Theor Appl Genet (1990) 79:145–152

THEORETICAL AND APPLIED GENETICS

The allotetraploidization of maize

5. The utilization of zygomeres *

G. G. Doyle

U.S. Department of Agriculture, Agricultural Research Service, and the Agronomy Department, University of Missouri, Columbia, MO 65211, USA

Received January 25, 1989; Accepted September 18, 1989
Communicated by K. Tsunewaki

Summary. Artificial allotetraploidization is the derivation of synthetic allotetraploids. In an allotetraploid, chromosomes of similar genomes pair with their homologues in similar genomes rather than with their homoeologues in the dissimilar genomes. The basis of this discrimination is not completely understood because the mechanisms of chromosome pairing are not adequately known. Sybenga has hypothesized the existence of special units of DNA (zygomeres) that are responsible for the initiation of synapsis of chromosomes during meiosis. Zygomeres, if they exist, should be detectable by preferential pairing studies. In the work reported here, trisome 3 maize plants had two standard chromosomes 3 marked with the genes *al sh2* or *al Sh2,* and an odd chromosome 3 from a commercial inbred line (or derivatives thereof) marked with the dominant alleles *A1 Sh2*. In a previous study, three inbred lines (B41, Hy, and 38-11) were found to have chromosomes 3 that caused a great amount of preferential pairing. It may be assumed that they have different zygomeres than those of the standard chromosome 3. Hybrids between these inbred lines and hybrids between the inbreds and the standard were used as the donors of the odd chromosome. Segregation for preferential pairing (and presumably for zygomeres) was observed. The data can be explained on the basis of only two zygomeres per chromosome. Zygomeres should be able to be mapped as though they were genes.

Key words: Maize – Allotetraploidization – Trisomes – Synapsis – Zygomeres

* Contribution from the Agricultural Research Service, U.S. Department of Agriculture, and the Agronomy Department University of Missouri, and the Missouri Agricultural Experiment Station, Journal Series No. 10667

Introduction

Allotetraploids have two pairs of dissimilar genomes and thus may be symbolized as AABB. The genomes (A and B) were derived from related species or genera that had a common ancestor and whose chromosomes were therefore once homologous. During evolutionary divergence chromosomal structural rearrangements, mutations in the pairing code, and mutations of genes affecting the general expression of differential pairing affinity (DPA) have arisen, so that when diploid species (AA and BB) are hybridized and their chromosome number is doubled, almost all the chromosome pairing in the resulting allotetraploid is between homologues of like genomes.

Artificial allotetraploidization is the derivation of synthetic allotetraploids. This process has been discussed by Bender and Gaul (1966), Gaul and Friedt (1975), and Sybenga (1969, 1973).

Maize is a single species. Therefore, to produce allotetraploid maize it is necessary to convert the maize genome (Z) into a restructured genome (R). The chromosomes of the Z and R genomes should then pair autosydetically in the synthetic allotetraploid, ZZRR. The R genome can be created by concentrating induced or naturally occurring DPA factors into stocks by a recurrent selection breeding system. Allotetraploid maize would be a true breeding hybrid. Also, because virtually no aneuploid gametes would be formed, an allotetraploid population would not have the reduction in vigor and fertility due to aneuploidy as found in autotetraploid populations (Doyle 1986a). It was shown (Doyle 1979a) that DPA factors occur naturally between different races of maize and that they can be readily induced by X-rays and chemical mutagens. A comprehensive model was presented (Doyle 1979b) to explain how DPA affects the

relative frequencies of various chromosome pairing configurations and, consequently, the genetic ratios expected in segmental allotetraploids. A similar study on the effects of DPA in trisomes has been presented (Doyle 1982). Cytological and genetic evidence indicating substantial progress toward allotetraploidization has been given (Doyle 1986b).

To understand the process of allotetraploidization (or cytological diploidization), it is necessary to understand the mechanisms of chromosome pairing. Some investigators (Sved 1966; Woollam et al. 1966) believe that homologous chromosome ends (telomeres) are attached to the nuclear membrane in close proximity. This would allow synapsis to occur very easily. However, telomere attachment would not explain how ring chromosomes (which have no ends or telomeres) could pair, and how such internal configurations as inversion loops could be formed. It has been demonstrated that internal structural differences (a series of inversions in chromosome 3 of maize) affect pairing (Doyle 1969). Also, the work of Burnham et al. (1972) indicates that pairing can be initiated anywhere along the chromosome, although it most commonly occurred in the subterminal segments. For a review of the problems of chromosome pairing, the reader is directed to the work of Maguire (1984).

DPA is known to be under the control of genes in some cases. Notable is the effect of the *Ph* gene in wheat (Okamoto 1957; Riley and Chapman 1958).

Sybenga (1966) has hypothesized the existence of "zygomeres", units responsible for the initiation of chromosome pairing. Among evidence suggesting that a limited part of the genome, rather than all parts, is responsible for pairing initiation is the fact that the length of the synaptonemal complex (SC) is very much shorter than the length of the DNA. In corn, e.g., the SC : DNA ratio is 1.5 : 10,000 (Gillies 1973). This implies that there is a special class of DNA responsible for chromosome pairing, because a random sample of DNA from each chromosome would have a very low probability of being homologous. These specialized DNA segments are zygomeres.

When more than two chromosomes that are capable of pairing with each other are present at meiosis, preferential pairing may occur. In the case of a trisome with two standard chromosomes and an odd chromosome (that may have altered pairing affinities), preferential pairing means that the two standard chromosomes will pair with each other with a frequency greater than would be expected if random pairing were occurring. Preferential pairing will affect the relative frequencies of the various pairing configurations given in Fig. 1. Disjunction of the chromosomes from these configurations will affect genetic ratios as shown in Table 1.

The standard chromosomes 3 and those from the inbred lines are not cytologically different, so that the

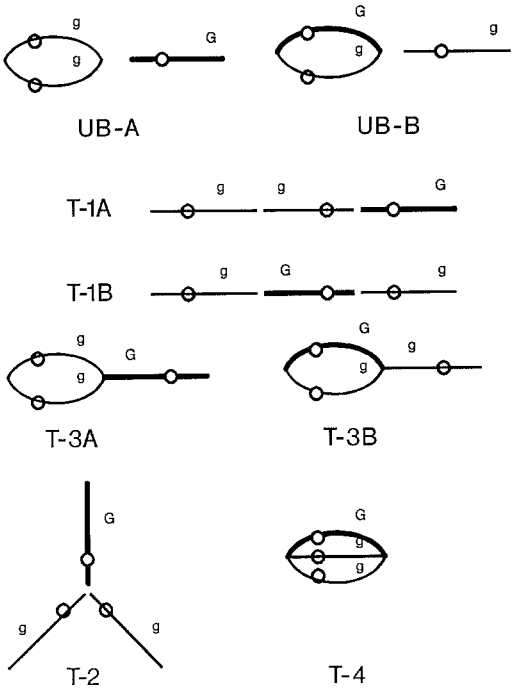

Fig. 1. Pairing configurations possible in a heterozygous trisome. These configurations may be classified as homogenetic if all chiasmata are between like chromosomes (UB-A), heterogenetic if all chiasmata are between unlike chromosomes (UB-B and T-1B), semi-homogenetic if chiasmata between like chromosomes exceed the random pairing value of 1/3 (T-1A and T-3A), semi-heterogenetic if chiasmata between unlike chromosomes exceeds the random pairing value of 2/3 (T-3B), or neutral if associations between like chromosomes is 1/3 and that between unlike chromosomes is 2/3 (T-2 and T-4)

Table 1. The effect of preferential pairing on genetic ratios

Pairing configuration[a]	Frequency[b]	Monosomic gametes expected	
		G	*g*
Bivalent and univalent	(1-*t*)		
Homogenetic (UB-A)	(1/3+*p*)	0	all
Heterogenetic (UB-B)	(2/3−*p*)	1/2	1/2
Trivalent	(*t*)		
Semihomogenetic (T-1A)	(2/3+*p*)	0	all (alt. disj.)
		1/2	1/2 (adj. disj.)
Heterogenetic (T-1B)	(1/3−*p*)	all	0 (alt. disj.)
		0	all (adj. disj.)
Semihomogenetic (T-3A)	(1/3+*p*)	0	all
Semiheterogenetic (T-3B)	(2/3−*p*)	1/2	1/2
Neutral			
T-2		1/3	2/3
T-4		1/3	2/3

[a] Refer to Fig. 1

[b] The symbols used are as follow: *t* is frequency of trivalent formation, (1-*t*) is the frequency of bivalent and univalent formation, and *p* is the preferential pairing factor (see Doyle 1982 for a more detailed discussion)

frequencies of the configurations are inferred from genetic data. When the trisomes are used as the pollen parent, only the monosomic gametes need to be considered because disomic gametes function in fertilization only very rarely. If only homologous pairing occurs, then only homogenetic bivalents (UB-A) will be formed, and all the gametes will be g. If the preferential pairing factor (p) has a value, then the random ratio of $1G:2g$ will change. The "frying pan" trivalents (T-3A and T-3B) behave like the univalent and bivalent types (UB-A and UB-B), because the chromosomes forming the "pan" will disjoin and go to opposite poles. Because the chromosomes are all spatially equivalent in the triradial trivalents (T-2) and "birdcage" trivalents (T-4), the gametes from these configurations must be the random values of $1G:2g$. The chain trivalents (T-1A and T-1B) will not give a $1G:2g$ ratio if the frequency of alternate segregation is greater than the random value of 1/3. The genetic ratios given are for configurations where the chromosomes are all reductional (*GG* or *gg*) and not equational (*Gg*). Equational chromosomes result from crossing-over between the gene marker and the centromere. The effect of equational chromosome formation in the trivalents is to reduce the effect of preferential pairing on genetic ratios, as was discussed previously (Doyle 1982). The frequency and placement of chiasmata are probably affected by the environment, and different relative frequencies of pairing configurations will occur, with concomitant changes in genetic ratios. Therefore, the expression of preferential pairing is somewhat variable.

Alonso and Kimber (1981) have devised a scheme based upon trivalent and bivalent (ring and rod) frequencies to assess the affinity of genomes. Unfortunately, this method is not adaptable to maize because of the presence of complex trivalents (T-2, T-3, and T-4).

Materials and methods

Trisome 3 plants (*a1 Sh2/a1 Sh2/a1 sh2* or *a1 Sh2/a1 sh2/a1 sh2*) with all standard chromosomes 3 were crossed with many sources of possible structurally altered chromosomes or chromosomes with modified pairing codes, that were marked with *A1 Sh2* in a previous study (Doyle 1979a). The *a1* gene is one of a series of complementary genes that control anthocyanin formation. Kernels that are homozygous for *a1* have colorless aleurones. The gene *sh2* is very closely linked to *a1* (0.02). It gives shrunken kernels when homozygous. Hereafter, for the sake of brevity the numbers in these gene symbols will not be used. The trisomic progeny of these crosses (*A Sh/a Sh/a Sh*, *A Sh/a Sh/a sh*, or *A Sh/a sh/a sh*) were crossed as the male with *a sh/a sh* testers.

Three inbred lines (B41, Hy, and 38-11) whose chromosomes 3 produced a strong preferential pairing response were selected for an intensive study. To determine the inheritance of DPA, hybrids of these lines (all *A Sh/A Sh*) were used as the odd chromosome donor and crossed with the trisomes with all standard chromosomes. The resulting trisomic progeny were tested for the preferential pairing. Also, hybrids between the inbred lines and the standard (*A Sh/a Sh*) were crossed with the standard trisome 3 (*a sh/a sh/a sh*) plants. The two types of trisomes formed by these crosses, *A Sh/a sh/a sh* and *a Sh/a sh/a sh*, were crossed with *a sh/a sh* females to detect preferential pairing. Recombinant chromosomes 3 with different patterns of zygomeres were anticipated (see Fig. 2, which shows the pattern of crosses used).

For the sake of statistical simplicity, all progenies with fewer than 500 kernels were discarded.

Also, another inbred line, Tr, was used. It had given anomalous results which will be explained.

Results

The results of the genetic experiments are given in Table 2. Except for the standard trisome, the male transmission rates of *A* or *Sh* are very variable, as indicated by the interaction Chi-squares. The p values are all below 0.0005 except for the Std (standard) where $p=0.005-0.001$. When the data in Table 2 are plotted graphically (Fig. 3), in many cases a normal curve is approximated. In some cases, such as B41, a possible bimodal distribution was found. In all cases, the variability of preferential pairing allows for the upper tail of these distributions to extend over the random pairing point (33.3%) and gives readings for normality. Preferential pairing is a behavioral phenomenon and thus is expressed like a quantitative trait.

As a check on the possibility that factors other than preferential pairing were affecting genetic ratios, diploid sibs were crossed as the male with the *a sh* tester. Here we would expect 50% transmission of *A* if such disturbing factors as pollen competition, differential viability of spores or zygotes, or gametophyte factors are absent. The results are given in Table 3. It may be seen that the transmission rates of *A* are very close to 50%, except for Tr. The anomalous results for the Tr trisome in Table 2 are thus explained by transmission abnormalities; there are probably genes on the Tr chromosome 3 linked to the *A Sh* markers that make the pollen containing them able to compete more successfully than pollen with the standard genes. The 38-11/Std (*A Sh/a sh*) showed a slight excess of *A Sh* gametes, but it would not explain the results found in the trisomes because it works counter to the effects of preferential pairing.

When the tested plant had the genotype of *A Sh/a Sh/a sh* (see Table 4, which is a subset of the data in Table 2) instead of *A Sh/a Sh/a Sh* or *A Sh/a sh/a sh*, the almost equal frequency of *a Sh* and *a sh* phenotypes in the progeny indicates that the two standard chromosomes bearing the *a Sh* or *a sh* gene markers pair with the odd chromosome equally and, therefore, are homologous to each other in terms of pairing affinity. However, there tends to be a small excess of *a Sh* phenotypes over *a sh* ones, as found in the diploid tests given in Table 3. This probably

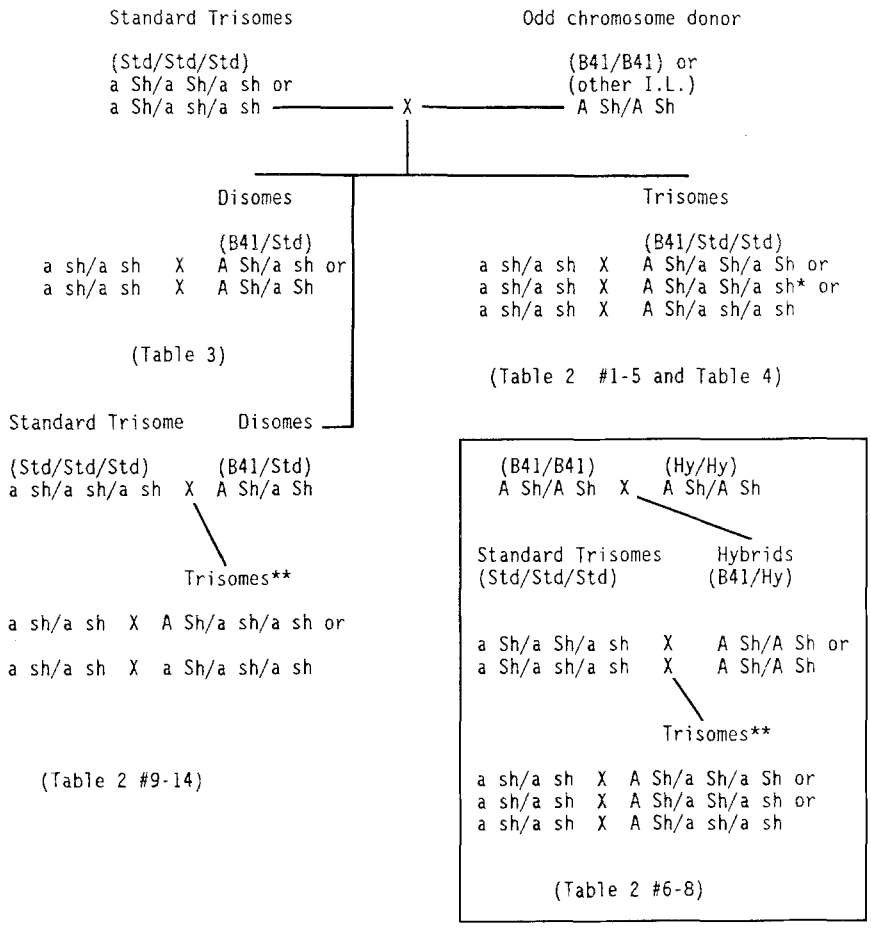

Fig. 2. Pattern of crosses used in this study. * genotype used for data in Table 3. ** disomic siblings were also produced but were not used

Table 2. Genetic data from trisomic heterozygotes crossed as the male onto *a sh/a sh* testers

Source of the odd chromosome	No. of plants tested	No. of gametes tested	Percent of odd gene	χ^2 ($A=1/3$) ($Sh=1/3$)	Interaction χ^2	No. of plants significant at[a]				
						0.01 (−)	0.05 (−)	N	0.05 (+)	0.01 (+)
1 Std.	51	59,007	33.25	0.19	81.05**	1	2	46	1	1
2 B41	69	70,523	21.42	4,503.08**	1,324.37**	66	0	3	0	0
3 Hy	60	63,138	24.01	2,471.75**	859.92**	55	0	5	0	0
4 38-11	64	72,959	23.62	3,000.17**	782.22**	60	1	3	0	0
5 Tr	32	35,131	36.64	172.85**	151.51**	1	0	14	3	14
6 B41/Hy	17	15,652	24.36	567.00**	330.28**	11	4	2	0	0
7 B41/38-11	15	16,717	22.98	805.96**	308.96**	14	0	1	0	0
8 Hy/38-11	36	42,437	23.86	1,715.06**	790.84**	29	4	2	1	0
9 B41/Std (*A*)	26	28,691	24.77	945.81**	638.57**	20	1	3	0	2
10 B41/Std (*Sh*)	14	17,978	28.04	226.22**	169.06**	6	3	5	0	0
11 Hy/Std (*A*)	28	28,836	29.39	202.38**	361.65**	13	1	14	0	0
12 Hy/Std (*Sh*)	35	38,768	31.98	32.07**	386.57**	11	3	13	3	5
13 38-11/Std (*A*)	20	25,596	28.62	255.28**	73.61**	11	3	5	1	0
14 38-11/Std (*Sh*)	22	26,238	27.41	414.71**	541.83**	11	3	7	0	1

[a] The number of plants whose transmission frequencies of the marker gene were significantly lower (−) or higher (+) than 1/3 at the 0.01 and 0.05 levels using Chi-squares.

* and ** indicate significance at the 0.05 and 0.01 level, respectively

Table 3. Genetic data from disomic sibs of the trisomes crossed as the male onto *a sh/a sh* testers

Plants tested		No. plants	No. of gametes	% *A Sh*	χ^2 $A=1/2$	Interaction χ^2	No. of plants significant at				
							0.01 (−)	0.05 (−)	*N*	0.05 (+)	0.01 (+)
B41	*A Sh/a sh*	5	4,812	50.74	1.08	4.17	0	0	5	0	0
	A Sh/a Sh	6	6,484	49.12	2.00	14.94*	0	2	4	0	0
	Total	11	11,296	49.81	0.16	22.03*	0	2	9	0	0
Hy	*A Sh/a sh*	9	9,959	50.51	1.02	10.54	0	0	9	0	0
	A Sh/a Sh	8	10,437	49.76	0.25	5.08	0	0	8	0	0
	Total	17	20,396	50.12	0.12	17.77	0	0	17	0	0
38-11	*A Sh/a sh*	10	9,441	51.26	5.95*	7.43	0	0	8	1	1
	A Sh/a Sh	3	3,115	50.63	0.49	7.77*	0	0	2	1	0
	Total	13	12,556	51.10	6.07*	15.78	0	0	10	2	1
Tr	*A Sh/a sh*	8	6,374	53.50	31.21**	10.94	0	0	4	2	2
	A Sh/a Ah	6	5,319	53.36	23.96**	6.59	0	0	3	0	3
	Total	14	11,693	53.43	55.14**	17.57	0	0	7	2	5

* and ** Significant at 0.05, and at 0.01, respectively

Table 4. Genetic data from *A Sh/a Sh/a sh* trisomes used as the male parent onto *a sh/a sh* testers

Source of odd chromosome	No. of plants tested	No. of gametes tested	Percent of gametes				Chi-square *a Sh = a sh*
			A sh[a]	*A Sh*	*a Sh*	*a sh*	
Std.	23	32,312	0.0062	33.2044	34.1916	32.5978	12.29**
B41	45	48,505	0.0082	20.1113	40.4329	39.4475	5.89*
Hy	33	36,715	0.0054	24.4968	38.3358	37.1619	6.70**
38-11	31	34,554	0.0029	23.5834	39.3268	37.0869	22.69**

* and ** significant at 0.05 and 0.01 level, respectively
[a] Crossovers between *A* and *Sh*

Table 5. Results of crossing-over in hybrid odd chromosome donors (Fig. 4)

Parental chromosomes	Chromosomes produced							
	ZAShZ	*ZAShz*	*zAShZ*	*zAShz*	*ZaShZ*	*ZaShz*	*zaShZ*	*zaShz*
no. 4 no. 1 *ZAShZ/zaShz*								
No crossovers	1/2	–	–	–	–	–	–	1/2
c.o. in I	1/4	–	1/4	–	–	1/4	–	1/4
c.o. in II	1/4	1/4	–	–	–	–	1/4	1/4
c.o. in I & II*	1/8	1/8	1/8	1/8	1/8	1/8	1/8	1/8
no. 2 no. 1 *ZAShz/zaShz*								
No crossovers	–	1/2	–	–	–	–	–	1/2
c.o. in I	–	1/4	–	1/4	–	1/4	–	1/4
c.o. in II	–	1/2	–	–	–	–	–	1/2
C.o. in I & II*	–	1/4	–	1/4	–	1/4	–	1/4

* Summation of 2-, 3-, and 4-strand double exchanges

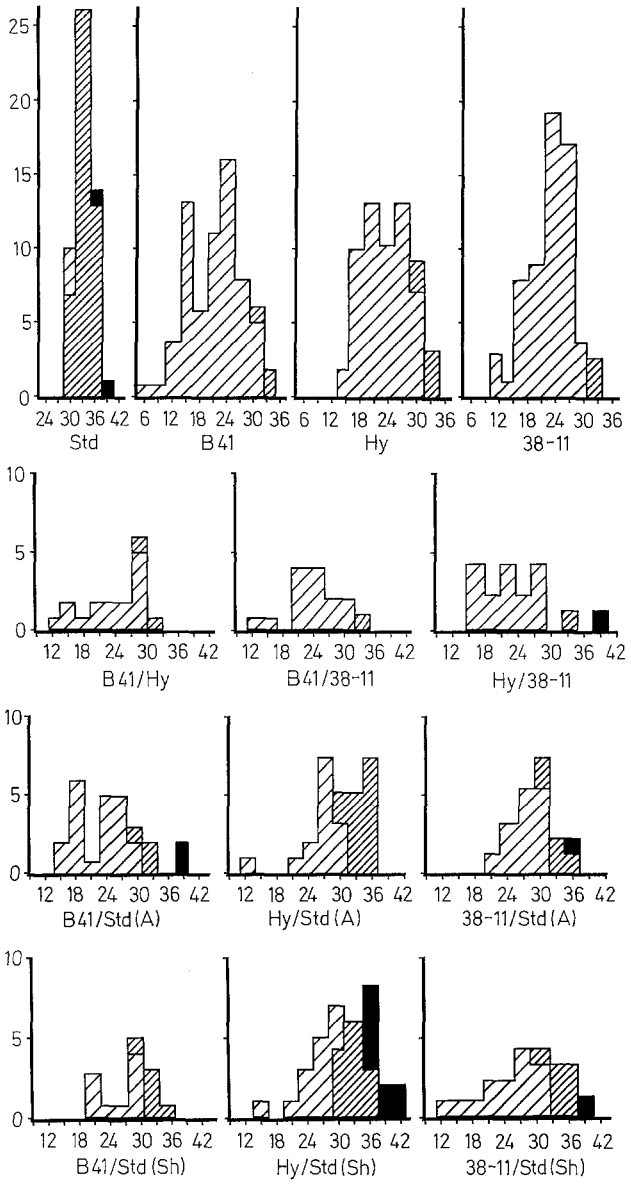

Fig. 3. Histograms showing the distributions of transmission frequencies of chromosomes bearing the *A* or *Sh* markers from heterozygous trisomes used as the male parent on *a sh* testers. The number of plants is shown on the vertical axis. The numbers on the horizontal axis are midpoints of classes that cover three percentage points. Thus 9 represents a class with transmission rates that run from 7.51 to 10.50 transmission rates. The shadings indicate whether these rates are significantly lower (light), equivalent to (medium), or significantly higher (solid) than 33.33%

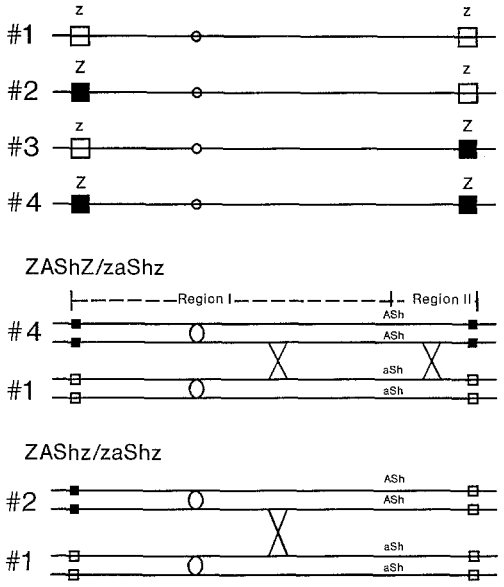

Fig. 4. Four possible zygomeric constitutions. The placement of these zygomeres is arbitrary. The effect of crossing-over in hybrids is shown. The crossover patterns indicated would produce *A Sh* chromosomes with standard zygomeres and *a Sh* chromosomes with non-standard zygomeres

indicates pollen competition and differential viability. The data will not be corrected for this factor, as its expression is variable.

Discussion

The data in Table 2 can be explained by a simple model. It may be assumed that chromosome pairing is initiated by two zygomeres, one each at or near the ends of the chromosome. There are four possible patterns, as shown in Fig. 4. The standard chromosome 3 is no. 1; the B41, Hy, and 38-11 chromosomes 3 are no. 2, no. 3, or no. 4. The zygomeres indicated by the black squares have different pairing affinities from the standard white-square zygomeres. Chromosome pairing is initiated at zygomeres and the tendency for like zygomeres to associate will cause a higher than random frequency of homogenetic bivalents and semi-homogenetic trivalents to be formed, which will affect the genetic ratios. There is probably affinity between the allelic zygomeres on the standard chromosomes and the ones on three inbred lines used, but it is reduced in strength. In the diploid there is no choice possible.

The results from using the hybrids B41/Hy, B41/38-11, and Hy/38-11 as the source of the odd chromosome permit the definition of the zygomere patterns of the hybrids as no. 2/no. 4, no. 3/no. 4, no. 2/no. 2, no. 3/no. 3, or no. 4/no. 4. None can be no. 2/no. 3 because crossing-over would produce about 1/2 no. 1 chromosomes, assuming that the terminal or near-terminal zygomeres would show 50% recombination. The highest frequency of apparent no. 1 chromosomes, showing normal (33%) transmission, was from B41/Hy, where there was 11.76%. There was no visible transgressive segregation for DPA, which suggests that all pairs of zygomeres are allelic.

The results from using the inbred line/standard hybrids as the source of the odd chromosome are quite instructive. The consequences of crossing over are shown in Table 5. If the Hy/Std hybrid is no. 2/no. 1, we would

Table 6. Observed and expected genetic ratios

Odd chromosome donor	Observed or expected[a]	Zygomeric constitution	Plants with normal or statistically significant different transmission rates for *A* or *Sh*					
			Number			Percent		
			(−)	*N*	(+)	(−)	*N*	(+)
B41	0	no. 4/no. 4	66	3	0	95.7	4.3	0.0
Hy	0	no. 2/no. 2–no. 3/no. 3	55	5	0	91.7	8.3	0.0
38-11	0	no. 4/no. 4	60	4	0	93.8	6.2	0.0
B41/Hy	0	no. 4/no. 2 or no. 3	15	2	0	88.2	11.8	0.0
	E		15.9	1.1	0	93.7	6.3	0.0
B41/38-11	0	no. 4/no. 4	14	1	0	93.8	6.2	0.0
	E		14.2	0.8	0	94.8	5.2	0.0
Hy/38-11	0	no. 2 or no. 3/no. 4	29	6	1	80.1	16.7	2.3
	E		33.4	2.6	0	92.8	7.2	0.0
B41/Std	0	no. 4/no. 1	21	3	2	80.8	11.5	7.7
(A)	E		19.5	6.5	0	75.0	25.0	0.0
B41/Std	0		9	5	0	64.3	35.7	0.0
(Sh)	E		10.5	3.5	0	75.0	25.0	0.0
Hy/Std	0	no. 2 or no. 3/no. 1	14	14	0	50.0	50.0	0.0
(A)	E		14.0	14.0	0	50.0	50.0	0.0
Hy/Std	0		14	13	8	40.0	37.1	22.9
(Sh)	E		17.5	17.5	0	50.0	50.0	0.0
38-11/Std	0	no. 4/no. 1	14	5	1	70.0	25.0	5.0
(A)	E		15.0	5.0	0	75.0	25.0	0.0
38-11/Std	0		14	7	1	63.7	31.8	4.5
(Sh)	E		16.5	5.5	0	75.0	25.0	0.0

[a] Expected values (E) for the inbred/inbred hybrid donors are the average percent of normal readings for each component inbred. The expected values for the inbred/standard donors are based on two exchanges per chromosome as given in Table 5

expect equal frequencies of *A Sh* no. 1, *A Sh* no. 2, *a Sh* no. 1, and *a Sh* no. 2 chromosomes following crossing-over. The data show that this appears to be true, although there is an unexpected enhancement of transmission of the *a Sh* chromosomes in the *a sh*/*a sh* × Hy/Std (*Sh*) cross. The other two inbred line/standard hybrids (B41/Std and 38-11/Std) are probably no. 4/no. 1. If there are two exchanges, the frequencies of *A Sh* and *a Sh* chromosomes with patterns of no. 1, no. 2, no. 3, and no. 4 are all 1/8. The chromosomes no. 2, no. 3, and no. 4 will give preferential pairing. The data are analyzed in Table 6 and are in fairly close agreement. However, the presence of transmission frequencies greater than 33.3% cannot be explained, except in a few cases, by sampling error.

Conclusions

This work does not definitely establish the existence of zygomeres, but it indicates that pairing affinity is inheritable. The system used will only detect zygomeres that are different, so that the number of zygomeres per chromosome is unknown. Using the simplest hypothesis to explain the results requires only two.

There are probably other synaptic initiation sites that act later than these primary initiation sites or zygomeres. This would allow the formation of inversion loops and other configurations that are observable at pachytene.

If DPA resides in a limited number of zygomeres instead of the whole genome, it would greatly facilitate the process of allotetraploidization. If zygomeres are like genes, then they are mutable and recombinable. The mapping of zygomeres, while difficult, should be possible. Once the existence of zygomeres and the cytological location are established, then it should be possible to characterize them by using the methods of molecular biology.

References

Alonso LC, Kimber G (1981) Analysis of meiosis in hybrids. Triploid hybrids. Can J Genet Cytol 23:221–234

Bender K, Gaul H (1966) Zur Frage der Diploidisierung autotetraploider Gerste. Z Pflanzenzuecht 56:164–183

Burnham CR, Stout JT, Weinheimer WH, Kowles RV, Phillips RL (1972) Chromosome pairing in maize. Genetics 71:111–126

Doyle GG (1969) Preferential pairing in trisomes of *Zea mays*. In: Darlington CD, Lewis KR (eds) Chromosomes today, vol 2. Oliver and Boyd, Edinburgh, pp 12–20

Doyle GG (1979a) The allotetraploidization of maize. 1. The physical basis – differential pairing affinity. Theor Appl Genet 54:103–111

Doyle GG (1979b) The allotetraploidization of maize. 2. The theoretical basis – the cytogenetics of segmental allotetraploids. Theor Appl Genet 54:161–168

Doyle GG (1982) The allotetraploidization of maize. 3. Gene segregation in trisomic heterozygotes. Theor Appl Genet 61:81–89

Doyle GG (1986a) Aneuploidy and inbreeding depression in random mating and self-fertilizing autotetraploid populations. Theor Appl Genet 72:799–806

Doyle GG (1986b) The allotetraploidization of maize. 4. Cytological and genetic evidence indicative of substantial progress. Theor Appl Genet 71:585–594

Gaul H, Friedt W (1975) Progress in the diploidization of autotetraploid barley. In: Gaul H (ed) Barley genetics III. Thiemig, Munich, pp 378–387

Gillies CB (1973) Ultrastructural analysis of maize pachytene karyotypes by three-dimensional reconstruction of the synaptonemal complexes. Chromosoma 43:145–176

Maguire MP (1984) The mechanism of meiotic homologue pairing. J Theor Biol 106:605–615

Okamoto M (1957) Asynaptic effect of chromosome V. Wheat Inf Serv 5:6

Riley R, Chapman V (1958) Genetic control of the cytological diploid behavior of hexaploid wheat. Nature 182:713–715

Sved JA (1966) Telomere attachment of chromosomes. Some genetical and cytological consequences. Genetics 53:747–756

Sybenga J (1966) The zygomere as a hypothetical unit of chromosome pairing initiation. Genetica 37:186–198

Sybenga J (1969) Allopolyploidization of autopolyploids. 1. Possibilities and limitations. Euphytica 18:355–371

Sybenga J (1973) Allopolyploidization of autopolyploids. 2. Manipulation of the chromosome pairing system. Euphytica 22:433–444

Woollam DHM, Ford EHR, Millen JW (1966) Attachment of pachytene chromosomes to nuclear membrane. Exp Cell Res 42:657–661