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1. Disjunction and preferential fertilization in TB-9b.

Several studies have been made in which it has been possible to estimate the rate of disjunction and preferential fertilization of the B^9 chromosome in the A-B translocations B-9b. Roman⁴ found normal disjunction only occurred in a frequency of 1.8% and that preferential fertilization occurred in 66.3% of the pollinations involving pollen grains in which nondisjunction had occurred. Bianchi, Bellini, Contin and Ottaviano³ found normal disjunction in frequencies of 33.3% and 22.1% in two sets of crosses and preferential fertilization 59.5% and 65.3%, respectively. Carlson¹ found preferential fertilization values ranging from 64% to 69%. However, he did find in some crosses that if one particular stock was used as a female parent no preferential fertilization was observed. The rates of normal disjunction ranged from 2% to 18%.

In recent crosses to test for the presence of I on the B^9 chromosome, plants of the putative genotype B^9 (I) $9^B/9(C)$ were crossed as males onto a homozygous purple aleurone stock which was homozygous for the R_2^{scm} allele. This r allele is not only responsible for colored aleurone but also produces color in the scutellum. If the genotype of the male parents is correct then it should be possible to determine the following facts from the resulting seeds: 1) the frequency with which pollen grains carrying a normal chromosome nine and those carrying the translocated chromosomes participated in fertilizations, 2) the rate of normal disjunction of the B^9 chromosome and 3) the rate of preferential fertilization. The results of the above crosses are given in Table 1.

Before considering the results, two characteristics of the I allele should be reviewed. First, in crosses of I to CC plants, heterozygous seeds will frequently not be completely devoid of aleurone color but will show a tinge of pigment. Secondly, seeds heterozygous for I in such crosses will have spots of color where I has been lost

Table 1. Classes of seeds produced from the cross purple aleurone ($R_2^{Scm} R_2^{Scm}$) X $B^9(I)9^B/9(C)$

Phenotypic Classes Observed	$R_2^{Scm} R_2^{Scm}$ X $B^9(I)9^B/9(C)$								Total	
	Purple Pl.scut	Purple Yel.scut	Pl.tinged spotted Pl.scut	Yel.- spotted Pl.scut	Yel.non- spotted Pl.scut	Pl.tinged spotted Yel.scut	Pl.tinged non-spotted Yel.scut	Yel. spotted Yel.scut		Yel.non- spotted Yel.scut
<u>71-9187-2</u> <u>8181-2</u>	97	72	2	1	26	17	1	14	5	235
<u>71-8184-4</u> <u>8181-2</u>	113	66	0	3	32	23	0	16	3	256
<u>71-8189-3</u> <u>9181-1</u>	165	86	5	3	44	28	0	37	8	376*
<u>71-9183-4</u> <u>9181-3</u>	138	50	1	9	25	12	3	33	5	276
<u>71-8182-1</u> <u>9181-3</u>	151	71	0	1	44	24	6	14	8	319
<u>71-8182-2</u> <u>9181-5</u>	134	64	0	7	34	31	3	17	1	291
<u>71-8182-4</u> <u>9181-5</u>	121	67	6	1	28	26	0	22	2	273
<u>71-8182-3</u> <u>9181-5</u>	110	51	0	3	19	29	1	13	2	228
<u>71-9185-6</u> <u>9181.1-5</u>	140	57	0	3	21	45	0	39	3	308**
<u>71-8186-2</u> <u>9192-6</u>	106	62	0	6	36	11	0	17	2	240**
	1275	646	14	37	309	246	14	222	39	2,802

* 3 seeds questionable classification not included in total.

** 2 seeds questionable classification not included in total.

from a cell lineage. The number of spots expected is inversely proportional to the number of I alleles present.

In Table 2, the probable genotypes of the phenotypes listed in Table 1 are given. The class A seeds are the result of the functioning of pollen grains carrying normal (non-translocated) chromosomes. Class

Table 2. Probable genotypes of the phenotypes shown in Table 1.

Phenotype	Genotype		Class
	Endosperm	Embryo	
Purple endosperm; purple scutellum	999 (<u>CCC</u>)	99 (<u>CC</u>)	A
Purple endosperm; yellow scutellum	$9^B 99$ (<u>CC</u>)	$B^9 B^9 9^B 9$ (<u>IIC</u>)	B
<u>Purple tinged, spotted endosperm; purple scutellum</u> <u>yellow, spotted endosperm; purple scutellum</u> <u>yellow, non-spotted endosperm; purple scutellum</u>	$B^9 B^9 9^B 99$ (<u>IICC</u>)	$9^B 9$ (<u>C</u>)	C
<u>Purple tinged, spotted endosperm; yellow scutellum</u> <u>Purple tinged, non-spotted endosperm; yellow scutellum</u> <u>yellow, spotted endosperm; yellow scutellum</u> <u>yellow, nonspotted endosperm; yellow scutellum</u>	$B^9 9^B 99$ (<u>ICC</u>)	$B^9 9^B 9$ (<u>IC</u>)	D

B seeds have deficient endosperms and hyperploid embryos and thus are the result of nondisjunction. The class C seeds have a hyperploid endosperm and a deficient embryo. Notice that in this class there is a low frequency of purple-tinged seeds and seeds with purple spots. (Spots were counted by using a binocular microscope and a magnification of 19.5 x). This is as expected if these seeds have two I alleles in the endosperm. This class is also the result of nondisjunction. Seeds of D class result

from the fertilization by pollen grains in which nondisjunction did not take place and thus the endosperm and embryo have only one I. This is shown in the embryo by yellow scutellum color and in the endosperm by a higher frequency of purple-tinged seeds and spotted seeds than observed in class C. The higher frequency of purple-tinged and spotted seeds is expected because only one I allele is present.

From Table 3 it can be seen that pollen grains carrying the A-B translocation function more frequently (54.5%) than those that had a normal chromosome (45.5%). This is a very significant difference ($X^2 = 22.6$). Purple scutellum in the seeds with the normal chromosome was determined by cutting the germ. Why translocation bearing pollen grains should be more successful in accomplishing fertilizations is not obvious.

Table 3. An analysis of the data presented in Table 1.

Types of fertilizations	Phenotypic class (see Table 2)				Total
	A	B	C	D	
All classes of fertilizations	1275	646	360	521	2802
Fertilizations involving translocation and normal gametes	1275 (45.5%)		1527 (54.5%)		2802
Translocation fertilizations only		646 (42.3%)	360 (23.6%)	521 (34.1%)	1527
Translocation fertilizations involving non-disjunction		646 (64.2%)	360 (35.8%)		1006

If only the fertilizations which resulted from pollen grains with TB-9b are considered, it can be seen from Table 3 that normal disjunction is occurring 34.1% of the time (Class D). Table 4 summarizes the rates obtained for normal disjunction of TB-9b from several workers. It is obvious that the rate with which normal disjunction occurs is very variable and probably depends upon the genotype of the male parent although environmental factors can not be ruled out. In Carlson's paper,¹ two different TB-9b pollen sources were used to pollinate the same two female lines. In one source (678-5) the pollination on the two female lines revealed normal disjunction in 2% and 4% of the progeny. In crosses involving the second line (808-1) the values of 16% and 18% were observed. The different rates may reflect genotypic differences in the two male lines. However, environmental influences can not be ruled out since nothing is reported on the differences, if any, in environmental conditions surrounding the growth of these plants (e.g., planting dates, position in field with respect to each other, maturity dates, etc.).

Table 4. A summary of rates of normal disjunction and preferential fertilization of TB-9b from several studies.

Source	Rate of normal disjunction	Rate of preferential fertilization
Roman ⁴	1.8%	66.3%
Bianchi, et al. ³	33.3% & 22.1%	59.5% and 65.3%
Carlson ¹	range from 2% to 18%	64% to 69%
Carlson ²	18%	67%
This report	34.1%	64.2%

The rate of preferential fertilization in Table 3 is 64.2% (Class B). Table 4 gives the rates of preferential fertilization from several sources. It is obvious that the rate of preferential fertilization is relatively constant and not greatly influenced by the environment. However, Carlson¹ found a female tester line which, when used in crosses

with TB-9b plants, did not show preferential fertilization. This would seem to indicate that there is a genetic basis for determining whether or not preferential fertilization will occur.

References:

1. Carlson, W. R. Genetics 62:543-554, 1969.
2. Carlson, W. R. Maize Genetics Cooperation News Letter 44:91-92, 1970.
3. Bianchi, A., Bellini, G., Contin, M. and Ottaviano, E. Z. Vererb. 92:213-232, 1961.
4. Roman, H. Proc. Nat. Acad. Sci. U.S. 34:36-42, 1948.

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2. Location of the modifier gene of the cl_1 locus.

The white-albino mutant cl_1 is located on chromosome three. Two alleles of this mutant are known w_{7716} and cl_p . These mutants have the white (or pale yellow) endosperms and albino seedlings typical of this class of mutants. Four dominant, allelic modifiers of these genes have been described (Heredity 21:1-7, 1966) which, when present, partially or completely suppress the albino phenotype. Depending upon the modifier present, the seedling can be pale green (pastel) or green. The modifiers do not alter the endosperm phenotype.

Attempts to locate the locus of the modifier alleles have been frustrated by the rather widespread occurrence of modifier genes in genetic stocks. In the F_2 's of crosses of the cl_1 alleles to the inbred Ml^4 , pale green (pastel) or green seedlings segregated in the white endosperm class. These results indicate that this inbred carries two modifiers, one responsible for pale green seedlings and the other for green seedlings. To verify that the green Ml^4 modifier was allelic to the other known modifiers of the cl_1 locus, plants of the following genotypes were self pollinated: $w_{7716} \frac{Cl^{Ml^4}}{Cl^4} / \pm \frac{Cl^4}{Cl^4}$, $\pm \frac{cl^{Ml^4}}{Cl^4} / \frac{cl_p}{Cl^4} \frac{Cl^4}{Cl^4}$ and $w_{7716} \frac{Cl^{Ml^4}}{Cl^4} / \frac{cl_p}{Cl^4} \frac{Cl^4}{Cl^4}$. From these selfs, the white or pale yellow seeds were planted in a seedling bench. If Cl^{Ml^4} is allelic to Cl^4 , no albino seedlings will be observed. Out of 2,221 seedlings grown, no albinos were found. Another allele test was made involving the Cl_M^3 modifier.