5. Genetic study of B^3 chromosome.

A. Types of pollen produced by "3 3^B B^3 B^3" plant.

The A-B translocation involved here is TB-3a. Progenies from the cross 3^{a} sh 3^{a} sh x 3^{a} Sh 3^B B^3 A Sh B^3 A Sh were analyzed in detail for the kernel phenotype, plant color, pollen abortion, and degree of glume clumping, and were crossed by and onto 3^{a} sh 3^{a} sh tester plants. The expected pollen types produced by the original male parent would be "3^B B^3" and "3 B^3". All possible plant types produced by these two kinds of pollen, taking account of nondisjunction of B^3 at the 2nd microspore division and of crossing-over between the translocation point and A locus, were considered. Most of the plant types are distinguishable from each other in some way. The types of pollen and sperm involved in fertilization were determined on the basis of analysis of each individual plant from the parental cross.

About 55% of pollen functioning in the parental cross was the "3^B B^3" type. Then 43%, (2% being unclassified), should have been the "3 B^3" type. Among F_1 plants which came from colored, full kernels (Cl Sh), 75 individuals have the "3 3" genotype. They may have come from "3 B^3" pollen. However, if "3" pollen had been produced by the "3 3^B B^3 B^3" plant, the resulting plants would also be "3 3". These "3 3" plants of different origins can not be distinguished.

However, Roman (Genetics 35:132, 1950) reported that the B^4 chromosome in "4 B^4" type pollen undergoes nondisjunction rarely if at all. If this is the case with B^3 in "3 B^3" type pollen, almost all "3 3" type plants must have come from "3" type pollen, except two colorless plants from colored Sh kernels. These two plants can be explained as a result of heterofertilization. The absence of "3 3 B^3 B^3" type plants is in agreement with Roman's statement.

As a result the percentages of the 3 types of pollen which functioned in the parental cross could be roughly estimated.

Parental Cross	Type of Pollen Functioning	Percentage
3 3 X 3 3^B B^3 B^3	3^B B^3	55%
	3 B^3	3%
	3	40%
	Unclassified	2%
		100%

B. Nondisjunction of the B^3 chromosome in the "3 3^B B^3 B^3" plant.

(1) Nondisjunction of B^3 on the male side.

a. Nondisjunction of B^3 at meiosis.

The types of pollen produced by the "3 3^B B^3 B^3" plant turned out to be "3^B B^3", "3 B^3", and "3". To get the "3" type pollen, nondisjunction of the B^3 chromosome must have taken place either at AI or at AII in meiosis. A cytological study of MII of microsporogenesis will clarify when this nondisjunction occurs. If any dyads show (10 + 12) chromosome distribution at MII, nondisjunction has occurred at AI. In fact Blackwood confirmed cytologically that nondisjunction of B chromosomes occurs at AI (Heredity 10:345,1956). Therefore it is conceivable that nondisjunction of B^3 chromosomes also takes place at AI.

As a result of the meiotic nondisjunction of B^3 in the "3 3^B B^3 B^3" plant, we have "3", "3^B B^3 B^3", "3^B", and "3 B^3 B^3" pollen. "3^B" is apparently aborted. "3^B B^3 B^3" pollen would produce a variety of plant types from crosses with normal egg parents. These plant types are as follows:

Endosperm type	Plant type
3 3 3^B B^3 B^3	3 3^B B^3 B^3
3 3 3^B B^3	3 3^B B^3 B^3 B^3
3 3 3^B B^3 B^3 B^3	3 3^B B^3
3 3 3^B B^3 B^3 B^3 B^3	3 3^B
3 3 3^B	3 3^B B^3 B^3 B^3 B^3

Three of the five plant types are distinguishable from plant types produced by "3^B B^3" and "3 B^3" pollen. These plant types were not found in the progeny.

"3 B^3 B^3" pollen is not expected to function because of its highly unbalanced chromosomal makeup which fails to compete with the normal or less unbalanced pollen in pollen tube growth.

b. Nondisjunction of B^3 at the 1st microspore division.

If the pollen is the "3^B B^3" type, nondisjunction of B^3 at the 1st microspore division would produce either a deficient tube nucleus or a deficient generative nucleus. The deficient tube nucleus would prevent the pollen from functioning. The deficient generative nucleus will result in two hypoploid gametes which, after fertilization, produce hypoploid endosperm and hypoploid embryo. These were not found in the progeny studied.

If the pollen is the "3 B^3" type, the consequence is different.

	Tube nucleus	Generative nucleus
After nondisjunction of B^3	3 B^3 B^3	3
	3	3 B^3 B^3

The plant type resulting from the generative nucleus of "3" type is not distinguishable from the type produced by "3" pollen. But the other type of generative nucleus results in a clearly distinguishable plant type; however, this type was not found in the progeny. Therefore it seems that the B^3 chromosome disjoins normally at the 1st microspore division. Another support on this matter comes from Blackwood. She observed no nondisjunction of B chromosomes at the 1st microspore division (ibid., 1956).

Table 1. Types of Pollen Which Functioned in Parental Cross $3^{\underline{a}}\ \underline{sh}\ 3^{\underline{a}}\ \underline{sh}$ X $3^{\underline{a}}\ \underline{Sh}\ 3^{B}\ B^{3\underline{A}}\ \underline{Sh}\ B^{3\underline{A}}\ \underline{Sh}$

Kernel phenotype	Number of kernels	Number of plants analysed	Type of pollen											Unclassified
			$3^B\ B^3$			$3\ B^3$						3		
			Resulting plant type			Resulting plant type						Resulting plant type		
						$3\ 3\ B^3$		$3\ 3$		$3\ 3\ B^3\ B^3$		$3\ 3$		
			33^BB^3	33^B	$33^BB^3B^3$	colored plant	colorless plant	colored plant	colorless plant	colored plant	colorless plant	colored plant	colorless plant	
Cl Sh	184	175	10	78		4		0	(2)	0	0	75		6
cl Sh	99	96	2	26			5	0	0	0	0		61	2
cl sh	98	72			72									0
Total	381	343	188			(11)						136		8
%			55%			(3%)						40%		2%

c. Nondisjunction of B^3 at the 2nd microspore division.

In this particular cross (cf. Table 1), the percentage of nondisjunction of B^3 in "3^B B^3" pollen was 93%. If all colorless, shrunken kernels (cl *sh*), which were obviously hypoploid endosperm with hyperploid embryo, had germinated, the percentage would be higher. It would seem that hypoploid gametes tended to fertilize eggs more frequently, the apparent percentage being 59%. But if we take account of all cl *sh* kernels, including ones which could not be analyzed because they failed to germinate, the percentage would approach 50%. This indicates random fertilization by both types of gametes, "3^B" and "3^B B^3 B^3".

As discussed in section A, nondisjunction of B^3 in "3 B^3" type pollen is not a common event. This can be checked genetically by planting colorless and colored kernels from 3^{a} 3^{a} X 3^{a} 3^{a} B^{3A} cross separately and scoring for the occurrence of colored and colorless plants respectively.

(2) Nondisjunction of B^3 on the female side.

a. Nondisjunction of B^3 at meiosis.

When 3^{a} *Sh* 3^B B^3 *A* *Sh* B^3 *A* *Sh* plants were crossed by 3^{a} *sh* 3^{a} *sh* tester plants and the ears were analyzed, about 17.6% of kernels were cl *Sh*. According to a rough calculation the expected frequency of cl *Sh* occurrence due to crossing-over within the T-*A* segment is about 14% at maximum. The excessive cl *Sh* kernels could be accounted for by meiotic nondisjunction of B^3 followed by formation of a "3" type megaspore. There is no way to tell the difference between nondisjunction of B^3 at AI and at AII except by cytological study. The actual ratio of expected megaspore types can be obtained by planting all kernels from the original cross and by classifying plants according to kernel phenotype, plant color, pollen abortion and degree of glume clumping.

b. Nondisjunction of B^3 at embryo sac formation.

If nondisjunction of B^3 takes place some time at embryo sac formation, the genotypes of polar nuclei and egg might be different. They can be determined by planting cl *Sh* and Cl *Sh* kernels separately and scoring for the occurrence of colored and colorless plants respectively.

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6. The effect of a-x deficiencies on crossing over in T β α sh/ N a-x plants.

Of the 109 alpha-bearing strands reported by Laughnan (Mutation and Plant Breeding Symposium, 1961) among offspring of T-marked hemizygotes (T *β* *α* *Sh* / N *a-x*), none carried the marker (N) proximal to the *a-x* deficiency. As was reported, their complete absence is somewhat surprising since they might be expected, at least occasionally, as a result of a coincidental exchange in the T-*β* segment.