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A Test of Distributive Pairing in *Zea mays* Utilizing Doubly Monosomic Plants[1]

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Summary. The r_{x1} deficiency in *Zea mays* induces chromosomal nondisjunction during the megagametophyte divisions after meiosis producing large numbers of monosomes, trisomes, double monosomes, double trisomes, and even triple monosomes. In this study, microsporogenesis in six doubly monosomic combinations was analyzed. Double monosomes in a diploid organism provide the ideal material to determine if there is an interaction between two nonhomologous univalent chromosomes because two nonhomologous chromosomes lacking partners are present in each meiotic cell.

At diakinesis and metaphase I, the two nonhomologous monosomic chromosomes were infrequently "paired" (3.76% and 2.18% respectively). These estimates are the upper estimates of "pairing" of nonhomologous monosomic chromosomes and probably represent an overestimate of these values because cells with any connections between the monosomic chromosomes were scored as having nine pairs and similar connections are not infrequently observed between two bivalents.

The transmission of two nonhomologous unpaired chromosomes was deduced by studying the progeny of maize plants hyperploid for two chromosomes (a B^4 and *Wd* ring). The two nonhomologous univalents disjoined randomly.

Since no evidence for an interaction between nonhomologous univalent chromosomes which leads to their non-random disjunction to opposite poles was found in this study, these data confirm my earlier conclusion (Weber, 1966, 1969) that "distributive pairing does not occur in maize (and probably most other plants) or that it occurs with a much lower efficiency than in *Drosophila* females". The frequent "pairing" between nonhomologous chromosomes at diakinesis and metaphase I and the non-random distribution at anaphase I in doubly trisomic maize plants reported by Michel and Burnham (1969) was found neither in my earlier studies (Weber, 1966, 1969) nor in the present study. The current study is far more sensitive than any of the previous studies because two nonhomologous chromosomes lacking pairing partners are found in every cell of a doubly monosomic plant.

The distributive pairing hypothesis was proposed by Grell (1962) to account for the non-random transmission of nonhomologous univalent chromosomes to the progeny of *Drosophila melanogaster* females (Bridges and Anderson, 1925; Gowen, 1933; Cooper, Zimmerling, and Krivshenko, 1955; Sandler and Novitski, 1956; Grell, 1957; and others). It hypothesizes that there is an achiasmatic pairing between univalent chromosomes (distributive pairing) subsequent to pairing between homologous segments of chromosomes for recombination (exchange pairing). Her genetic evidence is convincing, but for technical reasons, cytological confirmation of the putative pairing between univalents in meiotic cells has not been possible with female *D. melanogaster*.

Two studies (Weber, 1966, 1969; Michel and Burnham, 1969) were initiated to determine if distributive pairing occurred in *Zea mays* where analogous situations could be established and where meiotic cytology is favorable. In my work (Weber, 1966, 1969), singly trisomic plants with an accessory B chromosome and doubly trisomic plants were analyzed. A heterozygous paracentric inversion was used to increase the frequency of univalents in these plants (Doyle, 1963). At diakinesis and metaphase I, bivalent-like configurations between nonhomologous chromosomes were rarely seen. At anaphase I, the frequency of 11-11 disjunctions was not higher than the 10-12 disjunctions, thus the univalents were distributed randomly to the two poles. Also, the progeny of plants containing two chromosomes which are found as univalents essentially 100 per cent of the time (a ring fragment and a B chromosome) were examined. The two nonhomologous univalents were transmitted independently to the progeny of plants containing the univalents. Since no evidence for an interaction between nonhomologous univalents was found, I concluded that "distributive pairing" does not occur in maize or that it occurs at a much lower frequency than in *Drosophila* females.

Michel (1966) and Michel and Burnham (1969) also analyzed doubly trisomic maize plants and reported frequent associations between nonhomologous chromosomes at diakinesis and metaphase I. In cells where two nonhomologous univalents are available for pairing (cells with 10 bivalents and 2 univalents or cells with 11 "pairs"), the two univalents were found as a "pair" in an average of 28.1 per cent of the

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diakinesis cells and 25.0 per cent of the metaphase I cells. They also analyzed prophase II cell pairs to determine the chromosome distribution at anaphase I. In the doubly trisomic combinations analyzed, the frequency of cell pairs each containing 11 chromosomes was greater than the 10-12 cell pairs, thus the chromosomes were disjoined nonrandomly at anaphase I. However, because the excess of 11-11 disjunctions was greater than would occur if each of the paired heterologs passed to opposite poles, it was felt that there was no need to invoke a model of meiosis which included "distributive pairing".

A recently-discovered system in maize (Satyanarayama, unpublished) produces large numbers of monosomes and trisomes by inducing non-disjunction during the megagametophyte divisions. This system also produces a low frequency of doubly monosomic plants. These plants provide the most sensitive possible test of the interaction between two non-homologous chromosomes because each meiotic cell contains two chromosomes lacking homologs. The doubly monosomic plants are sufficiently vigorous to permit microsporocyte samples to be taken from these plants. These have been studied intensively in an attempt to resolve the differences reported in the above studies. Preliminary results of this work have been presented (Weber, 1970a). The present study appears to be the first cytological study of doubly monosomic individuals in a true diploid organism. Extensive tests of the transmission of two unpaired chromosomes are also reported.

Materials and Methods

The doubly monosomic *Zea mays* plants utilized in this study were generated by the r_{x1} deficiency. The stock carrying this deficiency and the Mangelsdorf's tester stock were generously provided by Kante Satyanarayama. The *Wd*-ring containing stock was provided by M. M. Rhoades and the B^4-containing stock by A. Ghidoni.

Microsporocyte samples were fixed in a freshly-prepared mixture of 3 parts of 94 per cent ethanol and 1 part propionic acid and then stored at −10 °C until used for cytological study. Customary methods of smearing anthers and staining with propiocarmine were followed.

Results

Production of Doubly Monosomic Plants

The r_{x1} deficiency was induced by L. J. Stadler with X-rays and includes the *R* locus on chromosome 10. Satyanarayama (unpublished) at the University of Wisconsin noted that when gametes carrying the r_{x1} deficiency are fertilized by haploid pollen, numerous monosomes and trisomes are produced in addition to the diploid progeny. A low percentage of doubly monosomic and doubly trisomic plants were also produced. He generously provided this deficiency to our laboratory where it is under intensive investigation.

R/r_{x1} plants in inbred W22 were crossed as females by a second inbred, Mangelsdorf's multiple chromosome tester, which bears a recessive gene on each chromosome. The markers listed in order for chromosomes 1 to 10 are: bm_2 (brown midrib), lg_1 (ligule less), a_1 (lack of anthocyanin), su_1 (sugary endosperm), *pr* (red aleurone), y_1 (white endosperm), gl_1 (glossy seedling leaves), j_1 (white striped plant), *wx* (waxy endosperm), and g_1 (golden plant). As the R/r_{x1} line carries a dominant gene corresponding to each recessive marker in Mangelsdorf's tester, the appearance of a recessive phenotype in the F_1 indicates a loss of the chromosome carrying the corresponding allele from the maternal parent. I have produced three or more plants monosomic each for 9 of the 10 maize chromosomes (chromosomes 1, 2, 3, 4, 6, 7, 8, 9, and 10) and these plants have been confirmed cytologically (Weber, 1970a and unpublished). This is the first time that most of the possible monosome types have been produced in a true diploid organism. Doubly and triply monosomic plants are also produced with this system (Weber, 1970b). Simultaneous appearance of two recessive markers in a single plant indicates monosomy for two different chromosomes. Double monosomes 1—8 (*bm* and *j*), 2—8 (*lg* and *j*) and 8—10 (*j* and *g*) were detected in this way.

Of the mutants in Mangelsdorf's tester, five are for traits expressed in sporophyte tissue (*bm, lg, gl, j,* and *g*) and five are for traits expressed in the endosperm (*a, su, pr, y,* and *wx*). Because the r_{x1}-induced non-disjunctive event is post-meiotic (Weber, unpublished), there is non-correspondence between endosperm and embryo chromosome constitutions. Consequently, loss of a chromosome which is marked by an endosperm trait of Mangelsdorf's tester from the embryo of a kernel is not accompanied by a loss of the same chromosome in the endosperm of that kernel. Consequently, the endosperm would not express this recessive; appropriate testcrosses are necessary to make this determination. However, because of the lower vigor and high sterility of the doubly monosomic plants, these testcrosses were not possible. Plants expressing a given mutant marker (monosomic for a given chromosome) are relatively uniform in height; however, occasionally a plant is strikingly smaller or morphologically different from other plants in this monosome class. Microsporocyte samples were taken from these exceptional plants and certain of these plants were also doubly monosomic. One smaller *j* plant (monosomic for chromosome 8) had extremely short internodes and one of the two invalent chromosomes was consistently associated with the nucleolus at diakinesis (Fig. 1). Therefore, the other monosomic chromosome in this plant was chromosome 6 which bears the nucleolar organizing region. Two other smaller *j* plants were doubly monosomic. One had narrow leaves and the other had normal leaves. Because the morphologies of these plants were different, the second unidentified mono-

somic chromosomes in these plants were also different. These plants will be designated 8—? narrow-leaved and 8—? normal-leaved respectively.

Diakinesis and Metaphase I Configurations in Doubly Monosomic Plants

The 1—8 doubly monosomic plant was desynaptic with an average of only 4.56 bivalents per diakinesis cell (163 cells). Numerous univalents were also present at metaphase I. As two other plants monosomic only for chromosome 1 were also desynaptic and monosome 8 plants were normal at diakinesis, the desynapsis is due to monosomy of chromosome 1. This confirms Baker and Morgan's (1966) report that monosome 1 plants in maize are desynaptic. The desynapsis appears to be due to hemizygosity of the *as* locus on chromosome 1 (Baker and Morgan, 1969).

Table 1. *Frequency of different pairing configurations at diakinesis in doubly monosomic of maize pollen mother cells*

Monosomic chromosomes	Number of cells with		Total	Per cent of cells with 9 "pairs"
	$8^{II} + 2^{I}$	9 "pairs"		
2 and 8	550	26	576	4.5
6 and 8	94	2	96	2.1
8 and 10	375	5	380	1.3
8 and ? narrow-leaved	374	28	402	7.0
8 and ? normal leaved	196	8	204	3.9
Total	1589	69	1658	
Average of per cents found in doubly monosomic plants				3.67

Table 2. *Frequency of different pairing configurations at metaphase I in doubly monosomic of maize pollen mother cells*

Monosomic chromosomes	Number of cells with		Total	Per cent of cells with 9 "pairs"
	$8^{II} + 2^{I}$	9 "pairs"		
2 and 8	296	4	300	1.3
8 and 10	162	4	166	2.4
8 and ? narrow-leaved	321	8	329	2.4
8 and ? normal-leaved	186	5	191	2.6
Total	965	21	986	
Average of per cents found in doubly monosomic plants				2.18

The frequencies of the various types of diakinesis configurations in other doubly monosomic plants are given in Table 1 and those of metaphase I in Table 2. Diakinesis and metaphase I cells with 8 bivalents and 2 univalents are shown in Figs. 1 and 2 respectively. Diakinesis and metaphase I cells with 9 "pairs" are shown in Figs. 3 and 4 respectively.

Diakinesis and metaphase I were exceptionally favorable in this material, and very few cells were

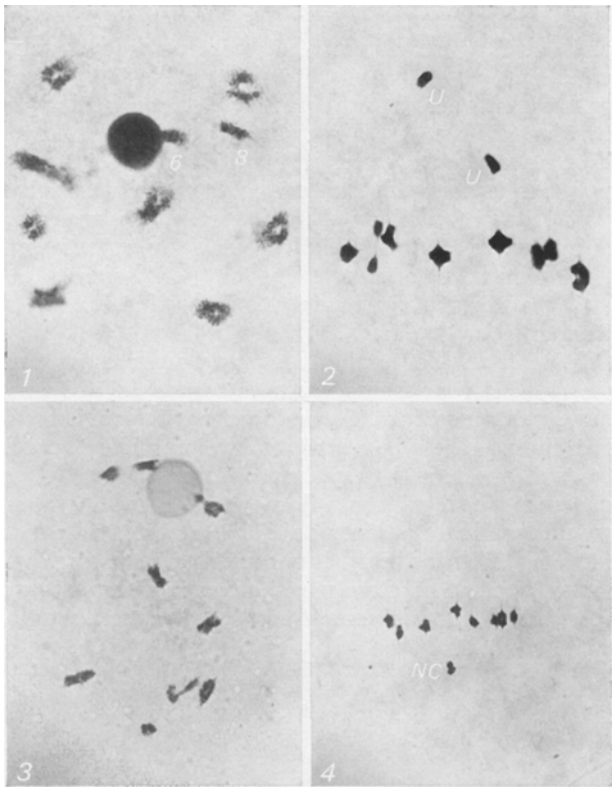


Fig. 1. Pollen mother cell at diakinesis in maize plant monosomic for chromosomes 6 and 8. The univalent chromosome 6 (6) contains the nucleolous organizing region and is attached to the nucleolus; the univalent chromosome 8 (8) is free

Fig. 2. Metaphase I in doubly monosomic maize. Pollen mother cell with 8 bivalents and 2 univalents (U)

Fig. 3. Diakinesis in doubly monosomic maize. Pollen mother cell with 9 "pairs"

Fig. 4. Metaphase I in doubly monosomic maize. Pollen mother cell with 9 "pairs". Note the atypical morphology of the "pair" composed of the two nonhomologous chromosomes (NC) lying off the metaphase plate. The centromeres are not pulled from the chromosome mass toward the opposite poles

present which could not be accurately classified. Any classification of bivalents is somewhat subjective because a continuous gradation from long, thin, barely resolvable, filamentous attachments between nonhomologous chromosomes to intimate end-to-end attachments between nonhomologous chromosomes is found in various cells. Furthermore, the two univalents are frequently positioned close to each other but not visibly connected. I have shown that nonhomologous univalents in doubly monosomic diakinesis microsporocyte cells are not randomly positioned in the cell but are located closer together than expected by chance (Weber, 1970a). A detailed discussion of this phenomenon will be presented in a subsequent paper. Also, in certain cells two univalents positioned adjacent to each other due to chance would be classified as a bivalent. In this study, I wanted to determine the absolute upper estimate of

the bivalent frequency; thus, cells in which there was any visible attachment between univalents were classified as having 9 "pairs". As filamentous attachments are not infrequently seen connecting two bivalents (Fig. 5), this value is an overestimate. Therefore, the estimates in this part of the study are upper estimates which are probably much higher than would be obtained by other investigators analyzing this same material. Filamentous attachments were not observed at anaphase I, thus these values probably represent a more accurate determination of the frequency of "pairing".

Most "pairs" of nonhomologous chromosomes were clearly different from bivalents composed of homologous chromosomes. At diakinesis and metaphase I, the "pair" often appeared as two univalents stuck to each other, and they were frequently at slightly different focal planes. Sometimes, one univalent would terminate at the side of the other univalent to form a "T", and only infrequently was a configuration seen that closely resembles and end-to-end association that is sometimes seen between homologous bivalents. At metaphase I, centromeres of homologous bivalents are characteristically directed towards opposite poles and stretched from the chromosome. Only rarely was a nonhomologous chromosome "pair" oriented near the metaphase plate with its centromeres stretched towards opposite poles. Thus, most "pairs" between nonhomologous chromosomes appear to be atypical and the frequency of chiasmatic association between nonhomologous chromosomes is certainly considerably lower than the frequency of "pairs" determined above. However, recombination can take place between paired nonhomologous chromosomes because reciprocal translocations are frequently found in the progeny of monoploid maize but rarely in progeny of diploids (Alexander, 1964; Weber and Alexander, 1972).

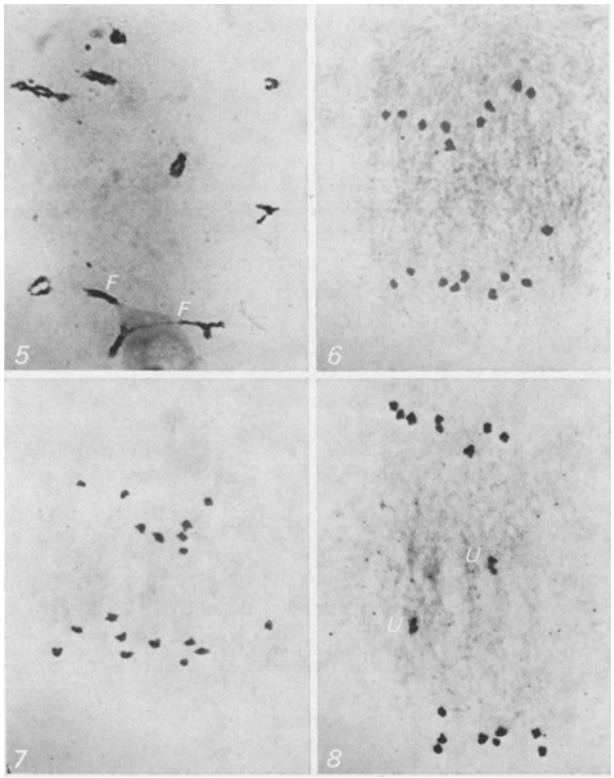


Fig. 5. Diakinesis in diploid maize. Pollen mother cell with two pairs of bivalents connected by filaments (F)

Figs. 6–8. Anaphase I in doubly monosomic of maize pollen mother cells:

Fig. 6. 9 univalents are passing to each pole

Fig. 7. 8 univalents are passing to the upper pole and 10 to the lower pole

Fig. 8. 2 univalents (U) are lagging at the metaphase plate and 8 univalents are passing to each pole

Chromosome Distribution at Anaphase I in Doubly Monosomic Plants

Anaphase I configurations were scored to determine if univalent chromosomes pass independently to the poles at anaphase I. The two monosomic chromosomes may pass to opposite poles giving a 9-9 configuration (Fig. 6), to the same pole giving a 8-10 configuration (Fig. 7), or one or both of the monosomic chromosomes may lag near the metaphase plate (Fig. 8). The frequency of cells in which the nonhomologous monosomic chromosomes passed to the same pole was not different from the frequency of cells in which they passed to opposite poles (Table 3), thus the monosomic chromosomes assort independently at anaphase I.

Table 3. *Frequency of different disjunction configurations at anaphase I in doubly monosomic of maize pollen mother cells*

Monosomic chromosomes	Anaphase I configurations[a]				Total
	9	8	8 U	8 UU	
	9	10	9	8	
6 and 8	74	62	109	78	323
8 and 10	42	47	27	11	127
8 and ? narrow-leaved	13	12	11	20	56
Total	129	121	147	109	506

[a] These diagrams represent anaphase I spindles and the number of chromosomes at each end is the number of chromosomes going to each pole. A U represents a lagging univalent chromosome.

Prophase II configurations were also scored to determine if univalent chromosomes pass independently to the poles at anaphase I. The two univalent chromosomes may pass to opposite poles to give prophase II cells pairs with 9 chromosomes in each cell (Fig. 9), may pass to the same pole at anaphase I giving a prophase II cell pair with 10 chromosomes in 1 cell and 8 in the other (Fig. 10), or one or both

of the univalents may divide equationally at anaphase I to give a cell pair with 1 or 2 monads (half univalents) in each cell. The frequency of 9-9 cell pairs was not significantly higher than 8-10 cell pairs (Table 4), thus the univalents disjoined independently at anaphase I.

Table 4. *Frequency of different prophase II cell pairs in doubly monosomic of maize pollen mother cells*

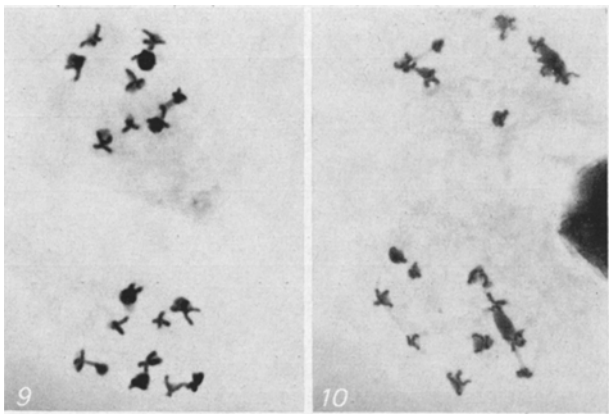
Monosomic chromosomes	Prophase II cell pairs with				Total
	9 9	8 10	8 + M[a] 9 + M	8 + 2 M 8 + 2 M	
2 and 8	59	53	94	32	238
6 and 8	34	41	2	0	77
8 and 10	73	78	12	5	168
8 and ? narrow-leaved	28	22	55	8	113
Total	194	194	163	45	59

[a] M = monad (half univalent)

The Distribution of Unpaired Chromosomes in the Progeny of Plants Hyperploid for two Chromosomes

The progeny of plants containing two chromosomes in addition to the normal diploid complement were studied to determine the transmission of two univalent chromosomes. Because both extra chromosomes (a B^4 chromosome and the *Wd* ring fragment of chromosome 9) could be followed genetically, a large population could be readily analyzed. As the B^4 chromosome is found as a univalent chromosome in 41.6% of the cells (411 cells scored in two of the plants used in these crosses) and the ring fragment in essentially all cells at diakinesis (Randolph, 1928; McClintock, 1932, 1938), 41.6% of the cells contain two univalents. This provides an extremely sensitive system to detect non-random assortment of non-homologous univalents.

Plants containing two normal chromosome 4's, a B^4, and the *Wd* ring chromosome were established. The normal 4's carried su_1 (wrinkled endosperm) and the B^4 carried Su_1 (smooth endosperm), thus, the presence of a B^4 chromosome in the endosperm of a kernel could be detected by its smooth phenotype. The *Wd* (white deficiency) ring chromosome was obtained by McClintock (unpublished) and contains the C^I (color inhibitor) allele of the C_1 locus on chromosome 9, a gene necessary for anthocyanin formation in the aleurone layer of the endosperm. C^I is dominant to *C* and inhibits anthocyanin formation in the heterozygote. If the triploid endosperm carries three chromosome 9's with *C*, the aleurone is fully colored. However, if a ring chromosome carrying C^I is also present, the aleurone is white (where the ring is present) with colored sectors (where the ring chromosome is lost). Examples of the four phenotypes are shown in Fig. 11.



Figs. 9—10. Prophase II in doubly monosomic of maize pollen mother cells:

Fig. 9. 9 univalents are present in each cell

Fig. 10. 8 univalents are present in the upper cell and 10 in the lower cell

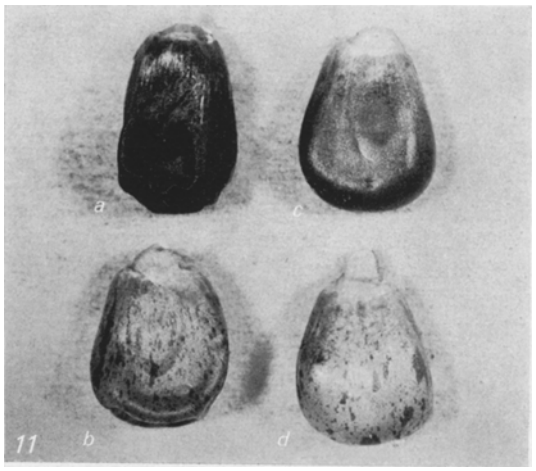


Fig. 11. Progeny of $4^{su}4^{su}B^{4^{Su}}$; 9^C9^C-Wd^{C^I} plants crossed by $4^{su}4^{su}$; 9^C9^C plants. Kernels A and B do not carry B^4; consequently, they are sugary in phenotype. Kernels C and D carry B^4 and are smooth. Kernels A and C do not carry the ring and are colored. Kernels B and D carry the ring; consequently, they are variegated

The above plants were crossed by diploid plants that were *su su*; *C C*. If the ring and B^4 chromosomes interacted and disjoined non-randomly to opposite poles at anaphase I, the frequency of B^4 chromosomes would be lower in the progeny with the ring than in progeny without the ring. On the other hand, if the two chromosomes segregated independently, the frequency of the B^4 chromosomes would be the same in progeny with and without the ring. The results of this experiment are presented in Table 5. The frequency of B^4 chromosomes in ring-containing kernels is no lower than in kernels without the ring in either of the reciprocal crosses. Therefore, the two univalent chromosomes did not interact to cause them to disjoin to opposite poles at anaphase I. There was, however, a slightly higher frequency of B^4 chro-

Table 5. *Frequency of B^4 chromosome in ring-containing and ring-deficient progeny from crosses of maize plants containing a supernumerary Wd ring chromosome and a supernumerary B^4 chromosome*

Female parent	Male parent	Number of progeny with				Frequency of B^4 in ring-deficient progeny	Frequency of B^4 in ring-containing progeny
		no supernumerarys	B	*Wd* ring	B^4 + *Wd* ring		
2 N + B^4 + *Wd* Ring	2 N	4297	2273	836	492	34.06%	37.05%*
2 N	2 N + B^4 + *Wd* Ring	12.969	3742	1834	545	22.39%	22.91%*

* Chi square tests without a priori hypothesis utilizing Yates correction factor were not significant at the 0.05 level in either of these crosses.

mosomes in the ring-containing progeny than in the ring-deficient progeny. This might suggest that the two univalents tended to pass nonrandomly to the same pole at anaphase I; however, the deviation in either cross is not significant. These results are in agreement with those obtained previously (Weber, 1969) and indicate that there is no interaction between two nonhomologous univalents in maize which cause them to disjoin to opposite poles at anaphase I.

Discussion

This study was initiated to clarify the apparently contradictory reports of the behaviour of nonhomologous univalents in maize plants containing two univalents (Weber, 1966, 1969; Michel and Burnham, 1969). In Michel and Burnham's study, an average of 9.7% and a maximum of 14.5% of the cells had two chromosomes available for pairing at diakinesis and in my study a maximum of 21.9% were present. In a doubly monosomic plant, all meiotic cells have two chromosomes lacking homologs; thus, this is the most sensitive possible system to test for an interaction between two nonhomologous univalents. However, doubly monosomic plants were previously not available in a diploid organism and the current study appears to be the first cytological study of this interesting aneuploid type.

Michel and Burnham (1969) found that in cells where two nonhomologous chromosomes are available for pairing (cells with 10 bivalents and two univalents or cells with 11 "pairs"), the two univalents were found as a "pair" in an average of 28.1% of the diakinesis and 25,0% of the metaphase I cells. Only one questionable "pair" between nonhomologous chromosomes was seen at diakinesis and one at metaphase in my study (Weber, 1969). A low frequency of pairing between nonhomologous chromosomes was observed in the present study at diakinesis (3.8%) and metaphase I (2.2%). These frequencies are considerably lower than the surprisingly high frequencies found by Michel and Burnham (1969). In the current study, all associations, however tenuous, were scored as "pairs"; thus, the frequencies reported in this study represent the highest estimates of these frequencies and are higher than others might have obtained scoring the same material. Furthermore, the associations observed usually are not of the type characteristic of associations between homologous chromosomes, and many of the associations are probably achiasmate. Pairing between nonhomologous chromosomes is also found in monoploid maize (McClintock, 1933; Ford, 1952; Ting, 1966; Snope, 1967; and others) and other monoploids (Kimber and Riley, 1963). Furthermore, at least part of these bivalents are chiasmate associations because reciprocal translations are frequently found in the progeny of monoploid maize and rarely in progeny of dipliods (Alexander, 1964; Weber and Alexander, 1972). We have recently shown that at least part of the translocations from monoploid parentage in maize appear to be generated by recombination between paired redundant segments of the genome, because 12 of 22 independently isolated reciprocal translocations from monoploid parentage had cytologically indistinguishable breakpoints (6L.2-3 and 7L.2-3) and two of the remaining ones had a second pair of cytologically indistinguishable breakpoints (2L.9 and 6L.4) (Weber and Alexander, 1972). The points at which translocations were repeatedly generated appear to represent two pairs of redundant segments in the normal chromosomes between which recombination took place. Translocations are also found in the progeny of singly monosomic maize plants (Weber 1972); these are being used to map additional redundant segments in the diploid maize genome. Similarly, part of the associations in doubly monosomic plants might be chiasmate associations if the two chromosomes contain a redundant segment.

It was also noted that nonhomologous unpaired univalent chromosomes are not randomly positioned in the diakinesis pollen mother cells; rather they are found closer to each other than expected by chance. A preliminary description of this phenomenon was presented (Weber, 1970a), and a detailed discussion will be published later. Michel and Burnham (1969) also noted that the two univalents at metaphase I were oriented "such that they could be in the process of pairing or perhaps had already paired and were disjoining"; thus, they might have been observing this same phenomenon. This phenomenon is not distributive pairing (Grell, 1962) because it does not result in a non-random distribution of nonhomologous

univalents at anaphase I. It could, however, be a phenomenon related to distributive pairing.

In an earlier study (Weber, 1966, 1969), I scored anaphase I configurations to determine if two nonhomologous univalents were distributed non-randomly to the poles at anaphase I. Michel and Burnham (1969) scored prophase II cells to answer the same question. Both methods of scoring should provide equivalent data; however, I found the distribution to be random, whereas Michel and Burnham found it to be non-random with the extra chromosomes passing non-randomly to opposite poles. In the current study, both anaphase I and prophase II cells were scored to determine if the different results could somehow be ascribed to the different methods of scoring. Both methods of scoring demonstrated that the nonhomologous univalent chromosomes disjoined randomly to the two poles at anaphase I (Tables 3 and 4). Extensive genetic data on the transmission of two nonhomologous univalent chromosomes (Table 5) extent and confirm these data. These data support the earlier conclusion (Weber, 1966, 1969) that nonhomologous univalents are disjoined randomly to the two poles at anaphase I. Thus, "distributive pairing" is either not present or it is operating with a much lower efficiency in maize (and probably most plants) than in *D. melanogaster*.

It is not understood why the high frequency of pairing between heterologous univalents at diakinesis and metaphase I and the non-random distribution of chromosomes at anaphase I was found in doubly trisomic plants by Michel and Burnham (1969). The differences might be ascribed to differences in genetic background or growing conditions, but this seeems unlikely. Standard cytological procedures were used in all studies.

Acknowledgement

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Literature

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