

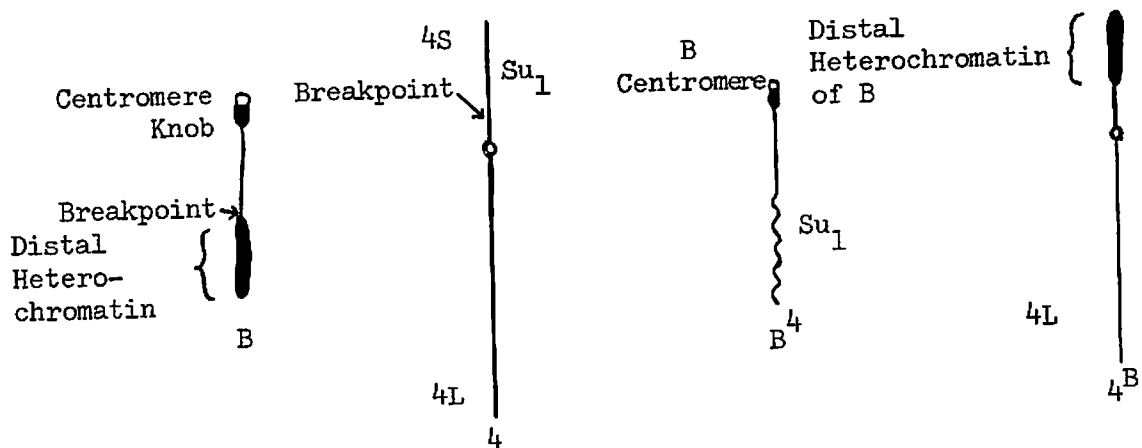
to be determined. Some kind of interaction between the heterochromatin of knobs and that of B chromosomes which leads to loss of all or part of the knob-bearing A chromosome would appear to be likely. Unfortunately, the second spore division occurs at a stage when the cytoplasm is full of starch grains and it is not a favorable stage to observe. It may also be difficult to distinguish between B chromosomes which undergo nondisjunction at this time and aberrantly behaving A chromosomes.

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2. An interaction of B chromosomes and abnormal 10.

Y. C. Ting has proposed that abnormal chromosome 10 was derived from a normal 10 and a B chromosome. (*Chromosoma*: 9:286). Since then, attempts have been made to determine whether homology exists between B chromosomes and the extra chromatin of abnormal 10. Rhoades and Dempsey looked for pairing in pachytene between a single B and abnormal 10, as an indication of homology. Little if any pairing was found. (*MNL*:33:58). Ting found some association between B's and abnormal 10, which, however, also occurred between abnormal 10 and other heterochromatic knobs. (*MNL*:33:37). Even if we assume that pairing between abnormal 10 and B's is a rare event, some homology between the two cannot be ruled out. It is possible that some rearrangement in abnormal 10 has occurred since its hypothetical origin from a B chromosome. So a different approach to the problem was used.

It was first determined by Roman, and since confirmed by other workers, that the distal heterochromatin of the B chromosome is responsible for the nondisjunction of the B centromere region at the 2nd microspore division. Roman used the B-4a translocation.



Since the B^4 chromosome undergoes nondisjunction and the 4^B chromosome does not, the B centromere (or an adjacent region) is the site of nondisjunction. However, nondisjunction of the B^4 chromosome occurs only in the presence of the 4^B chromosome. Microspores that contain a normal chromosome 4 plus a B^4 show little, if any, nondisjunction of the B^4 chromosome. (The $4 + B^4$ sperm, while unbalanced, does function often enough to be tested.) The same result has been found in other B translocations. Apparently the 4^B chromosome is required for nondisjunction because it contains the distal heterochromatin of the B chromosome.

If abnormal 10 arose from an interchange between a B chromosome and a normal 10, it may contain some or all of the distal heterochromatin of the B chromosome, including the region responsible for nondisjunction of the B centromere. As previously mentioned, microsporocytes that contain a normal chromosome 4 plus a B^4 do not show nondisjunction of the B^4 chromosome. The addition of abnormal 10 to such a microsporocyte will test whether or not abnormal 10 contains the region responsible for nondisjunction. This was done, but, for reasons of convenience, the translocation used was B-9b rather than B-4a. The break point in chromosome 9 is in the short arm, between sh and wx. The break point in the B chromosome is a short distance into the distal heterochromatin, but apparently does not include the region controlling nondisjunction. Plants were produced that contained two normal chromosomes 9 plus a B^9 . One half of the plants were expected to be heterozygous for abnormal 10 and one half should have normal chromosomes 10. The presence of abnormal 10 was determined by examination of sporocytes. The plants were crossed as males onto a c sh wx tester:

$$\underline{c} \underline{sh} \underline{wx} \text{ X } \frac{\underline{c} \underline{sh} \underline{wx}}{9} \quad \frac{\underline{c} \underline{sh} \underline{wx}}{9} \quad B^9 \underline{C} \underline{Sh}$$

The B^9 chromosome carries the dominants for C and Sh. Colored, full seeds produced in the cross indicate the presence of the B^9 chromosome in the endosperm. If nondisjunction has occurred, there should be two B^9 's in the endosperm and none in the embryo. If it has not occurred, there should be one B^9 in each. The C Sh seeds were grown and the resulting plants used as female parents in backcrosses to a c sh wx tester. The occurrence of C Sh seeds in the backcross progeny at a rate of about 30% demonstrates the presence of one B^9 in the female parent. (The rate does not reach 50%, apparently because of poor pairing with the normal chromosomes 9 and lagging at anaphase. Some of the plants from C Sh kernels do give 50% C Sh when backcrossed. These plants contain a cross-over chromosome 9 carrying C Sh wx.) The absence of C Sh on the backcrossed ear indicates that nondisjunction has occurred. (This could also result occasionally from heterofertilization, rather than nondisjunction.) Results of the backcrosses are given below:

Male Parent	Constitution of Plants from		
	C Sh Kernels		
$\frac{c}{9} \frac{sh}{9} \frac{wx}{9}$	$\frac{c}{9} \frac{sh}{9} \frac{wx}{9}$	$B^9 \frac{C}{9} \frac{Sh}{9}$	
	No B^9	One B^9	Crossover
Normal 10			
202-3	1	14	1
202-28	1	30	2
203-2	1	9	3
203-3	3	17	2
203-17	0	32	3
Totals	6	102	11

$$\% \text{ Nondisjunction} = 6/108 = 5.6\%$$

Abnormal 10	Constitution of Plants from		
	C Sh Kernels		
	No B^9	One B^9	Crossover
202-23	0	19	2
202-27	2	66	8
203-1	0	18	5
203-8	2	10	6
203-9	1	51	12
203-16	0	9	5
Totals	5	173	38

$$\% \text{ Nondisjunction} = 5/178 = 2.8\%$$

The results show that abnormal 10 cannot replace the distal heterochromatin of the B in producing large scale nondisjunction.

However, it was still considered possible that abnormal 10 might increase the amount of nondisjunction occurring in the presence of the distal heterochromatin. For this reason, the effect of abnormal 10 on nondisjunction of B^9 was tested in the presence of the 9^B chromosome. In the presence of 9^B , nondisjunction should occur at a relatively high rate. The plants used were heterozygous for the translocation, and segregated abnormal 10 in a 1:1 ratio. Markers present are shown below:

$$\frac{c}{9} \frac{sh}{9} \frac{wx}{9} + 9^B \frac{Wx}{9} + B^9 \frac{c}{9} \frac{Sh}{9}$$

The following classes of spores will be found after meiosis:

1. $\frac{c}{9} \frac{sh}{9} \frac{wx}{9}$
2. $\frac{c}{9} \frac{sh}{9} \frac{wx}{9} + B^9 \frac{c}{9} \frac{Sh}{9}$
3. $9^B \frac{Wx}{9}$
4. $9^B \frac{Wx}{9} + B^9 \frac{c}{9} \frac{Sh}{9}$

The 9^B class will abort. The two classes containing a normal 9 will be waxy. If Wx seeds are selected following the cross onto a wx tester, only the $9^B + B^9$ class will be represented. Crossing over between Wx

and the break point is negligible. (Bianchi estimates it at 0.2% in MNL 40:75). The nondisjunction of the B^9 can, therefore, be measured in the presence of 9^B , without the need for a homozygous translocation. In this experiment, sporocytes from 22 plants heterozygous for TB-9b were examined for the presence or absence of abnormal 10. Each plant was used as a male parent onto 4-6 ears of a sh bz wx B Pl tester. Wx seeds were selected from the ears. Wx kernels which are also bronze result from nondisjunction of the B^9 , with the endosperm being deficient for B^9 and the embryo carrying two doses. Purple kernels which give rise to bronze plants also indicate that nondisjunction has taken place, with the embryo, in this case, being deficient. Classification of seedlings has not yet been attempted, however, and only the one type of nondisjunction (bronze seeds) has been scored. The following table gives the frequency of this type of nondisjunction. There is good reason to believe that, when the total rate of nondisjunction is determined, the relative differences between the normal 10 and abnormal 10 groups will remain the same (see Catcheside Heredity 10:345).

Normal 10 Group			Abnormal 10 Group		
Male parent	Total Wx	% bronze	Male parent	Total Wx	% bronze
771-1	509	46.6%	771-7	710	23.5%
-3	825	43.0	-8	524	30.0
-4	935	56.6	-10	679	20.0
-15	791	52.9	-11	1176	3.4
-17	779	38.5	-14	623	49.0
-21	634	35.2	-20	1134	32.5
-22	579	55.0	-36	1174	25.5
-23	761	63.3	-39	827	33.0
-24	758	49.0	-41	928	54.9
-25	610	66.0		Av.	30.2%
-32	605	66.0			
-33	507	63.0			
-34	647	47.0			
	Av.	52.5%			

It is obvious from these results that abnormal 10 does not increase the rate of nondisjunction of the B^9 . In fact, the rate is decreased in plants with abnormal 10. While the lowest member of the normal 10 group shows 35.2% nondisjunction, 7 of the 9 members of the abnormal 10 group fall below this level of nondisjunction, with one abnormal 10 plant having a rate of only 3.4%. It is possible that the difference here is not due to abnormal 10, but to a factor linked to it on chromosome 10. It is also possible that the presence of abnormal 10 changed the time of flowering of these plants slightly, and thereby changed the environmental condition at the time of nondisjunction. Bianchi has reported an apparent environmental effect on nondisjunction (Z. f. Vererbungslehre 92:213).

If abnormal 10 has the ability to reduce the rate of nondisjunction of a B chromosome, an explanation may be advanced for Longley's data on distribution of B chromosomes in different maize stocks. (J. Agric. Res. 56:177). Longley found that B chromosomes were seldom present in stocks with large numbers of heterochromatic knobs. If knobs in general, and not just abnormal 10, are capable of reducing the rate of nondisjunction among B chromosomes, they would tend to eliminate B chromosomes from the stock. Nondisjunction of B chromosomes together with preferential fertilization of the egg by the hyperploid sperm increases the B chromosome number in a population. In the absence of nondisjunction, it seems likely that a lack of selective advantage and irregularities in segregation at meiosis would result in the elimination of B's. The effect of other knobs on the rate of nondisjunction in TB-9b will be tested this summer. There is no evidence yet that knobs other than abnormal 10 can affect nondisjunction.

Wayne Carlson

3. Further study of the transmission of B^4 derived from the TB-4a standard stock.

In last year's News Letter (1966) preliminary data on the transmission of the supernumerary B^4 in normal genotypes were reported. A more intensive study of its genetic behavior is underway. Crosses were made using hyperploid plants ($4,4,B^4$) homozygous for Su as the male parent on a su₁ tester in order to investigate the transmission of B^4 together with chromosome 4 through the male gametophyte. In addition, the ability of such hyperploid gametes to fertilize the egg, as well as the nondisjunction rate of B^4 in the absence of 4^B at the 2nd microspore division, was studied.

The F_1 , heterozygous Su/su and expected occasionally to be hyperploid for B^4 , was backcrossed as female parent to the su₁ tester in order to recover the hyperploid plants. Three hundred thirty ears were scored for the ratio Su:su. The presence of B^4 would be indicated by an excess of ears showing a significant deviation from the expected 1:1 ratio (with a majority of Su kernels) over those deviating by chance. Also, 19 ears obtained by selfing were scored for the ratio 3:1. A total of 108,273 kernels were classified.

In Table 1 the P value corresponds to the χ^2 deviation calculated on each of the ears examined. These results show a considerable excess of ears deviating from the expected ratios. The 6 ears deviating from the 1:1 ratio in the opposite direction (towards su) give an idea of the deviation by pure chance. In the backcrosses, among the significantly deviating ears, variations of ratios from 1.88:1 to 1.30:1 are presumably due to different rates of loss of the single B^4 in female meiosis or in the later stages of embryo sac development. These variations could be partially ascribed to the different backgrounds originally involved. The few data available from the ears obtained by selfing confirm those available from backcrosses. Here pollen transmission of B^4 occurs in addition to the main source of transmission through the female gametogenesis, but at a low rate since the B^4 -hyperploid pollen is competitively selected