Theor. Appl. Genet. 54, 161-168 (1979)

The Allotetraploidization of Maize

Part 2: The Theoretical Basis – The Cytogenetics of Segmental Allotetraploids*

G.G. Doyle

U.S. Department of Agriculture, Science and Education Administration and Agronomy Department, University of Missouri, Columbia, Missouri (USA)

Summary. Allotetraploidization is the creation of artifical allotetraploids from a normally diploid species. The possible value of allotetraploid maize has been discussed in Section I of this series. Allotetraploidization of maize can be achieved by restructuring a maize genome so that its chromosomes will not pair with those of the standard maize genome. This restructuring can be done by concentrating differential pairing affinity (DPA) factors into a single line by a recurrent selection type of breeding program. Because the divergence of the maize genome is a gradual process, it is necessary to devise a model for chromosome pairing and gene segregation in segmental allotetraploids. This has been done by considering pairing in each arm separately and then combining paired arms to form pairing configurations for whole chromosomes. The chromosome disjunction patterns are hypothesized and genetic ratios in relation to different levels of DPA are suggested.

Key words: Preferential pairing – Quadrivalents – Non-disjunction

Introduction

Allotetraploidization is the creation of artificial allotetraploids. Allotetraploidization of maize can be achieved by restructuring the maize genome so that its chromosomes will no longer pair with those of the parental form. The restructuring can be done by concentrating induced or naturally occurring visible or cryptic chromosome aberrations and qualitatively different genetic material into a single line by a recurrent selection type of breeding program. Allopolyploidizing genes like the *Ph* gene in wheat will be used if they can be found or induced in maize.

The physical basis of allotetraploidization is the presence of differential pairing affinity (DPA) between normal and restructured chromosomes. It was found that DPA factors occur naturally among different lines of maize and that DPA factors can be easily induced by X-irradiation and chemical mutagens. These results were reported in Section I of this series (Doyle 1979). DPA was detected by its effects on gene segregation. The interpretation of these data is difficult because there is no adequate model for chromosome pairing in segmental allopolyploids. Those presented by Collins and Longley (1935) and Buzzell (1965) are inadequate because they assume that the chromosomes of multivalents disjoin at random and consider only the relative frequencies of homogenetic and heterogenetic bivalents. These terms will be discussed later.

The term segmental allopolyploid was coined by Stebbins (1947). It implies that some chromosome segments are homologous in all genomes and would pair at random and that other segments are different and would pair exclusively or preferentially with their homologous counterparts. However, even in true allotetraploids with complete homogenetic bivalent pairing there are homologous segments common to all genomes so the term is ambiguous.

A cytogenetic study of segmental allopolyploids is complicated by all the factors found in autopolyploids plus a few new ones. Genetic ratios in autopolyploids and segmental allopolyploids are determined by the kind of heterozygosity, the frequency of double reduction (the formation of gametes with a given gene which was on sister chromatids), the frequency of numerical non-disjunction (3-1 chromosome disjunctions in tetraploids), the loss of univalent chromosomes and the relative frequencies of transmission of euploid and aneuploid gametes formed by the latter events.

Autopolyploid gene segregation has been discussed by

* Contribution from the Science and Education Administration, U.S. Department of Agriculture, and the Agronomy Department, University of Missouri, Columbia, Missouri, Agricultural Experiment Station Journal Series No. 8090

0040-5752/79/0054/0161/$ 1.60

many writers: Muller 1914; Haldane 1930; Mather 1935, 1936; Fisher and Mather 1943; Catcheside 1956, 1959; Doyle 1973. Space does not permit a detailed review.

In diploids, there is only one kind of heterozygote. In tetraploids there are four kinds. They are quadri-allelic ($a_1 a_2 a_3 a_4$), tri-allelic ($a_1 a_1 a_2 a_3$), balanced di-allelic ($a_1 a_1 a_2 a_2$), and unbalanced di-allelic ($a_1 a_1 a_1 a_2$). Polyploids can also be heterozygous for chromosome type. If one type of chromosome is called standard (S) and others restructured (R_n) then there can be different types of structural heterozygotes, which are designated in a similar fashion with the replacement of the term 'allelic' by 'type.' Thus, $SSR_1 R_2$ would be a tritype.

The expression of DPA will be different in balanced and unbalanced ditypes, tritypes and tetratypes. A model using arbitrary values will be helpful. Let us assume that there are four types of pairing units, A, B, C and D. The pairing affinity of the pairing units for each other is assumed to be AB = 8, AC = 6, AD = 4, BC = 5, and BD = 3 and CD = 2. AA, BB, CC and DD all equal 10. In a tetraploid there are four chromosomes which will be called W, X, Y and Z. At any point along these chromosomes there are three possible kinds of pairing combinations: WX and YZ, WY and XZ, or WZ and XY. Chromosome pairing in a polyploid is a competitive process and the relative frequencies of the above three modes of pairing combinations will vary with the pairing affinity of their pairing units. We can make various combinations of the pairing units as shown in Table 1 and predict the probability of a pairing mode if we assume that it can be determined by dividing its pairing affinity by the total of that of all three modes.

The hypothetical results indicate that preferential pairing is not possible in an unbalanced ditype (AAAB). The greatest expression of DPA is possible in a balanced ditype (AABB). However, some tritypes may have greater preferential pairing than some balanced ditypes; it depends on the DPA of their pairing elements. Also tetratypes may have preferential pairing.

A segmental allotetraploid produced by doubling the chromosome number of a hybrid between pure diploid lines will be a balanced ditype. If it is carried to later generations unbalanced ditypes, tritypes and tetratypes from crossing over will be produced.

One difficulty with this model is that it will not simulate complete autosyndesis unless the pairing affinity of one pair of units is zero. In nature there is probably a pairing affinity level which becomes critical if it becomes too low. Also the effect of different pairing elements may not be additive but might be very synergistic.

In segmental allotetraploids because the chromosomes do not pair at random the relative frequencies of different types of pairing configurations and the positions of chromosomes within these configurations will not be at random. Because of the non-random disjunctional patterns of some of these configurations, the gene segregation is profoundly affected.

All possible pairing configurations found in balanced

Table 1. Hypothetical frequencies of segmental pairing configurations in different types of heterozygotes

Type	Pairing modes				
WXYZ	WX – YZ	WY – XZ	WZ – XY	Total	% WX – YZ
AAAA	AA + AA = 20	AA + AA = 20	AA + AA = 20	60	33.33
AAAB	AA + AB = 18	AA + AB = 18	AA + AB = 18	54	33.33
AABB	AA + BB = 20	AB + AB = 16	AB + AB = 16	52	38.46
AACC	AA + CC = 20	AC + AC = 12	AC + AC = 12	44	45.45
AADD	AA + DD = 20	AD + AD = 8	AD + AD = 8	36	55.55
BBCC					
BBDD	BB + DD = 20	BD + BD = 6	BD + BD = 6	32	62.50
CCDD	CC + DD = 20	CD + CD = 4	CD + CD = 4	28	71.43
AABC	AA + BC = 15	AB + AC = 14	AC + AB = 14	43	34.88
AABD	AA + BD = 13	AB + AD = 12	AD + AB = 12	37	35.14
AACD	AA + CD = 12	AC + AD = 10	AD + AC = 10	32	37.50
BBAC	BB + AC = 16	AB + BC = 13	BC + AB = 13	42	38.10
BBAD	BB + AD = 14	AB + BD = 11	BD + AB = 11	36	38.89
BBCD	BB + CD = 12	BC + BD = 8	BC + BD = 8	28	42.86
CCAB	CC + AB = 18	AC + BC = 11	BC + AC = 11	40	45.00
CCAD	CC + AD = 14	AC + CD = 8	CD + AC = 8	30	46.67
CCBD	CC + BD = 13	BC + CD = 7	CD + BC = 7	27	48.15
DDAB	DD + AB = 18	AD + BD = 7	BD + AD = 7	32	56.25
DDAC	DD + AC = 16	AD + CD = 6	CD + AD = 6	28	57.14
DDBC	DD + BC = 15	BD + CD = 5	CD + BD = 5	25	60.00
ABCD	AB + CD = 10	AC + BD = 9	AD + BC = 9	28	35.71

AA, BB, CC, DD = 10; AB = 8; AC = 6; AD = 4; BC = 5; BD = 3; and CD = 2

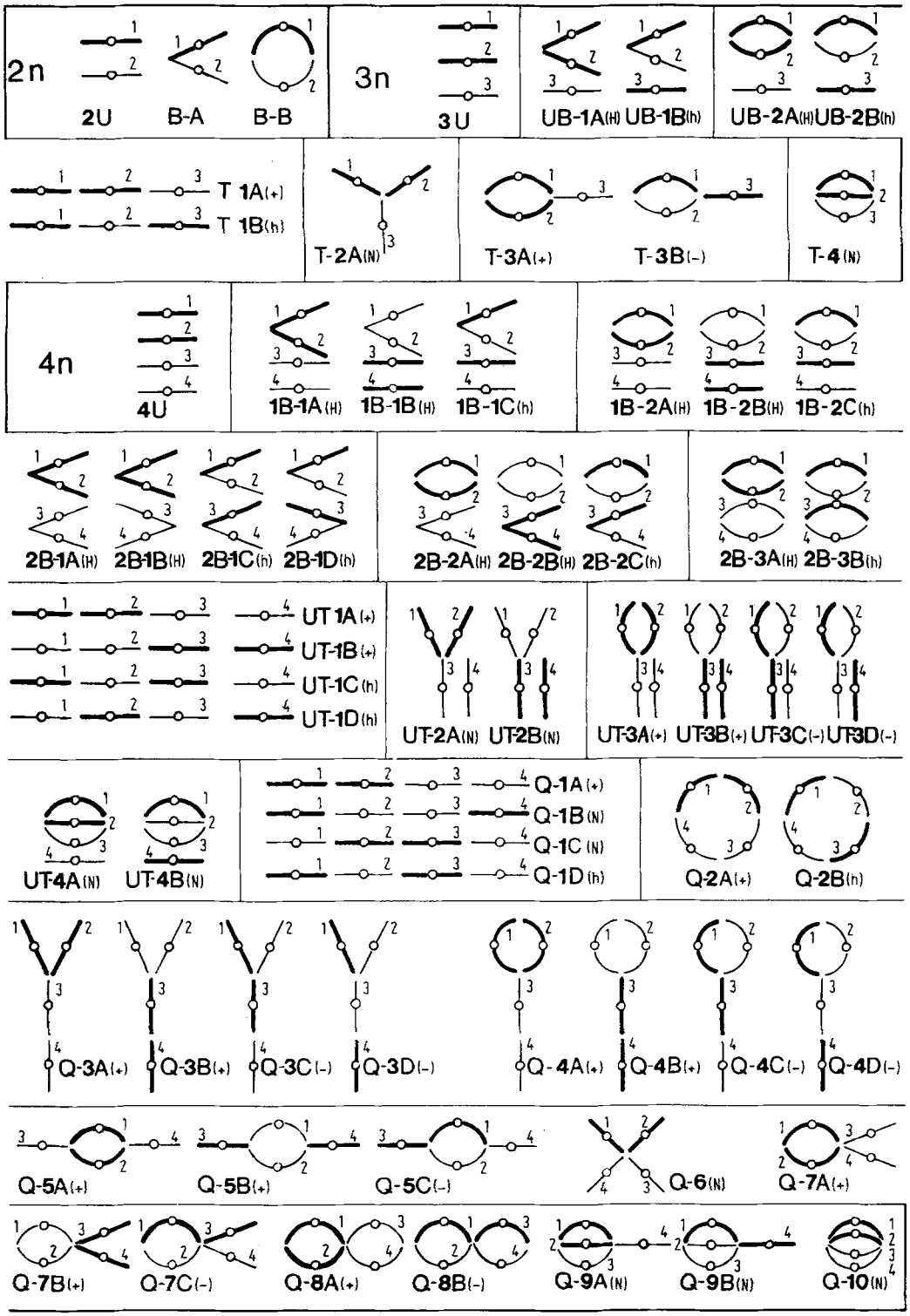

Fig. 1. All possible pairing configuration for structurally heterozygous diploids, triploids, and tetraploids. The symbols in parenthes indicate the type of pairing (H) = homogenetic, (h) = heterogenetic, (+) = semi-homogenetic, (−) = semi-heterogenetic and (N) = neutral

ditype tetraploids are given in Fig. 1, in accordance with the 10 general types of quadrivalents (Q) presented by Darlington (1931). If pentaploids and hexaploids were to be considered, there would be 23 quinquevalents and 66 sexavalents. (Pentasomics (4n + 1) and hexasomics (4n + 2) are found in autotetraploid populations.) These different configurations are the result of different pairing patterns and chiasma placement.

The general pairing types have been divided into subtypes indicated by letters to show the different arrangements possible within the configuration. Chromosomes have been given positional numbers which will be used in later discussions of chromosome disjunction. It may appear that there are additional subtypes possible; for example, if chromosomes 3 and 4 were reversed in Q-8B, a different appearing configuration would result. If we assume that the chromosomes rotate freely where they are attached at one end, this 'new' configuration is the same as Q-8B. Other rotations are possible with the other multivalents and are not given. Certain multivalent types such as T-4, UT-4, Q-9 and Q-10 cannot be shown adequately in two dimensions. For example, Q-10 resembles a bird cage; the 'inner' chromosomes are not positionally different from the 'outer' chromosomes.

Most of these configurations exist in two forms if we consider which arm is involved. If we mark one pair of chromosomes with *A* in one arm and *B* in the other arm and their homoeologues with *a* and *b*, there will be two subtypes of Q-1A: *A-B B-A a-b b-a* and *B-A A-B b-a a-b*. These would be called Q-1A1 and Q-1A2.

It may be noted that the configurations differ in the number of associations between homologous and homoeologous arms. Q-1A has two homologous associations and one homoeologous association. Q-1D has no homologous associations and three homoeologous ones. If pairing were at random, we would expect an average frequency of 1/3 homologous associations. The multivalents are termed semi-homogenetic (+), semi-heterogenetic (−) or neutral (N) depending on whether the number of homologous associations is more, less, or equal to 1/3, respectively. Some multivalents have no homologous associations and are termed heterogenetic (h), only bivalents can be homogenetic (H). Where three or four arms are paired it is assumed that 1/3 of the associations are homologous and that there are three associations in a triad and six in a quartet. Configurations differ in the amount of recombination possible between homologous and homoeologous chromosomes.

How do these configurations arise? A chromosome has two arms which may be called left and right arms. Consider the chromosomes diagrammed in Fig. 2, in which each arm is numbered. The types of chromosome pairing for an arm are given on the sides and tops of Table 2. There are several types of pairing in tetraploids such as a single pair of arms (13), two pairs of arms (13-57), a triad (135) or a quartet (1357). If there is no pairing it is symbolized by 0. Pairing triads or quartets are the result of pairing partner exchange. For the sake of brevity, these arm configurations have been coded. For example, one

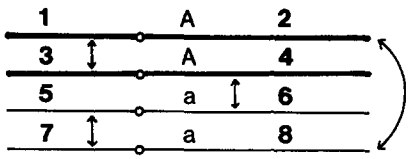

Fig. 2. Model for explaining pairing configurations. Chiasmata can arise between any two homologous arms. The pattern of chiasmata formation shown (13, 57, 28 and 46) would give rise to a Q -2A quadrivalent (Fig. 1)

Table 2. Pairing configurations in tetraploids

			A	B	B	B	B	C	D	E	E	F	F	F	F	G
		0	24	26	28	46	48	68	24-68	26-48	28-46	246	248	268	468	2468
0	0	4U														
A	13	1B-1A	1B-2A													
B	15	1B-1C	UT-1A	1B-2C												
B	17	1B-1C	UT-1A	UT-1D	1B-2C											
B	35	1B-1C	UT-1A	UT-1C	2B-1D	1B-2C										
B	37	1B-1C	UT-1A	2B-1D	UT-1C	UT-1D	1B-2C									
C	57	1B-1B	2B-1B	UT-1B	UT-1B	UT-1B	UT-1B	1B-2B								
D	13-57	2B-1A	2B-2A	Q-1A	Q-1A	Q-1A	Q-1A	2B-2B	2B-3A							
E	15-37	2B-1B	Q-1C	2B-2C	Q-1D	Q-1D	2B-2C	Q-1B	Q-2A	2B-3B						
E	17-35	2B-1B	Q-1C	Q-1D	2B-2C	2B-2C	Q-1D	Q-1B	Q-2A	Q-2B	2B-3B					
F	135	QT-2	UT-3A	UT-3C	Q-3C	UT-3C	Q-3C	Q-3A	Q-4A	Q-4C	Q-4C	UT-4A				
F	137	UT-2	UT-3A	Q-3C	UT-3C	Q-3C	UT-3C	Q-3A	Q-4A	Q-4C	Q-4C	Q-5A	UT-4A			
F	157	UT-2	Q-3B	UT-3D	UT-3D	Q-3D	Q-3D	UT-3B	Q-4B	Q-4D	Q-4D	Q-5C	Q-5C	UT-4B		
F	357	UT-2	Q-3B	Q-3D	Q-3D	UT-3D	UT-3D	UT-3B	Q-4B	Q-4D	Q-4D	Q-5C	Q-5C	Q-5B	UT-4B	
G	1357	Q-6	Q-7A	Q-7C	Q-7C	Q-7C	Q-7C	Q-7B	Q-8A	Q-8B	Q-8B	Q-9A	Q-9A	Q-9B	Q-9B	Q-10

pair of configurations for each arm is homologous (13-57) and is coded C, the other two pairs (15-37, 17-35) are homoeologous and are coded D. It is assumed that configurations having the same code will have the same frequencies.

In Table 2 the pairing configurations of the left and right arms are combined to obtain the pairing configurations of the whole chromosomes. If the arm pairing types are given arbitrary frequencies as shown in Table 3, the hypothetical frequencies of the different pairing configurations may be determined as is done in Table 4.

Two kinds of autotetraploids are used in this model: $A_1 A_1 A_1 A_1$, where there is a great amount of pairing partner exchange, $A_2 A_2 A_2 A_2$, where there is less pairing partner exchange. Note the lower values of F and G for the A_2 tetraploid. Two kinds of segmental allotetraploids are used, one where A = 2B and D = 2E and one where A = 5B and D = 5E. The relationship of triad and quartet frequencies to the others is difficult to hypothesize. It is assumed that they decrease with increasing DPA. It may be seen that frequencies of some configurations are related as they have common formulae such as UT-4 and Q-5 (2FF) or they have common factors, such as G in the formulae for quadrivalents 6 through 10. The frequencies of types of configurations should be related to each other. Theoretically it should be possible to set up simultaneous equations and predict the frequencies of some configurations from the observed frequencies of others. However, the model assumes that all chromosome arms have the same pairing configurations, which is not true.

The hypothetical results in Table 4 are summarized in Table 5, which gives some observed data cited by Shaver (1962) and Shcherbak (1971). There is a rough correspondence between theoretical and observed data. The values used to produce the array of theoretical frequencies were chosen to match observed values for two bivalents (2B), the ring quadrivalent (Q-2) and the 'bird cage' quadrivalent (Q-10) and a few others. It is not possible to hypothesize values like that shown in Table 3 which would produce a close alignment with observed values because the situation is very complex; each chromosome arm has its own particular values. Nonetheless, the model is useful in that it shows predictable relationships between types of pairing configurations and the effect of DPA on changes in their relative frequencies.

Table 3. Pairing configurations for chromosome arms in hypothetical tetraploids

	$A_1 A_1 A_1 A_1$	$A_2 A_2 A_2 A_2$	$A_1 A_1 A_3 A_3$	$A_1 A_1 A_4 A_4$
0	.005	.010	.005	.005
A	.010	.020	.016	.025
B	.010	.020	.008	.005
C	.010	.020	.016	.025
D	.200	.230	.400	.600
E	.200	.230	.200	.120
F	.015	.010	.005	.002
G	.275	.140	.111	.077

The relative frequencies of the various configurations are important because they determine the types of chromosome disjunction and the frequencies of double reduction and numerical non-disjunction, and therefore genetic ratios and the amount of crossing over expected between homologous and homoeologous chromosomes.

The expected patterns of chromosome disjunction are given in Table 6.

In tetraploids there are five general types of pairing configurations: four univalents, one bivalent and two univalents, two bivalents, a trivalent and a univalent, or a quadrivalent.

Cases of four univalents have not been observed (Table 5). We might expect them in hybrids of two allotetraploids (AABB × CCDD = ABCD). It is assumed that the chromosomes would be randomly assorted, giving a higher frequency of 3-1 separations than 2-2 ones, and that they would be lost at rates derived from the z value.

One bivalent and two univalents are also not observed. The chromosomes of the bivalent (1 and 2) would always disjoin and the univalent chromosomes (3 and 4) would go at random to either pole. An equal frequency of 2-2 and 3-1 disjunction would result. One or both univalents may be lost at rates z or z^2, respectively.

In the two bivalent cases the bivalents always separate and the disjunction is always 2-2.

The trivalent and univalent configuration should have a 1:1 ratio of 3-1 and 2-2 disjunction because the trivalent will separate 2-1 and the univalent will got to either pole. The univalent (4) is lost at a frequency of Z. The false univalent lost in the case of UT-3 is chromosome '3'.

The quadrivalent types are probably all unique in their patterns of chromosome disjunction. Here the general pattern of chromosome disjunction is 2-2, with a low frequency of numerical non-disjunction (expressed as x), giving 3-1 disjunctions and a few cases of false univalent formation (expressed as y), giving 2-1 disjunctions, except for Q-5, Q-8, and Q-9. Q-5 is the 'two handled frying pan.' Chromosomes 3 and 4, which are the 'handles,' cannot co-orient themselves to opposite poles and will go to the same pole about half the time, giving a 3-1 disjunction. Chromosome 1 and 2 always go to opposite poles. Similarly Q-9 is an unbalanced configuration and chromosome 1, 2, and 3 will generally disjoin 2-1 leaving chromosome 4 to go to either pole and giving a 3-1 disjunction one half of the time. Q-8 is equivalent to two bivalents and probably always disjoins 2-2.

The quadrivalents, except for Q-8, probably form false univalents with different frequencies. It is assumed that

Table 4. Excepted frequencies of pairing configurations and gene segregation in hypothetical tetraploids

Configuration	Formula	H/T	Type of configuration	Configuration frequencies A_1 A_1 A_1 A_1	A_2 A_2 A_2 A_2	A_1 A_1 A_3 A_3	A_1 A_1 A_4 A_4	Gene segregation 2-2 gg	3-1 g	2-1 gg	g
40	00	0/0	–	.000025	.000100	.000025	.00025	1/6	1/4	1/12	1/4
1B-1A	2AO	1/1	H	.000100	.000400	.000160	.000250	0	0	0	0
1B-1B	2CO	1/1	H	.000100	.000400	.000160	.000250	0	1/2	0	1/2
1B-1C	8BO	0/1	h	.000400	.001600	.000320	.000200	1/4	1/4	1/8	1/4
1B-2A	AA	2/2	H	.000100	.000400	.000256	.000625	0	0	0	0
1B-2B	CC	2/2	H	.000100	.000400	.000256	.000625	0	1/2	0	1/2
1B-2C	4BB	0/2	h	.000400	.001600	.000256	.000100	1/4	1/4	1/8	1/4
2B-1A	2DO	2/2	H	.002000	.004600	.004000	.006000	0	–	–	–
2B-1B	2AC	2/2	H	.000200	.000800	.000512	.001250	0	–	–	–
2B-1C	4EO	0/2	h	.004000	.009200	.004000	.002400	1/4	–	–	–
2B-1D	4BB	0/2	h	.000400	.001600	.000256	.000100	1/4	–	–	–
2B-2A	2AD	3/3	H	.004000	.009200	.012800	.030000	0	–	–	–
2B-2B	2CD	3/3	H	.004000	.009200	.012800	.030000	0	–	–	–
2B-2C	8BE	0/3	h	.016000	.036800	.012800	.004800	1/4	–	–	–
2B-3A	DD	4/4	H	.040000	.052900	.160000	.360000	0	–	–	–
2B-3B	2EE	0/4	h	.080000	.105800	.080000	.028800	1/4	–	–	–
UT-1A	8AB	1/2	+	.000800	.003200	.001024	.001000	1/8	1/8	0	1/8
UT-1B	8BC	1/2	+	.000800	.003200	.001024	.001000	1/8	3/8	1/8	3/8
UT-1C	4BB	0/2	h	.000400	.001600	.000256	.000100	1/4	1/4	0	1/4
UT-1D	4BB	0/2	h	.000400	.001600	.000256	.000100	1/4	1/4	1/4	1/4
UT-2A	4FO	1/3	N	.000300	.000400	.000100	.000040	1/6	1/6	0	1/6
UT-2B	4FO	1/3	N	.000300	.000400	.000100	.000040	1/6	1/3	1/6	1/3
UT-3A	4AF	2/4	+	.000600	.000800	.000320	.000200	0	0	0	0
UT-3B	4CF	2/4	+	.000600	.000800	.000320	.000200	0	1/2	0	1/2
UT-3C	8BF	1/4	–	.001200	.001600	.000320	.000080	1/4	1/4	0	1/4
UT-3D	8BF	1/4	–	.001200	.001600	.000320	.000080	1/4	1/4	1/4	1/4
UT-4A	2FF	2/6	N	.000450	.000200	.000050	.000008	1/6	1/6	0	1/6
UT-4B	2FF	2/6	N	.000450	.000200	.000050	.000008	1/6	1/3	1/6	1/3
Q-1A	8BD	2/3	+	.016000	.036800	.025600	.024000	1/8	1/4	1/12	1/4
Q-1B	4CE	1/3	N	.008000	.018400	.012800	.012000	1/8	1/4	1/12	1/4
Q-1C	4AE	1/3	N	.008000	.018400	.012800	.012000	1/8	1/4	1/12	1/4
Q-1D	8BE	0/3	h	.016000	.036800	.012800	.004800	1/4	1/4	1/12	1/4
Q-2A	4DE	2/4	+	.160000	.211600	.320000	.288000	1/8	1/4	1/12	1/4
Q-2B	2EE	0/4	h	.080000	.105800	.080000	.028800	1/4	1/4	1/12	1/4
Q-3A	4CF	2/4	+	.000600	.000800	.000320	.000200	1/6	1/4	1/12	1/4
Q-3B	4AF	2/4	+	.000600	.000800	.000320	.000200	1/6	1/4	1/12	1/4
Q-3C	8BF	1/4	–	.001200	.001600	.000320	.000080	1/6	1/4	1/12	1/4
Q-3D	8BF	1/4	–	.001200	.001600	.000320	.000080	1/6	1/4	1/12	1/4
Q-4A	4DF	3/5	+	.012000	.009200	.008000	.004800	0	0	0	0
Q-4B	4DF	3/5	+	.012000	.009200	.008000	.004800	0	1/2	0	1/2
Q-4C	8EF	1/5	–	.024000	.018400	.008000	.001920	1/4	1/4	1/8	1/4
Q-4D	8EF	1/5	–	.024000	.018400	.008000	.001920	1/4	1/4	1/8	1/4
Q-5A	2FF	2/6	N	.000450	.000200	.000050	.000008	0	1/2	0	0
Q-5B	2FF	2/6	N	.000450	.000200	.000050	.000008	0	0	0	1/2
Q-5C	8FF	2/6	N	.001800	.000800	.000200	.000032	1/4	1/4	1/8	1/4
Q-6	2GO	2/6	N	.002750	.002800	.001110	.000770	1/6	1/4	1/12	1/4
Q-7A	2AG	3/7	+	.005500	.005600	.003552	.003850	0	1/2	0	0
Q-7B	2CG	3/7	+	.005500	.005600	.003552	.003850	0	0	0	1/2
Q-7C	8BG	2/7	–	.022000	.022400	.007104	.003080	1/4	1/4	1/8	1/4
Q-8A	2DG	4/8	+	.110000	.064400	.088800	.092400	0	–	–	–
Q-8B	4EG	2/8	–	.220000	.128800	.088800	.036960	1/4	–	–	–
Q-9A	4FG	3/9	N	.016500	.005600	.002220	.000616	1/6	1/4	1/12	1/4
Q-9B	4FG	3/9	N	.016500	.005600	.002220	.000616	1/6	1/4	1/12	1/4
Q-10	GG	4/12	N	.075625	.019600	.012321	.005929	1/6	1/4	1/12	1/4

any of the chromosomes may be the false univalent except chromosomes 1 and 2 in the cases of Q-4, Q-5 and Q-7 where they form a bivalent-like configuration and are co-oriented.

The kind of disjunction may be alternate or adjacent in case of Q-1 and Q-2. These terms are not relevant for the other quadrivalents. It is assumed, using the maize translocation heterozygote model (Burnham 1950), that alter-

Table 5. Summary of hypothetical pairing frequencies from Table 4 and observed data of Shaver 1962 and Shcherbak 1971

	1*	2*	3*	4*	5*	6*	7*	8*
	A_1	A_2	A_1	A_1	A	A	A	A
	A_1	A_2	A_1	A_1	A	A	A	A
	A_1	A_2	A_3	A_4	A	A_x	A	A_x
	A_1	A_2	A_3	A_4	A	A_x	A	A_x
4U	.000	.000	.000	.000	.000	.000	.000	.000
1B2U	.001	.005	.001	.002	.000	.002	.000	.000
2B	.151	.230	.287	.463	.149	.670	.120	.687
UT	.008	.016	.004	.003	.000	.004	.004	.001
Q	.841	.749	.707	.532	.851	.323	.875	.312
Q-1	.048	.110	.064	.053	.101	.048	.022	.033
Q-2	.240	.317	.400	.317	.238	.194	.245	.104
Q-3	.004	.005	.001	.000	.018	.004	.016	.013
Q-4	.072	.055	.032	.013	.054	.012	.045	.040
Q-5	.003	.001	.000	.000	.000	.002	.009	.005
Q-6	.003	.003	.001	.001	.036	.003	.100	.024
Q-7	.033	.034	.014	.011	.149	.006	.114	.042
Q-8	.330	.193	.178	.129	.190	.041	.238	.037
Q-9	.033	.011	.004	.001	.000	.002	.029	.007
Q-10	.076	.020	.012	.006	.065	.011	.056	.007

* 1, 2, 3, and 4 = from pairing model
5 = Shaver 1962b Autotetraploid maize
6 = Shaver 1962b Autotetraploid maize/Perennial teosinte
7 = Shcherbak 1971 Autotetraploid maize
8 = Shcherbak 1971 Autotetraploid maize/Perennial teosinte

Table 6. Chromosome disjunction in tetraploids

				2-2			3-1				2-1(1)(y) Chromosome lost			
	2-2	3-1	2-1(1)	12/34	13/24	14/23	123/4	124/3	134/2	234/1	1	2	3	4
B + 2U	1/2	1/2	z,(z^2)	0	1/2	1/2	0	0	1/2	1/2	–	–	(1/2 z)	(1/2 z)
2B	1	0	0	0	1/2	1/2	–	–	–	–	–	–	–	–
UT-1	1/2	1/2	y,z	1/4	1/2	1/4	0	1/3	1/3	1/3	1/3	1/3	1/3	(z)
UT-2	1/2	1/2	y,z	1/3	1/3	1/3	0	1/3	1/3	1/3	1/3	1/3	1/3	(z)
UT-3	1/2	1/2	y,z	0	1/2	1/2	0	0	1/2	1/2	0	0	1	(z)
UT-4	1/2	1/2	y,z	1/3	1/3	1/3	0	1/3	1/3	1/3	1/3	1/3	1/3	(z)
Q-1	1	x	y	1/4	1/2	1/4	1/4	1/4	1/4	1/4	1/4	1/4	1/4	1/4
Q-2	1	x	y	1/4	1/2	1/4	1/4	1/4	1/4	1/4	1/4	1/4	1/4	1/4
Q-3	1	x	y	1/3	1/3	1/3	1/4	1/4	1/4	1/4	1/4	1/4	1/4	1/4
Q-4	1	x	y	0	1/2	1/2	0	0	1/2	1/2	0	0	1/2	1/2
Q-5	1/2	1/2	y	0	1/2	1/2	0	0	1/2	1/2	0	0	1/2	1/2
Q-6	1	x	y	1/3	1/3	1/3	1/4	1/4	1/4	1/4	1/4	1/4	1/4	1/4
Q-7	1	x	y	0	1/2	1/2	0	0	1/2	1/2	0	0	1/2	1/2
Q-8	1	0	0	0	1/2	1/2	–	–	–	–	–	–	–	–
Q-9	1/2	1/2	y	1/3	1/3	1/3	0	1/3	1/3	1/3	1/4	1/4	1/4	1/4
Q-10	1	x	y	1/3	1/3	1/3	1/4	1/4	1/4	1/4	1/4	1/4	1/4	1/4

nate disjunction occurs one-half of the time.

In the case of Q-4, Q-5 and Q-7 the chromosome segregations of 12/34 are not possible since chromosomes 1 and 2 are presumed always to disjoin.

These patterns of disjunction can be used to predict gene segregation patterns for each configuration. These are shown in Table 4 on the right. By multiplying the frequency of gametes times the frequency of a configuration it is possible to predict the genetic ratios of each kind of polyploid if we assign arbitrary values of x = 2%, y = 0.5% and z = 10%. These computations are somewhat lengthy. The results are given in Table 7.

The two types of autotetraploids show about the same genetic ratios. There are fewer aneuploid gametes in the $A_2A_2A_2A_2$ tetraploid where the more complex types of quadrivalents are less frequent than in the $A_1A_1A_1A_1$ tetraploid. The effect of DPA on the genetic ratios in the segmental allotetraploids is large.

However, there are additional problems. For example, this model of gene segregation assumes that there is no crossing over between chromosomes. When there is crossing over there is a possibility of double reduction, which would modify the genetic ratios somewhat. As DPA increases, the frequency of double reduction should decrease because of lower multivalent frequencies. Many complications arise. For example, if a four strand double exchange occurs in a Q-1A1 type as shown in Fig. 3, the genetic ratio of the *A* locus will now be 1/4*AA*:1/2*Aa*:1/4*aa*, equivalent to that of Q-1D, and the *B* locus will be unchanged-1/8*BB*:3/4*Bb*:1/8*bb*. The results of crossing over undo some of the effects of preferential pairing. If all the types of quadrivalents are considered along with the non-random disjunction of their chromosomes the effect of crossing over becomes very complex and beyond the scope of this paper.

Table 7. Gene segregation in hypothetical *GGgg* tetraploids

Tetraploid	Gametes expected			
	GG or gg	Gg	G or g	GGg or Ggg
$A_1A_1A_1A_1$	.161183	.644733	.008673	.007777
$A_2A_2A_2A_2$	.161880	.647524	.007854	.006504
$A_1A_1A_3A_3$	.123322	.736376	.004667	.003823
$A_1A_1A_4A_4$	.070759	.846340	.003375	.002696

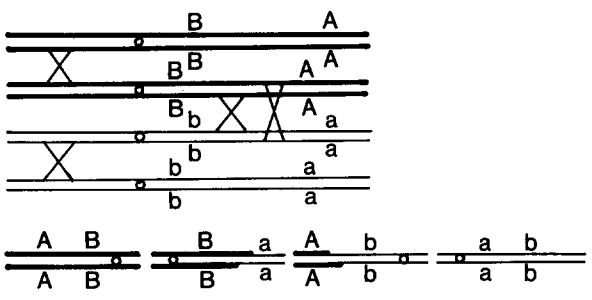

Fig. 3. Results of crossing over (4 strand double exchange) on gene segregation. A chain quadrivalent is formed. It is Q-1A for the B locus, and Q-1D for the A locus

Conclusions

This model of chromosome pairing and gene segregation in segmental allotetraploids needs refinement. The approximate values used to demonstrate the model need to be more closely aligned with real ones. Nonetheless, the model shows the major features of the cytogenetics of segmental allotetraploids.

Literature

Burnham, C.R.: Chromosome segregation in translocations involving chromosome 6 in maize. Genetics **35**, 446-481 (1950)

Buzzell, R.I.: Tetraploid genetics. I. Effects of variation in bivalent preferential pairing. Can. J. Genet. Cytol. 7, 478-483 (1965)

Catcheside, D.B.: Double reduction and numerical non-disjunction in tetraploid maize. Heredity **10**, 205-218 (1956)

Catcheside, D.B.: Segregation in tetraploid potatoes. Heredity **13**, 403-407 (1959)

Collins, G.N.; Longley, A.E.: A tetraploid hybrid of maize and perennial teosinte. J. Agric. Res. **40**, 123-133 (1935)

Darlington, C.D.: Meiosis in diploid and tetraploid *Primula sinensis*. J. Genet. **24**, 65-69 (1931)

Doyle, G.G.: Autotetraploid gene segregation. Theor. Appl. Genet. **43**, 139-142 (1973)

Doyle, G.G.: The allotetraploidization of maize. I. The physical basis – differential pairing affinty. Theor. Appl. Genet. (in press)

Fisher, R.A.; Mather, K.: Inheritance of style length in *Lythrum salicaria*. Ann. Eug. **12**, 1-23 (1943)

Haldane, J.B.S.: The theoretical genetics of autotetraploids. J. Genet. **22**, 359-373 (1930)

Mather, K.: Reductional and equational separation of chromosomes in bivalents and tetravalents. J. Genet. **30**, 53-78 (1935)

Mather, K.: Segregation and linkage in autotetraploids. J. Genet. **32**, 287-314 (1936)

Muller, H.J.: A new mode of segregation in Gregory's Primulas. Am. Nat. **48**, 508-512 (1914)

Shcherbak, V.S.: Meiosis in amphidiploid maize and teosinte. Maize Genetics Coop. News Letter **45**, 257-259 (1971)

Shaver, D.L.: A comparison of meiosis in perennial teosinte (4n), tetraploid maize and their hybrid. Caryologia **15**, 53-57 (1962)

Stebbins, G.L., Jr.: Types of polyploids: their classification and significance. Adv. Genet. **1**, 403-429 (1947)

Received September 20, 1978
Communicated by P.L. Pfahler

Dr. G.G. Doyle
215 Curtis Hall
Agronomy Department
University of Missouri
Columbia, MO 65211 (USA)