AN ANALYSIS OF FREQUENCIES OF CHROMOSOME CONFIGURATIONS IN WHEAT AND WHEAT HYBRIDS[1]

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ABSTRACT

Presynaptic association of homologous chromosomes is a prerequisite to the sequence of events that lead to chiasma formation. This association of homologous chromosomes, as entire units, occurs with probability *a*, and chiasma formation occurs independently in opposite chromosome arms with probability *c*. *a* and *c* have been estimated from frequencies of different chromosome configurations at metaphase I of euhexaploid wheat and several derived lines. In the euploid, *a* is essentially unity and *c* is of the order of 95%. All changes in the aneuploidy studied involved *c* rather than *a*, whereas the change induced by colchicine application primarily involved *a*.—— Observed and expected frequencies of configurations were compared in wheat hybrids in which only homoeologues were present. The expected frequencies of configurations were estimated from the data, based on *a* being unity for entire groups of homoeologues and *c* being the probability of chiasma formation between random homoeologous arms. Observed and expected frequences of configurations were in general agreement; however, an excess of observed closed bivalents at the expense of multivalents is interpreted to mean that not all homoeologues are effectively associated in all cells.——In euhexaploid wheat, we suggest that homologues associate with almost certainty, whereas homoeologous pairs of chromosomes associate less efficiently. The aneuploidy examined in this study does not appear to affect the association of chromosomes, but rather the number of chiasmata that eventuate and, in the case of deficiency of chromosome *5B*, the distribution of chiasmata within homoelogues, perhaps by way of rendering sites for chiasma formation of homoelogues more similar.

DURING the period 1965 to 1975, a number of pollen mother cells of wheat (*Triticum aestivum* L.) and of hybrids of wheat and related genera were analyzed by us for frequencies of different chromosome configurations at metaphase I. These analyses were carried out for a variety of reasons and included a range of materials such as euploid and hypoploid wheat, wheat-rye (*Secale cereale* L.) substitution lines, wheat-rye hybrids, wheat-*Aegilops variabilis* Eig hybrids, with and without deficiency for various chromosomes and also material treated pre-meiotically with colchicine.

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These data are now examined collectively on the basis of a proposed theory of the formation of various configurations of homologous and homoeologous chromosomes. There is sufficient internal consistency in these data to lend credence to the assumptions incorporated in the theory.

The theory is presented in three parts, the first of which ignores configured homoeologues. The second relates to instances where homologues are absent; thus all configured chromosomes are homoeologues. The third attempts a synthesis of the first two parts and relates to configured homologues and homoeologues.

MATERIALS AND METHODS

The data analysed are taken from the publications of DRISCOLL and QUINN (1968, 1970), BIELIG and DRISCOLL (1970a, b) DRISCOLL and DARVEY (1970), DRISCOLL (1972) and from unpublished observations of the authors. Plants were raised under glasshouse conditions, whole spikes were fixed in Carnoy's solution and the chromosomes were stained with aceto-carmine. Samples of the same material were pooled, except in the cases of nullisomic *5B*, nullisomic *5D* and colchicine treatment. In these cases, samples are listed separately in order to emphasize differences or similarities between replicates. The method of colchicine application has been described previously (DRISCOLL and DARVEY 1970). Aneuploids for chromosomes of groups *5* and *3* are included because of their known influence on chromosome configurations at metaphase I. (SEARS and OKAMOTO 1958; RILEY and CHAPMAN 1958; MELLO-SAMPAYO 1971; DRISCOLL 1972).

RESULTS AND DISCUSSION

Basis of the theory and terminology used

The theory states that the formation of chromosome configurations occur in at least two stages, as proposed by DRISCOLL, DARVEY and BARBER (1967). In the first stage, related chromosomes enter an association. This is presynaptic and involves closer spatial relationship of chromosomes, but not physical exchange. Association occurs with a probability *a*, which applies to entire chromosomes: *i.e.*, one pair of chromosome arms is not independent of the opposite pair of chromosome arms. Association is a prerequisite to the later stages, which involve the sequence of events that lead to chiasma formation. Thus, failures of association result in univalents at metaphase I. The various stages after the association stage are not separable in these experiments. These include synaptinemal complex formation and molecular crossing over, which lead to chiasma formation. These are collectively referred to by the cytologically observable end-product at metaphase I, chiasmata. Chiasma formation occurs in a pair of chromosome arms with a probability *c*, and its occurrence in one pair of chromosome arms is independent of its occurrence in the opposite pair of chromosome arms. Instances of more than one chiasma in a pair of chromosome arms are ignored in this theory. Thus, *a* relates to the probability of obtaining closer spatial relationship, and *c* relates to the probability of physical exchange. The three terms used in this paper are *association* (which is presynaptic), *chiasma formation* and *chromosome configuration*. The last term refers to two or more chromosomes held together by one or more chiasmata. Chromosomes in the same configuration must have involved association and the various steps leading to chiasma formation. Homologous

configurations refer to configurations involving homologues only, homoeologous configurations refer to configurations involving homoeologues only, and homologous and homoeologous configurations refer to configurations involving both homologues and homoeologues.

Homologous configurations : expectations

A closed bivalent results from association, with probability a and chiasma formation in both pairs of arms, with probability c^2. An open bivalent results from association with probability a, and chiasma formation in one pair of arms only, with probability $2c(1-c)$. Two univalents result from failure of association, with probability $1-a$, or from association with probability a, and chiasma formation in neither pair of chromosome arms, with probability $(1-c)^2$. It is assumed that one value of a and one value of c apply to all pairs of homologues.

Expected frequencies are thus:

(II)	*i.e.*, closed (or ring) bivalents	$= a \times c^2$
|II|	*i.e.*, open (or rod) bivalents	$= a \times 2c(1-c)$
2I	*i.e.*, two univalents	$= (1-a) + a(1-c)^2$

c can be estimated from the ratio of observed (II) and observed |II| as follows:

$$\frac{(\text{II})}{|\text{II}|} = \frac{a \times c^2}{a \times 2c(1-c)} = \frac{c}{2-2c}$$

$$c = \frac{2(\text{II})}{2(\text{II})+|\text{II}|} \tag{1}$$

The estimate of c is independent of a.

The value of a is estimated by the method of maximum likelihood from equations (2) and (3) below.

$$\frac{(\text{II})}{(\text{II})+|\text{II}|+2\text{I}} = ac^2$$

$$a = \frac{(\text{II})}{(\text{II})+|\text{II}|+2\text{I}} \cdot \frac{1}{c^2} \tag{2}$$

and

$$\frac{|\text{II}|}{(\text{II})+|\text{II}|+2\text{I}} = a \times 2c(1-c)$$

$$a = \frac{|\text{II}|}{(\text{II})+|\text{II}|+2\text{I}} \cdot \frac{1}{2c(1-c)} \tag{3}$$

Homologous configurations : observations

Frequencies of chromosome configurations of euploid wheat and eleven derived types are shown in Table 1, along with the values of c and a calculated from equations (1), (2) and (3), respectively. With the sample of euploids studied, association of homologues occurred with certainty and chiasma formation occurred in each pair of chromosome arms with a probability of 0.95. High inci-

TABLE 1

Frequencies of chromosome configurations of the entire chromosomes of the following material and the calculated values of a *and* c

Stock	No. cells	ⓘ	|II|	2I	*a*	*c*
Euploid	100	18.96	2.00	0.04	1.00	0.95
N3A	100	14.96	4.92	0.12	1.01*	0.86
3Rt(3A)†	56	16.98	2.96	0.06	1.00	0.92
3Rtt(3A)‡	40	18.53	1.45	0.02	1.00	0.96
N3B	100	7.14	9.41	3.45	0.98	0.60
3Rt(3B)†	76	14.33	5.26	0.41	1.00	0.84
3Rtt(3B)§	50	15.90	3.94	0.16	1.00	0.89
N3D	100	17.13	2.68	0.19	1.00	0.93
3R″(3D)	100	19.67	1.32	0.01	1.00	0.97
N5A	33	19.12	0.88	0.00	1.02*	0.97
N5B (sample 1)	100‖	15.79	3.93	0.28	1.00	0.89
N5B (sample 2)	63¶	15.35	4.22	0.43	0.99	0.87
N5D (sample 1)**	100	2.44	9.59	7.97	1.07*	0.34
N5D (sample 2)	100	10.51	7.47	2.00	0.97	0.74
N5D (sample 3)	100	13.26	5.19	1.51	0.95	0.84

* Values of a numerically greater than 1.00 are equated to unity.

† Rye telocentric unpaired in all cells.

‡ Rye telocentrics paired with one another in 85% of cells and both unpaired in 15% of cells.

§ Rye telocentrics paired with one another in 86% of cells and both unpaired in 14% of cells.

‖ The first 100 cells scored, of a total of 150, that did not contain multivalents. The average of the 150 cells was 15.35ⓘ, 3.87|II|, 0.61 I, 0.08 III, 0.08ⓘⓥ and 0.10|IV|.

¶ The 63 cells, of a total of 85, that did not contain multivalents. The average of the 85 cells was 14.94ⓘ, 4.14|II|, 0.73 I, 0.06 III, 0.09ⓘⓥ, and 0.13|IV|.

** One cell, excluded from the 100, exhibited 11 II, 6 II, 3 I and 1 III.

Examples of abbreviations used in Table 1: N3A = nullisomic *3A*. 3Rt(3A) = monosomic substitution of a telocentric of rye chromosome *3R* for chromosome *3A*. 3Rtt(3A) = disomic substitution of a telocentric of rye chromosome *3R* for chromosome *3A*. 3R″(3D) = disomic substitution of entire rye chromosome *3R* for chromosome *3D*. ⓘ = closed bivalent, *i.e.*, ring bivalent. |II| = open bivalent, *i.e.*, rod bivalent. I = univalent. III = trivalent. ⓘⓥ = closed quadrivalent. |IV| = open quadrivalent.

dence of association is evident in all derived lines, the range being from 0.95 to 1.0.

By contrast, large variation is seen in the values of *c*, ranging from 0.34 in one sample of nullisomic *5D* and 0.60 in nullisomic *3B* up to normal values in other materials. Obviously the homoeologous groups *3* and *5* chromosomes affect chiasma frequencies.

In homoeologous group *3*, results obtained with the three nullisomics show that removal of chromosome *3B* has a greater effect on chiasma frequency than removal of *3A*, whereas *3D* does not seem to have any detectable effect. Deficiency for *3A* is compensated for by rye telochromosome *3Rt*, especially in two doses. Similarly, deficiency for chromosome *3B* is, to a large measure, compensated for by rye telochromosome *3Rt*, especially in two doses.

In homoeologous group 5, the major interest involves chromosome *5B* because of its known affect on restricting configurations to homologous ones. Analysis of cells deficient for *5B*, that did not exhibit multivalents, reveals that association of homologues is not impaired, but chiasma frequency is reduced, though not

dramatically so in comparison with the other nullisomics analysed. (The result of removal of *5B* will be referred to again below.) Absence of chromosome *5A* has no detectable affect, and absence of chromosome *5D* results in considerable reduction in chiasma frequency. The *c* values for the samples of nullisomic *5D* vary considerably. This may reflect variation in temperature during the early stages of meiosis; absence of chromosome *5D* results in meiotic instability at low temperatures (RILEY 1966).

In contrast to the estimates of *a* (all greater than 0.95 in the materials listed in Table 1), the main affect of premeiotically applied colchicine is to reduce the association of homologoues, as reflected in the low values of *a* (all less than 0.5 in Table 2). In some samples shown in Table 2, chiasma frequency in associated homologues is affected. The variation in this parameter (0.82 to 0.96) could reflect environmental effects or treatment differences.

In summary, colchicine primarily reduces the frequency of association of homologues, whereas the kind of aneuploidy examined reduces the frequency of chiasma formation in associated homologues. The colchicine effect is in agreement with that proposed by DRISCOLL, DARVEY and BARBER (1967) and DRISCOLL and DARVEY (1970).

These conclusions are in accord with those of THOMAS and KALTSIKES (1977), who analysed chromosome configuration data in pentaploid material with a modified formula derived by GAUL (1958), which relates parabolically the number of chromosomes in configurations with the number of chiasmata.

Homoeologous configurations : expectations

In the second part of the theory homoeologous configurations are assessed in the absence of homologues, such as in a wheat-rye hybrid. It is assumed that chromosomes that are homoeologous to one another are equally associated in the one group. (This assumption of $a = 1.0$ for all homoeologues will be referred to again later.) Chiasmata occur between homoeologous arms at random with probability *c*. It is assumed that the one value of *c* applies to all homoeologues within any homoeologous group. Instances of involvement of one chromosome arm in more than one chiasma are ignored, and chromosome arms are inde-

TABLE 2

Frequencies of chromosome configurations of normal chromosomes following premeiotic application of colchicine and the calculated values of a *and* c

Stock	No. cells	(II)	[II]	2I	*a*	*c*
Euploid						
(sample No. 1)	128	6.85	3.07	11.16	0.49	0.82
(sample No. 2)	39	8.03	2.26	10.69	0.49	0.88
(sample No. 3)	28	7.00	3.04	10.96	0.49	0.82
Mo5DL	100	8.28	1.03	10.69	0.47	0.94
Mo7DS	50	4.68	0.40	14.92	0.25	0.96

Abbreviations used in Table 2: Mo5DL = Monoisosomic for the long arm of chromosome *5D*. Mo7DS = Monoisosomic for the short arm of chromosome *7D*.

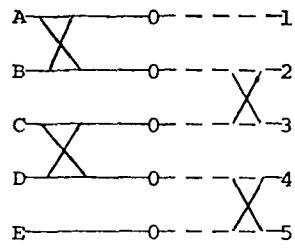

FIGURE 1.—A homoeologous group of five chromosomes, with arms designated A to E, which are homoeologous to one another, and 1 to 5, which are homoeologous to one another. Homoeologous arms are not identical to one another, thus the figure is the first approximation only.

penden of one another in participating in chiasma formation. (This assumption of independence will also be referred to again later.)

Consider a hybrid of hexaploid wheat by a tetraploid species in which five different genomes are involved. This hybrid has seven groups, each with five homoeologous chromosomes. Considering one homoeologous group only, the maximum number of chiasmata that can form in one group is four, according to the theory as shown in Figure 1. In the example shown, the only arms not involved in pairing are E and 1, which are heteroeologous arms, *i.e.*, opposite arms of homoeologous chromosomes. No other distribution of chismata results in more than four chiasmata in one group of homoeologous chromosomes. Thus, the maximum possible number of chiasmata for this hybrid is four multiplied by the number of different homoeologous groups (*i.e.*, 7), which in this case is 28.

The observed number of chiasmata is equal to the number of open bivalents + 2 (closed bivalents) + 2 (trivalents) + 3 (open quadrivalents) + 4 (closed quadrivalents) + 4 (quinquevalents). c can be estimated as follows:

$$c = \frac{\text{observed number of chiasmata}}{\text{maximum possible number of chiasmata}} \tag{4}$$

The expected frequencies of the various configurations can then be determined as follows. Figure 1 illustrates one placement of four chiasmata in five homoeologues. Keeping the place of the first chiasma constant as AB, there are a total of 45 ways of deploying the remaining three chiasmata. These and their results are shown in Table 3. The results of four, and of fewer chiasmata which have been obtained in the same manner, are shown in Table 4. Expressed in another way, the probability of each possible type of configuration emanating from a group of five homoeologues is given in Table 5. Similar probabilities, derived in the same manner, for a group of four homoeologues and for a group of three homoeologues are given in Tables 6 and 7, respectively. The expected frequencies of configurations can be determined from the value of c as calculated from equation (4) and Tables 5, 6 and 7 where appropriate. For example, in a 34-chromosome hybrid of a monosomic × *Ae. variabilis*, there are six homoeologous groups having five chromosomes and one homoeologous group having four chromosomes. The one calculated value of c would be entered into Table 5, the results multi-

TABLE 3

The 45 ways four chiasmata can be distributed among five homoeologues and their results

1	Chiasma number 2	3	4	Results I	II	III	IV	V
AB	12	34	CD	1		2		
			CE			1	1	
			DE			1	1	
		35	CD			1	1	
			CE	1		2		
			DE			1	1	
		45	CD			1	1	
			CE			1	1	
			DE	1		2		
	13	24	CD	1			1	
			CE					1
			DE					1
		25	CD					1
			CE	1			1	
			DE					1
		45	CD					1
			CE					1
			DE			1	1	
	14	23	CD	1			1	
			CE					1
			DE					1
		25	CD					1
			CE					1
			DE	1			1	
		35	CD					1
			CE			1	1	
			DE					1
	15	23	CD					1
			CE	1			1	
			DE					1
		24	CD					1
			CE					1
			DE	1			1	
		34	CD			1	1	
			CE					1
			DE					1
	23	45	CD					1
			CE					1
			DE			1	1	
	24	35	CD					1
			CE			1	1	
			DE					1
	25	34	CD			1	1	
			CE					1
			DE					1

Result:	No.	Ratio
2 (II) + I	3	1
(IV) + I	6	2
(II) + III	12	4
V	24	8
Total	45	

TABLE 4

Results of various numbers of chiasmata in one homoeologous group of five chromosomes

No. of chiasmata	Probability	I	|II|	(II)	III	|IV|	(IV)	V
0	$(1-c)^4$	5						
1	$4c(1-c)^3$	3	1					
2	$\frac{1}{13} \times 6c^2(1-c)^2$	3		1				
	$\frac{6}{13} \times 6c^2(1-c)^2$	2			1			
	$\frac{6}{13} \times 6c^2(1-c)^2$	1	2					
3	$\frac{1}{5} \times 4c^3(1-c)$	1	1	1				
	$\frac{2}{5} \times 4c^3(1-c)$	1				1		
	$\frac{2}{5} \times 4c^3(1-c)$		1		1			
4	$\frac{1}{15} \times c^4$	1		2				
	$\frac{2}{15} \times c^4$	1					1	
	$\frac{4}{15} \times c^4$			1	1			
	$\frac{8}{15} \times c^4$							1

TABLE 5

Expected frequencies of chromosome configurations in a homoeologous group of five chromosome, e.g., $III = 1.44c^4 - 3.94c^3 + 2.77c^2$

	c^4	c^3	c^2	c	1
I	0.49	−0.98	3.69	−8.00	5.00
|II|	−0.86	3.32	−6.46	4.00	
(II)	0.06	−0.12	0.46		
III	1.44	−3.94	2.77		
|IV|	−1.60	1.60			
(IV)	0.13				
V	0.53				

TABLE 6

Expected frequencies of chromosome configurations in a homoeologous group of four chromosomes

	c^4	c^3	c^2	c	1
I	1.14	—2.29	5.14	—8.00	4.00
[II]	—1.90	6.48	—8.57	4.00	
(II)	0.19	—0.38	0.86		
III	3.43	—6.86	3.43		
[IV]	—2.67	2.67			
(IV)	0.67				

plied by six and then added to the results obtained by entering the value of c into Table 6.

Homoeologous configurations : observations

Comparisons of observed and predicted frequencies of configurations, with and without chromosome *5B*, are shown in Tables 8 and 9, respectively. In general terms, there is reasonable agreement in that observed and expected frequencies of configurations show the same sequence from the most frequent to the least frequent type, *viz.*, univalents, open bivalents, trivalents, closed bivalents, open quadrivalents, quinquevalents and closed quadrivalents. Thus, the relative frequencies of the various configurations can be predicted if the overall chiasma frequency is known.

On closer examination, as shown in Table 10, the observed number of closed bivalents is higher than the expected number, and this is at the expense of the number of observed multivalents. This indicates that the association of homoeologues is less than fully efficient in that all homoeologues are not effectively associated in all cells. This would result in a second chiasma giving rise to a closed bivalent more often than expected, since all homoeologues are not available for chiasma formation on the other side of the centromere. The discrepancy between observed and expected closed bivalents is numerically greater in the case of deficiency of *5B*; thus, the absence of this chromosome does not lead to greater association of homoeologues, otherwise the discrepancy would have been less in the absence of *5B*. This indicates that the *5B* gene(s) affects chiasma formation rather than association of chromosomes.

TABLE 7

Expected frequencies of chromosome configurations in a homoeologous group of three chromosomes

	c^2	c	1
I	1.33	—4.00	3.00
[II]	—2.00	2.00	
(II)	0.33		
III	0.67		

TABLE 8

Observed frequencies of chromosome configurations of hybrids, the calculated values of c *and the expected frequencies of chromosome configurations*

Hybrid (Chromosome No.)	No. cells	I	III	II	III	IV	IV	V	c
Poso × *Ae. variabilis*	1,500	30.69	1.97	0.03	0.10	0.002	...	...	0.08
(35)	Exp	30.68	1.96	0.02	0.11	0.005	0.000	0.000	
Federation × *Ae. variabilis*	495	30.82	1.99	0.02	0.05	...	...	...	0.08
(35)	Exp	30.68	1.96	0.02	0.11	0.005	0.000	0.000	
Ae. variabilis × A. R. Falcon	600	31.08	1.73	0.02	0.13	0.010	...	...	0.07
(35)	Exp	31.20	1.75	0.02	0.09	0.004	0.000	0.000	
Bearded Yalta × *Ae. variabilis*	495	33.20	0.86	0.002	0.030	...	...	...	0.03
(35)	Exp	33.34	0.78	0.003	0.017	0.000	0.000	0.000	
Ae. variabilis × Gamut	590	34.13	0.43	0.002	0.003	...	...	...	0.02
(35)	Exp	33.89	0.54	0.000	0.010	0.000	0.000	0.000	
Chinese Spring ×	1,000	33.96	0.52	...	...	...	...	...	0.02
Ae. variabilis	Exp	33.89	0.54	0.000	0.010	0.000	0.000	0.000	
(35)									
Ae. variabilis × Eureka	300	34.24	0.37	0.003	0.003	...	...	...	0.01
(35)	Exp	34.44	0.28	0.000	0.002	0.000	0.000	0.000	
Chinese Spring monosomic	300	30.08	1.87	0.02	0.05	...	...	...	0.07
3A × *Ae. variabilis*	Exp	30.21	1.74	0.02	0.09	0.004	0.000	0.000	
(34)									
Chinese Spring monosomic	200	33.40	0.30	...	...	...	...	...	0.01
3B × *Ae. variabilis*	Exp	33.44	0.28	0.000	0.002	0.000	0.000	0.000	
(34)									
Shinese Spring monosomic	300	28.44	2.52	0.05	0.14	...	...	...	0.10
3D × *Ae. variabilis*	Exp	28.67	2.35	0.04	0.17	0.011	0.000	0.000	
(34)									
Chinese Spring monosomic	100	33.68	0.16	...	...	...	...	...	0.01
5A × *Ae. variabilis*	Exp	33.44	0.28	0.000	0.002	0.000	0.000	0.000	
(34)									
Chinese Spring monosomic	52	32.46	0.77	...	...	...	...	...	0.03
5D × *Ae. variabilis*	Exp	32.58	0.80	0.003	0.017	0.000	0.000	0.000	
(34)									
Chinese Spring ×	200	26.13	0.91	...	0.015	...	...		0.03
Imperial Rye	Exp	26.35	0.79	0.005	0.020	0.000	0.000		
(28)									

TABLE 9

Observed frequencies of chromosome configurations of 5B*-deficient hybrids, the calculated values of* c *and the expected frequencies of chromosome configurations*

Hybrid (Chromosome No.)	No. cells	I	III	II	III	IV	IV	V	c
Chinese Spring monosomic	250	14.42	6.36	0.81	1.33	0.25	0.01	0.03	0.41
5B × *Ae. variabilis*	Exp	15.18	5.14	0.55	1.61	0.50	0.04	0.09	
(34)									
Chinese Spring monosomic	295	19.75	2.80	0.39	0.27	...	...		0.16
5B × Imperial Rye	Exp	19.45	2.94	0.13	0.39	0.055	0.001		
(27)									

TABLE 10

Observed and expected numbers of various chromosome configurations in hybrids with and without chromosome 5B

Hybrid (No. of cells)		<2 Chiasmata	Closed bivalents	Multivalents
Euploid × *Ae. variabilis*	Obs	197,755	91	337
(5,932)	Exp	197,680	71	394
Monosomic *5B* × *Ae. variabilis*	Obs	5,195	202	405
(250)	Exp	5,080	137	560
Monosomic *5B* × Imperial rye	Obs	6,652	115	80
(295)	Exp	6,605	38	132

Thus, the frequencies of configurations when homoeologues only are present is interpreted as (1) homoeologues associate as a group with an efficiency less than that of homologues and (2) chiasmata occur at random between associated homoeologous arms. The low efficiency of association of homoeologues as a group results in opposite arms of the same chromosomes being involved in chiasmata on both sides of the centromere more often than expected on the basis of chance alone. This may be accentuated by some homoeologues being more closely related than others in the same group.

Removal of some of the chromosomes of homoeologous group *3* or *5* alters the frequencies of configurations by increasing the number of chiasmata (see Tables 8 and 9). In group *3*, removal of *3B* has no effect, removal of *3A* an intermediate effect and removal of *3D* has the most effect on increasing the number of chiasmata. In group 5, removal of *5A* has no effect, removal of *5D* has an intermediate effect and removal of *5B* has a dramatic effect on increasing the number of chiasmata. None of these changes seem to affect association of homoeologues; otherwise, expected and observed frequencies of configurations would exhibit less agreement in cases of deficiencies of chromosomes than in euploid cases.

Homologous and homoeologous configurations

The third part of the theory is a synthesis of the first two parts. From the analysis of the first part of the theory, we concluded that homologous chromosomes associate with almost certainty and that no genetic alteration examined in this study affected this association. From the analysis of part two of the theory, we concluded that homoeologous chromosomes associate as a group with less efficiency and that no genetic alteration examined in this study affected this association. Thus, we propose that homologues and homoeologues in euploid wheat associate as groups of six chromosomes with each pair of homologues being associated efficiently, but the three pairs of chromosomes associated inefficiently with respect to one another. Removal of any one chromosome of homoeologous group *3* or *5* does not affect the process of association.

The affect of removal of some of the group *3* or group *5* chromosomes is to alter the number of chiasmata, either by decreasing the number from almost

unity if homologues are present (see Table 1) or by increasing the number from almost zero if only homoeologues are present (see Tables 8 and 9). Alterations in the directions indicated are the only ones that could have been detected in this study. Nevertheless, in the case of *3A* and of *5B*, removal of the one chromosome leads to changes in opposite directions, as follows. Removal of *3A* results in a decrease in the value of *c* from 0.95 to 0.86 in the case of homologous configurations and an increase in the value of *c* from 0.02 to 0.07 in the case of homoeologous configurations. This same pattern is seen dramatically in the case of removal of *5B*, which results in a decrease in the value of *c* from 0.95 to 0.88 in the case of homologous configurations and an increase in the value of *c* from 0.02 to 0.41 in the case of homoeologous configurations. In the case of nullisomic *5B*, the total number of chiasmata is reduced; however, the distribution within a homoeologous group is increased, perhaps by rendering sites for chiasma formation of homoeologues more similar. In *5B*-deficient hybrids, the potential lowering of the chiasma frequency is outweighed by the opportunity to realize chiasmata between homoeologues, perhaps by way of greater similarity of sites for chiasma formation. This greater opportunity of homoeologous chiasma formation is maximized in the hybrid because of the lack of preferential chiasma formation between homologues. A similar situation may be involved with deficiency of chromosome *3A*; however, the effect is not strong enough to result in homoeologous chiasma formation in nullisomic *3A* because of the preferential chiasma formation of homologues.

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