspring of monosomic-tetrasomics

Chromosomes involved		No. grown	No. analysed	No. nulli-tetra
Mono	Tetra			
1A	1D	19	1	1
1D	1A	18	2	1
1D	1B	12	5	1
2A	2B	20	8	6
2A	2D	20	2	1
2B	2A	33	10	4
2D	2A	20	2	1
3A	3B	19	2	1
3A	3D	20	1	1
4A	4B	14	2	1
4A	4D	40	4	3
4B	4A	35	9	5
4B	4D	19	1	1
4D	4A	20	2	1
4D	4B	18	3	3
5A	5B	40	11	8
5A	5D	40	10	2
5B	5A	37	6	1
5B	5D	40	3	2
5D	5A	20	6	1
6A	6D	12	4	1
6B	6A	20	2	1
6B	6D	39	3	2
6D	6A	20	2	2
6D	6B	20	7	7
7A	7D	23	1	1
7B	7A	20	10	7

to the amount and kind of pollen selection that occurred. In nearly every case, the first few plants to reach the sampling stage were the ones analysed. In some cases, particularly those involving nulli-6D, this undoubtedly involved a selection in favour of nulli-tetras; whereas in other cases the nulli-tetras tended to be late and thus were poorly represented in the sample taken. In a few families—for example, those involving mono-4B and -6B—the nullisomics could be recognised by their awnedness, and the number of plants examined was thereby reduced.

The few data obtained from selfing of monosomic-trisomics conform to the conclusion previously reached (Sears, 1944) for mono-2D tri-2B

and mono-3D tri-3A that nulli-di pollen may compete fairly successfully with normal pollen—that is, that an extra chromosome can compensate to a large extent for a missing homoeologue in the pollen as well as in the plant itself. The only significant addition to the 1944 data is for mono-2B tri-2D, which yielded three nulli-tetra, eight nulli-tri, and one normal in 34 plants analysed. As with 2D-2B, this is in reasonable accordance with prediction based on competition on even terms between normal and nulli-di pollen.

TABLE 2

Chromosome constitution of offspring of nullisomic-trisomics

Chromosomes involved		No. grown	No. analysed	No. nulli-tetra	No. nulli
Nulli	Tri				
1B	1A	20	20	9	1
1B	1D	20	2	1	0
2B	2D	40	27	5	3
2D	2B	104	62	29	0
3B	3D	22	8	1	2
3D	3B	19	1	1	0
6A	6B	13	6	2	0
7A	7B	51	29	5	4
7B	7A	22	13	1	2
7B	7D	20	10	1	3
7D	7A	9	9	2	0
7D	7B	20	4	1	0

Another measure of the degree of compensation of one chromosome for another in the pollen is the frequency of nulli-tetra and nullisomic offspring obtained from nulli-tri plants (table 2). If compensation is complete, nulli-tri plants should behave like the corresponding monosomics, except for differences based on the divergent meiotic behaviour of trisomes and monosomes. Whereas monosomics produce only about 25 per cent. of 21-chromosome gametes, a nulli-tri individual should give rise to about 40 per cent. of 21-chromosome (19+2) gametes. This means a ratio of 40:60 of 21- to 20-chromosome pollen instead of 25:75 and should result in the functioning of only about half as much 20-chromosome pollen. Also, only 60 per cent. of the functioning 20-chromosome pollen of the nulli-tri will give rise to nullisomic plants, compared with 75 per cent. from monosomics. Therefore, assuming full compensation, only about 0·4 per cent. to 3·0 per cent. nullisomics would be expected instead of the 0·9 per cent. to 7·6 per cent. reported (Sears, 1954) for monosomics. Nulli-tetras, on the other hand, would be expected to be more frequent than are disomics from monosomics—about 40 per cent. instead of 25 per cent.

For the combination 2D-2B (table 2), it is clear that nulli-tri pollen functions almost to the exclusion of nulli pollen, and the same may be

true for 1B-1A. In 2B-2D, 3B-3D, 7A-7B, 7B-7A and 7B-7D, the rather meagre data suggest that nulli pollen competes fairly successfully with nulli-di, and this indicates less than complete compensation in the male gametophyte.

(ii) *Characteristics*

Most of the 42 nulli-tetra combinations involving chromosomes of the same homoeologous group are far superior to the corresponding nullisomics, and all are superior in some way.

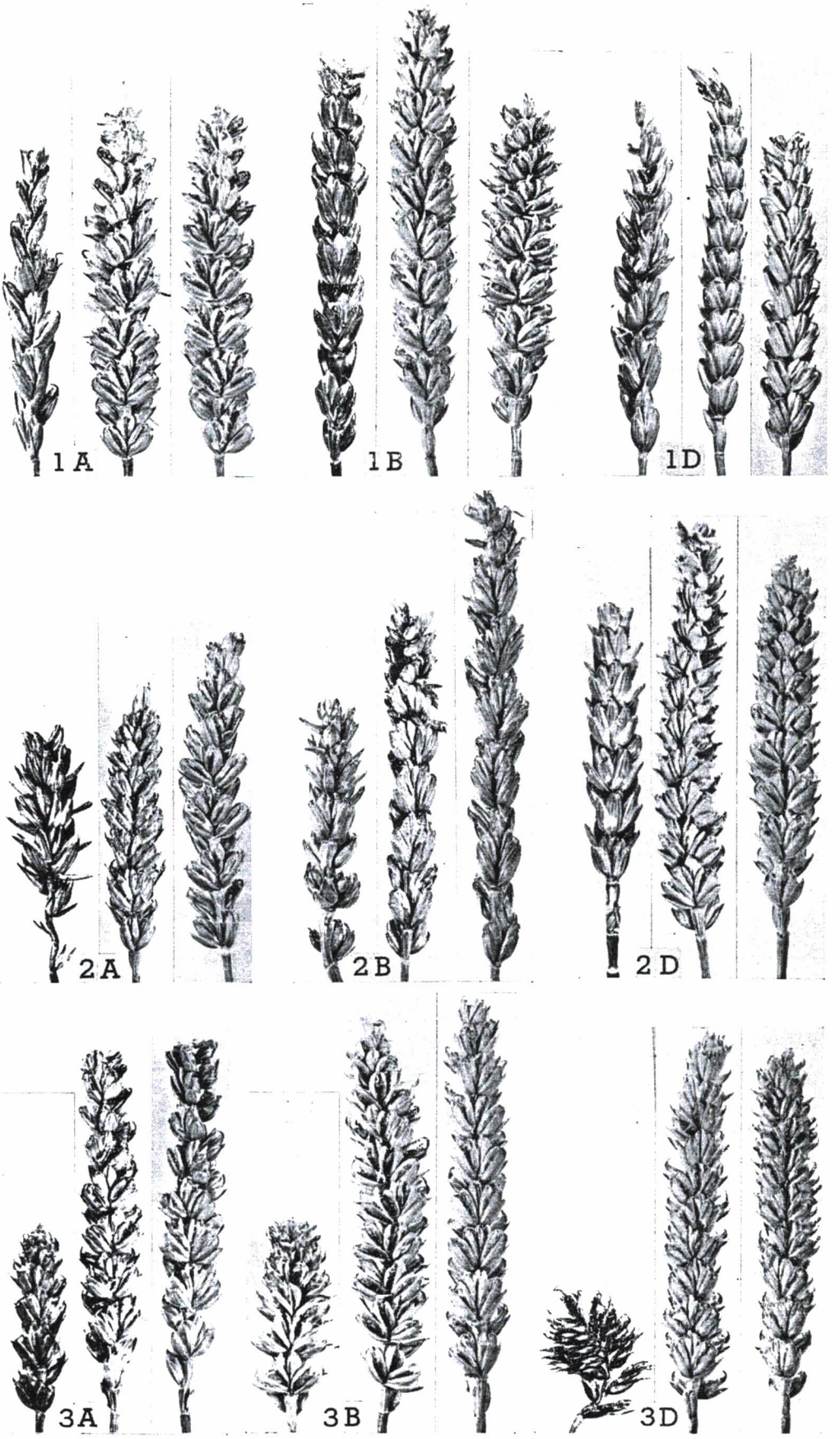
TABLE 3

Number of seeds obtained on single plants having compensating nullisome-tetrasomes

Nullisome involved	Tetrasome involved	Season grown	No. seeds	Tetrasome involved	Season grown	No. seeds
1A	1B	1953S*	183	1D	1953S	425
1B	1A	1951S	118	1D	1951F	127
1D	1A	1957F	40	1B	1954S	97
2A	2B	1951F	109	2D	1952F	129
2B	2A	1959F	17	2D	1951S	8
2D	2A	1952S	211	2B	1951S	129
3A	3B	1952S	118	3D	1951F	148
3B	3A	1953S	190	3D	1951S	203
3D	3A	1951S	117	3B	1951S	136
4A	4B	1955F	0	4D	1954F	0
4B	4A	1959F	35	4D	1954S	90
4D	4A	1952S	124	4B	1959F	7
5A	5B	1951F	58	5D	1951F	78
5B	5A	1959F	25	5D	1951F	63
5D	5A	1955F	53	5B	1963F	139
6A	6B	1951S	128	6D	1952F	162
6B	6A	1959F	47	6D	1959F	17
6D	6A	1951F	102	6B	1951F	107
7A	7B	1951S	62	7D	1953S	187
7B	7A	1951F	91	7D	1952S	229
7D	7A	1951S	91	7B	1951F	144

* S = spring; F = fall.

One of the major criteria used in establishing the superiority of the nulli-tetra to the nullisomic was fertility as measured by seed set from selfing. Since the plants scored for fertility were not all grown at the same time (table 3), the values obtained involve more than the usual amount of error due to environmental differences. Also, in some cases the most fertile plant was chosen from among several nulli-tetras, while in 15 cases only a single nulli-tetra plant was grown. Nevertheless, the plants were all raised in a greenhouse under such similar conditions that substantially the same seed sets were obtained on


1A
1B
1D
2A
2B
2D
3A
3B
3D

normal plants from season to season and year to year. Large differences in the recorded seed sets almost certainly reflect real differences in fertility.

Many of the nulli-tetras are of nearly normal fertility. It is an unusually fertile plant of normal constitution that has as many as 500 seeds, and 300 would be closer to the average value for plants handled as the nulli-tetras were (*i.e.*, grown in 6-inch pots until meiosis could be studied and then transferred to 8-inch pots). Thus any plant that bears as many as 200 seeds is approaching normal fertility, and a set of 100 seeds represents a fair degree of fertility.

In homoeologous group 3, all six nulli-tetra combinations had more than 100 seeds. In three other groups (1, 2 and 6), all exceeded 100 except the two combinations involving a particular nullisome (1D, 2B and 6B). Group 4 appears to have the poorest fertility, with the nulli-4A combinations completely sterile and 4D-4B nearly sterile. The group-5 combinations are consistently low, except for 5D-5B.

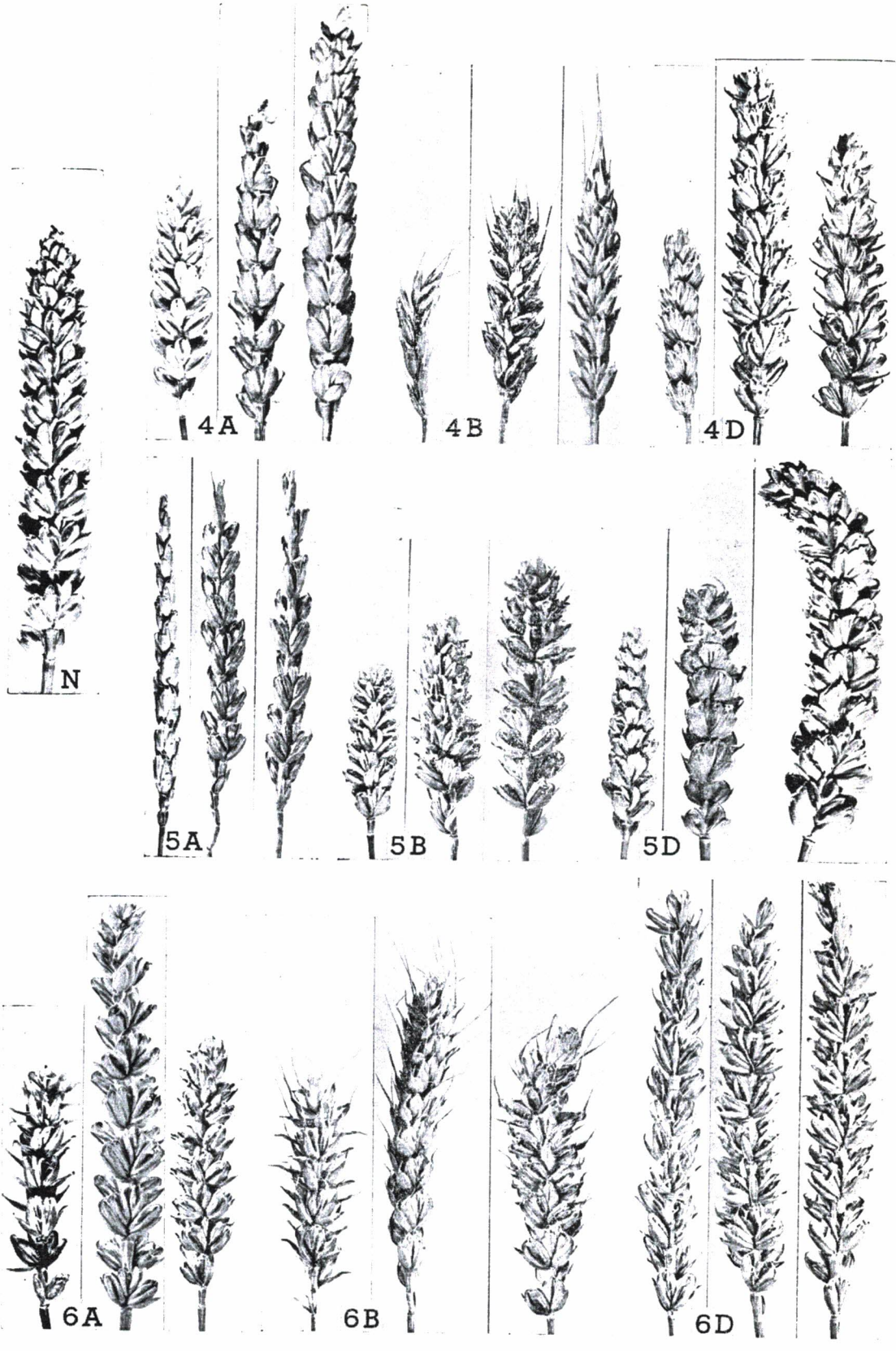
In comparison with the respective nullisomics, only the combinations 4A-4B, 4A-4D, and possibly 7B-7A and 7D-7A showed no increase in fertility. In about half the combinations, the increase over the nullisomic is particularly obvious because the nullisomics concerned set no selfed seeds (Sears, 1954). This is true of all three nullisomics of group 2, which are female-sterile; of groups 4 and 5, which are male-sterile; and of nullisomic 6B, which is male-sterile. Several other nullisomics, 1A, 1D, 3D, 6A and 6D, are only marginally fertile, and nullisomics 3A and 3B are poorly fertile. Nulli-7A has not been observed to set as many as 60 seeds, but nullisomics 7B and 7D have set as high as 112 and 126, respectively.

To supplement the data in table 3 and the information obtainable from the photographs of nullisomics and nulli-tetras in plates 1, 2 and 3, the following additional observations concerning the various groups are presented.

Group 1. The compensation is excellent, the spike peculiarities of the nullisomics (long internodes, stiff glumes) being fully suppressed in the nulli-tetras. In the one combination of low fertility (1D-1B), the plant is of nearly normal size.

Group 2. Here the compensation of 2A and 2D for each other, and that of 2B for 2A and 2D, are very good, but 2A and 2D compensate only partially for 2B. Not only is fertility low in these two combinations, but certain of the floral abnormalities of nulli-2B remain. Tetra-2A largely but not completely corrects the tendency of nulli-2B toward reduplication of floral parts. Tetra-2D restores nearly the normal number of spikelets to nulli-2B, but it does not restore normal internode length. This results in a long, lax spike. Both tetrasomes largely

PLATE I (*opposite*). Nullisomic-tetrasomics within homoeologous groups 1, 2 and 3. Each series of three spikes includes the simple nullisomic (left) and the two combinations of this nullisomic with homoeologous tetrasomes. Combination nulli-A tetra-B is to the left of A-D, B-A to the left of B-D, and D-A to the left of D-B. ×4/5.



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correct the coarseness and reduced tillering of nulli-2B. Full compensation in all combinations is exhibited for papery glumes and reduced awns.

Group 3. The degree of compensation in this group is probably best of all, particularly when plant characters are taken into account. Whereas all three nullisomics are narrow-leaved dwarfs, all six nulli-tetras are of essentially normal size and vigour. Even the tendency of nulli-3B toward asynapsis is less pronounced in the nulli-tetras.

Group 4. Nulli-4A and -4D are very similar in plant and spike characters, while -4B is narrower-leaved, bushier, and shorter in plant and spike. Tetra-4D does not compensate for the infertility of nulli-4A, however, although the plant and spike become decidedly more nearly normal. In the reverse direction compensation of tetra-4A for nulli-4D is the best in the group. Tetra-4B compensates poorly for both nulli-4A and -4D, but in part this is attributable to a necrotic condition that affects the leaves of tetra-4B and is independent of the dosage of 4A and 4D. Trisomic-4B does not show this necrosis, and a nulli-4A tri-4B plant obtained was more vigorous than the nulli-tetra, but it also set no seed. It appears that chromosome 4A carries a gene or genes essential for male fertility not present on the other two chromosomes, whereas 4B contributes more to length of spike than do the other two chromosomes. Since the hooded gene of 4B is not duplicated on 4A or 4D, neither of the latter two tetrasomes is able to suppress the awnedness of nulli-4B.

Group 5. Results with this group are confounded by the large effect of the gene *Q* carried by 5A. Although the spike characters of nulli-5A are changed very little by tetra-5B or -5D, tetra-5A spikes are considerably less compact in combination with the nullisomes, especially 5D. The aberrant plant characters, particularly the narrow leaves and slender culms, of all three nullisomes are substantially corrected by addition of the tetrasomes. Under certain conditions, both nulli-5D tetra-5A and nulli-5D tetra-5B show a pronounced tendency toward asynapsis.

Group 6. With respect to fertility it is clear that chromosome 6B carries a gene or genes not present on 6A or 6D, since the latter two tetrasomes do not restore full fertility to nulli-6B. Plant characters are reasonably normal in all the nulli-tetras. Tetrasome 6D is unable to restore normal spike length to nulli-6A and -6B, showing that 6A and 6B carry genes essential to normal spike length that are not present on 6D. As is already well known, the awn inhibitor B_2 on 6B has no duplicates on 6A and 6D; hence both nulli-tetras involving nulli-6B are awned.

Group 7. This is the group in which least compensation could be expected, because the nullisomics, particularly 7B and 7D, are themselves so nearly normal. It is obvious, however, from the fertility data

PLATE II (*opposite*). Nullisomic-tetrasomics within homoeologous groups 4, 5 and 6, together with the respective simple nullisomics and a normal spike (N). ×4/5.

and the photographs of spikes (plate 3, row 1) that both tetra-7B and -7D compensate strongly for nulli-7A, and that tetra-7D gives essentially full compensation for nulli-7B. Tetra-7A can also be said to compensate for nulli-7D, although the spike of nulli-7D photographed is neither quite as large nor as fertile as some that have been obtained. The spike shown of nulli-7D tetra-7B bears no more seeds than can be obtained on individual spikes of nulli-7D, but the 144 seeds set on the nulli-7D tetra-7B plant in table 3 are more than have been recorded for nulli-7D. The remaining combination, nulli-7B tetra-7A, is no less fertile than nulli-7B; it makes a taller plant; and its spikes are almost completely normal, whereas those of nulli-7B tend to be sterile in the upper portion. Therefore it may be concluded that all the nullisomic-tetrasomics in this group exhibit compensation, although necessarily of a lower order than that in some of the other groups.

TABLE 4

Chromosome constitution of offspring of nullisomic-tetrasomics

Chromosomes involved		No. grown	No. nulli-tetra	No. nulli-tri
Nulli	Tetra			
1B	1A	3	3	0
1D	1A	5	4	1
2B	2D	1	1	0
2D	2B	7	7	0
3A	3B	2	2	0
3B	3D	5	5	0
3D	3A	11	7	4
3D	3B	2	2	0
4B	4A	2	2	0
4D	4B	3	3	0
5B	5A	3	2	1
5B	5D	4	4	0
5D	5B	6	3	3
6A	6B	3	3	0
6A	6D	1	1	0
6B	6A	3	3	0
6B	6D	3	3	0
7A	7B	3	1	2
7B	7A	2	2	0
7D	7A	3	2	1
Totals		72	60	12

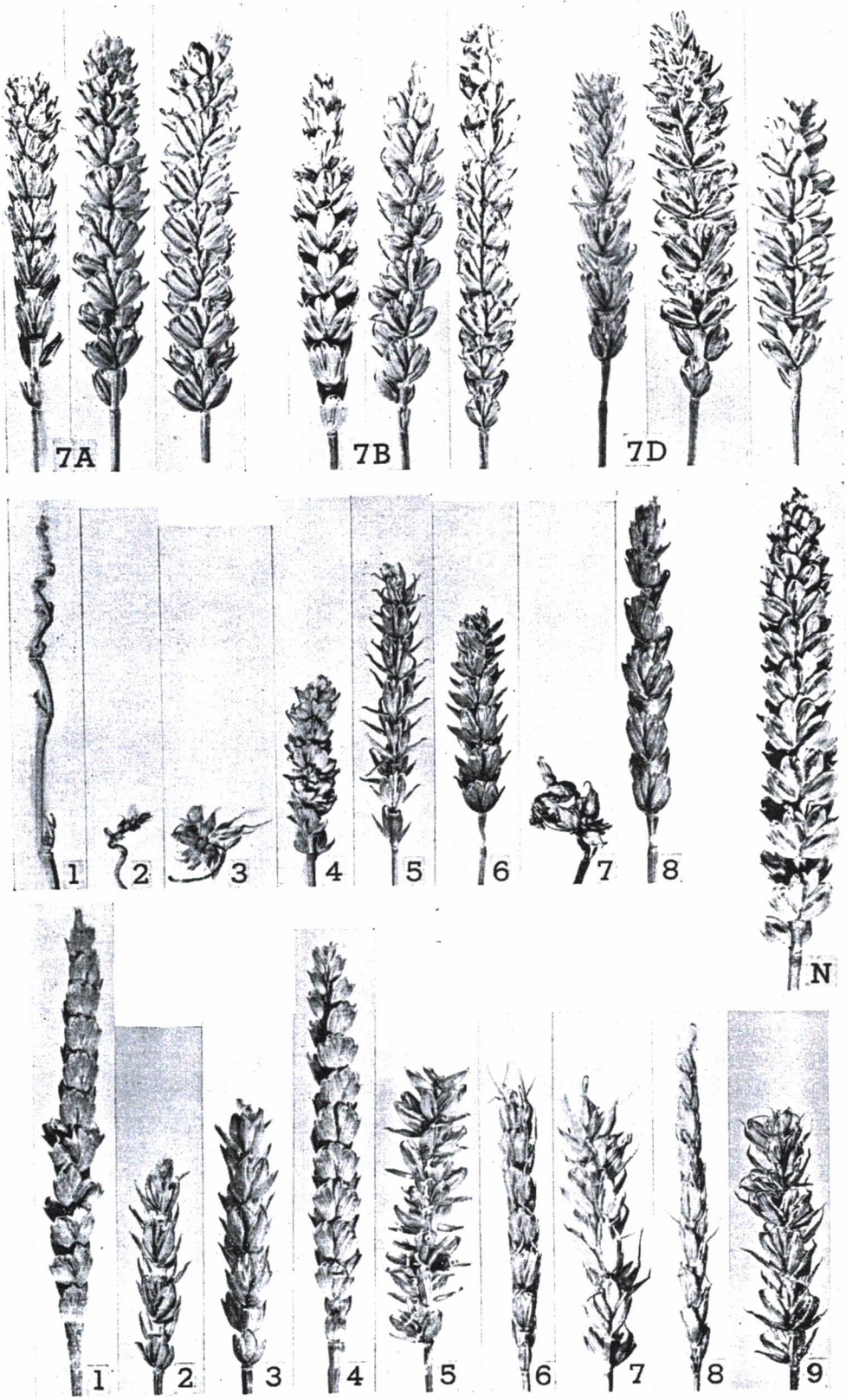
(iii) *Breeding Behaviour*

From cytological analysis of offspring of about half the compensating combinations (table 4), scattered through the seven homoeologous groups, it is clear that this type of nullisomic-tetrasomic forms a reasonably stable line. Of the 72 offspring 60 were nulli-tetra, and the remaining 12 were nulli-tri. This kind of stability was to be expected

TABLE 5

Nullisomic-tetrasomic (or otherwise deficient-duplicated) combinations obtained involving chromosomes of different homoeologous groups

Groups involved	Genomes involved							
	A-A	A-B	A-D	B-B	B-A	B-D	D-A	D-B
1-2						X		
1-3					X			
1-4					X			
1-5						X		
1-6				X	X			
1-7					X		X	
2-1							X	
2-3			X					
2-4			X					
2-5		X						
2-6	X	X						
2-7				X	X			
3-1			X					
3-2			X					
3-4	X							X
3-5			X					
3-6		X						
3-7			X					
4-1		X						
4-2			X	X				
4-3	X							
4-5				X	X	X		X
4-6								X
4-7			X					
5-1	X	X						
5-2			X					
5-3				X	X			
5-4		X		X			X	
5-6		X						
5-7	X		X					
6-1							X	
6-2	X							
6-3						X		
6-4			X					
6-5			X					X
6-7	X				X			
7-1		X	X					
7-2	X	X						
7-3			X					
7-4			X					
7-5			X					
7-6	X	X						
	9	10	16	6	8	4	4	4



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because of the competitive advantage 21-chromosome (nulli-di) pollen has over 20-chromosome pollen when the duplicated chromosome tends to compensate for the missing one. The occurrence of occasional nulli-tri plants must be very largely a consequence of irregular meiotic behaviour of the tetrasome on the female side. Failure of one or more members of the tetrasome to pair, which would usually be followed by univalent loss, must be a common type of irregularity, for simple 3:1 distributions from quadrivalents would lead to as many pentasomes as trisomes, and no pentasomes were observed in the sample of 72.

3. NON-COMPENSATING COMBINATIONS

The ability of each tetrasome to compensate to some extent for each of the two nullisomes of the same homoeologous group shows that the three chromosomes of each group have most of their genes in common. The possibility remains, however, that considerable relationship exists between certain chromosomes of different homoeologous groups.

To check every tetrasome for its ability to compensate for every non-homoeologous nullisome would require 378 tests, an inordinately large number. If one tetrasome from each homoeologous group is tested, however, with one nullisome from each other group, only 42 tests are necessary, and this perhaps constitutes a reasonably representative sample of the combinations possible.

Since some of the weaker nullisomics might become inviable if burdened additionally with a non-compensating tetrasome, the chromosome chosen to make nullisomic was in most cases the one whose nullisomic was the most vigorous in its homoeologous group. An exception was group 7, where nullisomics 7A and 7D are so nearly normal that a slight increase in vigour or fertility resulting from addition of a partially compensating tetrasome might not be detectable. In group 2, 2A was chosen because nulli-2A is less coarse than either nulli-2B or -2D; and since most of the tetrasomics of other groups tend to be coarse, their combinations with nulli-2B or -2D might be so excessively coarse as to conceal points of improvement.

Although nulli-3B is no less vigorous than -3A, it was not used because chromosome 3B carries a gene essential to normal synapsis. Nulli-4A is more vigorous than -4B, but the latter was used with three different tetrasomes of group 5 because its morphology suggested possible affinities with that group. Nulli-6D is somewhat more vigorous than -6A or -6B, but the latter two were also used.

PLATE III (*opposite*). Nullisomic-tetrasomics of homoeologous group 7, the respective group-7 nullisomics, a normal spike (N), and various non-compensating, between-group combinations (centre and bottom rows). Spikes in the centre row are from nullisomic-tetrasomics as follows: (1) 2A-4D, (3) 4B-5A, (4) 5D-4A, (5) 6D-1A, (6) 7A-1B, (7) 7A-4D, (8) 7A-6B, and (2) nullisomic-trisomic 3A-4A. In the bottom row are monosomic-tetrasomics (1) 1B-6A, (2) 1D-7A, (3) 2A-5B, (4) 2A-6A, (5) 2B-7A, (6) 3A-2D, (7) 4A-7D, (8) 5A-2D, (9) 6B-7A. ×4/5.

Four combinations were tested because Okamoto and Sears (1962) found translocations from haploids that involved the chromosomes concerned. The translocations were thought to have arisen through pairing and crossing over, which would mean structural, and presumably genetic, relationship. These combinations were 2B-4B, 3A-4A, 5A-7A and 5D-6A.

In all, 61 combinations were tested (table 5).

The method used for producing the between-group nulli-tetras was the same as for the majority of the within-group combinations; namely, (1) cross monosomic by tetrasomic, (2) backcross by tetrasomic, and (3) self the resulting mono-tetra.

As a rule little difficulty was experienced in obtaining the mono-tetra, as expected since there should be no selection of gametes in mono-tri × tetra. With tetrasomics of group 3, however, there was poor recovery of mono-tetras, which is presumably related to the pronounced tendency of tetrasomes of this group to revert to trisomes (Sears, 1954). In the nine combinations attempted involving group-3 tetrasomes, an average of 17·4 plants from mono-tri × tetra had to be examined to find one mono-tetra; whereas in 57 combinations involving tetrasomes of the other groups, only 4·4 plants were examined per mono-tetra.

In many cases it was clear from the characteristics of the mono-tetra that the tetrasome was not compensating for the missing chromosome but was making the plant more abnormal. This was particularly obvious in the effect on fertility, many mono-tetras setting few or no seeds (table 6), whereas the respective monosomics are fully fertile or nearly so. Spikes of several infertile mono-tetras are shown in plate III, bottom row, figs. 3, 4, 6, 7, 8. The remaining spikes in this row have a low degree of fertility.

Where seeds were produced by the mono-tetra, progeny were grown in an effort to obtain the nulli-tetra. In most cases this effort failed, in spite of some populations being sizeable (table 7). Although relatively few plants were examined cytologically, it is unlikely that nulli-tetras were overlooked. All seedlings with characteristics suggesting nullisomics were saved for cytological analysis. In several combinations the apparent nullisomic died before reaching the sampling stage, strongly suggesting that it was a semi-lethal nulli-tetra. In a few cases the nulli-like plants survived but produced spikes so abnormal that meiotic stages could not be obtained (plate III, figs. 1, 3, 7 in centre row). These and the pre-heading lethals are recorded as probable nulli-tetras in table 6. Of the remaining nulli-tetra spikes figured, all were sterile except no. 8, which set a single seed.

In two combinations (2A-6B and 5A-6B) no nulli-tetra was obtained, but a monotelosomic-tetrasomic did appear. In 3A-1D a monotelosomic-trisomic was obtained. In each of these cases no superiority was shown to the corresponding nullisomic. This indicated a lack of compensation by the tetrasomes or trisome, since without the extra

TABLE 6

Chromosomes involved in the non-compensating combinations, and kind of combination obtained

Groups involved	Combinations obtained and chromosomes concerned				
	Nulli-tetra	Probable nulli-tetra	Nulli-tri	Mono-tetra	
				With no seeds	With few seeds
1-2				1B-2D	
1-3				1B-3A	
1-4				1B-4A	
1-5					1B-5D
1-6					1B-6A, 1B-6B
1-7					1B-7A, 1D-7A
2-1				2D-1A	
2-3				2A-3D	
2-4		2A-4D			
2-5				2A-5B	
2-6				2A-6A	2A-6B
2-7				2B-7B	2B-7A
3-1			3A-1D		
3-2				3A-2D	
3-4			3A-4A	3D-4B	
3-5		3A-5D			
3-6			3A-6B		
3-7				3A-7D	
4-1		4A-1B			
4-2					4A-2D, 4B-2B
4-3			4A-3A		
4-5	4B-5D	4B-5A, 4B-5B		4D-5B	
4-6					4D-6B
4-7				4A-7D	
5-1			5A-1B		
5-2					5A-1A
5-3				5A-2D	
5-4	5D-4A				5B-3A, 5B-3B
5-6	5A-6B			5A-4B, 5B-4B	
5-7				5A-7D	5A-7A
6-1				6D-1A	
6-2		6A-2A			
6-3					6B-3D
6-4					6A-4D
6-5					6A-5D, 6D-5B
6-7					6A-7A, 6B-7A
7-1	7A-1B, 7A-1D				
7-2			7A-2A		
7-3					7A-2B
7-4		7A-4D			7A-3D
7-5					
7-6	7A-6B				7A-5D
					7A-6A

chromosomes the monotelosomic should have been superior to the nullisomic.

Where numerous offspring were grown from the monosomic-tetrasomic but no nulli-tetras were obtained, it was assumed either

TABLE 7

Chromosome constitution of offspring of monosomic-tetrasomics

Parents		Offspring								
			Constitution of plants analysed							
Mono	Tetra	No. grown	Nulli-tetra (or tri)	Monotelo- (or -iso-) tetra (or tri)	Mono-tetra	Tetra	Mono-tri	Tri	Mono	Nulli
1B	5D	16			5	2		2		
1B	6A	14			4	3				
1B	6B	67			8	2	4	1		
1B	7A	2			2					
1D	7A	2			1					
2A	4D	12			3		1			
2A	6B	131		1	13	5	1	1	1	
3A	1D	7		1					1	
3A	4A	79	1		7		1			
3A	5D	48	1		5		1			
3A	6A	40			2				2	
3A	6B	29	1							
3A	7D	1			1					
3D	4B	11			1	1				
4A	1B	102			6	5	1			
4A	2D	6			1	5				
4B	5A	130			12	8	5	1		1
4B	5B	319			16	6	1			
4B	5D	74	1	1	1					
4D	6B	15			2					
5A	1A	4			3					
5A	1B	30			1		1			
5A	6B	70		1						
5D	4A	34	1		1					
6A	2A	158			14	1	1			
6A	4D	131			17	7	3	1		
6B	3D	32								
6D	1A	77	3		2					
6D	5B	149			17	8	4	2		
7A	1B	35	2	1	3					
7A	1D	33	2							
7A	2A	117	2		16	8		2		
7A	4D	39			1		1			
7A	6B	25	1		3					

that male transmission of the nulli-di gametes was very low or that the nulli-tetra individuals produced were lethal at a very early stage. In either case it seemed very unlikely that the extra chromosome was

compensating for the missing one. As a further test, however, a comparison was made of the mono-tetra with the corresponding tetrasomic. If the mono-tetra was inferior, it seemed certain that the nulli-tetra would be still poorer, and therefore that no detectable compensation was involved. As a sensitive and convenient measure of vigour, the number of seeds set per plant was used. In no case was the mono-tetra more fertile than the corresponding tetrasomic.

In addition to the bizarre interactions of nullisomes and tetrasomes figured in plate III, tetrasome 7A affected mono-2B in an unexpected way. Both these two chromosomes are essential to normal floral development (Sears, 1954), with loss of 2B leading to a tendency for extra flowers or bracts to be inserted between glumes, and loss of 7A resulting in pistillody. In mono-2B tetra-7A, which has extra, not reduced, dosage of 7A, extreme pistillody, leading to almost complete sterility, was observed.

4. DISCUSSION

The results of the nullisomic-tetrasomic tests were unequivocal in showing some degree of compensation in each of the 42 combinations of chromosomes from the same homoeologous group and no compensation in any of the 61 tests of chromosomes from different groups. This would suggest that the main process by which the chromosomes of the A, B and D genomes have become structurally differentiated from each other is inversion. Inversions simply rearrange the chromatin within the individual chromosome and do not change the gene content. By this process homologous chromosomes in different genomes can become homoeologous.

Although combining tetrasomes with nullisomes revealed no relationships outside the homoeologous groups, this is a rather crude test, only capable of revealing substantial amounts of homology. If a tetrasome possesses relatively few of the same genes as the nullisome with which it is being combined, it restores the dosage of these genes but at the same time supplies an overdose of the rest of its own genes, with a net effect which may be detrimental. It is thus possible that considerable homology does exist between chromosomes of different homoeologous groups. Such homology would be most likely to arise through the process of reciprocal translocation.

In groups 1 and 3, the excellent within-group compensation indicates that the homoeologues have essentially the same genetic content. Therefore it is very unlikely that any substantial amount of homology exists between any chromosomes of these groups and non-homoeologous chromosomes. Although groups 5 and 7 show a somewhat lower level of compensation within themselves, no one chromosome is particularly anomalous, and there seems to be only little likelihood of a significant degree of homology with any non-homoeologous chromosomes. In each of groups 2, 4 and 6, however, there is one chromosome, 2B, 4A and 6B, for which the others compensate poorly.

This suggests that each of these chromosomes may have a segment, presumably derived from some non-homoeologue, that is not possessed by its two homoeologues.

One way of explaining this situation is to assume that 2B, 4A and 6B were involved in a double translocation, such that, for example, 2B had a segment replaced by one from 4A, 4A had a segment from 6B, and 6B had the segment from 2B. In this case nulli-2B would not be completely compensated for by tetra-2A or -2D, because neither of these would supply the missing 4A-segment. Neither would 4A be able to supply this segment; but 4B and 4D would have the segment and might show compensation for 2B. Similarly, tetra-6A and -6B would tend to compensate for nulli-4A, and tetra-2A and -2D for nulli-6B. The reciprocal combinations might also show compensation.

That the situation is not so simple as this is indicated by the fact that in each group the anomalous chromosome compensates very well as a tetrasome for each of the other two nullisomes. This would not be the case if it had lost an important segment through reciprocal translocation with a non-homoeologue. It is of interest to note, however, that one of the translocations obtained by Okamoto and Sears (1962) from haploids involved chromosomes 2B and 4B. If, as the authors assumed, these translocations arose through pairing and crossing-over, then 2B has a segment in common with 4B—a segment which 2B could have acquired from 4A.

Another translocation of Okamoto and Sears involved chromosome 4A, but the second chromosome was 3A, which belongs to a homoeologous group in which compensation is so nearly complete that substantial relationship of any of its three members to a member of another group seems unlikely. The other two non-homoeologous translocations from haploids involved 5A with 7A and 5D with 6A. These chromosomes belong to less well-defined homoeologous groups than does 3A, and thus relationship between them is not so improbable. Chromosomes 7A and 5D failed to compensate for 5A and 6A, respectively, but the reverse combinations were not tested. It is of course possible that these chromosomes have no common segment—that the non-homoeologous translocations of Okamoto and Sears originated through some process other than pairing and crossing over.

Although chromosomes 2B, 4A and 6B were included in as many or more compensation tests than the average for the other 18 chromosomes, additional tests of these three anomalous chromosomes would be desirable. However, it may be more productive to use a cytological method for checking possible relationships involving not only these chromosomes but also such chromosomes as the ones just mentioned that underwent translocation in haploids. A promising cytological method was indicated by the discovery by Okamoto (1957) and Riley (1958) of the suppressing effect which chromosome 5B exerts on homoeologous pairing. With chromosome 5B missing (or its effect suppressed), pairing may presumably be obtained between chromosomes

with only a small segment in common. Riley and Kempanna (1963) did not detect any pairing of non-homoeologues in nulli-5B material, but in their experiment pairing of homoeologues had to compete with pairing of homologues. To test for the possibility of pairing between two particular chromosomes, the ideal situation will be to have both chromosomes monosomic. Then neither will have a homologue with which to pair, and their homoeologues, being present as disomes rather than monosomes, will offer a minimum of pairing competition.

It is perhaps worth noting that two of the three anomalous chromosomes, 4A and 6B, are considerably longer than their homoeologues. This suggests that in these two cases the homoeologues have simply become deficient for a segment which 4A and 6B still retain. This would account for the fact that the tetrasomes of these two chromosomes are able to compensate well for the nullisomes of their homoeologues, whereas compensation is poor in the reverse direction. It would also explain that 6B is a nucleolar-organising chromosome while 6A and 6D are not. The behaviour of chromosome 2B cannot be explained in this way without some additional assumptions, for 2B is definitely shorter than 2A and little, if any, longer than 2D (Morrison, 1953; Sears, 1954).

The extent to which homology appears to be confined to the homoeologous groups suggests that differentiation of the chromosomes of the three genomes of wheat has involved very few translocations. Yet at least five different translocations with respect to the variety used here, Chinese Spring, have been identified in crosses of a relatively small number of varieties with monosomics of Chinese Spring (Sears, unpublished). Is it possible that translocations have been an important factor in the differentiation of the wheat chromosomes, but that the variety Chinese Spring happens to have a chromosome architecture which is more primitive than that of most other varieties? The answer is not necessarily in the affirmative, as a few translocations could in fact help to account for some of the anomalies reported here in the compensation tests within homoeologous groups. However, the data of Riley and Chapman (1960) show that at least the D genome of Chinese Spring does have a primitive arrangement. In a hybrid of this variety with *Aegilops squarrosa*, the source of the D genome, they found usually seven bivalents and never any multivalents.

5. SUMMARY

Combinations of tetrasomes with nullisomes showed that each chromosome of hexaploid wheat has a close relative in each of the other two genomes, making seven homoeologous groups of three. Within these groups all 42 possible combinations of tetrasomes with nullisomes have been made, and in every case the tetrasome compensates to some extent for the deleterious effect of the nullisome. Compensation is excellent in groups 1 and 3, whereas the tetrasomes homoeologous to

nullisomes 2B, 4A and 6B compensate rather poorly for them. It is suggested that the anomalous behaviour of these three chromosomes may be the result of translocation involving them; or that, in the case of 4A and 6B, a deficiency may have occurred involving their homoeologues.

At least one nullisome or monosome from each homoeologous group was combined with at least one tetrasome or trisome from each other group, for a total of 61 combinations, none of which gave evidence of compensation. Only 19 could be obtained as nullisomic-tetrasomic (or -trisomic), the rest being evaluated as monosomic-tetrasomic. Although the tests established that genetic homology is very largely confined to the homoeologous groups, they did not exclude the possibility that small amounts of homology, undetectable by the relatively insensitive nullisomic-tetrasomic test, may exist between certain non-homoeologues.

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