Theor. Appl. Genet. 61, 81–89 (1982)

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The Allotetraploidization of Maize

Part 3: Gene Segregation in Trisomic Heterozygotes

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Summary. Allotetraploidization is the creation of artificial allotetraploids. Allotetraploidization of maize can be accomplished by concentrating differential pairing affinity (DPA) factors into lines by a recurrent selection breeding system. Selection will be based on changes in genetic ratios which are the result of changes in the relative frequencies of various pairing configurations caused by DPA. Part 1 of this series gave extensive data on gene segregation in trisomic and tetraploid heterozygotes. Some of these tetraploids behaved like segmental allotetraploids. Part 2 presented a model for gene segregation in segmental allotetraploids. This paper presents an analogous model for gene segregation in trisomic heterozygotes. The pairing configurations of trisomes are analyzed by considering pairing in single arms which then are combined to obtain pairing configurations for whole chromosomes. The chromosome disjunction patterns of the various pairing configurations are hypothesized and expected genetic ratios are given that result from different levels of DPA expressed in several hypothetical trisomes. The model analyzes the effect of random pairing in one arm and non-random pairing in the other arms. Also, the effect of crossing over is taken into account. Because crossing over rates are affected by the environment, part of the variability in the data (Part 1) is explained. In addition, an hypothesis is advanced to explain the frequent enhancement of pairing affinity following x-irradiation.

Key words: Trisomes – Preferential pairing – Experimental evolution

Introduction

Allotetraploidization is the creation of artificial allotetraploids. Allotetraploidization of maize can be accomplished by restructuring a maize genome so that its chromosomes will not pair with those of the standard maize genome. This restructuring can be accomplished by concentrating induced or naturally occurring factors for differential pairing affinity (DPA) into a single line by a recurrent selection breeding system. Allopolyploidizing (or diploidizing) genes like the *Ph* gene in wheat (Sears 1958; Riley and Chapman 1958) could be used if they can be found or induced in maize.

Selection in the allotetraploidization breeding system will be made on the basis of changes in genetic ratios that are the result of DPA. The effect of DPA on genetic ratios in segmental allotetraploids and heterozygous trisomes was given in Part 1 (Doyle 1979a) of this series. Part 2 (Doyle 1979b) discussed the relationship between the relative frequencies of various pairing configurations (homogenetic bivalents, heterogenetic bivalents, heterogenetic quadrivalents, semi-heterogenetic quadrivalents, semi-homogenetic quadrivalents, and neutral quadrivalents) and genetic data. This paper presents an analogous model for gene segregation in heterozygous trisomes. As discussed in Part 1, the effects of DPA are more easily studied on the trisomic level. For this allotetraploidization experiment to be successful, it must rest on a sound theoretical basis.

Pairing Configurations in Heterozygous Trisomes

Let us consider a trisome that has two standard chromosomes that are marked with a recessive gene (g) and a third (or odd) chromosome which is marked with the corresponding dominant allele (G). The odd chromosome may be different from the standard chromosomes because it is from a different race, carries an inversion, or has been subjected to x-rays or chemical mutagens.

The possible kinds of pairing configurations in heterozygous trisomes are shown in Fig. 1. There are three general possibilities: three univalents (3U), a univalent and a bivalent (UB), and a trivalent (T).

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* Contribution from Agricultural Research/Science and Education Administration, US Department of Agriculture, University of Missouri, Columbia, Missouri, Missouri Agric. Exp. Sta. Jounal Series No. 8 670

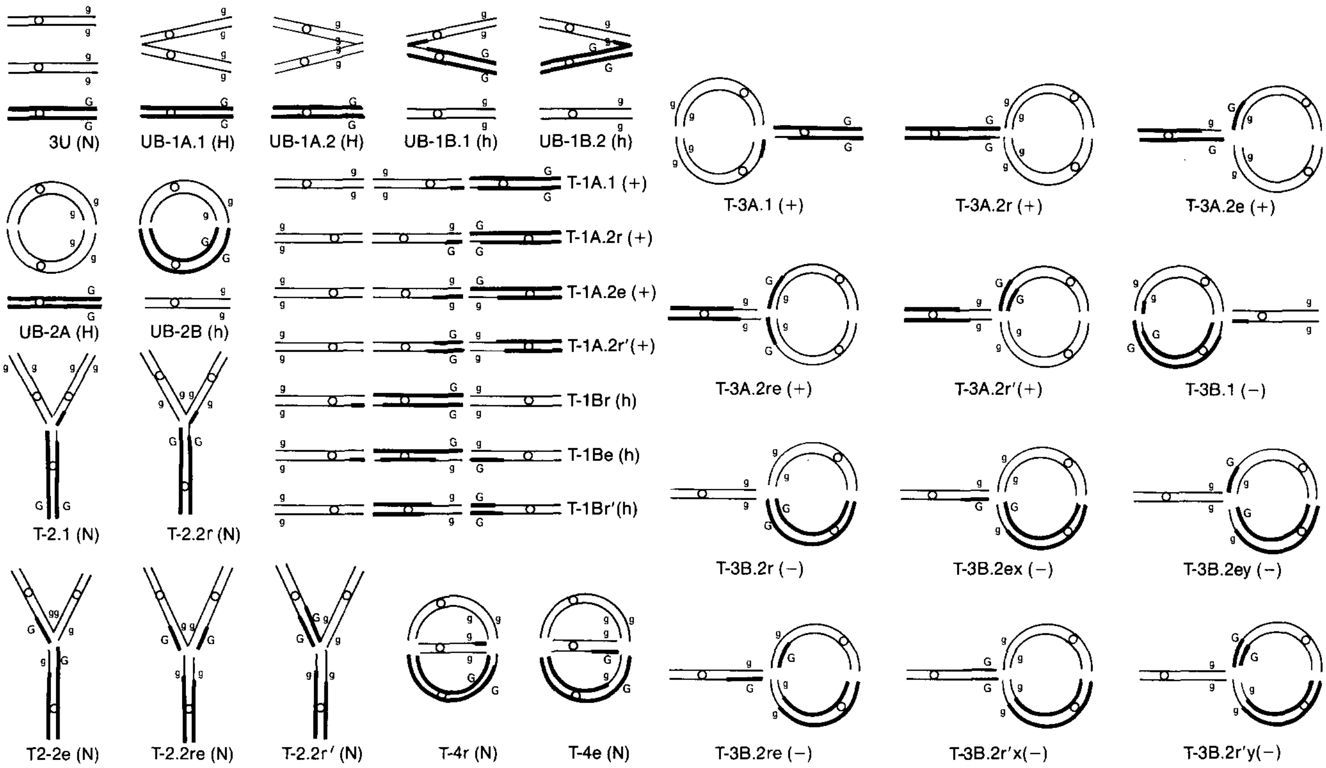

Fig. 1. Types of pairing expected in heterozygous trisomes. The symbols in the parentheses indicate nature of pairing: (H) homogenetic, (h) heterogenetic, (+) semi-homogenetic, (–) semi-heterogenetic, and (N) neutral

The bivalents can be rods (UB-1) with chiasmata in only one arm, or rings (UB-2) with chiasmata in both arms.

The trivalents can be chains (T-1), triradials (T-2), "frying pans" (T-3), or "bird cages" (T-4). These trivalent types have been recognized for a long time (Belling and Blakeslee 1923). To deal with trisomic heterozygotes, these general types must be subdivided according to how the chromosomes are arranged in the configuration. The symbol A, as in UB-1A, UB-2A, T-1A, and T-3A, indicates homogenetic (homologously associated) bivalents and semi-homogenetic (more than ⅓ homologous associations) trivalents. The symbol B indicates heterogenetic bivalents, heterogenetic trivalents, or semiheterogenetic (more than ⅔ homoeologous associations) trivalents.

Another subdivision indicates how the arms are involved in the configuration. For example, there are two types of T-1A which are called T-1A.1 and T-1A.2. There is no need to make this distinction in T-1B, because the two flanking standard chromosomes are alike.

Furthermore, the results of crossing over are shown when relevant. (There is no effect of crossing over on genetic ratios in the UB types.) If a chromosome has a Gg constitution it is called equational (e). This is the result of crossing over occurring proximally to the gene marker. Either there has been a single exchange or a 3-strand double exchange. If there has been no exchange or a 2- or 4-strand double exchange occurred proximally to the marker, the chromosomes will be GG or gg. This is called reductional (r). A 4-strand double exchange transfers both genes to another chromosome and it is signified by (r'). Note that T-1Ar = T-1Br' from the point of view of gene segregation for the G locus.

Three homologous or homoeologous arms are associated in T-2, T-3, and T-4. While only two chromosomes can be paired at any one point, exchanges of pairing partners at zygonema can bring three arms into association (Fig. 2). Different patterns of pairing-part-

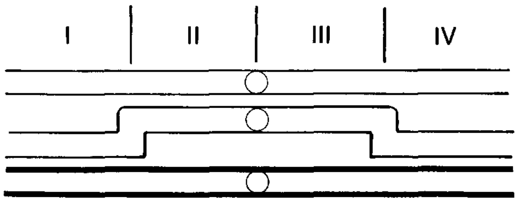

Fig. 2. One type of pairing partner exchange at pachynema in a trisome. Chiasmata at I, II, and III will produce a T-3A trivalent. Chiasmata at I, II, and IV will produce a T-3B trivalent. Other combinations of chiasmata will produce the array of configurations shown in Figure 1

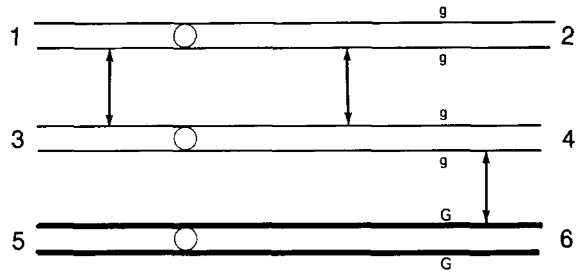

Fig. 3. The model used for explaining the pairing configuration shown in Figure 1. The exchanges shown above (13, 24, and 46) will produce at T-3 A.2 r trivalent as given in Table 2

ner exchange and chiasmata placement will yield all the trivalent types shown in Fig. 1.

When three arms are united by chiasmata, the situation after crossing over becomes complex. Some types such as T-2.2 re are possible if there are three chiasmata. Even if we limit our consideration to two chiasmata, there are two types of T-3 B.2 e, which are called T-3 B.2 ex and T-3 B.2 ey.

An Analysis of the Pairing Configurations

It is helpful to consider pairing in single arms and then to combine single-arm pairing configurations to form pairing configurations of whole chromosomes.

Let us consider a simple model. In Figure 3, there are three chromosomes whose arms have been numbered. Two of the chromosomes (1–2 and 3–4) are homologous and are marked with g. The odd chromosome (5–6) is homoeologous to chromosomes 1–2 and 3–4, and is marked with G.

Table 1. Hypothetical frequencies for pairing configurations in one arm

Pairing (per Fig. 3)		I	II	III	IV	V
None	O	0.01	0.05	0.01	0.01	0.01
13 or 24	A	0.27	0.30	0.44	0.70	0.10
15, 35, 26, or 46	B	0.27	0.30	0.22	0.10	0.40
135 or 246	C	0.18	0.05	0.11	0.09	0.09

Chiasmata can arise between any two arms. There can be homogenetic associations (A) 13 and 24, and heterogenetic associations (B), 15, 35, 26, and 46. Also, as a result of pairing partner exchanges as shown in Fig. 2, there can be triad associations (C), 135 or 246. Also, there may be a failure of pairing, a situation which is symbolized by O.

Different trisomic heterozygotes will have different values for A, B, C, and O. Let us consider some arbitrary hypothetical values as shown in Table 1. Five possibilities are considered (I through V). Pairing is at random in I and II, thus A = B. However, there is more triad formation in I than in II (C = .18 in I and .05 in II). Also, there is a greater frequency of pairing failure (O) in II than in I. In III and IV there is non-random pairing: A = 2 B in III, and A = 7 B in IV. There is a lower value for C in IV than in III. The relationship of C to A and B is difficult to hypothesize. The value of C is probably the mathematical product of A and B and some other factor (X) which represents the frequency of pairing partner exchange. Because X may not be a constant (it may be dependent on the ratio of A to B), the relationship may not be a simple one.

The V case may seem to be impossible. Here there is a greater pairing affinity of homoeologous chromosomes than that of homologues for each other (A = ¼ B). This runs counter to a basic assumption of cytogenetics; the more two chromosomes are alike, the greater is their pairing affinity. However, if we hypothesize that the strength of pairing initiation sites may vary, it is possible that the odd chromosome could have a greater "pairing power" than the standard chromosomes and consequently it could compete more successfully in pairing with a standard chromosome than another standard chromosomes could.

The expected frequencies of pairing configurations for whole chromosomes can be obtained by multiplying the frequency of pairing configurations in the left arm (A, B, C, and O) with those in the right arm (A′, B′, C′,

Table 2. Pairing configurations for whole chromosomes in trisomes obtained by combining pairing configurations of single arms

Code		0′ 0	A′ 24	B′ 26	B′ 46	C′ 246
0	0	3U	UB-1 A.2	UB-1 B.2	UB-1 B.2	T-2.2
A	13	UB-1 A.1	UB-2 A	T-1 A.2	T-1 A.2	T-3 A.2
B	15	UB-1 B.1	T-1 A.1	UB-2 B	T-1 B	T-3 B.2
B	35	UB-1 B.1	T-1 A.1	T-1 B	UB-2 B	T-3 B.2
C	135	T-2.1	T-3 A.1	T-3 B.1	T-3 B.1	T-4

Table 3. Pairing configurations in hypothetical trisomes

	Formula	1 I/I	2 II/II	3 III/III	4 IV/IV	5 V/V	6 I/II	7 II/I	8 I/IV	9 IV/I	10 I/V	11 V/I
3U	00′	0.0001	0.0025	0.0001	0.0001	0.0001	0.0005	0.0005	0.0001	0.0001	0.0001	0.0001
UB-A	[a]	0.0783	0.1200	0.2024	0.5040	0.0120	0.0975	0.0975	0.1987	0.1987	0.0307	0.0307
UB-B	[b]	0.1566	0.2400	0.1056	0.0240	0.3360	0.1950	0.1950	0.0614	0.0614	0.2294	0.2294
T-1A.1	2A′B	0.1458	0.1800	0.1936	0.1400	0.0800	0.1620	0.1620	0.0540	0.3780	0.2160	0.0540
T-1A.2	2AB′	0.1458	0.1800	0.1936	0.1400	0.0800	0.1620	0.1620	0.3780	0.0540	0.0540	0.2160
T-1B	2BB′	0.1458	0.1800	0.0968	0.0200	0.3200	0.1620	0.1620	0.0540	0.0540	0.2160	0.2160
T-2.1	C0′	0.0018	0.0025	0.0011	0.0009	0.0009	0.0090	0.0005	0.0009	0.0018	0.0009	0.0018
T-2.2	C′0	0.0018	0.0025	0.0011	0.0009	0.0009	0.0005	0.0090	0.0018	0.0009	0.0018	0.0009
T-3A.1	A′C	0.0486	0.0150	0.0484	0.0630	0.0090	0.0540	0.0135	0.0243	0.1260	0.0243	0.0180
T-3A.2	AC′	0.0486	0.0150	0.0484	0.0630	0.0090	0.0135	0.0540	0.1260	0.0243	0.0180	0.0243
T-3B.1	2B′C	0.0972	0.0300	0.0484	0.0180	0.0720	0.1080	0.0270	0.0486	0.0360	0.0486	0.1440
T-3B.2	2BC′	0.0972	0.0300	0.0484	0.0180	0.0720	0.0270	0.1080	0.0360	0.0486	0.1440	0.0486
T-4	CC′	0.0324	0.0025	0.0121	0.0081	0.0081	0.0090	0.0090	0.0162	0.0162	0.0162	0.0162

[a] AA′ + A0′ + A′0; [b] 2BB′ + 2B0′ + 2B′0

and O′). The expected pairing configurations are shown in Table 2 and their frequencies are shown in Table 3. This operation assumes that pairing in one arm is independent of pairing in the other arm. There is good evidence for this independence. As pointed out by Sved (1966), the common ⅔ frequency of quadrivalents in autotetraploids implies random association of chromosome arms.

Also, the work of Sallee and Kimber (1978), in which they predicted the pairing configuration of whole chromosomes from the pairing configuration of telocentrics, supports independent pairing of each arm of a chromosome.

There are 11 different possibilities shown in Table 3. Types 1–5 give the results when both arms have the same pairing affinities. Trisomes types 1 and 2 have random pairing, and there are twice as many heterogenetic bivalents (UB-B) as homogenetic bivalents (UV-A). Also, the relationship between the frequencies of the trivalents is in accordance with random pairing. For example, T-3A = ½T-3B. Trisome types 3 and 4 show the effects of preferential pairing (A > B). The frequencies of heterogenetic and semi-heterogenetic configuration are decreased. In trisome type 5, they are increased.

Types 6–9 show the effects of combining different single arm pairing frequencies. It may be seen that if pairing is random in one arm (I or II) and pairing in the other arm is preferential (III, IV or V), then there are modifications in the frequencies of homogenetic and semi-homogenetic configurations although it is not as great as when both arms are pairing preferentially. For example, in type 4 (IV/IV) the frequency of T-1B is .02, in type 8 (I/IV) it is .054 (the value from random pairing (I/I) is .1458).

Gene Segregation in Trisomic Heterozygotes

If we knew the exact proportions of each type of configuration, we could predict genetic ratios, because each type has an expected gametic output, as shown in Table 4.

There are two basic types of gametes: n+1 and n. One of the n+1 gametes, GG, has genes which were on sister chromatids and is derived from double reduction. For such a gamete to be produced, a trivalent must be formed, crossing over must occur in a fashion to produce two Gg chromosomes (an equational constitution), and the Gg chromosomes go to the same pole at the first division of meiosis (genetic non-disjunction), and the chromosomes will orient themselves one-half of the time so as to direct two G chromatids to the same pole. The sister spore, gg, is also a double reductional gamete but it cannot be distinguished from non-double reductional gg gametes from a Ggg heterozygote. Double reduction was explained first by Mather (1935, 1936).

The disjunction patterns of the various types of configurations are as follows:

When a bivalent and a univalent are formed, the chromosomes forming the bivalent regularly disjoin and go to opposite poles. The univalent chromosome may got to either pole, divide at the first division, or be lost.

The disjunction patterns of the trivalents are more complicated. The disjunction of the chromosomes of a chain trivalent (T-1) may be adjacent or alternate as shown in Fig. 4. In some genera such as *Oenothera, Triticum,* or *Datura,* disjunction is directed and it is almost all alternate. In maize, using the behavior of the chromosomes in translocation/normal heterozygotes as a model (Burnham 1950), the disjunction would be ½ alternate and ½ adjacent.

Table 4. Gametic output expected from the various pairing configurations shown in Figure 1.

Configurations	Type of Disjunction	Gametes expected				
		GG	Gg	gg	G	g
3U	random +U	0	1/3	1/6	1/6	1/3
	random −U or −2U	0	0	0	1/3	2/3
UB-1 A.1, UB-1 A.2, or UB-2 A	directed +U	0	1/2	0	0	1/2
	directed −U	0	0	0	0	1
UB-1 B.1, UB-1 B.2, or UB-2 B	directed +U	0	1/4	1/4	1/4	1/4
	directed −U	0	0	0	1/2	1/2
T-1 A.1, T-1 A.2r, or T-1 Br′	random	0	1/3	1/6	1/6	1/3
	1/2 alternate	0	3/8	1/8	1/8	3/8
	all alternate	0	1/2	0	0	1/2
T-1 A.2e or T-1 Be	random	1/24	1/4	5/24	1/6	1/3
	1/2 alternate	1/32	1/4	7/32	3/16	5/16
	all alternate	0	1/4	1/4	1/4	1/4
T-1 Br or T-1 Ar′	random	0	1/3	1/6	1/6	1/3
	1/2 alternate	0	1/4	1/4	1/4	1/4
	all alternate	0	0	1/2	1/2	0
T-2.1, T-2.2r, or T-4r	random	0	1/3	1/6	1/6	1/3
T-2.2e or T-4e	random	1/24	1/4	5/24	1/6	1/3
T-3 A.1, T-3 A.2r, or T-3 B.2r′x	directed	0	1/2	0	0	1/2
T-3 A.2e, T-3 B.2ex or T-3 B.2re	directed	1/16	1/4	3/16	1/8	3/8
T-3 B.1, T-3 B.2r, T-3 A.2r′, T-3 B.2r′y, T-3 A.2re, or T-3 B.2ey	directed	0	1/4	1/4	1/4	1/4
T-3 B.2ex + T-3 B.2ey/2	directed	1/32	1/4	7/32	3/16	5/16[a]

[a] If it is assumed that the T-3 B.2ex and T-3 B.2ey type occur with equal frequency the gametic output of T-3 B.2e is shown

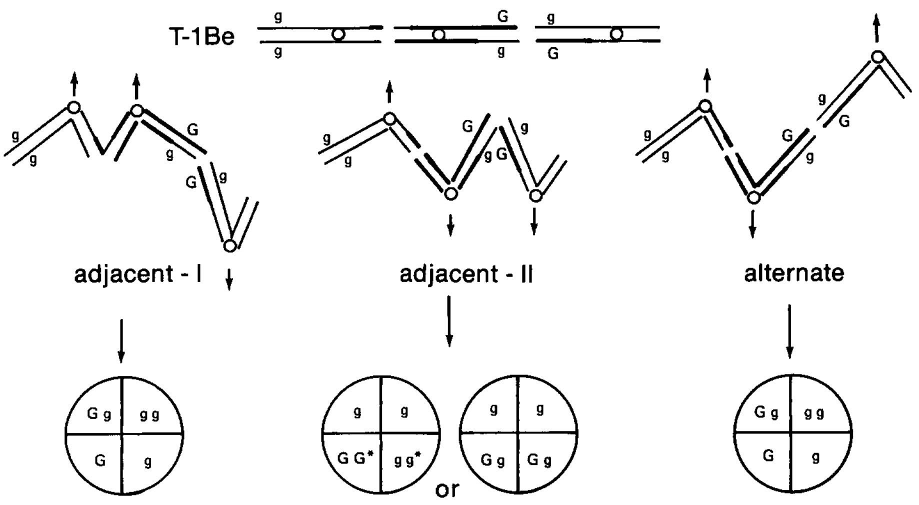

Fig. 4. The gametic output of a T-1 Be trivalent which depends on the relative frequencies of the disjunctional patterns (adjacent-1, adjacent-2, and alternate). The gametes marked with an asterisk are double reductional gametes

Table 5. Example of the derivation of expected gamete ratios using T-1 Be (see Figs. 1 and 4) with the assumption that alternate disjunction occurs at a 50% frequency

Disjunction	Frequency		GG	Gg	gg	G	g
adj.-I	1/4	x	(0	1/4	1/4	1/4	1/4)=
adj.-II	1/4	x	(1/8	1/4	1/8	0	1/2)=
alt.	1/2	x	(0	1/4	1/4	1/4	1/4)=
adj.-I				1/16	1/16	1/16	1/16
adj.-II			1/32	1/16	1/32	0	1/8
alt.				1/8	1/8	1/8	1/8
Expected ratio			1/32	1/4	7/32	3/16	5/16

Because all the chromosomes in the triradial (T-2) and "bird cage" (T-4) trivalents are spatially equivalent, the disjunction of the chromosomes must be at random.

In "frying pan" trivalents (T-3), the chromosomes forming the "pan" are co-oriented like those of a bivalent and are directed to opposite poles leaving the "handle" chromosomes to go to either pole at random.

It may be seen that whether the chromosomes have equational or reductional constitutions greatly affects the proportion of gametes expected.

To show how these ratios are derived, an example is given in Table 5.

A complication that is neglected is the rare occurrence of "false univalent" formation, which results from one of the chromosomes of a trivalent being left on the metaphase plate. For example, a chain trivalent (T-1) may orient linearly perpendicular to the plate and the center chromosome may not orient to either pole and may be left as a "false univalent."

Using the pairing configuration frequencies shown in Table 3, and the expected gametic output for each configuration shown in Table 4, we can compute the genetic ratios for the hypothetical trisomic heterozygotes (1–11) given in Table 3. The results are given in Table 6.

Two possible results are given: one in which all the configurations were reductional, and the other in which they were all equational. Except where the gene locus is completely linked with the centromere–and thus always reductional–gene segregation patterns would be a mixture of "r" and "e".

To simplify the model, some of the sub-types resulting from crossing over were not considered. These are T-1 A.2 r′, T-1 Br′, T-2.2 r′, T-3 A.2 re, T-3 A.2 r′, T-3 B.2 re, T-3 B.2 r′x, and T-3 B.2 r′y. These sub-types

Table 6. The expected gametic output of hypothetical trisomic heterozygotes

Constituion		Gametes						
		n+1			n		n only	
		GG	Gg	gg	G	g	G	g
1 I/I	r[a]	0.0000	0.2942	0.1471	0.1862	0.3725	0.3333	0.6667
	e[b]	0.0166	0.2610	0.1637	0.1862	0.3725	0.3333	0.6667
2 II/II	r	0.0000	0.2729	0.1365	0.1969	0.3937	0.3334	0.6666
	e	0.0133	0.2462	0.1498	0.1969	0.3937	0.3334	0.6666
3 III/III	r	0.0000	0.3106	0.1124	0.1388	0.4382	0.2406	0.7594
	e	0.0141	0.2732	0.1356	0.1479	0.4291	0.2563	0.7437
4 IV/IV	r	0.0000	0.3143	0.0537	0.0597	0.5723	0.0944	0.9056
	e	0.0099	0.2803	0.0778	0.0739	0.5581	0.1170	0.8830
5 V/V	r	0.0000	0.2333	0.1797	0.2637	0.3234	0.4492	0.5508
	e	0.0157	0.2203	0.1770	0.2453	0.3417	0.4179	0.5821
6 I/II	r	0.0000	0.2845	0.1422	0.1911	0.3822	0.3333	0.6667
	e	0.0122	0.2601	0.1544	0.1911	0.3822	0.3333	0.6667
7 II/I	r	0.0000	0.2845	0.1423	0.1911	0.3822	0.3333	0.6667
	e	0.0176	0.2493	0.1599	0.1911	0.3822	0.3333	0.6667
8 I/IV	r	0.0000	0.3355	0.0995	0.1148	0.4502	0.2032	0.7968
	e	0.0233	0.2552	0.1565	0.1486	0.4164	0.2630	0.7370
9 IV/I	r	0.0000	0.3355	0.0995	0.1148	0.4502	0.2032	0.7968
	e	0.0071	0.3212	0.1066	0.1148	0.4502	0.2032	0.7968
10 I/V	r	0.0000	0.2672	0.1677	0.2251	0.3399	0.3984	0.6016
	e	0.0148	0.2545	0.1657	0.2082	0.3568	0.3685	0.6315
11 V/I	r	0.0000	0.2672	0.1677	0.2251	0.3399	0.3984	0.6016
	e	0.0173	0.2327	0.1850	0.2251	0.3399	0.3984	0.6016

[a] r = reductional; [b] e = equational

arise from three or more chiasmata in a group of three arms. The r′ types arise from 4-strand double exchanges and thus are rare. Also, the neglect of these types is mitigated because there is some compensation. For example, if the frequencies of T-1 A.2 and T-1 B.2 are equal, then as many T-1 A.2 r′ will be formed as T-1 B.2 r′, which are equivalent to T-1 Br and T-1 Ar, respectively.

If it is not clear how these genetic ratios were derived, an example of the computations is given in Table 7.

If the trisomes are used as the male parent, only the relative frequencies of the n gametes, G and g need to be considered, because n + 1 pollen rarely functions in fertilization. Thus, on the right side of Table 6 the expected n ratios are given.

In trisomes 1, 2, 6, and 7 there is random pairing and there is a ratio of 1 G : 2 g. Whether the mode is equational or reductional makes no difference if we only consider n gametic ratios.

In the other trisomes there is non-random pairing and the effect of different frequencies of pairing configurations is apparent. There is an effect of the e and r modes, except in trisomes 7, 9, and 11 where the gene locus followed is in the arm which is pairing at random.

The effect of crossing over is to cause the genetic ratios to move toward the random 33% value.

The Relationship of this Model to Observed Data

Part 1 of this series gave extensive data on gene segregation in many types of trisomic heterozygotes. A portion of these results are reproduced in Table 8.

The gene followed in these experiments was *A*, which is one of a series of complementary alleles controlling the production of anthocyanin in the aleurone. This gene is located near the end of the long arm of chromosome 3.

The trisomic heterozygotes were produced by crossing *a*/*a*/*a* trisomes with all standard chromosomes with various *A*/*A* pollen parents.

The control trisomes with all standard chromosomes gave ratios very close to 1 *A* : 2*a* with deviations attributable to random sampling. If the inbred lines, N6 or W23, were the *A* chromosome donors, there is also random pairing, indicating that their chromosomes 3 are equivalent to the standard chromosome 3. However, when the inbreds Kys, 38-11, Hy, or B41 contributed the *A* chromosome, there is evidence for non-random pairing as in the hypothetical trisomes 3 or 4. Also the presence of an inversion produces non-random pairing.

The data from the Tr trisomes and some of the three radiation derived trisomes ("C", Kys, and In 3 aKys) indicate that the "V" case in Table 1 and the correspond-

Table 7. An example of how genetic ratios in Table 6 were computed using trisome type 1(I/I)

	Frequency	GG		Gg		gg		G		g	
3 U	0.00010	0.00000		0.16677	0.00002	0.08333	0.00001	0.25000	0.00002	0.50000	0.00005
UB-A	0.07830	0.00000		0.25000	0.01958	0.00000		0.00000		0.75000	0.05872
UB-B	0.15660	0.00000		0.12500	0.01958	0.12500	0.01958	0.37500	0.05872	0.37500	0.05872
T-1 A.1	0.14580	0.00000		0.37500	0.05468	0.12500	0.01822	0.12500	0.01822	0.37500	0.05468
T-2.1	0.00180	0.00000		0.33333	0.00060	0.16667	0.00030	0.16667	0.00030	0.33333	0.00060
T-3 A.1	0.04860	0.00000		0.50000	0.02430	0.00000		0.00000		0.50000	0.02430
T-3 B.1	0.09720	0.00000		0.25000	0.02430	0.25000	0.02430	0.25000	0.02430	0.25000	0.02430
					0.14305		0.06241		0.10156		0.22137
r T-1 A.2	0.14580	0.00000		0.37500	0.05468	0.12500	0.01822	0.12500	0.01872	0.37500	0.05468
T-1 B	0.14580	0.00000		0.25000	0.03645	0.25000	0.03645	0.25000	0.03645	0.25000	0.03645
T-2.2	0.00180	0.00000		0.33333	0.00060	0.16667	0.00030	0.16667	0.00030	0.33333	0.00060
T-3 A.2	0.04860	0.00000		0.50000	0.02430	0.00000		0.00000		0.50000	0.02430
T-3 B.2	0.09720	0.00000		0.25000	0.02430	0.25000	0.02430	0.25000	0.02330	0.25000	0.02430
T-4	0.03240	0.00000		0.33333	0.01080	0.16667	0.00540	0.16667	0.00540	0.33333	0.01080
					0.15113		0.08467		0.08467		0.15113
e T-1 A.2	0.14580	0.03125	0.00456	0.25000	0.03645	0.21875	0.03189	0.18750	0.02734	0.31250	0.04556
T-1 B	0.14580	0.03125	0.00456	0.25000	0.03645	0.21875	0.03189	0.18750	0.02734	0.31250	0.04556
T-2.2	0.00180	0.04167	0.00008	0.25000	0.00045	0.20833	0.00037	0.16667	0.00030	0.33333	0.00060
T-3 A.2	0.04860	0.06250	0.00304	0.25000	0.01215	0.18750	0.00911	0.12500	0.00608	0.37500	0.01822
T-3 B.2	0.09720	0.03125	0.00304	0.25000	0.02430	0.21875	0.02126	0.18750	0.01822	0.31250	0.03038
T-4	0.03240	0.04167	0.00135	0.25000	0.00810	0.20833	0.00675	0.16667	0.00540	0.33333	0.01080
			0.01663		0.11790		0.10127		0.08468		0.15112

Table 8. The genetic ratios observed from *Aaa* trisome 3 maize plants used as the pollen parent

Source of A chromosome	No. of plants tested	No. of gametes tested	%A	Number of plants with *A* transmission rates														Number of plants deviating significantly from expected					Inter. X^2	P
				<6	9	12	15	18	21	24	27	30	33	36	39	42	45[a]	–			+			
																		0.01	0.05	N	0.05	0.1[b]		
C (control)	30	25,117	33.80	–	–	–	–	–	–	–	–	4	16	10	–	–	–	–	–	29	1	–	35.23	0.0–0.10
N 6	22	20,731	33.59	–	–	–	–	–	–	–	–	4	11	6	1	–	–	–	–	19	–	3	70.75	<0.0005
W 23	10	12,212	33.93	–	–	–	–	–	–	–	–	–	7	3	–	–	–	–	–	9	–	1	14.17	0.20–0.10
Kys	37	38,394	29.56	–	–	–	–	–	–	1	10	21	2	3	–	–	–	14	9	14	–	–	67.85	<0.05–0.025
38-11	40	39,866	25.06	–	–	–	–	1	4	6	10	15	2	2	–	–	–	37	1	2	–	–	285.44	<0.0005
Hy	43	43,037	24.07	–	–	–	1	8	9	5	8	9	3	–	–	–	–	36	–	7	–	–	557.26	<0.001
B 41	27	26,133	25.14	–	–	–	2	–	3	9	9	3	1	–	–	–	–	25	–	2	–	–	210.76	<0.0005
Tr	3	2,553	39.71	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–	3	1.72	0.50–0.40
In3a(Kys)	12	7,791	15.17	–	1	1	5	4	1	–	–	–	–	–	–	–	–	1	1	8	–	2	48.98	<0.0005
C (1000r)	32	26,373	32.44	2	–	–	–	2	–	–	2	5	8	7	5	1	–	5	1	19	4	3	141.62	<0.0005
Kys (1000r)	38	34,183	28.30	1	1	–	–	–	–	5	9	10	9	3	–	–	–	5	3	26	2	2	557.91	<0.0005
In3a (Kys) 1000r	59	76,358	16.00	3	3	10	14	15	9	5	–	–	–	–	–	–	–	14	–	17	3	25	1394.56	<0.0005

[a] The numbers in this row indicate the midpoints of classes of percent *A* transmission (33 = 31.51% – 34.50%)

[b] The numbers below 0.01(–), 0.05(–), 0.05(+) and 0.01(+) indicate the cases of significant deviations at the 0.01 and 0.05 levels from the expected transmission rates. The deviations may be (–) or (+); N indicates normal expected rates

ing trisomic types (5, 10, or 11) in Table 6 may have occurred in these experiments.

In the radiation derived trisomes there are 24 minus and 30 plus deviations from the transmission rates of the untreated controls at the .01 level of singificance out of a total of 127 cases.

An hypothesis to explain the enhancement of pairing affinity may be suggested. It assumes that the pairing initiation sites on chromosomes are composed of many tandemly repeated identical units whose numbers may fluctuate as a result of unequal exchanges between sister chromatids that may be induced by x-irradiation or by oblique pairing and crossing over.

One of the disturbing features of the data is the wide range in the transmission rates of certain types of trisomic heterozygotes; note the interaction chi squares in Table 8. This variability seems to increase as the mean deviates from 33%. Thus the interaction X^2 for the W 23 trisomes is 14.17 (p = .20–.10) and that of the B 41 trisomes is 210.76 (p = < .0005). In Table 6 it may be seen that there is a great difference in the n gametic ratios from the reductional and equational modes in the cases of trisome 3, 4, and 5 where there is non-random pairing. There is no effect of e and r in trisomes where pairing is at random. Because the value of e is dependent on crossing over which is known to be affected by the environment, we have an explanation for part of the variability in the B41, Hy, Kys, and 38-11 trisomic data. We can conclude that the long arms of these chromosomes 3 (which carry the *A* locus) must have DPA factors.

Some cytological data have been collected. The configurations were determined at diakinesis, which does not give reliable data for the types of trivalents because of the poor terminalization of chiasmata at this stage in maize. Although chain trivalents are easily recognizable, the other three types may be confused. The trivalent frequencies were as follows: 68.9% (591 cells) for control trisomes, 67.0% (291 cells) for Kys trisomes, and 52.6% (226 cells) for In 3 a Kys trisomes. Because of the great difference in the gametic output of different trivalent types, gross trivalent frequencies are not usable for predicting genetic data.

Discussion and Conclusions

Recently (Kimber and Hulse 1978; Driscoll et al. 1979; Driscoll 1979; Driscoll et al. 1980; Kimber et al. 1981; Alonso and Kimber 1980; Kimber and Alonso 1981) mathematical models have been developed which allow the comparison of observed chromosome pairing (univalents, rod bivalents, ring bivalents, and multivalents) with expectations based on calculations of the relative affinity or similarity of chromosomes.

These models assume that only two arms can be united by chiasmata. This is essentially valid in wheat and its relatives and many other species of plants; *Hordeum, Avena, Collinsia,* and *Gossypium* (Kimber and Alonso 1981). However, maize has frequent exchanges of pairing partners and the types of trivalents and quadrivalents are more complex; therefore it cannot be readily adapted to the aforementioned models.

The use of genetic data to study DPA is advantageous because it is affected by the relative frequencies of homogenetic and heterogenetic bivalents and the two types of chain trivalents T-1A and T-1B (which are found in the above models) which cannot be distinguished cytologically unless heteromorphic chromosomes are used.

Ideally, DPA should be studied by cytological and genetic methods which are then correlated. Pairing configurations must be analyzed at metaphase rather than at diakinesis. Also, at this stage the disjunction patterns of the chromosomes may be determined. The usefulness of genetic data would be enhanced by following genes closely linked with the centromere. Variability due to different values of "e" could be eliminated.

This model needs refinement. The arbitrary values used to demonstrate the model need to be more closely aligned with real ones. Nonetheless, it shows the major features of gene segregation in trisomic heterozygotes.

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Received April 2, 1981
Communicated by Å. Gustafsson

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