CROSSING OVER AND ANAPHASE I DISTRIBUTION OF THE CHROMOSOMES OF A MAIZE INTERCHANGE TRIVALENT¹

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PREDICTION of genetic segregation ratios from polyploids and polysomics is usually complicated by the necessity of simultaneous estimation of crossover frequencies and frequencies of the modes of anaphase I distribution. In a special hyperploid maize stock, the frequency of chiasma formation in one arm of a trivalent configuration and the relative frequencies of disjunctive and nondisjunctive distribution of the chromosomes involved in these chiasmata can be estimated genetically with only the one assumption (and this for only part of the data) that random distribution occurs at anaphase II. This maize stock carries *Zea-Tripsacum* interchange chromosomes such that a trivalent configuration is almost always found at pachytene. Two of the three chromosomes involved in these trivalents regularly disjoin from each other, and preferential pairing effectively limits the type of configuration formed so that crossing over occurs between the remaining chromosome and only one of these two. The genetic constitution has been made such that recessive progeny arise only from such crossing over. The relative frequency of the recessive progeny among 20- and 21-chromosome plants is a direct indication of the relative frequencies of disjunctive and nondisjunctive distribution of chromosomes involved in these chiasmata.

There are numerous accounts in the literature of deviations from standard recombination frequencies in the multivalents of polyploids, polysomics and translocation configurations. Where a decrease in crossover frequency is found, this is usually attributed to synaptic failure. Thus OLIVER and VAN ATTA (1932) noticed that if translocated regions of *Drosophila* chromosomes paired with their homologues in oogonial cells the crossover frequency was normal or nearly normal, but that otherwise it was reduced. BURNHAM (1934) reported similar observations in maize, where crossover frequencies from translocated regions were markedly reduced except in an unusual case where pachytene pairing was complete in the cross configuration found in such structural hybrids. BEADLE (1933), DOBZHANSKY (1930, 1935) and BROWN (1940) found a reduced crossover frequency in translocated regions in *Drosophila*. RHOADES (1931, 1936) reported decreased crossover frequencies in duplicated regions of *Drosophila* and maize, and DOBZHANSKY reported similar results in *Drosophila*. UPCOTT (1939) found a lower chiasma frequency per chromosome in tetraploid *Primulas* than would have been deduced from diploid chiasma frequencies.

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Precise comparisons of observed and expected recombination frequencies based on extent of synapsis have not appeared because direct observations of the extent of pairing in pachytene configurations, and therefore estimates of the degree of crossover inhibition expected as a direct result of pairing failure, are usually impossible.

Increases in crossover frequencies above standard expectation in multivalents of polyploids, polysomics and structural hybrids, though not easily explained, have also been reported repeatedly. DOBZHANSKY (1930, 1935) and BROWN (1940) found some increase in crossing over in chromosome arms opposite translocation exchange in *Drosophila*. RHOADES (1936) found a greatly increased crossover frequency in maize in an arm opposite one for which a duplicating fragment was present. Regional increases in crossover frequencies per chromosome were found in triploid *Drosophila* by BRIDGES and ANDERSON (1925) and by REDFIELD (1930, 1932). Increases in chiasma frequency were found in triploid *Tulipa* by DARLINGTON and MATHER (1932), in triploid *Hyacinthus* by STONE and MATHER (1932) and in trisomic maize by DARLINGTON (1934). CALLAN (1949) found similar increases in chiasma frequencies in tetraploid *Forficula*, as did OKSALA (1952) in tetraploid *Odonata*, and JOHN and HENDERSON (1962) in tetraploid *Schistocerca*. On the other hand RHOADES (1933) calculated a linkage strength between two maize loci in a trisome to be similar to that found in diploid maize, and WELCH (1962) found linkage strength to be approximately equal in diploid and tetraploid maize. However, as RHOADES (1933) pointed out, genetical studies of crossover frequency in polyploids and polysomics are subject to the bias of selective anaphase I distribution following chiasma formation, which may lead in many cases to an underestimation of crossover frequency. Estimations of crossover frequency from chiasma frequency are rarely free from uncertainties of interpretation and possible error introduced by terminalization.

PRITCHARD (1960) has reasoned that increases in crossover frequency per chromosome in polyploids are consistent with expectation if crossing over occurs at a very early stage when only very short chromosome intervals are effectively paired, since the likelihood of pairing would, with the simplest model, be expected to be increased when more than two members are present. However, the complexity of the situation is emphasized by the fact that, as mentioned above, where multivalent configurations are expected, increases in crossover frequency are sometimes found in regions present only in duplicate, and reductions or no change may be found in regions present in more than duplicate. Deviations from the normal diploid expectation of crossover frequency with changes in ploidy or structural hybridity may in fact be causally related to changes in synaptic configuration. It has been suggested by CALLAN (1949) that a change of pairing partner such as that found in multivalents reduces interference, and OKSALA (1952) has presented some evidence that it may be the synaptic failure that usually locally accompanies the pairing partner change which is responsible for interference reductions. Others have attempted to account for inter- and/or intrachromosomal crossover effects in the more general terms of disturbances of coiling and synapsis (see RAMEL [1962] for review of literature). It is clear that more data are needed

from situations where more of the pertinent variables can be either controlled or independently observed.

It is one of the purposes of the present study to examine crossover frequency in a region usually involved in a multivalent configuration at pachytene, in material where genetic recombination frequencies can be directly estimated independently of anaphase I distribution, and pachytene configurations with maximum clarity can be studied.

While this study also tests the relative frequencies of disjunctive and nondisjunctive distribution of chromosomes involved in chiasmata, critical evaluation of the importance of chiasma formation in the determination of anaphase I distribution in this case must be postponed until tests are also available for distribution frequencies in the absence of such chiasma formation. As indicated earlier, the fact that chiasmata may strongly influence such distribution has long been recognized. RHOADES (1933) noted not only that chromosomes of multivalents mutually involved in a chiasma probably tend to disjoin from each other at anaphase I, but also that the likelihood of such selective disjunction would be expected to decrease with greater distance of the chiasma from the centromere. BROWN (1940) and PIPKIN (1940) deduced a negative correlation between nondisjunction and crossing over of adjacent members of translocation configurations of *Drosophila*. BURNHAM (1950), in studies of spore types from chromosome 6 translocation heterozygotes in maize, found that in this special case, homologous centromeres of chromosomes involved in a crossover in the region between the centromere and the breakpoint of the translocation generally go to opposite poles at anaphase I. Relative lengths of the two axes was not a factor in determining segregation. From ring configurations, nondisjunction of homologous centromeres occurred only when there was no crossing over. From chain configurations, this type of nondisjunction occurred rarely if at all, even without crossing over. However, in BURNHAM's work it was impossible to distinguish adjacent distribution, involving disjunction of homologous centromeres, from alternate distribution, following chiasma formation. In the present study of another special case, the relative frequencies of these two types of distribution following chiasma formation are estimated genetically.

MATERIALS AND METHODS

The maize used in this study was a 21-chromosome stock in which a portion of the short arm of the distal region of chromosome 2 had been exchanged for a corresponding partially homologous region of a *Tripsacum* chromosome in an earlier generation. The constitution of these chromosomes is diagrammed in Figure 1. The genetic map of chromosome 2 is shown in Figure 2. Cytologically the original interchange point between maize chromosome 2 and the *Tripsacum* chromosome was located at 24-25 percent of the pachytene length of chromosome 2 from the distal end of the short arm (MAGUIRE 1960b). Since the arm ratio of chromosome 2 in this stock has been estimated to be 1.4:1 (MAGUIRE 1962b) the most proximal location for the original interchange is estimated to be at 60 percent of the distance from the end of the short arm to the centromere. On the basis of unpublished data made available by DR. EARL B. PATTERSON and DR. ERNEST G. ANDERSON and cytological findings of LONGLEY (1958), it is possible to approximate the cytological location of genetic markers. From Table 1, it seems probable that the most proximal possible location of *sk* is at 63 percent of the distance from the distal end of the short

FIGURE 1.—Genetic constitution of plants having a normal chromosome 2 of maize and two chromosomes involved in a reciprocal interchange between chromosome 2 and a *Tripsacum* chromosome. Broken lines indicate the chromosome segments derived from *Tripsacum*. The transverse lines indicate centromeres.

FIGURE 2.—The genetic map of chromosome 2 of maize (RHOADES 1955). The arrow indicates the most proximal probable location of the interchange point. The double crossbar is the centromere. *ws*—white sheath, *al*—albescens, *lg*—liguleless, *B*—Booster (a plant-color intensifier), *sk*—silkless, *fl*—floury endosperm, *ts*—tassel seed, *v*—virescent seedling, *Ch*—chocolate pericarp.

TABLE 1

Cytological and linkage data from various translocations involving chromosome 2S

Translocation	Cytological position	Linkage					
2-9a	2S.36	<i>B</i>	1.6 (884)	<i>sk</i>	0.6 (1224)	T*	
		<i>B</i>	1.2 (81)	<i>sk</i>	1.2 (81)	T	
1-2b	2S.36	<i>B</i>	3.9 (412)	T*			
2-3c	2S.46	<i>B</i>	0.5 (3317)	T	4.9 (183)	<i>sk</i> *	
		<i>B</i>	2.0 (199)	T	4.0 (199)	<i>sk</i>	
2-3 5304	2S.62	<i>gl</i> ₂	2.8 (109)	T	4.6 (109)	<i>B</i>	
2-6b	2S.69	<i>gl</i> ₂	3.9 (2008)	T	0.9 (3553)	<i>B</i> *	
2-5g	2S.79	<i>gl</i> ₂	2.1 (146)	T	4.1 (146)	<i>B</i>	

Cytological data are from LONGLEY (1958). Figures to the right of the decimal in column 2 indicate the position of the interchange as percent of its distance from the centromere to the end of the arm. Genetic data have been made available by DR. EARL B. PATTERSON or by DR. ERNEST G. ANDERSON (DR. ANDERSON'S data are marked with an asterisk). The linkage values for each region are based on the number of plants, italicized in parentheses. This table was compiled by DR. PATTERSON.

arm to the centromere. If 0.9 map units are allotted to each one percent of cytological distance in the short arm, the most proximal possible location of the Zea-Tripsacum interchange is estimated to be at 54 on the genetic map. This would include in the interchanged region 24 crossover units proximal to gl_2 . This is thought to be a maximal estimate because at each step a value considered maximum was selected, and because it is based on the assumption that there is a linear relationship along the chromosome between the genetical and cytological maps, although crossing over is known to be somewhat more concentrated toward the distal region.

In 21-chromosome plants carrying the interchange pachytene trivalent configurations are found in about 95 to 98 percent of microsporocytes. Pachytene pairing failure in these trivalents has been found to occur in the region of pairing partner change such that on the average 20 percent of the normal maize chromosome 2 (48 percent of the short arm) is found synapsed with the interchange chromosome carrying its homologue (MAGUIRE 1960b). (Configurations usually formed are of the type illustrated in Figure 3). Therefore, it is estimated that at most an average of 14 crossover units proximal to gl_2 are synapsed in trivalent configurations at pachytene.

The Tripsacum segment transferred to the short arm of chromosome 2 (referred to as chromosome 2^T) has been shown to carry dominant alleles for at least three loci found in this region of chromosome 2 (MAGUIRE 1962a), Ws_3 , Lg_1 , and Gl_2 . Pairing between the Tripsacum segment (marked by a terminal knob) and either of the corresponding maize chromosome segments rarely or never occurs, in spite of their partial homology and the fact that the presence of this partially homologous Tripsacum segment may exert some influence on the synapsis of the maize homologues (MAGUIRE 1961). The remaining portions of chromosome 2 (in chromosomes 2 and 2^T) have always been found to be synapsed at pachytene.

To test the frequency of genetic recombination in trivalent configurations between the distal regions of the two homologous short arms of corn chromosome 2 (in chromosomes 2 and T^2), plants of the constitution shown in Figure 1 were constructed. They were pollinated by a chromosome 2 tester stock, homozygous recessive ws_3 , lg_1 , gl_2 . Progeny phenotypically recessive for any of the markers arise from such a cross as a result of crossing over in trivalent configurations. It is assumed that the frequency of crossing over between Tripsacum and maize segments is negligible, since pairing of these segments in trivalents is rare and since crossing over between these segments in disomic plants is also rare, even though synapsis is often regular in this latter case (MAGUIRE 1960a).

Twenty-chromosome recessive plants are therefore the result of crossing over between the two corn segments, followed by disjunctive distribution at the first anaphase of chromosomes 2 and T^2 (which were involved in the chiasma). Chromosome T^2 occasionally disjoins from the other two chromosomes (as discussed below), but gametes lacking both the normal chromosome 2 and chromosome 2^T do not survive. All other gametes are apparently fully viable. Twenty-one-chromosome recessive progeny are the result of similar crossing over followed by nondisjunctive distribution at anaphase I of the two chromosomes involved in the chiasma, and distribution of the crossover chromatids to opposite poles at anaphase II. The assumption of random distribution of chromosomes at anaphase II is a possible source of error in the analysis of 21-chromosome progeny.

FIGURE 3.—Camera lucida drawing of a typical trivalent configuration.

Direct cytological studies of microsporocytes of the stock used here (MAGUIRE 1957) have shown that trisome-2 plants produced by nondisjunction of chromosomes 2 and 2^T constitute about 4 percent of the progeny. If all of these arise from such nondisjunction at anaphase I, and the chiasma frequency in such sporocytes is as high as in the population as a whole, the total progeny from which the expected recombination fraction is derived should be decreased by a factor of 4 percent.

It is considered unlikely that there was selective distribution of chromosomes to functional megaspores since anaphase separation of trivalents was regular with no apparent lagging, and anaphase II appeared normal. It is also thought that there was no appreciable error introduced from differential viability, since ears were well filled and germination of seed was excellent (95 to 98 percent).

Reciprocal crosses were impossible since 21 chromosome plants of the type used in this experiment are completely pollen sterile, owing apparently to a factor or factors present in the non-homologous portion of chromosome T² (MAGUIRE 1957). Twenty-chromosome plants of this stock have always been found to have normal pollen, so pollen sterility was considered a reliable test for the presence of chromosome T².

Families were closely related genetically since the female parents were siblings derived from a 21-chromosome stock which had been pollinated for four successive generations by a chromosome-2 tester stock and then by inbred L289. The male parent was again the chromosome-2 tester line.

RESULTS AND DISCUSSION

Crossover frequencies: Results are listed in Table 2. Because of the small size of expected recessive classes within families, individual progenies are not analyzed and compared for heterogeneity among them. Heterogeneity among components of pooled data is therefore a possible source of error. With the assumption of random distribution at anaphase II, chiasma frequencies were estimated as indicated in Table 3, to have been 19.2 percent in the *ws₃-lg₁* region, 43.2 percent in the *lg₁-gl₂* region and 39.2 percent in the region proximal to *gl₂* and distal to the point of interchange. When standard expectations of recombination frequency based on map distances are corrected for the estimated 8 percent nondisjunction of maize centromeres (expected from past experience) observed recombination frequencies

TABLE 2

*Segregation data from five families (female parent of constitution shown in Figure 1 × *ws₃ lg₁ gl₂*)*

Phenotype	Family										Total	
	P6234 20- chrom.	21- chrom.	P6235 20- chrom.	21- chrom.	P6236 20- chrom.	21- chrom.	P6237 20- chrom.	21- chrom.	P6320 20- chrom.	21- chrom.		
Gl Lg Ws	63	76	39	32	73	65	24	43	62	66	261	282
Gl Lg ws	6	2	3	0	1	0	7	0	4	1	21	3
Gl lg ws	13	1	9	0	7	0	9	2	14	5	52	8
Gl lg Ws	0	0	0	0	1	0	0	0	2	0	3	0
gl Lg ws	0	0	0	0	0	0	0	0	0	0	0	0
gl Lg Ws	1	0	0	0	1	0	1	0	2	0	5	0
gl lg Ws	0	0	0	0	3	0	1	0	0	0	4	0
gl lg ws	10	0	7	0	14	1	13	0	11	1	55	2

in the ws_3 - lg_1 and lg_1 - gl_2 regions do not differ from them significantly at the 5 percent level from normal (chi-squares = 0.29 and 2.96 respectively). There is a significant increase, however, (1 percent level) in the region proximal to gl_2 if a maximum of 14 crossover units is available there (chi-square = 10.09). The validity of the correction for nondisjunction of maize centromeres can be questioned, since it is based on the possibly unjustified assumption that chiasma frequency was as high in the tested region in cells in which this kind of nondisjunction occurred as it was in the population as a whole. Without this correction (however), observed recombination frequency still does not deviate significantly from normal in the ws_3 - lg_1 or lg_1 - gl_2 regions (chi-squares = 0.45 and 1.67), and a significant increase remains in the region proximal to gl_2 (chi-square = 7.93) if the length available for crossing over here is estimated to be 14 units. The estimate of 14 units described above is considered maximal, based on a correlation of genetic and cytological maps and the extent of pachytene pairing found in this region in microsporocytes. The estimation of pairing extents in megasporocytes from microsporocyte measurements is probably reasonable, since the average metaphase I trivalent frequency in microsporocytes (90 percent) is close to the genetical estimate in this experiment of the frequency of megasporocytes having at least one chiasma in the pertinent region (88 percent). However, the precise period during which crossovers occur has not been established. It is possible that crossing over normally occurs at a stage prior to that at which pairing extents were measured, and that pairing was either more or less complete at this time.

On the other hand if the entire distal region of the short arm of chromosome 2 contained in the interchange (with either maximal or minimal estimates of its genetic length) is considered to have been available for crossing over, recombination frequency in the region proximal to gl_2 does not differ from standard expectation at the 5 percent level (with or without the correction for 8 percent nondisjunction of maize centromeres; chi-squares = 2.04 and 3.47). There are alternate explanations for such a result: Either (a) crossing over does indeed occur at an earlier time when the entire region is paired, or (b) it occurs at random in accord with the theory of PRITCHARD (1960) before synapsis is widespread, or (c) crossing over is limited to regions ordinarily found synapsed at pachytene; however, with interruption of synapsis and consequent crossover suppression in one region, an increase, possibly compensatory, occurs in adjacent regions. Critical evaluation of the possible explanations is impossible at present. While PRITCHARD's proposal that crossing over may occur at a very early stage when only extremely short intervals are effectively paired has been difficult to reconcile with accumulated evidence that crossover suppression accompanying chromosome aberrations consistently follows regions of pachytene synaptic failure, there are studies which suggest that likelihood of initiation of synapsis may be reduced by gross structural rearrangement of homologues (DOYLE 1959; SHAVER 1963). There are on the other hand (in addition to the cases mentioned earlier from multivalents) several reports in the literature of increases in crossover frequency which accompany crossover suppression elsewhere in the chromosome. WHITE and MORLEY (1955) found increases in chiasma frequency outside pericentric inversions which were

compensatory to decreases within these rearrangements in grasshopper spermatocytes. Likewise STEPHENS (1961) and GILES (1961) have noted in cotton that crossover reduction attributed to the presence of a nonhomologous region or heterozygous inversion is accompanied by a compensatory increase in crossover frequency in other regions of the chromosome. RUSSELL and BURNHAM (1950), MORGAN (1950) and RHOADES and DEMPSEY (1953) found increases in crossover frequency in regions adjacent to inversions in maize, although it is not clear whether these are compensatory to actual suppression of crossing over. KOMAI and TAKAKU (1940, 1942) found increases in crossover frequency in regions distal from heterozygous inversions in *Drosophila virilis*.

In the present case if the pachytene pairing failure found in trivalent configurations in the vicinity of the interchange is a result of opening of a region in which crossing over has actually occurred at an earlier stage, then it is necessary to assume a terminalization of chiasmata before or during pachytene such that non-sister chromatids are brought into extremely close proximity.

Further tests are needed for confirmation of the results. Tests are now in progress with additional genetic markers, proximal to gl_2 and in the long arm of chromosome 2.

Disjunction frequencies: Table 3 gives the estimated relative proportions of disjunctive and nondisjunctive distribution from single chiasmata in the tested arm of the trivalent configuration. The average frequency of nondisjunction following such chiasma formation for the entire arm was 19 percent, with individual frequencies of 29 percent for the ws_3 - lg_1 region, 26 percent for the lg_1 - gl_2 region and 8 percent for the region proximal to gl_2 . (There was no evidence that nondisjunction occurs following double chiasma formation.) Thus chiasma formation in this arm of the trivalent configuration was usually followed at anaphase I by disjunction of the chromosome involved. It also appears that proximal chiasmata may be more likely than distal chiasmata to be followed by disjunctive distribution although more data are needed to confirm this.

At least one chiasma is always or nearly always formed in the opposite arm of the trivalent configuration, which involves all of the long arm of chromosome 2, commonly thought to contain more than the 49 known map units, as well as approximately 25 units in the short arm. Nondisjunction of the two centromeres in this arm of the trivalent configuration has been found to occur in this stock, as mentioned earlier, with a frequency of about 8 percent (on the basis of 4 percent chromosome-2 trisomic progeny), if all of the chromosome-2 trisomes found can be attributed to anaphase I nondisjunction. This is probably a reasonable assumption, since nondisjunction of other chromosomes was not found. Conceivable reasons for a lower frequency of nondisjunction in this arm (as compared with the arm involved in the partner exchange) are purely conjectural at present, and include the following: (1) A higher frequency of double chiasmata occurs in this longer arm of the trivalent, and this may result in the more frequent coorientation of the centromeres of this region. (2) The centromere of one of the chromosomes of the shorter arm and its surrounding chromatin were derived from *Trip-sacum*. This fact in itself may reduce the probability of its coorientation with a

TABLE 3

Recombination and disjunction frequencies analyses. Pooled data from five families

Type of chiasma*		20-chromosome progeny										21-chromosome progeny									
		GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws	GI Lg Ws	GI Lg ws
none	{disjunction nondisj.	1/2										1/2									
single	{disjunction nondisj.	1/2										1/2									
single (1)	{disjunction nondisj.	1/4										1/4 (6.6%)									1/8 (0.3%)
single (2)	{disjunction nondisj.	1/2																			
single (3)	{disjunction nondisj.	1/4																			
2-strand doubles (1,2)	{disjunction nondisj.	1/2																			
3-strand doubles (1,2) a	{disjunction nondisj.	1/4																			
3-strand doubles (1,2) b	{disjunction nondisj.	1/2																			
4-strand doubles (1,2)	{disjunction nondisj.	1/2																			
2-strand doubles (2,3)	{disjunction nondisj.	1/4																			
3-strand doubles (2,3) a	{disjunction nondisj.	1/2																			
3-strand doubles (2,3) b	{disjunction nondisj.	1/2																			
4-strand doubles (2,3)	{disjunction nondisj.	1/2																			
2-strand doubles (1,3)	{disjunction nondisj.	1/4																			
3-strand doubles (1,3) a	{disjunction nondisj.	1/2																			
3-strand doubles (1,3) b	{disjunction nondisj.	1/2																			
4-strand doubles (1,3)	{disjunction nondisj.	1/2																			
Observed frequencies (total = 696)		37.5%	3.0%	0.4%	7.5%	0.7%	0	0.6%	7.9%	40.5%	0.4%	0	1.1%	0	0	0	0.3%				

* Region (1) = breakpoint to gl^1 ; Region (2) = gl^1 - lg ; Region (3) = lg - ws . Disjunction vs. nondisjunction refers to chromosomes 2 and 1². There was no evidence of triples.

Since GI Lg Ws, gl Lg Ws, gl Lg ws 21-chromosome classes are 0, there is no evidence for nondisjunction following double chiasmata; assumed to be 0.

Ratio of nondisjunction:disjunction following single in region (1) = $(0.3 \times 8) : (6.6 \times 4) = 1:11.00$

Ratio of nondisjunction:disjunction following single in region (2) = $(1.1 \times 8) : (6.4 \times 4) = 1:2.91$

Ratio of nondisjunction:disjunction following single in region (3) = $(0.4 \times 8) : (2.0 \times 4) = 1:2.50$

Chiasma frequency, region (1): 6.6×4 26.4

Chiasma frequency, region (2): 1.1×8 8.8

Chiasma frequency, region (3): 0.35×16 5.6

Observed frequencies (total = 696)

Observed frequencies (total = 696)

Observed frequencies (total = 696)

Observed frequencies (total = 696)

Chiasma frequency, region (3): 9.0×4 36.0

Chiasma frequency, region (3): 0.4×8 3.2

Chiasma frequency, region (3): 0.2×16 3.2

Chiasma frequency, region (3): 0.3×16 4.8

Chiasma frequency, region (3): 0.3×16 4.8

Chiasma frequency, region (3): 0.3×16 4.8

Chiasma frequency, region (3): 0.3×16 4.8

maize centromere. BURNHAM (1950) found that where chains were formed from translocation configurations, homologous centromeres rarely failed to disjoin. The findings of STURTEVANT (1936), NOVITSKI (1954) and SANDLER and BRAVER (1954) suggests that the centromeres or adjacent regions may exert an important influence in nonrandom segregation in *Drosophila*. (3) The mechanical difficulties of coorientation may be greater for the shorter arm, although the work of BURNHAM (1950) on frequencies of nondisjunction from various types of translocation configurations argues against this.

GRELL (1962) has presented convincing evidence that nonrandom distribution of noncrossover chromosomes occurs in *Drosophila*. It is of considerable interest whether a similar phenomenon occurs in maize where there is normally no clear advantage in a mechanism for orderly distribution in the absence of crossing over (as there is in the male of *Drosophila*) and where cytological events of the meiotic prophase may be readily followed.

Anaphase I chromosome distribution following failure of chiasma formation in the tested region cannot be traced by the experiment described above. Such chiasma failure occurred in these experiments with an average frequency of 12 percent, a figure in close agreement with the average metaphase I univalent frequency (10 percent) observed cytologically in microsporocytes of the tested plants.

In testcrosses of 21-chromosome plants in which dominant alleles for the *ws*, *lg*, *gl*₂ loci are carried only on the Tripsacum segment a test is readily available of the total frequency (irrespective of chiasma formation) of anaphase I nondisjunction of the two maize chromosome segments which correspond for this region. From such crosses, 20-chromosome recessives and 21-chromosome dominants arise from disjunction of these segments at anaphase I, while 21-chromosome recessives and 20-chromosome dominants arise from nondisjunction. Data are available at present from only one such progeny, with a frequency of 33 percent nondisjunction:

20-chromosome recessives:	50 plants	}	disjunction
21-chromosome dominants:	52 plants		
21-chromosome recessives:	25 plants	}	nondisjunction
20-chromosome dominants:	26 plants		

If (the average) 10 percent chiasma failure is assumed to have occurred with *random* distribution of univalents at anaphase I, the distribution following chiasma formation in this case would have been 31.5 percent nondisjunctive (or 29 percent nondisjunctive if 8 percent nondisjunction of maize centromeres is assumed to have occurred). This is a high value although well within the range of the results described above. Data from many more progenies are needed in order to estimate whether in the absence of crossing over and chiasma formation, the univalent tends to be distributed nonrandomly with respect to the two chromosomes 2 (or in the terminology of GRELL (1962) is involved in "distributive pairing"). If "distributive pairing" or some form of directed distribution occurs here, it is clearly a post-pachytene phenomenon with no cytologically observable pairing.

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SUMMARY

In maize stocks carrying certain reciprocal *Zea-Tripsacum* interchange chromosomes and a normal *Zea* homologue, trivalent configurations are found in most microsporocytes at pachytene. When stocks of this type are constructed which have a specific genetic constitution, frequencies of crossing over and nondisjunctive distribution from the trivalent following crossing over may be independently estimated. Evidence is reported that either crossing over occurs normally without regard to pachytene synaptic failure near the point of interchange in trivalent configurations, or an increase in crossover frequency which is apparently compensatory occurs in the region adjacent to this. Anaphase distribution from chiasmata is usually disjunctive but sometimes nondisjunctive.

Testcrosses of these stocks with a slightly different genetic constitution are a potential test for "distributive pairing" of a noncrossover chromosome in maize.

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