the theoretical distribution actually is a true representation of the distribution of non-associated chromosomes in squashed cells.

When K10 was present in one or two doses, the mean distances between the homologous chromosomes 6 were 0.336 and 0.315, respectively. These means deviated from the random distribution above the .01 level. The values of 0.336 and 0.315 did not differ significantly from each other. The occurrence of a non-random association of the two homologous chromosomes 6 indicates that K10 in some way has initiated or enhanced an attractive force which brings about somatic association of the homologues.

When association between the two K10 chromosomes was investigated no significant deviation from random was observed. This would indicate that the effect of K10 was interchromosomal in nature, affecting only the other homologous chromosomes in the complement. A similar interaction with non-homologous chromosomes has been reported for the effect of K10 on recombination; Rhoades has found that the increase in crossing over induced by K10 in meiotic cells was less in the K10 bivalent than in the other bivalents of the complement.

Since K10 increases the synapsis of meiotic homologues and induces a loose association in mitotic cells, it is possible that both forms of pairing are caused by a single attractive force. This would argue against the hypothesis that both long range and short range pairing forces are operative during meiosis.

Judith Miles

9. The induction of crossing over by B chromosomes.

In the 1960 Maize News Letter I reported that crossing over in the Sh-Wx region was not increased in plants homozygous for a piece of 3L inserted into the short arm of chromosome 9 despite the fact that the length of chromatin separating these flanking markers is approximately twice as great as in a normal chromosome 9. (The chromosome 9 with the inserted segment of 3L was originally designated Dp9 but we have since referred to it as Tp9 since the aberration is more accurately described as a transposition.) In the 1966 Maize News Letter the results of testcrosses of homozygous Tp9 plants heterozygous for the Yg, C, Sh and Wx loci were presented. An unusual feature of the data was the significant increase in recombination for the regions distal to the transposed segment of 3L and the complete, or nearly complete, absence of chiasma interference for double crossovers when one of the regions included the 3L piece. Extensive data from a large number of homozygous Tp9 plants showed no increase in crossing over above the control value for the C-Wx or Sh-Wx regions and the conclusion was reached that crossing over did not occur within the transposed segment of 3L. This conclusion would account for the unchanged recombination in the Sh-Wx region in Tp9 Tp9 and N9 N9 bivalents. Also intelligible are the high coincidence values for those double exchanges where one of the crossover regions is the Sh-Wx interval. The great majority of the exchanges in the Sh-Wx region occur to the right of the inserted piece. Although there is apparently no recombination

in the transposed segment, its presence decreases the interference distance for double exchanges involving the Sh-Wx region and an exchange in this interval does not affect the probability of a second exchange occurring in the adjacent C-Sh region. Interference is normally high for short adjacent regions in the short arm of chromosome 9 and decreases as the regions become longer. The transposed segment of 3L does not undergo crossing over but its physical presence in the Sh-Wx interval has the same effect in reducing interference as that achieved by increasing map distance.

The Df3 chromosome is shorter than the normal 3 by the deleted segment that was inserted into chromosome 9. Since the Lg_2 and A genes lie to the left and right of the deficiency, they are separated by considerably less chromatin and the amount of recombination between these two markers should be reduced in Df3 homozygotes. However, in testcrosses of Tp9 Tp9; Gl Lg Df A/gl lg Df a plants the percentage of recombination in the physically shorter Lg-A region was as great as in normal chromosome 3 homozygotes. Evidently no exchanges occur in the chromatin of the transposed segment when it is part of chromosome 3 or when placed in the Tp9 chromosome. This segment is not genetically inert since N9 Df3 spores abort and its immunity to genetic exchange, when in the Tp9 chromosome, is lost in the presence of supernumerary B chromosomes as is described below.

Subsequent to the extensive early experiments with Tp9 Tp9 plants where there was no change in C-Wx or Sh-Wx recombination values, segregating families were later encountered in which some individuals had the usual amount of recombination and others had two to three times as much. The genetic basis for high recombination, which has been followed for several generations, proved to be the presence of one or more supernumerary B chromosomes. Sib plants of C Tp wx/ c Tp Wx constitution with B's varying in number from none to three were testcrossed. As is shown in the tabulation below the average amount of recombination between C and Wx in sib plants of family 28064 was 17.7% in 0B, 37.0% in 1B, 40.4% in 2B, and 42.0% in 3B plants.

C-Wx Recombination in Plants with:

0 B	1 B	2 B	3 B
13.3%	40.7%	42.6%	42.5%
15.1	36.0	38.1	43.1
15.0	32.5	44.4	44.6
18.0	40.4	43.7	38.6
20.0		38.4	
21.4		36.4	
21.3			
14.4			
16.6			
Wt. M = 17.7	Wt. M = 37.0	Wt. M = 40.4	Wt. M = 42.0

Given below are C-Wx crossover values from a related family (28062):

0 B	1 B	2 B	3 B
11.9%	24.8%	26.7%	40.2%
23.0	22.4	36.9	40.4
10.9	31.8		
17.2	25.0		
16.6	30.0		
19.6	24.0		
19.3	32.3		
13.0			
14.6			
20.2			
16.1			
Wt. M = 16.7	Wt. M = 27.4	Wt. M = 30.6	Wt. M = 40.3

The increase in recombination in B-bearing plants compared to OB plants is not as striking as in the first experiment but the enhancement is highly significant and the data from the two sets of crosses are in agreement.

In contrast to the above two families in which the number of B's varied from none to three is the situation in family 28878 where all the plants had high C-Wx crossover values and one or more B chromosomes. These plants were homozygous for the Tp9 chromosome. The data given below likewise show a consistent dosage effect of B chromosomes, but the increase in recombination is less pronounced than that observed in comparisons of OB and 1B sibs in the first two sets of data.

1 B	2 B	3 B
30.1%	35.5%	43.0%
	40.0	42.6
	41.0	40.3
	38.0	
	38.0	
	39.2	
	40.5	
Wt. M = 30.1	Wt. M = 38.9	Wt. M = 42.0

Although there is variation in the amount of C-Wx recombination within and between the different classes of B chromosomes in the three families, the data were combined to determine the average increase produced by specific numbers of B chromosomes.

0 B	20 ears	M = 16.9	Population total = 5471
1 B	12 ears	M = 30.8	Population total = 3287
2 B	15 ears	M = 38.8	Population total = 4419
3 B	9 ears	M = 41.7	Population total = 2456

Before it was realized that B chromosomes were responsible for the enhanced C-Wx recombination values, testcrosses were obtained from homozygous Tp9 plants heterozygous for Yg, C and Wx. Some individuals had low C-Wx and some had high C-Wx recombination. Although the number of B chromosomes was not ascertained in these plants, they came from a duplicate planting in another season of the kernels giving rise to the populations reported above in the first set of data (family 28064). It is clear that the ears with low C-Wx and those with high C-Wx recombination values were borne on plants with OB and from 1-3 B chromosomes, respectively. When the kernels were planted and seedlings scored for Yg, the following data were obtained.

Per Cent Recombination

	Yg-C	C-Wx	Total	Coin.
Low C-Wx	28.8	13.0	41.8	0.65
High C-Wx	12.7	37.9	50.6	0.57

The average of 38% C-Wx recombination in those individuals assumed to carry from one to three B's is in good agreement with the recombination frequencies for sib plants with known numbers of B chromosomes. The most striking feature in the 3-point data is the negative correlation between crossover values in the Yg-C and C-Wx regions. Plants with high C-Wx crossing over (M = 38%) have low Yg-C values (M = 13%) and conversely those with low C-Wx recombination (M = 13%) have high Yg-C crossing over (M = 29%). A linear regression coefficient of -1.426 was obtained by plotting C-Wx against Yg-C recombination values. The failure to find individuals with high crossover percentages in both regions is indicative of an upper limit to the amount of recombination in the short arm of chromosome 9.

The plants in family 28878 were heterozygous for Yg, C and Wx. Recombination frequencies obtained from the 3-point testcross data are given below:

No. of B Chromosomes	Yg-C	C-Wx	Population Size	Total Recombination
1	15.6	30.1	379	45.7
2	9.6	35.5	271	
2	13.7	40.0	488	
2	10.4	41.0	424	
2	15.8	38.0	158	
2	16.8	38.0	297	
2	10.1	39.2	337	
2	6.1	40.5	412	
Wt. M =	11.8	Wt. M = 38.9	Σ = 2387	50.7
3	9.7	43.0	330	
3	10.1	42.6	286	
3	11.4	40.3	464	
Wt. M =	10.4	Wt. M = 42.0	Σ = 1080	52.4

These data confirm the conclusions reached above on the negative correlation between crossover percentages in the two regions and on the dosage effect of additional B chromosomes.

M. M. Rhoades

10. A molecular basis for heterosis.

Recent studies on the kinetic properties of alcohol dehydrogenase isozymes in corn scutella have revealed that the enzyme forms specified by the $Adh^{C(m)}$ and Adh^{S} alleles are strikingly different. For example, the C^{m} type isozyme found in $Adh^{C(m)}$ homozygotes shows optimal activity at pH 10.5 and a 10 fold reduction in activity at pH 8.0. On the other hand the S type isozyme formed in Adh^{S} homozygotes is most active around pH 8.0 and is completely inactive at pH 10.5. $Adh^{S}/Adh^{C(m)}$ heterozygotes which form both the S and C^{m} type isozymes show high activity at both pH levels as expected (Table 1). The striking difference between the isozymes is quite surprising in view of the fact that they are specified by allelic genes and do not show preferential dimerization.

Table 1
Units activity/gram kernel

	pH 8.0	pH 10.5
Adh^{S}/Adh^{S}	5898	0
$Adh^{S}/Adh^{C(m)}$	3399	3779
$Adh^{C(m)}/Adh^{C(m)}$	519	5702

The alcohol dehydrogenase system can serve as a model for explaining the phenomenon of hybrid vigor although we have no reason to believe that this particular enzyme is implicated in heterosis. We propose that the intracellular milieu such as pH, ionic strength, chemical composition, etc. is not constant and may vary significantly during growth. Furthermore, we propose that enzymes specified by various alleles of the same gene may have different optima for activity. The enzyme specified by one allele may be active in one environment but relatively inactive in a second, while another allelic enzyme may show the reverse relationship. Heterozygotes which contain both alleles would produce enzymes which are active in either environment. This would be expected to result in hybrid vigor since in such heterozygotes the range of intracellular conditions in which high enzyme activity persists is considerably broadened.

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William Laughner