that it appears that such "hybrid" A-B translocations are possible, reciprocal A translocations can be selected that will minimize the amount of the original chromosome arm incorporated in the new A-B translocation.

Not only would such hybrid A-B translocations be useful in placing new genes to chromosome arms not previously covered by A-B translocation, but they could be utilized to subdivide the regions of the present A-B translocations. If a new hybrid A-B translocation is tested with a gene that is uncovered by the original parent A-B translocation, the new A-B translocation will only uncover the gene if it is proximal to the break point of the reciprocal A translocation involved. For example, vp_5 is uncovered by TB-1b. Crossover studies have shown it to be very close to the break point of T1-2c. If it is proximal to this break point, then the "hybrid" A-B translocation produced by crossing over with this translocation will still have attached to the B centromere the segment of chromosome one which carries the vp_5 locus. Thus, vp_5 should be uncovered by the new "hybrid" translocation. However, if vp_5 is proximal to the break point of 1-2c, the vp_5 locus will be carried in the 2^1 chromosome and it will not be uncovered by the new translocation.

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2. Additional data on the genetics of TB-9b.

In last year's News Letter I reported upon the segregation in plants hyperploid for TB-9b (i.e., 9 $9^B B^9 B^9$). Hyperploid plants with the genetic and cytological constitutions shown in Figure 1 were pollinated by pollen from homozygous c sh_1 wx plants.
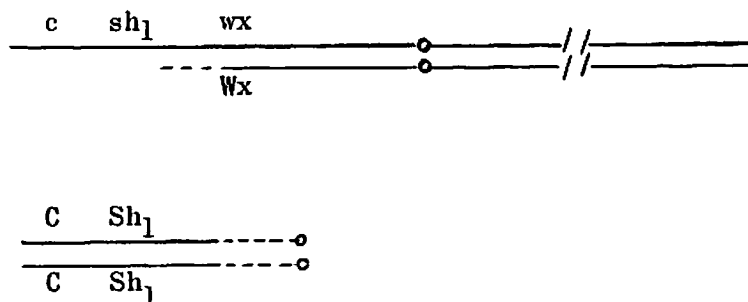

Figure 1. Genetic and cytological constitution of embryos of plants hyperploid for TB-9b.

Table 1 summarizes the testcross data and a suggested cytological configuration and genotype for each testcross phenotype observed.

Table 1

Testcross Data of Plants Hyperploid for TB-9b
($\underline{c}$ $\underline{sh_1}$ $\underline{wx}$/$\underline{C}$ $\underline{Sh_1}$-/$\underline{C}$ $\underline{Sh_1}$-/--$\underline{Wx}$ x $\underline{c}$ $\underline{sh_1}$ $\underline{wx}$/$\underline{c}$ $\underline{sh_1}$ $\underline{wx}$) and Suggested
Cytology and Genotype for Each of the Observed Testcross Phenotypes

Testcross phenotypes and frequencies	Suggested cytology and genotype of observed testcross phenotypes
$\underline{C\ Sh\ Wx}$ Freq. 1310 % 47.83	$\dfrac{c\ sh\ wx_o\!-\!/\!/\!-}{C\ Sh\ Wx_o\!-\!/\!/\!-}$ $\diagdown_o$
$\underline{c\ sh\ wx}$ Freq. 102 % 3.72	$\dfrac{c\ sh\ wx_o\!-\!/\!/\!-}{c\ sh\ wx_o\!-\!/\!-}$
$\underline{C\ sh\ wx}$ Freq. 0 % 0	
$\underline{c\ Sh\ Wx}$ Freq. 4 % 0.15	$\dfrac{c\ sh\ wx_o\!-\!/\!/\!-}{c\ Sh\ Wx_o\!-\!/\!/\!-}$ $\diagdown_o$
$\underline{C\ Sh\ wx}$ Freq. 1315 % 48.01	$\dfrac{c\ sh\ wx_o\!-\!/\!/\!-}{c\ sh\ wx_o\!-\!/\!/\!-}$ $\overline{C\ Sh}\diagdown_o$
$\underline{c\ sh\ Wx}$ Freq. 7 % 0.26	$\dfrac{c\ sh\ wx_o\!-\!/\!/\!-}{c\ sh\ Wx_o\!-\!/\!/\!-}$ $\diagdown_o$
$\underline{C\ sh\ Wx}$ Freq. 0 % 0	
$\underline{c\ Sh\ wx}$ Freq. 1 % 0.04	$\dfrac{c\ sh\ wx_o\!-\!/\!/\!-}{c\ sh\ wx_o\!-\!/\!/\!-}$ $\overline{c\ Sh}\diagdown_o$

Last year, directed segregation of the B and 9 centromeres, after crossing over in the $\underline{c}$-$\underline{sh}$ region, was suggested to explain the presence of four $\underline{c}$ $\underline{Sh}$ $\underline{Wx}$ seeds in the absence of the reciprocal crossover class ($\underline{C}$ $\underline{sh}$ $\underline{wx}$) and the extremely rare occurrence of the $\underline{c}$ $\underline{Sh}$ $\underline{wx}$ class. Additional data reported in Table 2 do not support such an explanation.

Table 2

Summary of Colorless Classes in Testcrosses of Plants Hyperploid for TB-9b ($\underline{c}$ $\underline{sh_1}$ $\underline{wx}$/$\underline{C}$ $\underline{Sh_1}$-/$\underline{C}$ $\underline{Sh_1}$-/--$\underline{Wx}$ x $\underline{c}$ $\underline{sh_1}$ $\underline{wx}$/$\underline{c}$ $\underline{sh_1}$ $\underline{wx}$)

Phenotypes	Frequency	Percentages
c sh wx	446	2.7
c Sh Wx	34	0.2
c sh Wx	63	0.4
c Sh wx	21	0.1
Total colored	15,805	96.6
	16,369	

The presence of 21 $\underline{c}$ $\underline{Sh}$ $\underline{wx}$ seeds suggests that crossing over between the B^9 and the normal 9 chromosomes in the $\underline{c-sh}$ region does not affect the independent assortment of the two pairs of chromosomes (i.e., the 9 and 9^B pair and the pair of B^9 chromosomes). If such independent assortment occurs, half the time the crossover B^9 chromosomes will end up in the same nucleus as 9^B chromosomes at the end of the first meiotic division. When this happens, one of the second meiotic division products of this nucleus will be $\underline{C}$ $\underline{Sh}$ $\underline{Wx}$ (non-crossover) and the other will be $\underline{c}$ $\underline{Sh}$ $\underline{Wx}$ (crossover). The $\underline{c}$ $\underline{Sh}$ $\underline{wx}$ class would be expected if the crossover B^9 chromosome went to the same first telophase pole as the crossover 9 chromosome. However, the $\underline{c}$ $\underline{Sh}$ $\underline{wx}$ class would be expected in only half the frequency of the $\underline{c}$ $\underline{Sh}$ $\underline{Wx}$ class since half the time the crossover B^9 chromosome will be aligned on the second metaphase spindle so that the crossover B^9 chromatid and the crossover 9 chromatid will go to the same pole resulting in a phenotype that cannot be distinguished from the non-crossover $\underline{C}$ $\underline{Sh}$ $\underline{wx}$ phenotype. The other 50 per cent of the time, when the chromosome alignment on the second metaphase spindle is such that the crossover B^9 chromatid and the non-crossover 9 chromatid go to the same pole, half of the second division products will be $\underline{c}$ $\underline{Sh}$ $\underline{wx}$. In summary, a crossover in the $\underline{c-sh}$ region followed by independent assortment of the chromosomes involved will result in two alignments of first metaphase chromosomes. The first, when the two crossover chromosomes go to opposite poles, will result in $\frac{1}{4}$ of the products being $\underline{c}$ $\underline{Sh}$ $\underline{Wx}$. The other alignment in which the two crossover chromosomes go to the same pole will result in 1/8 of the products being $\underline{c}$ $\underline{Sh}$ $\underline{wx}$. Thus, the $\underline{c}$ $\underline{Sh}$ $\underline{Wx}$ class is expected to be twice as frequent as the $\underline{c}$ $\underline{Sh}$ $\underline{wx}$ class as the data indicate. If the foregoing explanation of the origin of the $\underline{c}$ $\underline{Sh}$ $\underline{Wx}$ classes is correct, plants from these seeds when used as pollen parents should show the typical non-disjunction of plants carrying an A-B translocation. When plants from $\underline{c}$ $\underline{Sh}$ $\underline{Wx}$ seeds were crossed as pollen parents to plants carrying $\underline{yg_2}$, which is located near the end of the short arm of chromosome nine, 13 of the 14 F_1 ears produced segregated for $\underline{yg_2}$, thus confirming the cytology suggested in Table 1. The same plants when used as females for crosses involving $\underline{yg_2}$ pollen did not segregate any $\underline{yg_2}$ seedlings. As would be expected, reciprocal crosses of 12 plants of the $\underline{c}$ $\underline{Sh}$ $\underline{wx}$ to plants carrying $\underline{yg_2}$ did not segregate for this mutant.

The C sh wx class, which is the reciprocal of c Sh Wx, is rare (from the material summarized in Table 2, only one C sh wx seed was observed), because this class would be the result of two rare events: (1) a crossover in the c-sh region followed by (2) the non-disjunction of the B^9 centromeres.

In our 1963 report, three possible explanations for the c sh_1 Wx class were suggested. The most likely explanation involved a crossover between the sh_1 locus and the translocation point putting c and sh_1 on the B^9 chromosome (see Table 1). When upon independent assortment this crossover chromosome goes to the same pole as the 9^B chromosomes, one-fourth of the products will be c sh Wx. However, if the crossover B^9 chromosome ends up at the same pole as the crossover chromosome 9, the crossover products will form combinations that result in phenotypes classified as non-crossovers (i.e., c sh wx and C Sh wx). If the foregoing explanation of the origin of the c sh_1 Wx class is correct, these plants will be heterozygous for TB-9b and should show the typical non-disjunction when used as a pollen parent. Such plants were also reciprocally crossed to plants carrying yg_2. No yg_2 plants were found in the F_1 progeny when 26 c sh Wx plants were used as females. However, when these same plants were outcrossed as males to plants carrying yg_2, 18 of the F_1 ears obtained segregated for yg_2 seedlings while two did not. These two may be the result of the failure of B centromere to undergo non-disjunction or they could have been produced by a crossover in the region between sh-wx proximal to the translocation break point. This would yield a chromosome 9 of the genotype c sh Wx. Such a crossover event accompanied by non-disjunction would result in seeds of the c sh Wx phenotype that would have only normal chromosomes and thus would give only normal seedlings when crossed reciprocally with plants carrying yg_2.

Previously, we had suggested that the C Sh wx class resulted from the presences of a normal chromosome nine (c sh wx) and a B^9 chromosome (C Sh) in the same megaspore. However, there is a possibility that such a phenotype could be produced by a crossover in the region proximal to Sh and distal to the translocation point. Such an event if followed by either normal disjunction or non-disjunction of the B^9 chromosomes could produce some C Sh wx phenotypes. If the non-crossover explanation is correct, then on testcrossing C Sh wx plants, less than 50% C seeds should be observed. If the C Sh wx class was produced by crossing over followed by non-disjunction of B centromere so that the B^9 chromosomes did not end up in the same megaspore as the crossover C Sh wx chromosomes, then 50% of the testcross seeds should carry C. If this class was produced by crossing over followed by normal disjunction of the B^9 centromeres, then the C Sh wx seed would have 2 normal chromosomes nine, one carrying c sh wx and the other C Sh wx (C.O.) and a B^9 chromosome carrying c sh (C.O.) or C Sh. Testcrossing the plants from such seed should yield ears with slightly under 50% C seeds or considerably more than 50% C depending upon the genotype of the B^9 chromosome. In summary, if the C Sh wx class was produced by crossing over, testcrosses of this class would be expected to yield approximately 50% or more C seeds. Table 3 is a summary of testcross data in which C Sh wx plants were used as male and female parents. It will be noted that the total

Table 3

Summary of Testcrosses of C Sh wx Plants Used as Males and Females

	Male parent				Female parent			
	C Sh	C sh	c Sh	c sh	C Sh	C sh	c Sh	c sh
Number	509	21	5	2962	1719	5	12	4420
Per cent	14.56	00.60	00.14	84.70	27.92	00.08	00.19	71.80

percentage of C in both sets of data is considerably below the 50% level. In the individual ear data, the highest percentage of C seeds observed in the male data was 32.39% and in the female data 35.26%. These data support the non-crossover origin of the C Sh wx class.

Both Rhoades (Genetics 21:491-502, 1936, Genetics 25:483-520, 1940) and Maguire (Genetics 49:69-80, 1964) have studied plants which were hyperploid for duplications similar to those carried by the C Sh wx plants. The genetic results would suggest that segregation in the hyperploid C Sh wx plants most closely resembles that described by Rhoades for plants which were hyperploid for a telocentric short arm of chromosome 5.

Plants of the C Sh Wx phenotype from the testcross progeny of original 9 $9^B B^9 B^9$ hyperploid plants were testcrossed as females. These should be heterozygous for TB-9b and have the genotype c sh wx/C Sh Wx with the dominant alleles carried on the translocated chromosomes. A summary of this testcross is given in Table 4.

Table 4

Summary of Testcross Data for Plants of the Constitution

$$\frac{c \quad sh \quad wx \quad \_\_o\_\_}{C \quad Sh \quad \diagdown_o \quad Wx}$$

	C Sh Wx	c sh wx	C sh wx	c Sh Wx	C Sh wx	c sh Wx	C sh Wx	c Sh wx
Number	784	1054	18	19	812	66	1	19
Per cent	28.27	38.01	0.65	0.69	29.28	2.38	0.04	0.69

The striking thing about these data is the high frequency of the C Sh wx class (29.28%). This value approximates those for the C Sh Wx and c sh wx classes. The most reasonable explanation for such a distribution would be that the B^9 chromosome in meiosis I moves at random with respect to chromosome 9 and 9^B so that the following distributions are produced in equal frequency $9 : 9^B B^9 : 9 B^9 : 9^B$. Since 9^B gametes do not function, 1/3 of the non-crossovers would be expected to be C Sh Wx, 1/3 c sh wx and 1/3 C Sh wx.

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