A New Property of the Maize *B* Chromosome

Wayne R. Carlson and Robin R. Roseman

Botany Department, University of Iowa, Iowa City, Iowa 52242

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ABSTRACT

TB-9Sb is a translocation between the *B* chromosome and chromosome *9* in maize. Certain deletions of *B* chromatin from the translocation cause a sharp decrease in *B-9* transmission compared to the rate for standard *TB-9Sb*. The deletions remove components of a *B* chromosome genetic system that serves to suppress meiotic loss in the female. At least two distinct *B*-chromosome regions suppress meiotic loss: one on the *B-9* and one on *9-B*. The system operates by stabilizing univalent *B-type* chromosomes. It allows the univalents to migrate to one pole in meiosis, despite the absence of a pairing partner. The findings reported here are the first evidence for genetic control of meiotic loss by a *B* chromosome. However, it is proposed that the practice of suppressing meiotic loss is common to the *B* chromosomes of all species. The need to suppress meiotic loss results from the fact that *B* chromosomes are frequently unpaired in meiosis and subject to very high frequencies of loss. *B* chromosomes may utilize one or more of the following methods to suppress meiotic loss: (a) regular migration of univalent *B*'s to one pole in meiosis, (b) enhanced recombination between *B* chromosomes and (c) mitotic nondisjunction.

B chromosomes are nonessential, extra chromosomes that are found in hundreds of species of plants and animals (JONES and REES 1982). They seem to have little or no phenotypic effect on the organism and very few active genes. OSTERGREN (1945) proposed that *B* chromosomes are parasitic and exist only for self-perpetuation. This idea is consistent with the fact that many *B* chromosomes have "accumulation mechanisms," *i.e.*, systems that increase *B* chromosome frequency in the gametes by non-Mendelian methods (JONES 1985). The *B* chromosome of maize has an accumulation mechanism that involves mitotic nondisjunction. The chromosome undergoes nondisjunction at very high frequency at the second pollen mitosis. A single *B* chromosome produces sperm with zero and two *B*'s. Subsequently, the sperm with two *B* chromosomes will preferentially fertilize the egg (ROMAN 1948; CARLSON 1969).

Studies on nondisjunction of the maize *B* chromosome have identified four controlling regions (Figure 1). Regions 1, 2 and 3 are all essential for the occurrence of nondisjunction. Region 4 enhances the frequency of nondisjunction. In the course of our studies on nondisjunction, a number of *B*-deletion stocks were isolated (CARLSON 1978a). They were derived in the translocation *TB-9Sb* rather than an intact *B* chromosome. The *TB-9Sb* deletions, some on the *B-9* and some on *9-B*, were originally selected because they block *B-9* nondisjunction at the second pollen mitosis. (In *B*-translocations, nondisjunction occurs for the chromosome with the *B* centromere.) In this report, meiotic properties of the *B-9*'s in deletion stocks are examined.

For maintenance of deletion translocation stocks, a convenient cross has been: *9 9-B B9* (translocation heterozygote) *X* chromosome *9* tester. Passage of the translocation through the female parent avoids the complication of *B-9* nondisjunction. The cross utilizes genetic markers that detect transmission of *TB-9Sb* chromosomes. It was noted very early that this maintenance cross sometimes gives very low frequencies of *B-9* transmission. Low transmission can be explained if the chromosome is frequently lost during meiosis. The *B-9* is a small chromosome which sometimes fails to pair with the homologous *9S* region on chromosome *9*. The result is a univalent *B-9* that may lag at anaphase I and be excluded from daughter nuclei. Alternately, it may split "mitotically" at anaphase I, sending a single chromatid to each pole. Subsequently, at anaphase II, the single chromatids may lag and be excluded from daughter nuclei.

Certain deletion translocation stocks are much more susceptible to loss of the univalent B^9 than is the standard translocation. Data on meiotic loss for one deletion stock was reported earlier (CARLSON 1986). Tests presented here demonstrate that several different deletion stocks produce high rates of meiotic loss. At a minimum, two distinct regions on the *B* control meiotic loss. This is the first case in which genetic control of meiotic loss by a *B* chromosome has been demonstrated. The existence of such a system should not be surprising, since *B* chromosomes are, by their nature, frequently univalent. It is proposed that the avoidance of meiotic loss played a major role in the evolution of most or all *B* chromosomes.

FIGURE 1.—The *B* chromosome of maize. Regions that control nondisjunction of the centromere are numbered 1 to 4. Evidence for nondisjunctional control by these regions was given by: ROMAN (1949) and WARD (1973) (region 1); CARLSON (1973, 1978a) and LIN (1978) (region 2); RHOADES, DEMPSEY and GHIDONI (1967); RHOADES and DEMPSEY (1972) and CARLSON and CHOU (1981) (region 3); CARLSON (1978b) and LIN (1979) (region 4). Diagram reprinted from CARLSON and CHOU (1981) with permission.

MATERIALS AND METHODS

Genetic markers: The *9-B* and *B-9* chromosomes are marked by genes on the short arm of *9*. The *Wx* gene is located on *9-B* and is very near the translocation breakpoint. In practice, the segregation of *9-B* and *9* can be accurately followed by classification of *Wx* (*9-B*) *vs. wx* (*9*). No correction for crossing over is needed, due to the rarity of the event (ROBERTSON 1967). The *Bz, C* and *Yg2* genes are used to mark the *B-9* chromosome. Some recombination of these markers with chromosome *9* does occur.

The *Wx* gene produces a phenotype in both the endosperm and pollen. The *Wx* allele gives a dark stain with iodine whereas *wx* stains lightly. In the endosperm, the *Wx* allele is a simple dominant. In the pollen, segregation of *Wx* and *wx* alleles to different grains allows classification of *Wx Wx, Wx wx* and *wx wx* genotypes. The *Bz* gene is an endosperm marker. The dominant allele gives purple seed whereas the recessive phenotype is brown (*bronze*). The *C* gene is also an endosperm marker and the *C* allele allows aleurone color whereas *c* does not. The *Yg2* gene controls a plant phenotype. The *Yg2* allele produces a green plant while *yg2* gives yellow-green.

Cytology: Meiotic slides were prepared with propiocarmine stain in the conventional manner. All pachytene photographs are magnified to the same extent. (Enlargements of Figure 5c was approximated, since the original microscope magnification was not recorded.) Anaphase photographs are at a lower magnification than those in pachytene.

Classification of translocation type: Meiotic loss tests, described later, require classification of translocations into standard *vs.* deletion-type. In all cases reported here, the deletion translocations lack a region that is required for *B-9* nondisjunction. Consequently, classification of translocation type was usually carried out through a test of nondisjunction. However, for *TB-9Sb-1866,* a cytological classification was used, as discussed later. Also, for *TB-9Sb-1852,* a few plants were classified cytologically.

The nondisjunctional test requires that a plant be crossed as male parent to a stock that is recessive for a *B-9* marker. The male parent must be dominant for the marker in question. An example of such a cross is: *bz bz* × *9-B 9-B B-9* (*Bz*) *B-9* (*Bz*). If a number of recessive progeny arise in the cross, the translocation is the standard type. Recessive progeny arise from nondisjunction and the production of deficient, zero *B-9* sperm. If recessive phenotypes are not produced in the cross, the translocation is a deletion type (CARLSON 1978a).

Cytological classification of *TB-9Sb-1866* and *TB-9Sb-1852:* In the test of meiotic loss for *TB-9Sb-1866,* translocation type was classified cytologically. The cytological method was feasible because the difference between a standard *B-9* and the *B-9* from translocation *1866* can be easily seen in mitotic preparations. In prophase, the standard *B-9* has three separate heterochromatic regions whereas the *1866 B-9* displays two (CARLSON 1973). The deletion of intervening euchromatin between two heterochromatic sites makes two sites appear to be one. For the meiotic loss test of *TB-9Sb-1852,* classification of *B-9* type was made primarily with a test of nondisjunction. However, four plants were classified cytologically because their nondisjunctional crosses did not set seed. A cytological classification is possible in mitotic prophase due to the lack of centric heterochromatin in *TB-9Sb-1852* (CARLSON and CHOU 1981).

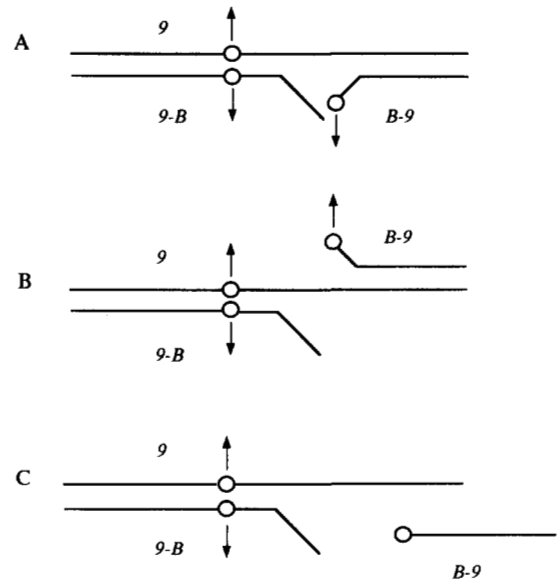

FIGURE 2.—Metaphase 1 orientation of the translocation heterozygote, *9 9-B B-9*. Three orientations are shown, depending on the poleward attachment of the *B-9* chromosome. (The translocation heterozygote has three chromosomes, instead of four, due to absence of the standard *B* chromosome.)

Calculation of meiotic loss: In tests of meiotic loss, the translocation heterozygote is used. *TB-9Sb* is usually marked with *Wx* on *9-B* and *Bz* or *C* on the *B-9*. A typical cross is: *9* (*bz wx*) *9-B* (*Wx*) *B-9* (*Bz*) × *bz bz wx wx*. The chromosomes in the female parent give three types of orientation at metaphase I, as shown in Figure 2. In all cases, the *9* and *9-B* chromosomes orient to opposite poles. The *B-9* may orient opposite chromosome *9* (Figure 2A) or may orient to the same pole (Figure 2B). In addition, the *B-9* may be unpaired and lack an initial polar attachment in metaphase I (Figure 2C).

The orientation shown in Figure 2C can have several consequences in anaphase. First, the *B-9* univalent may eventually move to one pole or the other and not undergo meiotic loss. Second, the *B-9* may lag at anaphase I and be excluded from daughter nuclei. Third, the *B-9* may split "mitotically" at anaphase I, with one chromatid going to each pole. Splitting at anaphase I may lead to lagging at anaphase II, with subsequent meiotic loss. Consequently, meiotic loss can occur by either of two mechanisms.

The metaphase orientations of Figure 2 lead to four classes of anaphase I disjunction:

1. Migration of *B-9* and *9* to opposite poles (from Figure 2, A and C)	*Gametes: 9* (*bz wx*) and *9-B B-9* (*Bz Wx*)
2. Migration of *B-9* and *9* to same pole (from Figure 2, B and C)	*Gametes: 9 B-9* (*Bz wx*) and *9-B* (*Wx* – lethal deficiency)
3. Lagging and loss of *B-9* (from Figure 2C)	*Gametes: 9* (*bz wx*) and *9-B* (*Wx* – lethal deficiency)

4. Mitotic splitting of the *B-9* (from Figure 2C)	*Gametes:* all categories of gametes can be produced. However, if meiotic loss occurs at anaphase II, the gametes will be the same as in (3) above.

The amount of meiotic loss is given by the total number of class 3 disjunctions, plus the percentage of class 4 disjunctions that result in *B-9* loss, divided by total meiotic divisions. The calculation is complicated by the fact that some meiotic products listed above are not viable and cannot be detected. Therefore, "total meiotic divisions" is not easily calculated. To compensate for inviable gametes, the products of meiosis can be divided into two categories: those receiving chromosome *9* and those receiving the *9-B*. The *wx* and *Wx* alleles are very tightly linked to chromosomes *9* and *9-B* respectively and classification for them is equivalent to classifying for chromosome type (ROBERTSON 1967). The chromosome *9* class of gametes, identified by the *wx* allele, can be used to accurately calculate meiotic loss rates. All gametes receiving chromosome *9* are viable, whereas some that receive *9-B* are not. The basic formula for meiotic loss is: *wx* gametes arising from meiotic loss divided by total *wx* gametes. The gamete frequencies are detected in testcrosses.

All *wx* gametes that arise from meiotic loss have the same genotype: *bz wx*. However, the *bz wx* genotype is not exclusive to meiotic loss. It is also produced by category 1 disjunction. To distinguish between *bz wx* gametes produced by "normal" disjunction *vs* meiotic loss is straightforward. The *bz wx* produced by normal disjunction occurs in equal frequency to its reciprocal class, *Bz Wx*. Therefore, any excess of *bz wx* over *Bz Wx* arises from meiotic loss. If meiotic loss is absent from a cross, the frequencies of *bz wx* and *Bz Wx* will be equal. Otherwise, there will be a surplus of *bz wx* gametes, corresponding to the rate of meiotic loss. The formula for meiotic loss is, therefore, *bz wx* − *Bz Wx* divided by total *wx*.

Crossing over requires some adjustment to the meiotic loss formula. Crossing over can occur between *9* and the *B-9* with transfer of *Bz* to *9* and *bz* to the *B-9*. It is assumed that crossing over between *9* and *9-B* for *Wx* and *wx* is negligible. The following crossover types must be considered: *9* (*Bz wx*); *9* (*bz wx*) *B-9* (*bz*) and *9-B* (*Wx*) *B-9* (*bz*). They affect the numerator of the meiotic loss formula. The simplest approach is to first restate the numerator in terms of gametic classes. The numerator equals the number of chromosome *9* gametes minus the number of *9-B B-9* gametes. The second term, *9-B B-9*, is easily calculated as total *Wx* (or *Bz Wx* + *bz Wx*). The *Wx* allele accurately identifies all *9-B B-9* gametes. The first term of the numerator, chromosome *9* gametes, is more difficult to calculate. A distinction must be made between two different *wx* gametes: *9 vs. 9 B-9*. For this calculation, the *Bz* locus is needed, along with a method for measuring its crossovers. The crossover *9* (*Bz wx*) class cannot be separated phenotypically from the noncrossover *9* (*bz wx*) *B-9* (*Bz*) type. However, it can be measured from the frequency of the reciprocal crossover product: *bz Wx*. Crossing over plus category 1 disjunction produces *9* (*Bz wx*) and *9-B B-9* (*bz Wx*) classes in equal frequencies. Therefore, the unique *bz Wx* class can be used as a measure of *9* (*Bz wx*) frequency. The second type of crossover to be accounted for is *9* (*bz wx*) *B-9* (*bz*). This type results from *9/B-9* crossing over to produce *B-9* (*bz*), followed by category 2 disjunction. On the assumption that category 2 disjunction occurs at equal frequency to category 1 disjunction following crossing over, the frequency of *9* (*bz wx*) *B-9* (*bz*) gametes can be calculated. It is directly proportional to the *bz Wx* crossover class since both types have a recombinant *B-9* (*bz*). The frequency of *9* (*bz wx*) *B-9* (*bz*) is one half that of the *bz Wx* class. It is formed at anaphase II by random segregation of *9* (*Bz/bz*) and *B-9* (*Bz/bz*) crossover chromatids.

The calculation of meiotic loss can now be corrected for crossing over. Meiotic loss is: chromosome *9* gamete class minus *9-B B-9* class divided by total *wx* gametes. Chromosome *9* gametes equal *bz wx* gametes plus *bz Wx* (correction for *9 Bz wx* crossover) minus 0.5 *bz Wx* (correction for *9 bz wx B-9 bz* crossover). The *9-B B-9* class equals total *Wx* gametes (*Bz Wx* + *bz Wx*). The formula for meiotic loss then becomes: (*bz wx* + *bz Wx* − 0.5 *bz Wx*) − (*Bz Wx* + *bz Wx*) ÷ total *wx*. The formula simplifies to: *bz wx* − *Bz Wx* − 0.5 *bz Wx* ÷ total *wx*.

The formula given is nearly complete, but two assumptions made in its formulation must be considered. The first assumption was made in the correction for *9* (*bz wx*) *B-9* (*bz*) crossovers. It was assumed that crossing over between the *9* and *B-9* leads equally often to category 1 and category 2 disjunction. ROBERTSON (1967) provided evidence that disjunction for the two types is equivalent following crossing over. However, more extensive data of CARLSON (1978c) suggest that type 1 disjunction is favored to some extent following crossing over. It is not possible to determine for the current data whether disjunction is biased toward category 1 disjunction or is random. On the extreme assumption that only category 1 disjunction occurs following crossing over, no correction for *9* (*bz wx*) *B-9* (*bz*) crossovers is needed, since none are produced. Therefore, the 0.5 *bz Wx* that was subtracted in deriving the formula above would be removed and the formula becomes *bz wx* − *Bz Wx* ÷ total *wx*. A modified formula that includes all possibilities is as follows: Meiotic loss = *bz wx* − *Bz Wx* − (0.0 to 0.5) *bz Wx* ÷ total *wx*. This formula gives a range of values for meiotic loss. Because the number

of *bz Wx* gametes in testcrosses tends to be small, the range is usually narrow.

A second assumption that was made in considering meiotic loss was that the *9* and *9-B* chromosomes always disjoin from each other in meiosis. However, KINDIGER, CURTIS and BECKETT (1991) reported an unusual type of meiotic segregation for certain *B-A* translocation heterozygotes. In some meiotic divisions, the heterozygote (*A A-B B-A*) may disjoin with both *A* and *A-B* going to one pole and *B-A* to the other pole. This can be classified as adjacent-2 disjunction from the trivalent. The *A A-B* gamete is duplicate and viable whereas the *B-A* gamete is deficient-lethal. For *TB-9Sb,* the cross *9* (*bz wx*) *9-B* (*Wx*) *B-9* (*Bz*) X *bz bz wx wx* can be used to detect adjacent 2 segregation. Any *9 9-B* gametes produced will have the *bz Wx* genotype. Since *bz Wx* can also arise as a *9-B B-9* crossover, the frequency of *bz Wx* gives an upper limit to the rate of adjacent 2 disjunction. The *bz Wx* gamete frequency in all crosses is low, suggesting that adjacent 2 segregation is not common. However, the meiotic loss formula must be reviewed to consider the possibility that some or all *bz Wx* gametes arise by adjacent 2 segregation, rather than crossing over. In the extreme case, all *bz Wx* gametes are the *9 9-B* type. If so, there would be no crossing over between *9* and *B-9*. In the absence of crossing over, meiotic loss is calculated simply as *bz wx* − *Bz Wx* divided by total *wx*. This formula is contained within the range of the formula presented earlier. Therefore, the formula remains: Meiotic Loss = *bz wx* − *Bz Wx* − (0.0 to 0.5) *bz Wx* divided by total *wx*. (Note: If adjacent 2 disjunction accounts for all *bz Wx* gametes, the denominator of the formula should, theoretically, be modified. The denominator should be: *total wx* plus *bz Wx*. The *bz Wx* term accounts for an inviable *wx* gamete type that is the reciprocal of the *bz Wx* class. However, the effect of adding *bz Wx* to the denominator is very small and can be disregarded.

Relation of crossing over between *9* and *B-9* to meiotic loss: In *9 9-B B-9* plants, the proportion of meiotic cells containing a univalent *B-9* is determined by the number that lack crossing over between *9* and the *B-9*. Therefore, the rate of *B-9* crossing over is an important factor that affects meiotic loss. Calculation of crossing over between the *9* and *B-9* is measured in crosses of the type: *9* (*yg2 wx*) *9-B* (*Wx*) *B-9* (*Yg2*) × *yg2 yg2 wx wx*. Transfer of the *Yg2* allele to *9* and of the *yg2* allele to *B-9* provide a measure of crossing over. *Yg2* is located near the distal tip of *9S* and, therefore, provides a measure of most crossing over between *9* and *B-9*. The *9-B* (*Wx*) *B-9* (*yg2*) crossover class from category 1 disjunction is the only crossover type with a unique phenotype. Its phenotype is not shared by any noncrossover class. Therefore, the *yg2 Wx* class is used to measure crossing over. To determine the percent of crossing over, *yg2 Wx* is divided by an appropriate denominator. The denominator cannot be total gametes, since *yg2 Wx* does not represent total crossovers. Instead, *total wx* is used as the denominator. The *wx* gametes represent exactly one-half of all meiotic events. Also, the *yg2 Wx* class represents one-half of all crossovers from category 1 disjunction. The formula is: crossing over = *yg2 Wx* divided by total *wx*.

It should be noted that the formula does not give a precise value for the rate of crossing over because not all *B-9* (*yg2*) chromosomes are accounted for by *yg2 Wx* gametes. Some crossover *B-9*'s segregate into the *9 B-9* class during meiosis. The rates of crossing over that have been calculated are, therefore, relative rates to be used only for comparison between groups. Actual rates of crossing over depend on the frequency of disjunctional types produced by the *9 9-B B-9* trivalent. If disjunctional types 1 and 2 (shown earlier) occur with equal frequency, the rate of crossing over is twice that which has been calculated. If there is a tendency for class 1 disjunction to be more frequent than class 2 (CARLSON 1978c), the actual rate of crossing over will be between 1.0 and 2.0 times the rate calculated.

Statistics: The analysis of a meiotic loss experiment requires comparison between unequal-sized groups. This occurs because the chromosome constitution of test populations is initially unknown. For example, if 30 siblings were selected for testing, their assortment into standard *vs.* deletion translocations would seldom be a precise 15–15 split. An added problem is present in the meiotic loss test of *TB-9Sb-1852*. Translocation *1852* is transmitted at a reduced rate compared to standard when the two translocations are combined in one plant and segregated by crossing (see RESULTS). Consequently, the number of standard *vs.* deletion ears in Table 1B is quite different.

Another aspect of the experiments is the conversion of classification results into rates of meiotic loss. A statistical test is needed that can utilize meiotic loss rates rather than original data. The method used to analyze most experiments is the Wilcoxan-Mann-Whitney test. This is a nonparametric test which analyzes rank order position rather than specific data. It can be used with unequal-sized groups. In the meiotic loss tests, ears were ranked at position 1, 2, 3, etc., according to their rate of meiotic loss. The Wilcoxan-Mann-Whitney test determined whether the rank order positions for standard translocation ears were significantly different from those of the deletion translocation ears. The method is described on pp. 542–543 of STEEL and TORRIE (1980).

In order to reduce a source of random variation from the experiments, small ears were not included in the data. Small ears were defined as those having

less than 200 kernels. However, two alternate methods for excluding small ears were also examined. If ears with less than 100 kernels are considered small, a few more ears are included in the experiments, but the results are unchanged. Similarly, if ears that fall outside two standard deviations from the mean kernel number are excluded, the assortment of ears changes slightly. However, statistical results are unchanged.

RESULTS

General experimental design: A test of meiotic loss was conducted for each of several deletion *TB-9Sb* stocks. The basic test begins with a cross of the type: standard *TB-9Sb* × deletion *TB-9Sb*. If homozygous translocation stocks are used as parents, all progeny receive two *9-B*'s and two *B-9*'s. Depending on the type of mutant being tested, the progeny may contain one normal *9-B* and one deficient *9-B* plus two normal *B-9*'s or one normal *B-9* and one deficient *B-9* plus two normal *9-B*'s. In the initial cross, heterozygous translocation plants can also be used as the parents. In this case, the *9-B* marker *Wx* allows selection of *9-B* (*Wx*) *9-B* (*Wx*) *B-9 B-9* progeny.

Once the standard/deletion crosses have been made, the progeny are crossed as females by a chromosome *9* tester stock. This cross segregates two classes of progeny: *9 9-B B-9* (deletion *TB-9Sb*) and *9 9-B B-9* (standard *TB-9Sb*). In the next step, a sample of the progeny is tested for translocation type by crossing as male to a tester of nondisjunction. Crosses that show nondisjunction by "uncovering" a recessive *9S* marker carry the standard *TB-9Sb*. When nondisjunction does not occur, the deletion *TB-9Sb* is indicated (MATERIALS AND METHODS). The same plants that are tested for translocation type are also backcrossed as female by the chromosome *9* tester.

The latter backcrosses are a test of meiotic loss. They utilize a genetic marker for the *9-B* (*Wx*) and one for the *B-9* (*Bz*) or (*C*). The normal *9* carries the recessive alleles. The general cross, using the *Bz* marker, is: *9* (*bz wx*) *9-B* (*Wx*) *B-9* (*Bz*) × *bz bz wx wx*. The formula for meiotic loss in terms of gametic genotypes is: *bz wx* − *Bz Wx* − (0.0 to 0.5) *bz Wx* divided by total *wx*. The value obtained from the formula is a direct measure of the frequency of meiotic divisions that result in *B-9* loss, as explained in Materials and Methods. The results of meiotic loss tests are given in Table 1. Endosperm classification data have been omitted from the table. However, an unabridged table is available from the senior author, on request. An example of endosperm classification for one ear is as follows. Plant 8211–46, from Table 1A, was classified as Bz Wx = 113, Bz wx = 104, bz Wx = 4, bz wx = 140. From this data, meiotic loss is calculated: 140 minus 113 minus 0 to 2 divided by 244 = 10 to 11%.

Deletion stocks: Five deletion translocation stocks were tested. Two of these have deletions on the *B-9*: *TB-9Sb-1866* and *TB-9Sb-1852*. Three others have deletions on the *9-B*: *TB-9Sb-2010, TB-9Sb-14* and *TB-9Sb-2150*. The stocks are diagrammed in Figure 3. Four of the deletions were originally isolated by selecting for "mutant" translocations that lack *B-9* nondisjunction. Translocations *1866, 2010, 14* and *2150* are of this type. Each was found to lack a segment of *B* chromatin. *TB-9Sb-1866* has an internal deletion on the *B-9* chromosome which probably arose as a simple, two break, event. *TB-9Sb-2010, TB-9Sb-14* and *TB-9Sb-2150* have terminal deletions on *9-B*. They probably originated as one-break events. However, their composition may be complex, since broken chromosome ends are often unstable (MCCLINTOCK 1942). The remaining translocation, *TB-9Sb-1852* had a multi-step origin. It was produced by two centric misdivision events. First, a pseudoisochromosome of the standard *B-9* was isolated. This chromosome lacks centric heterochromatin (region 3) on one side of its centromere but has heterochromatin on the other side. Misdivision of the pseudoisochromosome produced two classes of telocentrics. The *B-9* of *TB-9Sb-1852* derives from the chromosome arm which lacks region 3 (type 1 telocentric: CARLSON 1986).

Meiotic loss of *TB-9Sb-1866*: *TB-9Sb-1866* has a deficient *B-9* which lacks nondisjunctional region 2. It is missing most of the proximal euchromatin of the *B* and some of the centric heterochromatin (Figures 3 and 4b). Meiotic loss was tested for standard and deletion translocation heterozygotes in a sibling population. Results are given in Table 1-A. Average meiotic loss for the standard translocation was 14% and for the *1866* translocation was 46%. The two groups of data overlap slightly. However, the separation of classes is significant at the 1% level, using the nonparametric Wilcoxan-Mann-Whitney test.

Meiotic loss of *TB-9Sb-1852*: Translocation *1852* has a *B-9* that lacks nondisjunctional regions 3 and 4 (Figures 3 and 4c). Meiotic loss was tested for standard translocation heterozygotes and sibs containing the *1852*-translocation. Results are given in Table 1B. Average meiotic loss for the standard *TB-9Sb* was 10%, whereas the average for the *1852* translocation was 48%. The data are non-overlapping and the separation into two groups is significant at the 1% level using the Wilcoxan-Mann-Whitney test.

Additional test of meiotic loss for the *1852* translocation: In the course of establishing populations for meiotic loss tests, a cross with *TB-9Sb-1852* gave unusual results. The following cross was made: *9-B 9-B B-9* (std) *B-9* (*1852*) × chromosome *9* tester. This cross is expected to produce a 1:1 segregation of standard *vs.* deletion translocation heterozygotes. It soon became apparent, however, that an excess of

TABLE 1

Comparison of meiotic loss rates between standard *TB-9Sb* and various deletion stocks

Translocation type	Individual rates of meiotic loss (%)
A. Standard *TB-9Sb* (45 ears)	0, 0, 0, 0, 1.2–3.2, 2.0, 2.0–2.6, 4.0–4.6, 5.6–6.6, 6.2–6.8, 7.5–9.0, 7.7–9.7, 9.1–10, 10–11, 10–11, 10–12, 11, 12–13, 12–13, 12–13, 12–14, 13–14, 14–15, 14–17, 15–16, 16–17, 16–17, 16–17, 17, 17–18, 17–18, 18, 18–19, 18–20, 20–21, 20–21, 20–22, 20–22, 20–23, 21, 22–23, 26–27, 29–30, 34–35, 34–35 Range: 0–35% Average: 14%
Deletion *TB-9Sb-1866* (28 ears)	28, 31–32, 32–33, 33–34, 34, 36–37, 37–38, 40–41, 40–41, 40–42, 41, 44–45, 46, 46, 46–47, 48–49, 49–51, 50–51, 50–51, 50–51, 51–52, 51–52, 52–53, 54, 57–58, 58–59, 61, 62–63 Range: 28–63% Average: 46%
B. Standard *TB-9Sb* (25 ears)	0, 0, 0, 0.6–1.7, 2.5–4.2, 2.6–3.6, 6.7–8.3, 7.3–8.1, 7.6, 8.6–9.3, 9.1–11, 10–11, 11–12, 12–13, 12–13, 12–13, 12–13, 13, 14–15, 15, 15, 16, 19–20, 19–20, 20–21 Range: 0–21% Average: 10%
Deletion *TB-9Sb-1852* (8 ears)	22–23, 38–40, 38–41, 41–43, 49–50, 53–58, 65–66, 67 Range: 22–67% Average: 48%
C. Standard *TB-9Sb* (9 ears)	6.0–7.7, 7.0–8.5, 17–18, 19–21, 22–23, 24, 28–29, 28–29, 30–31 Range: 6.0–31% Average: 21%
Deletion *TB-9Sb-2010* (7 ears)	11–12, 12–14, 17–18, 21–22, 23–24, 28–30, 38 Range: 11–38% Average: 22%
D. Standard *TB-9Sb* (12 ears)	3.7–5.0, 15, 15, 15–16, 15–16, 19, 23–24, 26, 27, 31–32, 36–37, 38 Range: 3.7–38% Average: 22%
Deletion *TB-9Sb-2010* (13 ears)	2.3–4.0, 12, 13, 23–25, 24, 26–27, 27–28, 30–31, 31, 34–35, 39–40, 40, 40–41 Range: 2.3–41% Average: 27%

Each subdivision of the table represents one family of plants. The families segregated standard and deletion *TB-9Sb* heterozygotes. They were tested for meiotic loss in crosses as female parents and tested for translocation type in crosses as male parents. All ears produced by a family were included in the data, except for small ears with less than 200 kernels. Meiotic loss rates were calculated from endosperm data, as described in MATERIALS AND METHODS. The calculation often gives a range of values for an ear, rather than a single value, as seen in the tabulations. For each section of the table, standard and deletion meiotic loss rates were compared on the basis of rank order position using the Wilcoxan-Mann-Whitney statistical test. For example, in part A of the table, most standard ears have lower rates of meiotic loss than the deletion ears. When these ears are arranged in order of meiotic loss rates, the standard and deletion groups show a clear and significant separation from each other.

A. Comparison of standard *TB-9Sb vs.* deletion *TB-9Sb-1866*. There is a slight overlap in the range of meiotic loss between groups. However, the difference in rank order position is significant at the 1% level.

B. Comparison of standard *TB-9Sb vs.* deletion *TB-9Sb-1852*. There is no overlap between groups. The difference in rank order of meiotic loss is significant at the 1% level.

C and D. Two comparisons of standard *TB-9Sb vs.* deletion *TB-9Sb-2010*. There is considerable overlap between groups in both experiments. Rank order positions are not significantly different between standard and deletion groups.

progeny with the standard translocation was produced. When 37 individuals from the cross described were tested for *B-9* type, the population divided into 27 standard and 10 deletion translocations. The results differ significantly from a 1:1 ratio at the 1% level. The findings indicate that meiotic loss of *B-9–1852* occurs even when a standard *B-9* is present in the same cell. Consequently, the *B-9–1852* must lack a *cis*-active function that suppresses meiotic loss. A similar cross with *B-9–1866* gave ambiguous results. An excess of standard *vs. 1866* progeny was found (46 *vs.* 30). However, the deviation from 1:1 was not statistically significant.

Meiotic loss of *TB-9Sb-2010:* The *9-B* deletion of translocation *2010* involves loss of the distal euchromatic tip of the *B* (region 1) plus a small part of the adjacent heterochromatin (Figures 3 and 5b). A standard test of meiotic loss was conducted. Data from two

Translocation type	Individual rates of meiotic loss (%)
E. Standard *TB-9Sb* (17 ears)	0, 0–1.8, 0.5–1.0, 1.2–2.4, 2.8–3.2, 7.6–8.5, 7.9–10, 12–13, 13–14, 13–14, 13–15, 14–15, 15–17, 15–17, 17–18, 21–22, 21–23 Range: 0–23% Average: 11%
Deletion *TB-9Sb-14* (25 ears)	12–13, 13, 13–15, 18, 18–20, 20–21, 21, 25, 25, 27–28, 27–28, 30, 31–32, 34, 34–35, 35–36, 36, 36–37, 36–38, 38–39, 38–39, 39–40, 39–40, 42–43, 46–47 Range: 12–47% Average: 30%
F. Standard *TB-9Sb* (7 ears)	8.0–9.3, 8.3, 11–12, 16–17, 18, 19, 20–21 Range: 8.0–21% Average: 15%
Deletion *TB-9Sb-2150* (10 ears)	28–29, 35, 40, 40–41, 43, 46, 52–53, 52–53, 53–54, 60–61 Range: 28–61% Average: 45%
G. Standard *TB-9Sb* (13 ears)	1.5–3.0, 2.2–2.7, 10–11, 11–12, 13–15, 15, 16, 17–18, 18–19, 19–20, 21, 25–28, 27–28 Range: 1.5–28% Average: 16%
Deletion *TB-9Sb-2150* (7 ears)	40–41, 43, 50, 51, 51–52, 56–57, 65–66 Range: 40–66% Average: 51%

E. Comparison of standard *TB-9Sb vs.* deletion *TB-9Sb-14.* There is substantial overlap between groups. However, the rank order positions of the deletion crosses are significantly higher than for the standard *TB-9Sb* crosses (1% level).

F and G. Two comparisons of standard *TB-9Sb vs.* deletion *TB-9Sb-2150.* There is no overlap between groups in either experiment. The difference between standard and deletion groups is significant at the 1% level for both experiments.

experiments are given in Table 1, C and D. In both cases, the average rate of meiotic loss between groups is very similar. Apparently, the *2010* deletion has no effect on meiotic loss.

Meiotic loss of *TB-9Sb-14:* In *TB-9Sb-14,* the deletion on the *9-B* includes region 1 plus more than half of the distal *B* heterochromatin (Figures 3 and 5c). A meiotic loss comparison was made, with results given in Table 1E. Average meiotic loss for the standard group was 11% and for *TB-9Sb-14* meiotic loss was 30%. There is considerable overlap in rank order positions between the two groups. Nevertheless, the separation of classes is significant at the 1% level.

Meiotic loss of *TB-9Sb-2150:* The *9-B* deletion for translocation *2150* includes region 1 plus most of the distal *B* heterochromatin (Figures 3 and 5d). Results of two meiotic loss tests are given in Tables 1, F and G. In these experiments, meiotic loss by the standard translocation is much lower than for *TB-9Sb-2150* (15% *vs.* 45% and 16% *vs.* 51%). The separation of classes in both experiments is significant at the 1% level and the groups are nonoverlapping.

Crossing over in the meiotic loss experiments: The findings reported above demonstrate that both proximal and distal *B* chromosome regions act to suppress meiotic loss of the *B-9*. The effect can be explained in two ways. First, migration of univalent *B-9*'s to one pole may be directly controlled by *B* chromosome regions. Second, an indirect effect on *B-9* crossing over may occur. *B* chromosome regions may enhance crossing over between the *B-9* and chromosome *9*. Increased crossing over reduces the frequency of *B-9* univalents and, thereby reduces meiotic loss. Interestingly, the maize *B* chromosome is known to affect crossing over in certain chromosomal regions (RHOADES 1968; HANSON 1969; NEL 1973).

A test of crossing over was designed for the meiotic loss experiments. The test uses the *yg2* marker, located near the distal tip of *9*, plus the *wx* marker. The rate of crossing over on the *B-9* was calculated as *yg2 Wx* crossovers divided by total *wx*, as explained in MATERIALS AND METHODS. Tests of crossing over were performed for the ears of Table 1A (*TB-9Sb-1866*), Table 1B (*TB-9Sb-1852*), Table 1D (*TB-9Sb-2010*) and Table 1F (*TB-9Sb-2150*). Results are given in Table 2. An unusual aspect of the test with *TB-9Sb-2150* was the appearance of plants with fine yellow stripes or mottling in some of the crosses. The stripes suggest that *B-9* instability occurred late in development. The striping appeared in some crosses with the standard *TB-9Sb* and some with the deletion *TB-9Sb-2150*. It therefore seems unrelated to the meiotic loss effects of *TB-9Sb-2150*.

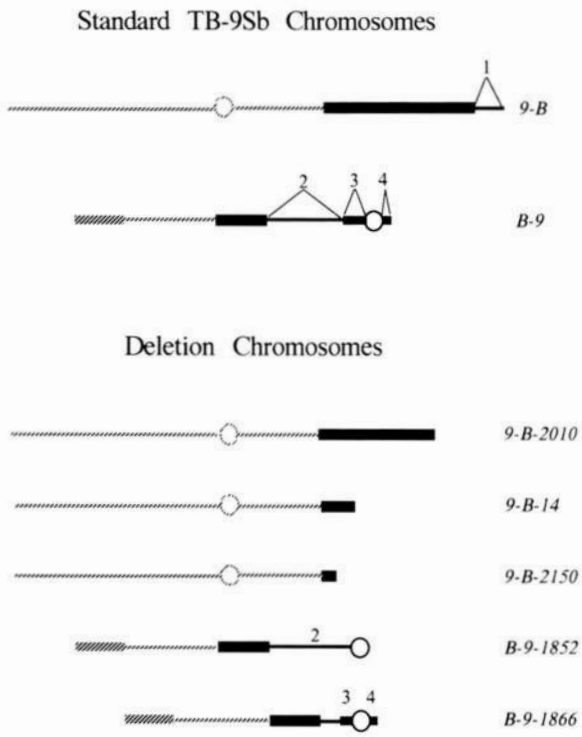

FIGURE 3.—Drawings of the *TB-9Sb* chromosomes. The standard *9-B* and *B-9* (top) can be compared to various deletion types (below). Solid lines are *B* chromosome segments and slashed lines are chromosome *9* regions. Circles represent centromeres. Widened lines are heterochromatic. Numbers indicate the presence of *B*-nondisjunctional regions. Note: *9L* is longer than it is depicted.

The data in Table 2 show that none of the deletion chromosomes causes a significant reduction in crossing over. The finding agrees with data of HANSON (1969) on the effect of *B* chromosomes on crossing over in chromosome *9*. He found that the presence of *B* chromosomes had little overall effect on *yg-wx* crossing over. An effect on crossing over is not, therefore, the reason that deletion chromosomes affect meiotic loss. The results also show that *B-9* crossing over is quite low, considering the map distance tested was at least 24 map units. (However, total *B-9* crossing over is higher than the rates shown: see note in Table 2 legend.) The low rate of crossing over may be caused by the combined effects of (a) reduced crossing over near a translocation breakpoint (BURNHAM 1962, 1981), (b) reduced crossing over in the presence of a knob at the end of the *B-9* (CHANG and KIKUDOME 1974) and (c) lower crossing over in the female (ROBERTSON 1984). In any case, the low rate of crossing over provides an ideal opportunity to test meiotic loss, since the univalent frequency should be high.

Cytological studies on meiotic loss: The experiments discussed thus far pertain to the female meiosis. Genetic tests of meiotic loss in the male are difficult, due mainly to pollen competition effects, and have not been attempted. It would be preferable to do cytological studies on meiotic loss in the female. However, the female meiosis is extremely difficult to study.

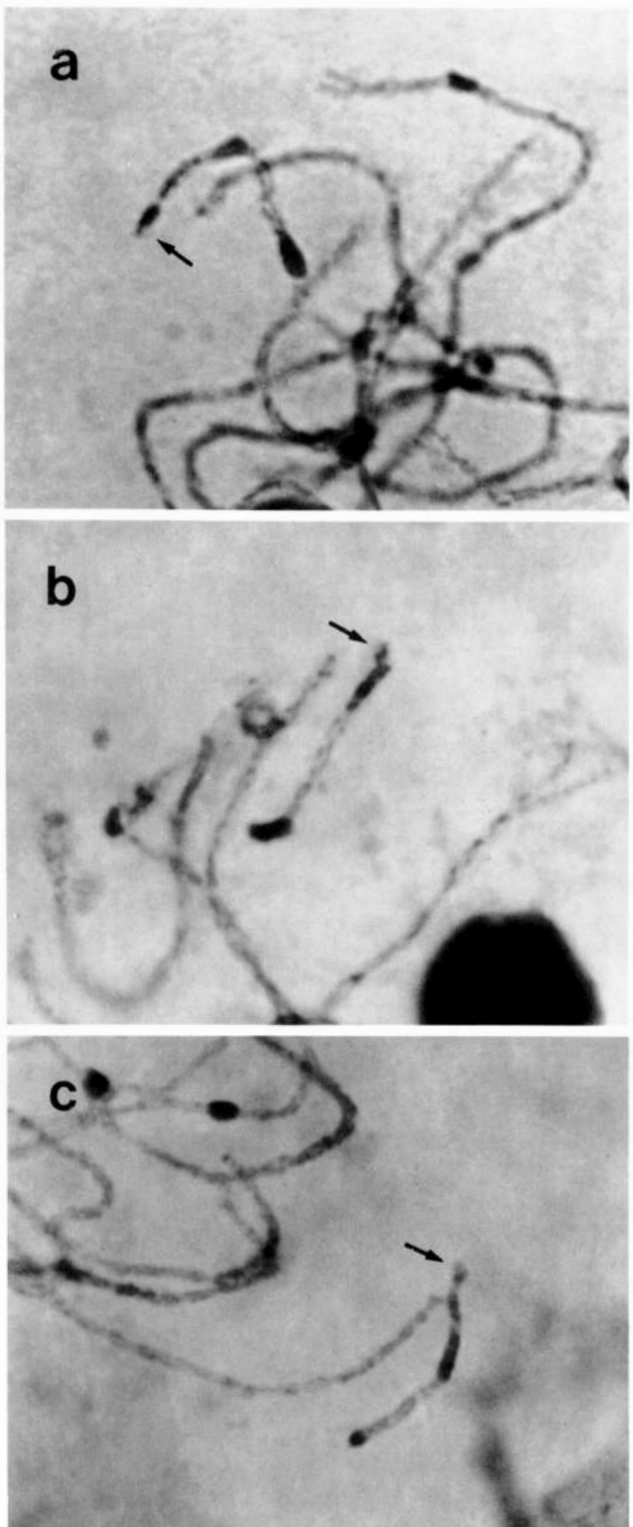

FIGURE 4.—Standard and deletion *B-9* chromosomes in pachytene. Arrows indicate the centromeric regions. (a) Complete (standard) *B-9* chromosome. (Reprinted from W. CARLSON, *Chromosoma* **30:** 356, 1970.) (b) Deletion *B-9–1866*. (c) Deletion *B-9–1852*. Note: the distal knob on each chromosome is a feature of chromosome *9*. The knob varies in size between stocks.

It cannot be used in any study that requires significant data collection. Therefore, cytological observations

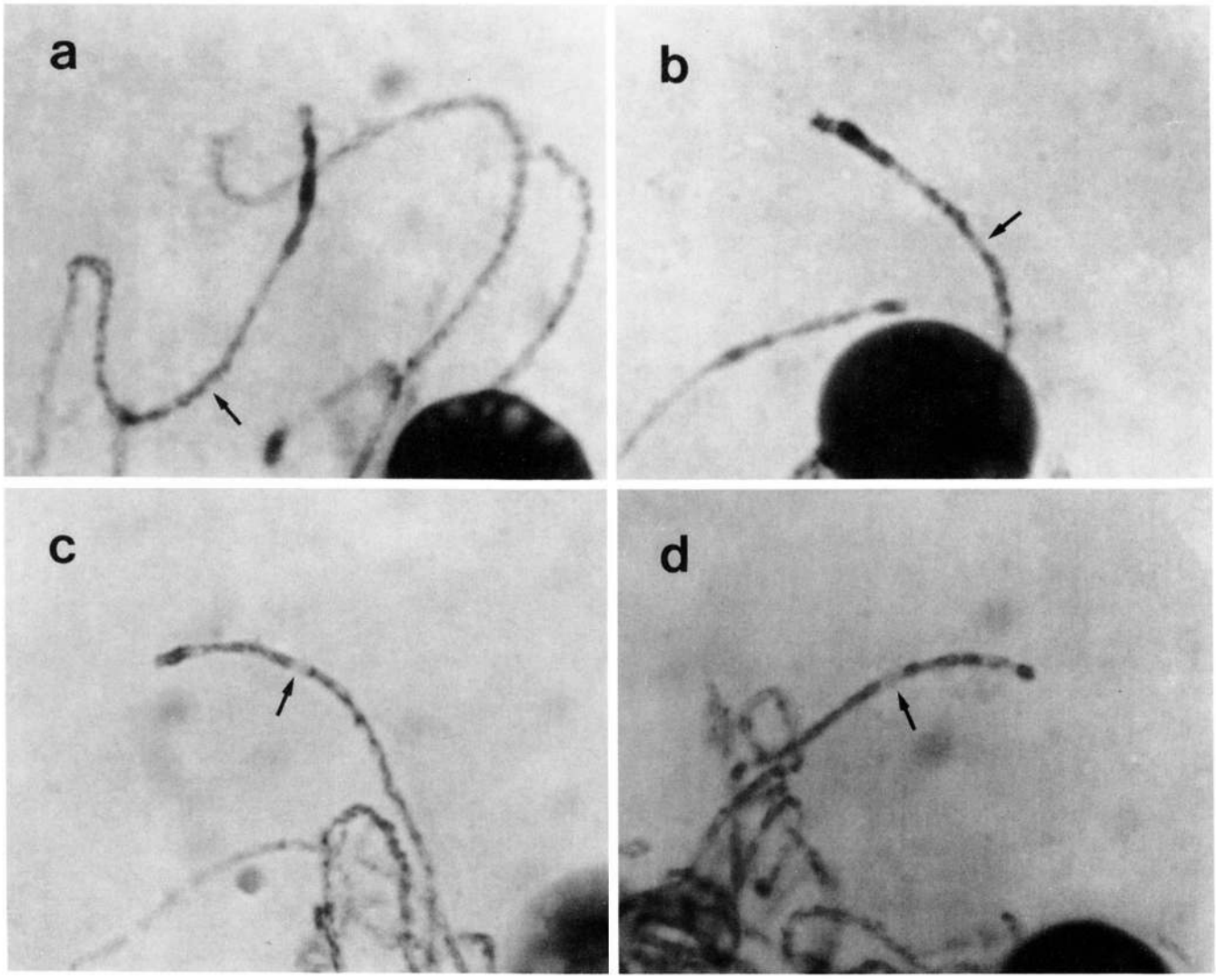

FIGURE 5.—Standard and deletion *9-B* chromosomes in pachytene. Arrows indicate the centromeres. For b, c and d, the centromere is clearly seen as a light, transluscent body. For a, the centromere is not well-stained and the arrow indicates its probable location. The euchromatic region of the short arm originates from *9S*, whereas the terminal heterochromatin is from the *B* chromosome. (a) Complete (standard) *9-B* chromosome. (b) Deletion *9-B-2010*. (c) Deletion *9-B-14*. (d) Deletion *9-B-2150*.

TABLE 2

Percent crossing over between *B-9* and *9* in various meiotic loss experiments

Reference	Chromosome tested	Classification groups	No. of ears	Average crossing over (%)	Percent range
1. Table 1A	*B9-1866*	*TB-9Sb*-standard	10	3.3	0.6–5.8
		TB-9Sb-1866	10	3.0	0.5–5.9
2. Table 1B	*B-9-1852*	*TB-9Sb*-standard	10	4.3	2.5–12.6
		TB-9Sb-1852	8	7.9	3.9–15.1
3. Table 1D	*9-B-2010*	*TB-9Sb*-standard	12	1.9	0.5–3.9
		TB-9Sb-2010	12	1.5	0.0–4.0
4. Table 1F	*9-B-2150*	*TB-9Sb*-standard	7	1.9	0.8–3.7
		TB-9Sb-2150	10	1.8	0.0–4.4

None of the deletion chromosomes produced a significant reduction in crossing over compared to standard. Note: the method of calculation does not identify all crossovers, as explained in MATERIALS AND METHODS. The actual rates of crossing over may be up to twice the values given.

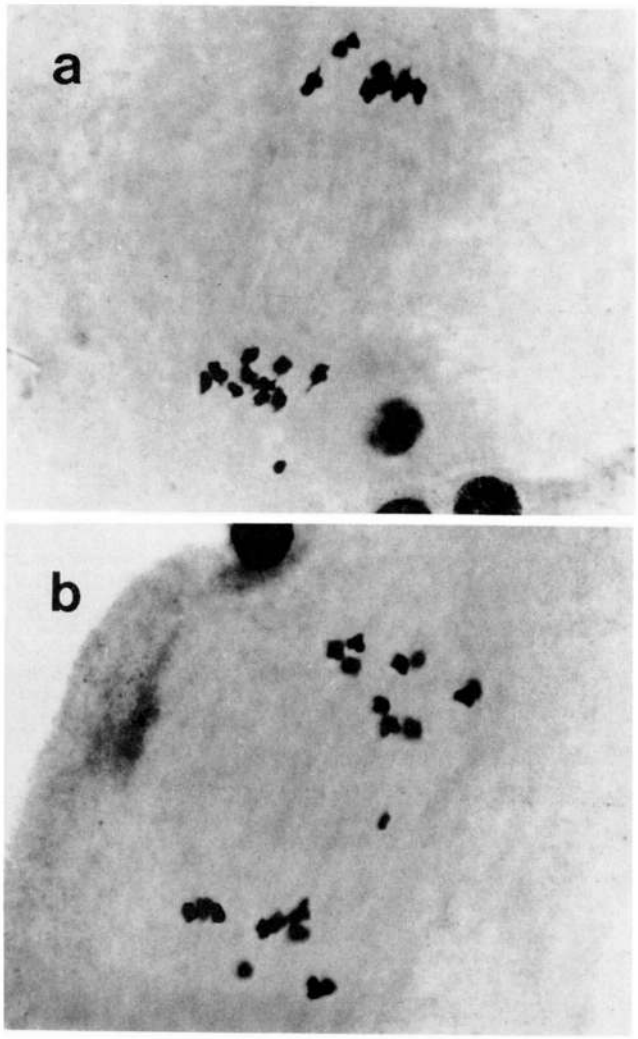

FIGURE 6.—Anaphase I in cells with univalent *B-9's*. (a) Standard *B-9* univalent moving precociously to one pole. (b) Deletion *B-9–1852* univalent lagging between disjoining sets of chromosomes.

have been made with the male meiosis.

CARLSON and CURTIS (cited by CARLSON 1988) compared meiotic behavior of the *B-9* in standard *TB-9Sb vs.* deletion *TB-9Sb-1852* plants. Hypoploid plants (*9-B 9-B B-9*) were utilized so that the *B-9* was always univalent in meiosis. With the standard *TB-9Sb,* the *B-9* univalent tended to move precociously to one pole at anaphase, rather than lag. With *TB-9Sb-1852,* lagging of the *B-9* in anaphase I was predominant (Figure 6). It was noted that lagging does not necessarily lead to meiotic loss. However, the findings suggested a cytological mechanism for meiotic loss: lagging and exclusion from daughter nuclei. Further data have been gathered recently and they correlate well with the earlier findings (Table 3). Anaphase I was classified for 11 hypoploid sibling plants. Six of the hypoploids had the standard *TB-9Sb* and five had the deletion *TB-9Sb-1852*. Fifty anaphases were classified for each plant. The categories of anaphase were: (a) "ahead to pole" (precocious migration of univalent to one pole), (b) "lag" (univalent remains behind) (c) "normal migration" (univalent is not separate from other chromosomes), (d) "split lag" (univalent splits mitotically but lags behind other chromosomes), (e) "split ahead" (univalent splits and moves ahead of other chromosomes to both poles). Only (a), (b) and (c) classes had significant numbers. The "ahead to pole" class is frequent for the standard *TB-9Sb* and much less frequent for the deletion translocation. The difference between groups is non-overlapping and significant at the 1% level. The "lag" class is frequent for *TB-9Sb-1852* and not frequent for the standard translocation. This difference is also non-overlapping and significant at the 1% level. The "normal migration" class is similar for both translocations. The findings suggest that the standard *B-9* univalent migrates to one pole much more efficiently than does the deletion *B-9*.

TABLE 3

Anaphase I in standard *9-B 9-B B-9 vs.* deletion-*1852 9-B 9-B B-9*

Type of TB-9SB	Plant No.	Ahead to pole	Lag	Normal migration	Split ahead	Split lag
Standard	8110-1	40	0	8	0	2
(6 plants)	-7	26	14	9	0	1
	-10	23	14	11	0	2
	-13	34	14	1	0	1
	-14	25	13	8	0	4
	-15	42	2	4	0	2
		190	57	41	0	12
		(63%)	(19%)			
Deletion	8110-3	10	25	15	0	0
B-9-1852	-9	7	34	6	0	3
(5 plants)	−11	10	29	10	0	1
	-12	13	25	10	0	2
	-25	10	25	3	1	11
		50	138	44	1	17
		(20%)	(55%)			

Fifty cells were classified per plant. The rank order difference between groups is significant at the 1% level when considering percent "ahead" or percent "lag" (see text). There is no overlap in the data.

DISCUSSION

Several functions have been attributed to the *B* chromosome of maize. In 1947, HERSCHEL ROMAN reported nondisjunction of the *B* at the second pollen mitosis. ROMAN (1948) also demonstrated that the *B* chromosome confers the property of preferential fertilization on sperm containing it. Several workers showed that the *B* chromosome modifies crossing over in certain regions of standard (*A*) chromosomes (RHOADES 1968; HANSON 1969; NEL 1973). BECKETT (1982) reported that the *B* chromosome gives pollen containing it a competitive advantage in fertilization. CARLSON (1986) provided evidence that the *B* chromosome suppresses its own meiotic loss.

The first *B* chromosome function to be localized to a specific site or sites on the *B* was nondisjunction at the second pollen mitosis. Four separate regions on the *B* were shown to control nondisjunction (reviewed by CARLSON 1986). In this report, a second function is localized to sites on the *B:* suppression of meiotic loss. The latter function allows unpaired *B*-type chromosomes to migrate poleward at anaphase I of meiosis. Data given in RESULTS show that suppression of meiotic loss is controlled by at least one proximal and one distal region on the *B* chromosome. The identification of these regions was accomplished through the use of *B*-deletion stocks that were derived in the *B-A* translocation, *TB-9Sb*. Five of these deletions were tested for meiotic loss. The translocations are diagrammed in Figure 3.

TB-9Sb-1866 and *TB-9Sb-1852* are *B-9* deletion stocks. The *1866* translocation lacks most of the proximal euchromatin of the *B,* including nondisjunctional region 2. The translocation also lacks part of the centric heterochromatin (CARLSON 1986). The *1852* translocation lacks the pericentric heterochromatin, including nondisjunctional regions 3 and 4 (Figures 3 and 4). A controlled comparison of meiotic loss rates was made between standard *TB-9Sb* and *TB-9Sb-1866* in Table 1A. A similar comparison between standard *TB-9Sb* and *TB-9Sb-1852* is reported in Table 1B. In both cases, the tested plants were translocation heterozygotes: *9 9-B B-9 vs. 9 9-B* deletion *B-9*. The *B-9* is frequently unpaired in these constructs and potentially subject to meiotic loss. Transmission of the *B-9* through the female parent was determined in testcrosses, and the rate of meiotic loss calculated. The formula is described in Materials and Methods. For both the *1866* and *1852* translocations, average meiotic loss was very high compared to that of the standard translocation. The rates for standard *vs. 1866* were 14% *vs.* 46%. The rates for standard *vs. 1852* were 10% *vs.* 48%. The difference was significant at the 1% level in both cases. Consequently, a proximal region or regions on the *B* acts to reduce meiotic loss. (Because *TB-9Sb-1866* lacks part of region 3 and, therefore, overlaps with *TB-9Sb-1852,* the possibility exists that only one factor controlling meiotic loss is identified by tests on the two deletion stocks.)

TB-9Sb-2010, TB-9Sb-14 and *TB-9Sb-2150* are *9-B* deletion translocations. All three translocations are deficient for the distal euchromatic tip of the *B,* which carries nondisjunctional region 1. In addition, *TB-9Sb-2010* is missing about 20% of the distal *B* heterochromatin, *TB-9Sb-14* lacks more than half of the heterochromatin and *TB-9Sb-2150* lacks most of the heterochromatin. (Figures 3 and 5). Meiotic loss tests were conducted in the same manner as described for *B-9* deletion translocations. The *2010* translocation showed no difference from standard *TB-9Sb* in meiotic loss, whereas *TB-9Sb-14* and *TB-9Sb-2150* did (Tables 1, C to G). The finding with *TB-9Sb-2010* indicates that the distal euchromatin is not required to suppress meiotic loss. However, the results with *TB-9Sb-14* and *TB-9Sb-2150* show that the distal *B* heterochromatin exerts control over meiotic loss. Meiotic loss rates for the standard translocation *vs. TB-9Sb-14* were 11% *vs.* 30%. The rates for standard *vs. 2150* (in two tests) were 15% *vs.* 45% and 16% *vs.* 51%. The data suggest, but do not prove, that *TB-9Sb-2150* has a more extreme effect on meiotic loss than *TB-9Sb-14*.

The findings discussed above show that at least one proximal region and one distal region on the *B* chromosome suppress meiotic loss. These regions could act directly by enabling univalent *B* chromosomes to migrate poleward in anaphase I. Alternately, they could act indirectly through an effect on crossing over. It was shown earlier (CARLSON 1986) that crossing over between *9* and the *B-9* prevents meiotic loss. The *B-9* must be univalent in order for meiotic loss to occur. Consequently, regions on the *B* which suppress meiotic loss could produce their effect indirectly by increasing crossing over between the *9* and *B-9*. Crossover rates were determined for each of the deletion-translocation stocks, except *TB-9Sb-14*. In each test, the deletion stock showed rates of crossing over that were similar to those for the standard translocation (Table 2). The tests of crossing over were conducted on the same ears that were used to measure meiotic loss rates. Consequently, the increased meiotic loss found in several deletion stocks is not due to an effect on crossing over. Instead, meiotic loss is controlled directly through an effect on chromosome movement in anaphase I. This conclusion is supported by cytological studies that compare standard *TB-9Sb* with the deletion stock, *TB-9Sb-1852* (Table 3 and Figure 6).

It was proposed earlier that the system which suppresses meiotic loss may be related to the *B*-nondisjunctional system (CARLSON 1988). The processes of univalent migration in meiosis and nondisjunction in mitosis are functionally equivalent. In both cases, two chromatids on one chromosome migrate to the same pole. Therefore, one of the systems may have evolved from the other and the two processes could share common genes. The findings reported here provide evidence both for and against this hypothesis. On the positive side, the *B-9* deletion of *TB-9Sb-1866* removes both a site for nondisjunction (region 2) and a site for suppressing meiotic loss. The *B-9* deletion of *TB-9Sb-1852* also removes both a nondisjunctional site (region 3) and a site that controls meiotic loss. The correlation of losing both nondisjunctional and meiotic loss sites in the same deletions could be coincidental. The functions could be located at different sites within the deleted regions. However, it is interesting that the

nondisjunctional and meiotic loss functions missing from *TB-9Sb-1852* are both *cis*-active functions [CARLSON (1978a) and RESULTS]. On the other hand, the deletion of nondisjunctional region 1 in *TB-9Sb-2010* has no effect on meiotic loss rates (Table 1, C and D). Also, the deletion of distal *B* heterochromatin, which lacks any nondisjunctional site (LIN 1978), has a strong effect on meiotic loss in *TB-9Sb-2150* (Table 1, F and G). No conclusions on a relationship between nondisjunction and meiotic loss can be drawn at this time.

The discovery of a system for controlling meiotic loss leads to a proposal on the significance of meiotic loss in the evolution of the maize *B* chromosome. The proposal assumes that the *B* arose from a standard (*A*) chromosome of maize or a maize relative or ancestor (JONES and REES 1982). The *B* chromosome is small in size and may have originated as a centric fragment rather than a simple trisome. The populational frequency of the *B* was, by definition, extremely low during the early stages of its evolution. Consequently, the chromosome frequently lacked a pairing partner in meiosis. The result was a high rate of meiotic loss, and the system described in this report was selected to suppress it. The system, however, was only partially effective. Data in Table 1 show that meiotic loss for standard *TB-9Sb* is substantial (also see ROBERTSON 1967, p. 442). Consequently, a second system for avoiding meiotic loss was developed. That system was nondisjunction at the second pollen mitosis.

Ordinarily, nondisjunction is discussed in the context of ROMAN'S (1947, 1948) accumulation mechanism. Nondisjunction together with preferential fertilization serve as a mechanism for increasing *B* chromosome frequency in a population. However, it seems likely that nondisjunction serves another purpose: it increases greatly the number of individuals with two *B*'s (and zero *B*'s) in a population. Even at very low populational frequencies of the *B* chromosome, nondisjunction has the ability to maximize the number of plants with two *B* chromosomes and thereby maximize bivalent pairing. Nondisjunction, therefore, acts to suppress meiotic loss. It is proposed that nondisjunction evolved originally for this purpose. Only later did preferential fertilization develop, adapting nondisjunction to an accumulation mechanism.

A related proposal concerns effects of the maize *B* chromosome on crossing over. Most functions of the *B* chromosome seem directed toward its own survival. However, several studies have shown that the maize *B* chromosome affects crossing over in standard (*A*) chromosomes. The effects are usually small, but they can be dramatic (RHOADES 1968). It has been proposed that *B* chromosomes serve a useful function by modifying crossing over in *A* chromosomes. *B*'s may increase the number of recombinant gamete types produced by an individual, and thus aid evolution (HANSON 1969; JONES and REES 1982 p. 110). However, we propose that the primary function of recombination effects is not to influence *A* chromosomes. Instead, recombination effects are directed toward the *B* chromosome itself. The standard chromosomes are influenced only incidentally. The purpose of recombination effects is to increase pairing and crossing over between *B* chromosomes so that meiotic loss is reduced. The need for a special system to increase *B* chromosome crossing over is explained by the fact that the chromosome is small and heterochromatic. Both conditions tend to reduce crossing over (JONES and REES 1982).

In summary, it is proposed that several activities of the maize *B* chromosome can be explained as responses to meiotic loss. These include a) direct suppression of univalent loss in meiosis b) nondisjunction at the second pollen mitosis, and c) recombination effects. It is also believed that similar properties are found with the *B* chromosomes of many other species. For example, the *B* chromosomes in some species display a regular migration of univalents to one pole in meiosis (JONES and REES 1982, pp. 47–53). Also, the *B* chromosomes of many species possess accumulation mechanisms. These systems may operate premeiotically, postmeiotically or during meiosis (JONES and REES 1982, Table 3.7). Despite the variety of accumulation mechanisms, most act by nondisjunction. Consequently, most or all accumulation mechanisms may have evolved originally as systems to reduce meiotic loss. Finally, several *B* chromosomes, in addition to the maize *B*, have been shown to influence crossing over among *A* chromosomes (JONES and REES 1982). We believe that these crossover effects function primarily to enhance bivalent pairing and crossing over between *B* chromosomes, thus suppressing meiotic loss.

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