

Table 1. (continued)

TB	Source	Chromosome arm(s)	Endosperm tester gene	Hypoploid endosperm phenotype	Comments
10a	Roman	10L	<u>r</u>	Non-purple (purple scutellum, see comments)	I have a homozygous TB stock, homozygous for purple aleurone and the <u>R-scm2</u> allele that colors the scutellum.
10b	Beckett	10L	<u>r</u>	Non-purple	
10c	Beckett	10S	<u>y9</u>	Pale yellow	

Tester genes lw, vp5, w3, lw2 and cl are all white-albino mutants and cannot be made homozygous. Thus, segregating populations must be used, and it is best to cross each putative TB plant with several plants suspected of carrying the marker gene. The al, y9 and o5 marker genes produce weak homozygotes, and it would be more efficient if a tester line were established by crossing homozygotes of these markers (as males) to a standard line to develop stocks of known heterozygotes.

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Additional studies on the differential recovery of crossover products from male and female in plants hypoploid for TB-10a — In 1970, I reported that more crossover products were recovered through the pollen than through the eggs of TB-10a hypoploid (deficient) plants (MGCNL 44:84-91, 1970). In these tests plants hypoploid for TB-10a and heterozygous for y9 were reciprocally crossed with homozygous y9 plants. The hypoploid plants carried y9 on the normal chromosome and the + allele on the deficient 10^B chromosome; most of the functional gametes from such plants will be expected to carry y9, but a few + gametes will be produced as a result of crossing over between the breakpoint and y9. The frequency of + (yellow endosperm) seeds in crosses involving hypoploid plants will therefore be a measure of the crossing over.

The crosses in the 1970 report (1969 crosses) were not exact reciprocals. In 1970 and 1971 paired reciprocal crosses were made so that in each set of crosses the two plants involved functioned as both male and female parents with respect to each other. The results of these tests (Table 1) are in agreement with those reported in 1970.

Table 1. Transmission of crossover products through pollen and ovules when exact reciprocal crosses were made between hypoploid $10/10^B$ ($y9/+$) plants and homozygous $y9$ plants.

Year	Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
1970	679	9.7	1018	21.0	11.3	37.05**
1971	564	13.7	692	20.8	7.1	10.5**
Total	1243	11.5	1710	20.9	9.4	44.5**

**Significant at the 1% level of probability.

When the crossover values of 1969, 1970 and 1971 are examined they are found to vary from year to year. This variation is systematically compared in Table 2. The only significant between-year variation occurred for the female crosses. In no cases were the differences in male crosses significant. From this limited test, it would appear that female transmission of crossovers is more sensitive to environmental factors than is the male transmission.

Table 2. Comparisons of the female crosses in 1969, 1970 and 1971 of hypoploid 10^B plants and of the male crosses for the same years.

Years compared	Total 1st year	% C.O. 1st year	Total 2nd year	% C.O. 2nd year	% Difference	Chi square
♀ Crosses						
1969 vs. 1970	1168	15.2	679	9.7	5.5	10.6**
1969 vs. 1971	1168	15.2	564	13.7	1.5	0.6 ^{N.S.}
1970 vs. 1971	679	9.7	564	13.7	4.0	4.3*
♂ Crosses						
1969 vs. 1970	2779	22.8	1018	21.0	1.8	1.2 ^{N.S.}
1969 vs. 1971	2779	22.8	692	20.8	2.0	1.1 ^{N.S.}
1970 vs. 1971	1018	21.0	692	20.8	0.2	0.002 ^{N.S.}

*Significant at the 5% level of probability.

**Significant at the 1% level of probability.

N.S. Not significant.

The different transmission rates of crossovers observed in male and female plants in these studies may be the result of some intrinsic factor in the normal chromosome 10 and have nothing to do with the hypoploid TB-10a condition. Previous studies on crossing over in normal chromosome 10 by other workers have

not revealed such differences. New crossover studies were made involving the y9-bf2 and bf2-g regions, which include the region being tested in the hypoploid crosses; the results of these crosses are given in Tables 3, 4, 5, 6 and 7. In none of the tests was there observed a significant difference in the male and female transmission of crossovers. For the whole region y9-g (Table 5) there is no indication of preferential transmission. There is apparently no differential transmission of crossovers that occur in the right hand portion of this segment of chromosome 10 (i.e., bf2-g, Tables 4, 5 and 7); however, the region closest to the breakpoint (i.e., y9-bf2, Tables 3, 5 and 6) exhibits a consistently higher transmission rate for male crossovers than for female crossovers. Although the difference is not significant (Table 6, Chi square 3.1), it comes very close to being significant at the 5% level (Chi square 3.8). If comparisons are made of the crossover and chi square values for this region in Tables 3, 5 and 6, it will be noted that male-transmitted crossovers are always higher; and as the numbers increase, so do the Chi square values. If this trend truly characterizes what is taking place in this region, one would expect a significant difference to be found if larger numbers of plants were tested.

Table 3. Male and female transmission of crossovers in the y9-bf2 region (two point tests) involving exact reciprocal crosses.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
183	9.8%	195	14.4%	4.6	1.4N.S.

N.S. Not significant.

Table 4. Male and female transmission of crossovers in bf2-g region (two point tests) involving exact reciprocal crosses.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
357	16.5%	296	16.9%	0.4	.004N.S.

Table 5. Male and female transmission of crossovers in a three-point test with y9, bf2 and g loci involving exact reciprocal crosses.

Region	Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
<u>y9-bf2</u>	322	2.8%	259	4.4%	1.6	0.8N.S.
<u>bf2-g</u>	322	18.0%	295	18.3%	0.3	0.0N.S.

Table 5. (continued)

Region	Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
<u>y9-g</u> *	322	20.8%	295	22.7%	1.9	0.2N.S.

*Total crossing over in the y9-g region (double crossovers have been included twice).

N.S. Not significant.

Table 6. Total male and female transmission in y9-bf2 region from two-point tests (Table 3) and three-point tests (Table 5).

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
505	5.3%	490	8.3%	3.0	3.1N.S.

N.S. Not significant.

Table 7. Total male and female transmission of crossovers in the bf2-g region from two-point tests (Table 4) and three-point tests (Table 5).

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
679	17.2%	591	17.6%	0.4	.01N.S.

N.S. Not significant.

The y9-bf2 region is located proximally to the TB-10a breakpoint and involves the region tested in the original hypoploid tests. There is a possibility that the preferential transmission of male crossovers in hypoploid plants may be characteristic of any crossing over in this region (y9-bf2 = "critical region") and may not be due to anything unique about the hypoploid condition. If the increased transmission of crossovers through the male in hypoploid plants carrying y9 is due to activity in the "critical region," then crossing over between bf2 and the breakpoint would lie outside the "critical region" and there would be no difference in male and female transmission of crossovers in this region. The results of such a test are given in Table 8. There is observed a significantly higher transmission of crossovers through the male, which would be expected if the "critical region"

extended beyond bf2 to the vicinity of the breakpoint; if this were the case, two-thirds of the bf2-g region would be included in the "critical region." However, there is no evidence for a higher transmission of crossovers through the male

Table 8. Male and female transmission of crossovers between bf2 and the TB-10a breakpoint in crosses involving hypoploid plants.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
1612	9.1%	4093	12.3%	3.2	11.1**

**Significant at the 1% level.

when this region is tested in the absence of any rearrangements (Tables 4, 5 and 7); if there is a "critical region" it does not seem to include the bf2 breakpoint region. In that case the higher male transmission of crossovers between bf2 and the breakpoint may be due to the hypoploid condition of the tested plants.

One additional test of crossover transmission in the TB-10a hypoploid was made with oy, which is about 12 crossover-units to the left of y9. The results of these tests are found in Table 9. Again a significantly higher transmission of crossovers through the male is observed. Crossing over in the oy-y9 region in normal chromosomes has not been tested for male and female transmission, and until such tests have been made it is perhaps too early to speculate on the significance of the data in Table 9.

Table 9. Male and female transmission of crossovers between oy and the TB-10a breakpoint in crosses involving hypoploid plants.

Total ♀	% C.O. ♀	Total ♂	% C.O. ♂	% Difference	Chi square
481	22.9%	664	32.5%	9.6	12.3**

**Significant at the 1% level.

Conclusion:

In tests of hypoploid plants carrying y9, bf2 or oy, male transmission of crossovers is consistently higher than female transmission; these results suggest that the hypoploid condition might be responsible for the differential transmission ("hypoploid effect"). However, tests of male and female transmission of crossovers by plants with normal chromosomes suggest that there might be a

"critical region" between y9 and bf2 that could account for some of the observed differential transmission. Whether or not this "critical region" really exists will require further tests. If it does exist, it will be necessary to determine how much of the "hypoploid effect" is due to events within this region and how much is due to hypoploidy per se.

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A case of genetic instability at the opaque-2 locus — In a 1971 field trial all the ears of the hybrid (FR 123 o2 x R 103 o2) x A 619 o2 segregated variegated kernels. This phenotypic variegation appeared particularly clear on the kernel surface, where sharply bordered horny and opaque patches were present side by side. In the last two years we have accumulated genetic data suggesting the existence in our material of a mutable system responsible for the somatic variegations observed. The attributes of the system, even though not carefully quantified, may be synthesized from the following data from two selected progenies (Tables 1 and 2).

1. Mutability is either autonomous or under the control of an independent factor. With some exceptions the segregation ratios of Table 1 are consistent with the 3:1 ratio expected in the case of autonomous control. The ratios of Table 2, on the other hand, imply the existence of a two-factor interaction.
2. A particular variegation pattern is not stable. Kernels of c or m phenotype (see Table 1) frequently produce N or c variegated kernels, respectively. For example, the 3472-1 plant was clearly heterozygous, bearing a mutable and a non-mutable o2 allele. This plant, when outcrossed to standard o2, gave 345 opaque and 347 variegated seeds (232 of c or m type and 115 N type). The N phenotype has been maintained in the subsequent generation (class 3 of Table 1).
3. When heterozygous with an unstable o2 allele, o2-R may segregate at unexpectedly low frequencies. This is the case with ears 5, 7, 13, 23 and 27 in Table 1. Abnormal segregation ratios have also been observed in progenies with independent control of mutability (i.e., ears 4, 17 and 18 selfed and 5/o2-R and 16/o2-R in Table 2).