

In female plants with the \underline{AA}^1 genotype the growth rate of the pollen tubes with and without B chromosomes would be intermediate between that in female plants with \underline{AA} or $\underline{A}^1\underline{A}^1$ genotypes. Assuming fertilization is at random, the frequency of 2B plants in the progeny would be intermediate, i.e., between 25% and 50% expected in \underline{AA} and $\underline{A}^1\underline{A}^1$ genotype plants.

Other explanations may be developed but these presented are worthy of consideration as working hypotheses since they can be tested experimentally.

The failure of the OB x 1B crosses (Table 1) to give exactly 50% 2B progeny is probably due to the presence of environmental or genetic modifier factors.

Some experimental studies regarding these two working hypotheses have been started during 1968.

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1. Further evidence for sister-strand crossing over in maize.

Schwartz (Genetics 38:251, 1953) presented evidence that sister-strand crossing over is a general phenomenon in meiotic cells of maize. Essentially that work has been repeated here using plants heterozygous for a ring and its homologous rod chromosome 10.

The ring chromosome 10 was derived from a long derivative of abnormal chromosome 10. Figure 1 gives a diagrammatic representation of the formation of the ring following a crossover between 10L and a second 10L fragment attached to the short arm of the chromosome. The knob is a large portion of the abnormal chromosome 10 knob.

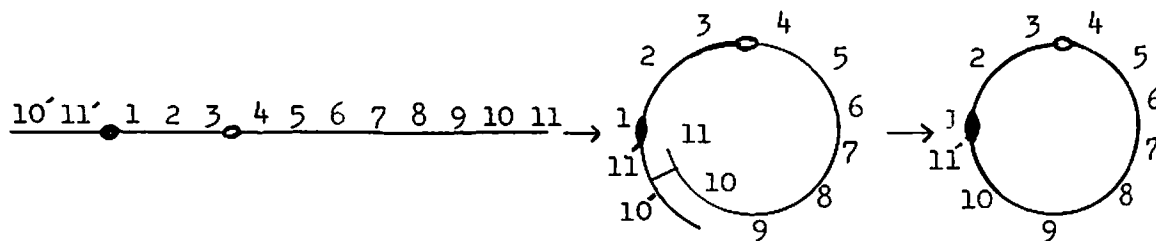


Figure 1. Diagrammatic representation of the formation of ring 10.

Certain crossovers between a ring and its homologous rod chromosome result in bridges being formed at anaphase I and/or at anaphase II. For example, a tetrad with a single crossover results in a single bridge at AI but no bridge at AII. Double exchanges result in specific AI and AII configurations depending on whether the exchanges are 2-strand doubles, type I 3-strand doubles, type II 3-strand doubles or 4-strand doubles, and on whether the two crossovers are in the same arm (Class A doubles) or are separated by the centromere (Class B doubles). The anaphase configurations resulting from single and double crossovers are shown in Table 1.

Table 1

Crossover type	Anaphase I (bridges)	Anaphase II (bridges)
None	None	None
Single	Single	None
Class A double crossovers (in one arm)		
2-strand double	None	None
3-strand double I	Single	None
3-strand double II	Single	Single
4-strand double	Double	None
Class B double crossovers (separated by centromere)		
2-strand double	None	None
3-strand double I	Double	None
3-strand double II	None	Single
4-strand double	Double	None

Schwartz used a ring chromosome 6 and could assume no crossing over in the very short arm. However when a ring chromosome 10 is used eight types of double crossovers must be considered rather than four. This consideration of crossing over in both arms makes the argument more complex but eventually leads to the same conclusion.

Three plants heterozygous for the ring chromosome 10 and its homologous rod were examined for anaphase I and anaphase II configurations. The frequencies of the various anaphase configurations are listed in Table 2. Anaphase I data are given for single cells counted; anaphase

Table 2
 Anaphase configurations observed in plants heterozygous for a ring
 and its homologous rod chromosome 10

	Anaphase I				Anaphase II (daughter cell pairs)			
	Single bridge	Double bridge	No bridge	Total	Single bridge	Double bridge	No bridge	Total
Number	332	70	126	528	242	36	386	664
Percent	62.8	13.3	23.9	100	36.4	5.4	58.2	100

Table 3
 Theoretical expectations from crossovers between a ring and its homologous rod chromosome 10

Crossover type	Anaphase I			Anaphase II		
	Single bridge	Double bridge	No bridge	Single bridge	Double bridge	No bridge
Part a. - non-sister chromatid crossovers only.						
None	-	-	100%	-	-	100%
Single	100%	-	-	-	-	100%
Double : Class A	50%	25%	25%	25%	-	75%
Double : Class B	-	50%	50%	25%	-	75%
Part b. - non-sister chromatid crossovers plus 50% effective sister-strand crossing over.						
None	-	-	100%	-	50%	50%
Single	100%	-	-	50%	-	50%
Double : Class A	50%	25%	25%	25%	12.5%	62.5%
Double : Class B	-	50%	50%	50%	-	50%

II data have been converted to daughter cell pairs which show a single or double bridge in one of the two cells.

The observed results (Table 2) can be compared with the theoretical expectations from each of the exchange possibilities (Table 3). The theoretical expectations are expressed as the percent of the total for each type of exchange. Table 3 is divided into Part a and Part b. Part a gives the expected results if crossing over is allowed between non-sister chromatids only. Part b will be discussed below.

Two discrepancies between the observed data and that expected if no sister-strand crossing over is allowed are obvious. The first is the high frequency of single bridges in anaphase II. When no sister-strand crossing over is allowed, these result from 3-strand type II double exchanges exclusively. If all 36.4% AII single bridges were due to one kind of double crossover, the total of the four types of double crossovers would exceed 100%. Since this is impossible, it is necessary to look for another source of AII single bridges.

The high frequency of AII single bridges can be accounted for by sister-strand crossing over. If the number of sister-strand crossovers per bivalent is high, an odd number occurring in any one region will appear as a crossover while an even number will appear as a noncrossover. Therefore, when a high number of sister-strand crossovers occurs per bivalent an effective sister-strand crossover occurs 50% of the time. Table 3 Part b indicates the frequency of anaphase bridges resulting from single and double crossovers plus 50% effective sister-strand crossing over. Note particularly that with 50% effective sister-strand crossing over AII single bridges result from half of the single exchanges and one-half of the Class B double exchanges.

To calculate the total percent of AII single bridges from all sources it is necessary to determine first the percent of AII single bridges expected irregardless of sister-strand crossing over, i.e. the percent of both Class A and Class B type II 3-strand double exchanges. First, assume that because of no chromatid interference 2-strand double exchanges equal 3-strand I double exchanges equal 3-strand II double exchanges equal 4-strand double exchanges. Second, assume the chromosome 10 arm ratio for crossing over is 2.8:1. It follows from the second

assumption that 61.2% of the double crossovers are in the same arm (Class A doubles) and 38.8% have the two crossovers separated by the centromere (Class B doubles). Third, observe that the 13.3% AI double bridges are the result of the two classes of 4-strand double exchanges and Class B 3-strand I double exchanges (Table 1), and that the proportions of these three classes are not changed by the occurrence of sister-strand crossing over. (Table 3). Combining these three statements it can be calculated that Class A double crossovers occur 23.6% of the time and Class B double crossovers occur 14.8% of the time, with 5.9% of each type of Class A exchange and 3.7% of each type of Class B exchange. Therefore only 9.6% (5.9% + 3.7%) AII single bridges are expected on the basis of non-sister chromatid crossing over.

Single bridges in anaphase I were observed 62.8% of the time. These result from single crossovers and half of the Class A double crossovers. The frequency of one-half of the Class A double crossovers is expected to be 11.8% ($\frac{1}{2} \cdot 23.6\%$). This leaves 51.0% AI single bridges due to single non-sister chromatid crossovers. As a result of sister-strand crossing over, half of these or 25.5% will form single bridges at AII. The third source of AII single bridges is Class B double exchanges. When 50% effective sister-strand crossing over occurs, 3.7% single bridges are expected at AII (Table 3). Thus, 38.8% (9.6% + 25.5% + 3.7%) single bridges are expected on the basis of abundant sister-strand crossing over; the observed frequency was 36.4%.

The second observation which can not be explained on the basis of no sister-strand crossing over is the appearance of double bridges (dicentric rings) at anaphase II. Double bridges at AII are not expected from either single or double non-sister chromatid crossovers. However, AII double bridges arise from sister-strand crossing over in tetrads which had no other crossovers and those which had 2-strand double exchanges in the same arm. The frequency of noncrossover tetrads is equal to the frequency of all AI cells showing no bridges less the percent of no bridge AI cells coming from double exchanges. The percent of no bridge AI cells coming from double exchanges is 13.3% since the number of these expected is the same as for double bridge AI cells (Table 1). Thus, 10.6% (23.9% - 13.3%) of all tetrads had no non-sister chromatid

crossovers. As a result of sister-strand crossing over, half of these or 5.3% will form double bridges at anaphase II. Class A 2-strand double exchanges occur 5.9% of the time; with 50% effective sister-strand crossing over half of these or 2.9% will form AII double bridges. Thus, 8.2% (5.3% + 2.9%) double bridges at AII are expected; the observed frequency was 5.4%.

The disparity between the observed anaphase configurations and those expected on the basis of non-sister chromatid crossing over between the ring chromosome 10 and its homologous rod is interpreted as due to sister-strand crossing over since the hypothesis of at least one sister-strand crossover per bivalent accounts for the experimental results. Two assumptions basic to the argument are no chromatid interference and a 2.8:1 arm ratio for crossing over in chromosome 10. Although the assumption of no chromatid interference probably holds in maize, the experimental results also discount the possibility of negative chromatid interference accounting for the high percent of AII single bridges. If there were negative chromatid interference we would expect more 2-strand doubles than type II 3-strand doubles. Since only part of the 23.9% AI cells with no bridges could be due to 2-strand doubles the 36.4% AII single bridges must not be a true indication of the number of type II 3-strand doubles. The 2.8:1 arm ratio was assumed since it is the cytological arm ratio. However, the arm ratio chosen is not critical to the argument. When the arms are assumed to be the same length, 40.3% AII single bridges and 7.4% AII double bridges are expected; both figures are reasonably close to the observed values. A third point is the dismissal of three or more crossovers to account for the data. One through seven exchanges were considered with an arm ratio varying from 20:1 to 1:1;* at no time did the percent of single bridges in AII exceed the percent of double bridges in AI. The observed percent of AII double bridges was reached only in situations where every tetrad had at least three crossovers and when the arm ratio was at least 19:1. Obviously, higher exchange levels could not account for the data.

*Computer program written by Roland Littlewood.