

Quantitative analysis of diploid translocation heterozygotes: test of models and equations

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Summary. Equations have been derived for two different models of chromosome pairing and chiasmata distribution. The first model represents the normal condition and assumes complete synapsis of homologous bivalents and the arms of interchange quadrivalents. This is followed by a nonrandom distribution of chiasmata among bivalents and multivalents such that each bivalent or bivalent-equivalent always has at least one chiasma. Univalents occur only as part of a III, I configuration at diakinesis or metaphase I. The second model assumes that a hologenomic mutation is present in which all chromosomes of a genome are equally affected. Two different assumptions can be made for such a mutation, and both give the same results: (1) homologous or homoeologous chromosome arms may be randomly paired or unpaired, but synapsis always leads to a crossover; (2) homologous or homoeologous arms always pair, but chiasmata are randomly distributed among the arms. The meiotic configurations at diakinesis or metaphase I are the same for both assumptions. Meiotic configurations of normal diploid interchange heterozygotes show good agreement with numbers predicted by the equations for nonrandom chiasmata distribution among configurations. Interspecific hybrids with supernumerary chromosomes produced meiotic configurations frequencies in agreement with predictions of equations for random chiasmata distribution, but a hybrid without supernumeraries fitted the nonrandom expectations.

Key words: Translocation heterozygote – Chromosome pairing models – Equations – Quantitative analysis

Introduction

Following the development and testing of mathematical models and equations that predict chromosome associations at diakinesis or metaphase I in diploid species and hybrids and in autopolyploids (Jackson and Casey 1982; Jackson and Hauber 1982; Jackson 1982, 1984; Murray et al. 1984), we believed it was possible to derive models and equations that would correctly predict meiotic associations in interchange heterozygotes. There is a need for such methods for the analysis of intra- and interspecific relationships and for the detection and investigation of mutant genes and supernumerary chromosomes that affect chromosome pairing and the distribution of chiasmata among bivalents and multivalents.

Previous analyses have shown that normal meiotic behavior in diploids is characterized by at least one chiasma per pachytene bivalent and not by a random distribution of chiasmata among bivalents (Jackson 1982, 1984). However, random pairing and/or crossing-over is found in some hybrids and inbred lines and is due to mutations that may cause changes in presynaptic positioning of the independently behaving genomes, either by a change of attachment sites on the nuclear membrane or by prezygotene movement on the membrane (Avivi and Feldman 1980; Jackson 1982). This could cause failure of synapsis in extreme cases or a delay in the processes sufficient to interfere with critical timing sequences in the molecular aspects of crossing-over (Jackson and Hauber 1983, pp 363–367). The details of such proposed mutations can only be hypothesized at this time, but their effects can be very accurately predicted by appropriate models and equations. We emphasize that mutations of this type affect all chromosomes of a genome as opposed to chromosome specific effects such as described by Parker (1975) and Tease and Jones (1976). Mutations that affect all chromosomes of entire genomes (hologenomic mutations) are the common types, and they can be detected in both diploids and polyploids and are responsible for what has been called differential affinity or preferential pairing in polyploids (Jackson 1982,

1984; Evans and Davies 1983). Premeiotic treatment with colchicine can disrupt preferential pairing and induce multivalents in ancient polyploids (Jackson and Murray 1983; Murray et al. 1983), so structural differences between genomes are not satisfactory explanations of differential affinity, and neither is a difference in timing of crossing over (Yacobi et al. 1982) unless proponents of such a model (Hobolth 1981) assume that colchicine is capable of changing the timing for recombination events.

In our proposed models and equations for translocation heterozygotes, we have considered both normal synapsis and crossing-over and the hologenomic mutations that affect these processes.

Models and equations

For both the normal nonrandom and the mutant random systems, we make the following assumptions. The chromosomes are of the same length, all are metacentric, there is equal probability that a crossover will occur in either arm, and each bivalent or bivalent equivalent has the same opportunity to form chiasmata. All interchanges involve entire arms so the karyotype remains symmetrical.

In the equations, the P value is a chiasma probability that is derived by dividing the average number of chiasmata per bivalent by the maximum number expected, which is 2 in these models. The Q value is $1-P$. The total number of chiasmata for each plant can be determined by $2(P) \times n \times \text{No. of cells}$, rounded to the nearest whole number. In both the normal nonrandom and the random methods, chiasmata are allocated by binomial distribution, but in the nonrandom method only some of the terms are used. In the derived coefficients and terms, P and Q replace p and q. Exponents of p represent the number of chiasmata and those of q the lack thereof. The following additional symbols and their meanings are used throughout the remaining part of the paper: oII = a two chiasmata bivalent; oIV = a four chiasmata quadrivalent; cII = a one chiasma bivalent; cIV = a three chiasmata quadrivalent; cIII,I = a two chiasmata trivalent and a univalent; I = a univalent; x = the basic chromosome number; n = the expected number of normal bivalents in the organism without interchange heterozygosity; Σ = sum of.

Normal pairing and non-random chiasma distribution model and equations

These methods require that the P value be greater than 0.5 and I's absent unless they are derived from a III,I configuration. All homologous chromosome arms are synapsed, and the interchange forms a IV at pachytene. Each II or its equivalent in a IV has a minimum of one and a maximum of two chiasmata. The translocation configuration with four equal arms (Fig. 1) may then have 2, 3, or 4 chiasmata. These chiasmata initially are distributed in the IV arms according to the binomial $(p+q)^4$. Coefficients of the terms multiplied by 4 yield the number of chromosomes used in each term, and they also give the number of different ways chiasmata may be allocated in the four arms of a IV. Thus $p^4 + 4p^3q + 6p^2q^2 + 4p^1q^3 + q^4$ is the distribution of 4 to 0 chiasmata in a random way. However, we can use only the first three terms because these represent the situations wherein there is always a minimum of one or a maximum of two chiasmata per bivalent-equivalent.

The first term (p^4) denotes a chiasma in each arm of the IV at pachytene and at diakinesis or metaphase I yields a oIV.

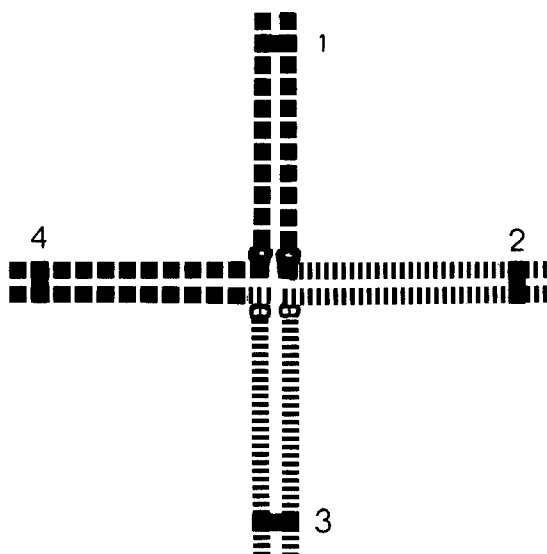


Fig. 1. Diagram of a pachytene quadrivalent with equal arm interchanges. Nos. 1-4 show possible positions of chiasmata. In the non-random chiasmata distribution model, the minimum number of chiasmata is always 2, but in the random system the number may vary from 4 to 0

The probability of this event must take into account the P value; thus $1(P^4) = \text{oIV}$ expected frequency. However, this result and that of the next term are overestimates and will be modified later by a correction coefficient. Similarly, $4(p^3q^1)$ represents a three chiasmata event so $4(P^3Q^1) = \text{a cIV}$ preliminary estimate, and the lack of a chiasma in any of the four arms gives the same results.

The term $6(p^2q^2)$ allows six ways to distribute two chiasmata among the four arms of the pachytene IV (Fig. 1). On a random basis, $4/6$ of the affected cells would form a cIII,I and $2/6$ would give 2 cII's. Thus, $4/6 \times 6 = 4(P^2Q^2) = \text{cIII,I}$ and $(2/6 \times 6) \times 2 = 4(P^2Q^2) = \text{cII}$ frequencies in a random situation. However, experience with IV's in autotetraploids having a low chiasma frequency has shown that the III,I class does not normally occur in some species (Jackson and Hauber 1982) because the two chiasmata are localized in opposite arms of the IV, yielding only 2 cII's. Our equations therefore do not consider that the cIII,I configuration occurs in this translocation heterozygote model. If the III,I should occur, it can be tested for agreement of expected numbers using the equation given, and this adds another degree of freedom for statistical analysis. The expected number of cII's is obtained as follows. After use of the correction coefficient on the oIV and cIV classes, the sum of all chromosomes found in expected oIV, cIV, cIII,I, and oII configurations is subtracted from the sum of all chromosomes in all cells analyzed. The remainder is then multiplied by 0.5 to yield cII's.

A correction coefficient is needed because not all terms of the $(p+q)^4$ binomial were used; omitted were $4(p^1q^3)$ and (q^4) . The correction coefficient in effect removes chromosomes and chiasmata from $1(p^4)$ and $4(p^3q^1)$ and allocates them to the part of the distribution that would otherwise result in I's. Thus the numbers of oIV and cIV configurations are decreased and the number of cII's increased. This allows all chromosomes and all chiasmata to be used, and the result is all oII and cII equivalent configurations characteristic of the normal

non-random model. From previous results (Jackson and Hauber 1982), we know that $1-2Q = oII$ and $2Q = cII$ frequencies in a normal situation. The oII equivalents in a random distribution of chiasmata in a IV are found only in $1(p^4)$ and $4(p^3q^1)$ terms. Thus, $1(p^4) = 2 oII$ and $4(p^3q^1) = 1 oII$ equivalents, so the new coefficients and terms for oII equivalents become $2(p^4) + 4(p^3q^1) = 2P^3(1+Q)$. In a normal non-random distribution of chiasmata among II's, the oII frequency is $1-2Q$, and since two II equivalents are needed for the interchange IV, this expression becomes $2(1-2Q)$. Because a binomial distribution allows some pachytene IV's to have three or four chiasmata while others have none, there is an abnormal excess of chromosomes and chiasmata in $1(p^4) + 4(p^3q^1)$. A correction coefficient can be obtained from the frequency of normal oII equivalents divided by the oII equivalents in a random distribution. Thus:

$$\frac{2(1-2Q)}{2P^3(1+Q)} = \frac{1-2Q}{P^3(1+Q)} = \text{Correction coefficient.}$$

Preliminary estimates of oIV and cIV frequencies are then multiplied by the correction coefficient to reduce them to a normal non-random frequency.

Table 1. Equations^a for determining the number of expected diakinesis or metaphase I configurations in a diploid translocation heterozygote with equal length metacentric chromosomes and whole arm interchanges between two non-homologous chromosomes. The equations are based on complete synapsis and a non-random distribution of 1 to 2 chiasmata per bivalent and 2 to 4 per quadrivalent

$$\begin{aligned} oIV &= (P^4) \times [(1-2Q + P^3(1+Q)) \times \text{No. Cells}] \\ cIV &= 4(P^3Q^1) \times [(1-2Q + P^3(1+Q)) \times \text{No. Cells}] \\ oII &= (n-2) \times (1-2Q) \times \text{No. Cells} \\ cII &= \text{No. Cells} \times (2n) - (\Sigma \text{chromosomes in} \\ &\quad oII + cIV + oIV) \times 0.5 \end{aligned}$$

^a The III,I class, derived from $4(P^2Q^2) \times \text{No. Cells}$, is not shown because the distribution of two chiasmata in a quadrivalent is not always predictable. This class is included in the expected cII class with each expected III,I counted as equivalent to two chain bivalents. Any observed III,I configurations should be multiplied by 2 and the results added to the observed cII class for statistical testing. See text for another treatment

Table 2. Equations for determining the number of expected diakinesis or metaphase I configurations of a diploid translocation heterozygote with equal length metacentric chromosomes and whole arm interchanges between two non-homologous chromosomes. The equations are based on complete pairing and random distribution of 0 to 2 chiasmata per bivalent and 2 to 4 per quadrivalent. These equations may be used also for random pairing of homologous arms always followed by a crossover

$$\begin{aligned} oIV &= (P^4) \times \text{No. Cells} \\ cIV &= 4(P^3Q^1) \times \text{No. Cells} \\ cIII &= 4(P^2Q^2) \times \text{No. Cells} \\ oII &= P^2(n-2) \times \text{No. Cells} \\ cII &= 4(P^1Q^3) \times \text{No. Cells} + [2(PQ) \times (n-2) \times \text{No. Cells}] \\ &\quad = 2(Q^2) \times n \times \text{No. Cells} \end{aligned}$$

The expected meiotic configurations for the normal II's are determined as shown previously (Jackson and Hauber 1982; Jackson 1984). At pachytene in a translocation heterozygote, the number of II's will constitute $(n-2)$ of the theoretical total, so $(n-2) \times (1-2Q) = oII$ frequency. The sum of all chromosomes minus those used in the described configurations yield the remaining chromosomes. The remainder is multiplied by 0.5 to yield the cII class.

Equations for determining the expected numbers of the different meiotic configurations in the non-random chiasmata distribution model are collected in Table 1.

Random pairing and/or chiasma distribution model and equations

These methods assume that the P value can be lower than 0.5 and that I's are present in addition to those that are derived from a III,I configuration. The higher the P value, the larger the sample size necessary to have a reasonable probability of observing a I. We can make two different assumptions in this model, and both lead to the same results. (1) Homologous or homoeologous chromosome arms may be paired or unpaired, but when they are synapsed a crossover always occurs. (2) Homologous arms always pair, but they may have 0 to 1 chiasma or 0 to 2 chiasmata per II or II equivalent. We will use the second assumption only because of ease of presentation. Thus a pachytene IV (Fig. 1) could have 4 to 0 chiasmata, and the chiasmata are distributed among the IV arms according to the binomial $(p+q)^4$.

The five terms of the expanded binomial, $p^4 + 4p^3q^1 + 6p^2q^2 + 4p^1q^3 + q^4$, are considered in order beginning at the left. As in the non-random model, the coefficients of the terms give the number of ways to allocate chiasmata among the four IV arms at pachytene. For each term, the fraction of a derived configuration is multiplied by the coefficient to obtain the coefficient for that particular configuration. The sum of all chromosomes in all configurations derived from a particular term must equal the product of the normal term coefficient multiplied by the four chromosomes involved in the interchange. This constitutes a test for unity.

The first term of the binomial, $1(p^4)$, yields only a IV at diakinesis or metaphase I; thus $1(P^4) = oIV$ frequency. The second term, $4(p^3q^1)$, can produce only a cIV at diakinesis, so $4(P^3Q^1) = cIV$ frequency. By random placement of two chiasmata in the four pachytene IV arms, the third term, $6(p^2q^2)$, yields a $cIII,I$ 4/6 of the time and 2 cII 's 2/6 of the time. This results in $4/6 \times 6 = 4(P^2Q^2) = cIII,I$ and $(2/6 \times 6) \times 2 = 4(P^2Q^2) = cII$ frequencies. The fourth term, $4(p^1q^3)$, has only one chiasma, and regardless of which arm is involved, the result at diakinesis or metaphase I is a cII and 2I's. Thus $4(P^1Q^3) = cII$, and $8(P^1Q^3) = I$ frequencies. The last term (q^4) can result only in I's and so $4(Q^2) = I$ frequency.

The II's not involved in the interchange may have 0, 1, or 2 chiasmata, and crossovers are randomly distributed among paired bivalents according to the working assumption used for pachytene IV's. The distribution of chiasmata is then a binomial $(p+q)^2$. Thus $P^2 = oII$, $2(P^1Q^1) = cII$, and $2(Q^2) = I$ frequencies.

The equations for determining all expected meiotic configurations in cell samples are collected in Table 2.

Results

The data in Table 3 show good agreement between numbers of expected and observed meiotic configura-

Table 3. Observed (O) and expected (E) numbers of meiotic configurations in microsporocytes of diploid *Alopecurus aequalis*, *A. bulbosus*, *Briza media*, and *B. spicata* ($x=7$) heterozygous for a translocation between two non-homologous chromosomes with approximately equal arm interchanges. e = the theoretical number of oII's and oIV's when the chiasma frequency is 2 per II or IV equivalent

Plant no.	Observed and expected	Configurations ^a						P value	No. cells	Chi-square <i>P</i>
		I	cII	oII	III,I	cIV	oIV			
<i>A. aequalis</i>										
1	O	0	1	64	0	(0 + 13)	0.9945	13	> 0.95	
	E	0	0.71	64.29	0	(0.28 + 12.72)				
	e	0	0	65	0	0 13				
2	O	0	0	75	0	0 15	1.0000	15	> 0.95	
	e	0	0	75	0	0 15				
3	O	0	3	97	0	(5 + 15)	0.9714	20	> 0.20	
	E	0	5.91	94.29	0	(2.10 + 17.81)				
4	O	0	7	93	0	(0 + 20)	0.9750	20	> 0.50	
	E	0	5.15	95	0	(1.85 + 18.07)				
165	O	0	6	94	0	(1 + 19)	0.9750	20	> 0.50	
	E	0	5.15	95	0	(1.85 + 18.07)				
<i>A. bulbosus</i>										
	O	0	4	96	0	2 + 18	0.9786	20	> 0.50	
	E	0	4.4	95.71	0	1.61 + 18.34				
	e	0	0	100	0	0 20				
<i>B. media</i>										
(273×131)–3	O	0	15	85	0	(3 17)	0.9357	20	> 0.50	
	E	0	13.80	87.14	0	(4.21 + 15.32)				
(131×273)–4	O	0	10	90	0	(0 20)	0.9643	20	> 0.30	
	E	0	7.44	92.86	0	(2.56 + 17.29)				
(273×131)–9	O	0	(30)+4	84	(2) ^b	6 5	0.8571	20	> 0.05	
	E	0	32.87	71.43	0	7.14 + 10.71				
71/162	O	0	11	89	0	(3 17)	0.9500	20	> 0.70	
	E	0	10.56	90	0	(3.43 + 16.29)				
71/131	O	0	5	95	0	(2 18)	0.9750	20	> 0.90	
	E	0	5.16	95	0	(1.85 + 18.07)				
<i>B. spicata</i>										
(06×04)–7	O	0	0	125	0	(1 + 24)	0.9971	25	> 0.90	
	E		0.72	124.28	0	(0.28 + 24.71)				
(06×04)–13	O	0	21	729	0	14 136	0.9833	150	> 0.20	
	E	0	25.50	725	0	9.51 140.24				
(06×03)–4	O	0	(49)+2	201	(1) ^b	10 40	0.9186	50	> 0.30	
	E	0	44.40	209.29	0	12.61 35.55				
(06×03)–10	O	0	(51)+2	449	(1) ^b	12 87	0.9536	100	> 0.30	
	E	0	48.89	453.57	0	16.10 82.67				
(06×03)–13	O	0	12	488	0	9 91	0.9850	100	> 0.50	
	E	0	15.28	485	0	5.73 94.13				
(06×03)–15	O	0	4	246	0	(3 47)	0.9900	50	> 0.50	
	E	0	5.06	245	0	(1.94 48.03				

^a Meiotic analyses were performed by B. G. Murray

^b The III,I number is multiplied by 2 and added to the number of cIIs

tions, and all plant samples had a fit to the H_0 with $P > 0.05$. The equations based on non-random chiasmata distribution were used exclusively to determine expected numbers, but the results may not differ significantly from those obtained with the random methods when the P values are high. To distinguish

between the two methods at high P values, a very large sample size would be needed. For example, if the equations for random chiasmata distribution were used for plant 1 of *Alopecurus aequalis*, a sample size of 7,130 meiocytes is necessary to have a 95% chance of observing a I that has an expected frequency of 0.0004 per cell.

Table 4. Observed (O) and expected (E) numbers of meiotic configurations in microsporocytes of diploid hybrids of *Briza media* and *B. elatior* ($x=7$) heterozygous for a translocation between two non-homologous chromosomes with approximately equal arm interchanges and 0, 1, 2, and 4 B-chromosomes. All plants except the one without a B-chromosome were analyzed with equations for random distribution of chiasmata in paired arms

Hybrids		Configurations ^a						P value	No. cells	Chi-square <i>P</i>
		I	cII	oII	III	cIV	oIV			
(81×023)–6 (0B)	O	0	11	95	0	–17–		0.9643	20	> 0.10
	E	0	7.44	92.86	0	(2.56 + 17.29)				
(023×71)–5 (1B)	O	85	122	119	11	15	10	0.6671	50	> 0.50
	E	77.62	125.85	111.22	9.86	19.76	9.90			
(81×023)–1 (2Bs)	O	19	75	180	5	25	14	0.8229	50	> 0.10
	E	21.97	78.05	169.28	4.25	19.74	22.92			
(81×E1)–8 (4Bs)	O	320	139	21	12	(6 + 0)		0.3186	50	> 0.50
	E	324.63	138.21	25.44	9.44	(4.42 + 0.52)				

^a Meiotic analyses were performed by B. G. Murray

In some samples of Table 3, the data were tested with the theoretical value (e) for oII and oIV configurations. Under conditions of two chiasmata per bivalent, only oII and oIV should occur, and this was observed in *Alopecurus aequalis* (No. 1). This method of testing was used for two other plants because it was a way of obtaining one degree of freedom for the chi-square test.

The data in Table 4 are of considerable interest because the plants with B chromosomes in varying numbers all show behavior characteristic of hologenomic mutations in that the chiasmata are distributed randomly among II's and II equivalents in the multivalents. In the one plant without B chromosomes, the expected numbers of meiotic configurations were determined by using both the non-random and the random methods. The chi-square value for the non-random expected numbers was 2.162 ($P > 0.10$) and 2.910 ($P > 0.05$) for the random numbers expected, so we chose the non-random fit although both were acceptable.

Discussion

The agreement between the observed and expected values for the different classes of meiotic configurations of translocation heterozygotes shows the accuracy of the equations for the model systems. A question to be answered by additional studies is: How will translocations involving less than whole arms affect the diakinesis or metaphase I configuration frequencies? This should depend on the genetic system being analyzed. For example, if chiasmata are localized in the distal regions, a translocation involving only this portion might be sufficient to yield results expected for whole arm interchanges. This may be true in *Briza media* (273×131) with an unequal interchange (Fig. 2) and in

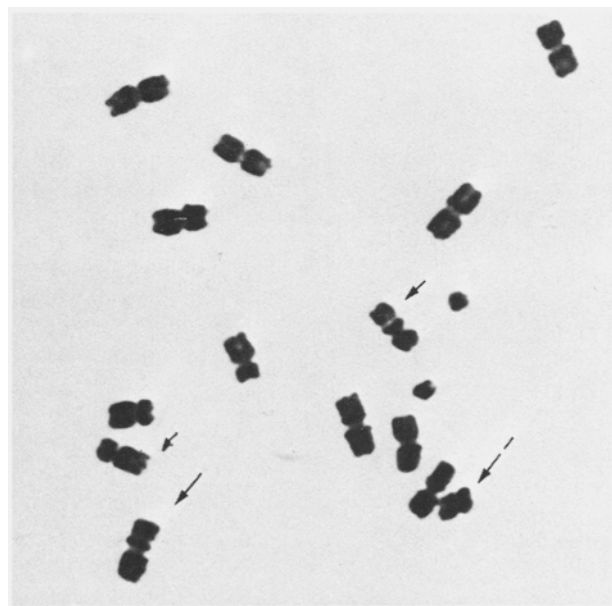


Fig. 2. Mitotic metaphase in *Briza media* $2n=14+2$ B chromosomes. Short arrows indicate interchange chromosomes, and long arrows show the two chromosomes with the normal arrangement

which three siblings (Table 3) gave an acceptable fit to the model. The situation is apparently different in cultivated strains of *Secale cereale*; only one interchange heterozygote analyzed by Sybenga (1970) in a different context gave a good fit for the values expected by our equations. Other examples he listed had too many oII configurations to fit our expected values, and this was likely caused by the occurrence of more proximal chiasmata at the expense of distal ones.

Interchanges that are unequal could yield excess III,I configurations while quadrivalents would be reduced below expected values. This may explain the higher than expected number of III,I and oII configurations in the hybrid *Aegilops longissima* × *A. searsii* (Feldman et al. 1979) whose genomes differ by a hologenomic mutation(s).

There was no evidence of negative interference across the breakpoints in either *Briza* or *Alopecurus* (Tables 3 and 4). As used by Sybenga (1970), negative interference constitutes excess crossovers in some arms of the multivalent. The phenomenon does occur in autotetraploids of *Haplopappus* and in *Triticum* (*Aegilops*) *longissimum* where III,I configurations are not found, or, if they do occur, they are significantly under-represented (Jackson and Hauber 1982). But cII's are over-represented because in two chiasmata IV's the crossovers occur in opposite arms. In deriving equations for predicting configurations in autopolyploids, cIII,I configurations were treated as 2 cII's that are equivalent in chiasmata and chromosome number. The same procedure was followed in equations for non-random chiasmata distribution in translocation heterozygotes (Table 1). However, for random chiasmata distribution equations (Table 2), III configuration equations were used, and there was reasonable agreement with expected numbers (Table 4). In cases where the observed III classes are too low and the cII classes are too high, negative interference probably is responsible if the other configurations give acceptable agreement with expectations. The III,I numbers then should be doubled and added to the cII class. Expected III,I calculations should be treated in the same way. If negative interference has occurred, the rearranged classes should give an acceptable overall fit to expected numbers.

There was only one plant of the normal diploids that had a low enough chiasma frequency and a large enough sample size to clearly differentiate between the equations based on random versus non-random chiasmata distribution. This was *Briza media* (273 × 139)-9 with a P value of 0.8571 (Table 3). Under the random system, 5.72 I's are expected, and none is predicted by the non-random system of equations. The chi-square value of the test for fit to random chiasmata distribution was 11.769, df=2, $P < 0.001$. Judging from experience with chiasmata behavior in normal autopolyploids, the meiotic configuration numbers derived from the random chiasmata distribution equations will not give acceptable agreement with observed numbers when the P value is low and the sample size is high. Normal genetic systems at the diploid level should not have I's, and interchanges in an otherwise normal system do not perturb the normal chiasmata distribution among II's or multivalents. Univalent numbers in normal inter-

change heterozygotes should not exceed the number of III's.

It should be clear that two separate interchanges in the model described here behave as expected. The frequency obtained for one event is multiplied by two to yield the final frequency. Some preliminary data from a two-interchange system give a good fit to expected numbers of the non-random system of equations (Murray, unpublished).

The data in Table 4 show that supernumerary chromosomes may drastically affect both chiasma frequency and distribution. Data from an earlier study of one plant of the hybrids without a B chromosome show a normal P value and a non-random distribution of chiasmata among the II's and multivalents. The three other plants have 1 to 3 B chromosomes, but none fitted the non-random chiasmata distribution model. They were then tested with the equations for random chiasmata distribution, and each gave an acceptable fit to the H_0 (Table 4). An earlier study of this hybrid demonstrated a correlated decrease in chiasma and II frequency with increasing number of B chromosomes (Murray 1976). Autotetraploids of hybrids with and without B chromosomes were synthesized. Seven tetraploids without B chromosomes had an average of 2.77 multivalents and 8 II's whereas tetraploids with 2, 4, and 8 B's showed significant linear decreases of multivalents and linear increases in II's (Murray 1978). In the diploid hybrid, homoeologues were more frequently associated when B chromosomes were absent, and homologues were most often associated in the tetraploids. Similar results have been found in other plants (Jones 1975; Jones and Rees 1982). Unfortunately, several otherwise excellent studies have not presented data in a manner that can be analyzed by our methods. However, several studies have conclusively demonstrated that B chromosomes decrease chiasma frequency, and Jones and Rees (1967) have shown that they cause an increase in variance of chiasmata among meiocytes. It has been shown also that B chromosomes may have an effect based on whether they are present in odd or even numbers (Jackson and Newmark 1960; Jones and Rees 1969).

We wish to emphasize a very significant effect of B chromosomes in our experiments. This is their capability of changing the normal non-random distribution of chiasmata among II's and multivalents to a random distribution among the configurations. This may be a more common phenomenon than generally realized, and we urge geneticists to re-examine their data with this in mind. Using the data of Evans and Macefield (1973, 1974), Jackson (1984) has tested the effect of B chromosomes on distribution of chiasmata in diploid hybrids of *Lolium temulentum* and *L. perenne* with equations that predict meiotic configurations for

normal and random chiasmata distribution among bivalents. The results were similar to our findings (Table 4); all plants with B chromosomes fitted the expectations of random chiasmata distribution while those without supernumerary chromosomes fitted the non-random model. The one exception in nine plants without B chromosomes showed a good fit ($P > 0.20$) to the random model and had 26 univalents in 20 meiocytes. This indicates that one of the parental species contributed one or more genes controlling pairing or crossing over, or both.

A major factor motivating our derivation of equations for non-random and random chiasmata distribution among bivalents and multivalents for interchange heterozygotes was to recognize pairing or chiasmata controlling genes in species or hybrids. With this information and the equations for diploids without interchanges (Jackson and Hauber 1982; Jackson 1984), it is now possible to analyze meiotic configurations in intra- and interpopulation crosses and in interspecific and intergeneric hybrids. As emphasized by Jackson (1982, 1984), the random behavior of chiasmata at the diploid level is positively correlated with II pairing in derived tetraploids regardless of taxonomic rank. Use of the equations for the two kinds of chiasmata distributions will allow plant breeders to select genotypes at the diploid level for chromosome doubling that should yield varying levels of intergenomal recombination or none at all in the derived tetraploids.

References

- Avivi L, Feldman M (1980) Arrangement of chromosomes in the interphase nucleus of plants. *Hum Genet* 55:281–295
- Evans GM, Davies EW (1983) Fertility and stability of induced polyploids. In: Brandham PE, Bennett MD (eds) Kew chromosome conference II. Allen & Unwin, London, pp 139–146
- Evans GM, Macefield AJ (1973) The effect of B chromosomes on homoeologous pairing in species hybrids. 1. *Lolium temulentum* × *Lolium perenne*. *Chromosoma* 41:63–73
- Evans GM, Macefield AJ (1974) The effect of B chromosomes on homoeologous pairing in species hybrids. 2. *Lolium multiflorum* × *Lolium perenne*. *Chromosoma* 45:369–378
- Feldman M, Strauss I, Vardi A (1979) Chromosome pairing of F_1 hybrids of *Aegilops longissima* and *Ae. searsii*. *Can J Genet Cytol* 21:261–272
- Hobolth P (1981) Chromosome pairing in allohexaploid wheat var. 'Chinese Spring,' transformation of multivalents into bivalents, a mechanism for exclusive bivalent formation. *Carlsberg Res Commun* 46:129–173
- Jackson RC (1982) Polyploidy and diploidy: new perspectives on meiotic chromosome pairing and its evolutionary implications. *Am J Bot* 69:1512–1523
- Jackson RC (1984) Chromosome pairing in species and hybrids. In: Grant WF (ed) Plant biosystematics. Academic Press, Canada, pp 67–86
- Jackson RC, Casey J (1982) Cytogenetic analyses of autopolyploids: models and methods for triploids to octoploids. *Am J Bot* 69:487–501
- Jackson RC, Hauber DP (1982) Autotetraploid and autotriploid cytogenetic analyses: correction coefficients for proposed binomial models. *Am J Bot* 69:644–646
- Jackson RC, Hauber DP (eds) (1983) Polyploidy. Benchmark papers in genetics, vol 12. Hutchinson Ross, Stroudsburg
- Jackson RC, Murray BG (1983) Colchicine induced quadrivalent formation in *Helianthus*: Evidence of ancient polyploidy. *Theor Appl Genet* 64:219–222
- Jackson RC, Newmark P (1960) Effects of supernumerary chromosomes on production of pigment in *Haplopappus gracilis*. *Science* 132:1316–1317
- Jones RN (1975) B chromosome systems in flowering plants and animal species. *Int Rev Cytol* 40:1–100
- Jones RN, Rees H (1967) Genotypic control of chromosome behavior in rye. 1. The influence of B chromosomes upon meiosis. *Heredity* 22:333–347
- Jones RN, Rees H (1969) An anomalous variation due to B chromosomes in rye. *Heredity* 24:265–271
- Jones RN, Rees H (1982) B chromosomes. Academic Press, London
- Murray BG (1976) The cytology of the genus *Briza* L. (Gramineae). 3. B chromosomes. *Chromosoma* 59:73–81
- Murray BG (1978) B chromosomes and multivalent formation in tetraploid hybrids between *Briza media* and *Briza elatior*. *Heredity* 41:227–231
- Murray BG, Jackson RC, Barker NR (1983) Cryptic genome homologies revealed by premeiotic treatment of meiocytes. In: Brandham PE, Bennett MD (eds) Kew chromosome conference, vol II. Allen & Unwin, London, pp 165–171
- Murray BG, Sieber VK, Jackson RC (1984) Further evidence for the presence of meiotic pairing control genes in *Alopecurus* L. (Gramineae). *Genetica* 63:13–17
- Parker JS (1975) Chromosome specific control of chiasma formation. *Chromosoma* 49:391–406
- Sybenga J (1970) Simultaneous negative and positive chiasma interference across the break point in interchange heterozygotes. *Genetica* 41:209–230
- Tease C, Jones GH (1976) Chromosome-specific control of chiasma formation in *Crepis capillaris*. *Chromosoma* 57:33–49
- Yacobi YZ, Mello-Sampayo T, Feldman M (1982) Genetic induction of bivalent interlocking in common wheat. *Chromosoma* 87:165–175