DIFFERENT FREQUENCY IN THE RECOVERY OF CROSSOVER PRODUCTS FROM MALE AND FEMALE GAMETES OF PLANTS HYPOPLOID FOR B-A TRANSLOCATIONS IN MAIZE

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ABSTRACT

The percentage of crossovers is consistently higher in plants hypoploid for six B-A translocations when crossed as males than when crossed as females; in most instances, this excess of male crossing over exceeds that found in control crosses (involving normal chromosomes). Thus, there seems to be something about the hypoploid condition that is responsible for the higher percentage of male crossovers. Several explanations for this "hypoploid effect" are possible, but none has been demonstrated to be responsible for the phenomenon.

NUMEROUS reports have been made on the comparison of the rates of crossing over in male and female plants of maize with variable and, in some cases, contradictory results. In Table 1, the results of some previous studies are summarized. Usually, if there is a difference in the amount of crossing over in the microspores and megaspores, more crossing over will be observed in the microspores. Higher crossover values have been found in the megaspores for a few regions (*i.e.*, *y-su2*, *c-wx*, and *c-sh*), whereas no differences in crossing over in microspores and megaspores have been observed in some instances. For a few regions, contradictory results have been reported by the same or different workers (*e.g.*, *a2-bt*, *bm-pr*, *bt-pr*, *ra-gl*, *c-wx*, *c-sh* and *sh-wx*). Such contradictory results suggest that environmental and (or) genic differences might be influencing the rate of crossing over for these regions in male and female inflorescences. Indeed, RHOADES (1978) has reported that the presence of a knobbed chromosome might be a prerequisite for greater male crossing over. The results of CHANG and KIKUDOME (1974) demonstrate such an effect in chromosome 9. In these tests, in which all plants had a terminal knob on the short arm of chromosome 9, there was consistently observed more crossing over through the male than female for all except the very short region II (*sh-bz*) of the three regions tested (*i.e.*, *yg-sh*, *sh-bz* and *bz-wx*). The presence of translocations and trisomics also can have an influence on the relative amounts of crossing over in microspore and megaspore (BURNHAM 1950, 1961; CLARK 1957; PHILLIPS 1969; GHIDONI 1975).

In this study, the rate of transmission of crossovers through the pollen and

TABLE 1

Summary of the results of tests on the rates of crossing over in male and female gametes of maize

Chromosome and region tested	Higher C.O. in male[a]	Higher C.O. in female[a]	No difference in C.O. between ♂ and ♀[a]	Author
Chromosome 2				
lg1-B			X	EMERSON and HUTCHINSON (1921)
gl2-v4			X	BURNHAM (1950)
Chromosome 3				
Rg-lg2	X			BURNHAM (1953)
Rg-d1	X			BURNHAM (1953)
gl6-lg2	X			HANSON (1969)
gl6-lg2	X		X	RHOADES (1978)
lg2-a1		X		HANSON (1969)
lg2-a	X		X	RHOADES (1978)
gl6-a	X		X	RHOADES (1978)
Chromosome 4				
su1-Tu	X			EYSTER (1921)
su1-Tu			X	EYSTER (1922)
su1-gl4			X	BURNHAM (1958)
la-su1	X			BURNHAM (1958)
Chromosome 5				
a2-bt1	X			RHOADES (1941)
a2-bt1	X			NEL (1971, 1973)
a2-bt1			X	PHILLIPS (1969)
a2-bm1	X			RHOADES (1941)
a2-bm1	X			PHILLIPS (1969)
bm1-pr	X			RHOADES (1941)
bm1-pr	X			PHILLIPS (1969)
bm1-pr			X	PHILLIPS (1969)
bm1-pr	X			RHOADES (1941)
bt-pr	X			NEL (1973)
bt1-pr			X	PHILLIPS (1969)
pr-ys	X			PHILLIPS (1969)
ys-v2			X	PHILLIPS (1969)
inv. 5a	X			MORGAN (1950)
Chromosome 6				
y1-pb	X			BURNHAM (1953)
y1-pl			X	PHILLIPS (1969)
y1-su2		X		PHILLIPS (1969)
Chromosome 7				
o2-v5			X	PHILLIPS (1969)
v5-ra1	X			PHILLIPS (1969)
in-gl1	X			BURNHAM (1950)
ra1-gl1	X			PHILLIPS (1969)
ra1-gl1			X	PHILLIPS (1969)

TABLE 1—Continued

Chromosome and region tested	Higher C.O. in male[a]	Higher C.O. in female[a]	No difference in C.O. between ♂ and ♀[a]	Author
Chromosome 9				
yg2-sh			X	GHIDONI (1975)
yg2-sh	X			CHANG AND KIKUDOME (1974)
c-wx	X			BREGGER (1918)
c-wx	X			STADLER (1926)
c-wx		X		COLLINS and KEMPTON (1927)
c-wx	X		X	RHOADES (1941, 1978)
c-sh1		X		EMERSON and HUTCHINSON (1921)
c-sh	X			STADLER (1926)
c-sh		X		NEL (1973)
c-sh		X		BURNHAM (1950)
c-sh	X		X	RHOADES (1978)
sh-wx	X		X	STADLER (1926)
sh-wx	X			NEL (1973)
sh1-wx	X			BURNHAM (1950)
sh1-wx			X	BURNHAM (1958)
sh-wx	X		X	RHOADES (1978)
sh1-wx			X	BURNHAM (1961)
sh-wx			X	GHIDONI (1975)
sh1-bz	X			CHANG and KIKUDOME (1974)
bz-wx			X	NELSON (1966)
bz-wx	X		X	CHANG and KIKUDOME (1974)
wx-v1			X	NELSON (1966)
wx-gl15	X			NEL (1973)
wx-gl#?	X			BURNHAM (1950)
wx^{coe}-wx^{90}	X			NELSON (1966)
Chromosome 10				
sp2-li			X	RHOADES and RHOADES (1939)
li-g1			X	RHOADES and RHOADES (1939)
g1-r			X	RHOADES and RHOADES (1939)
sp2-r			X	RHOADES and RHOADES (1939)

[a] Whether the difference in male or female crossing over was statistically different was not always determined by the original authors. In some instances, a judgment was made solely on the basis of unanalyzed numerical values by the present author. C.O., crossover.

ovules is determined for plants that are hemizygous for B-A translocations. Hemizygous individuals are produced when plants carrying a B-A translocation are used as male parents in crosses. ROMAN (1947) demonstrated that, during the mitotic division of the generative nucleus carrying a B-A translocation, the B^A element of the translocation frequently undergoes nondisjunction, which results in two sperms from a given pollen grain that differ with respect to this element. One has two B^A chromosomes (hyperploid), whereas the other lacks the B^A (deficient or hypoploid). If pollen grains in which nondisjunction has occurred function in pollination, some plants are produced that are hemizygous (deficient or hypoploid) for the segment of A chromosome translocated to the B centromere. This happens when the deficient sperm fertilizes the egg nu-

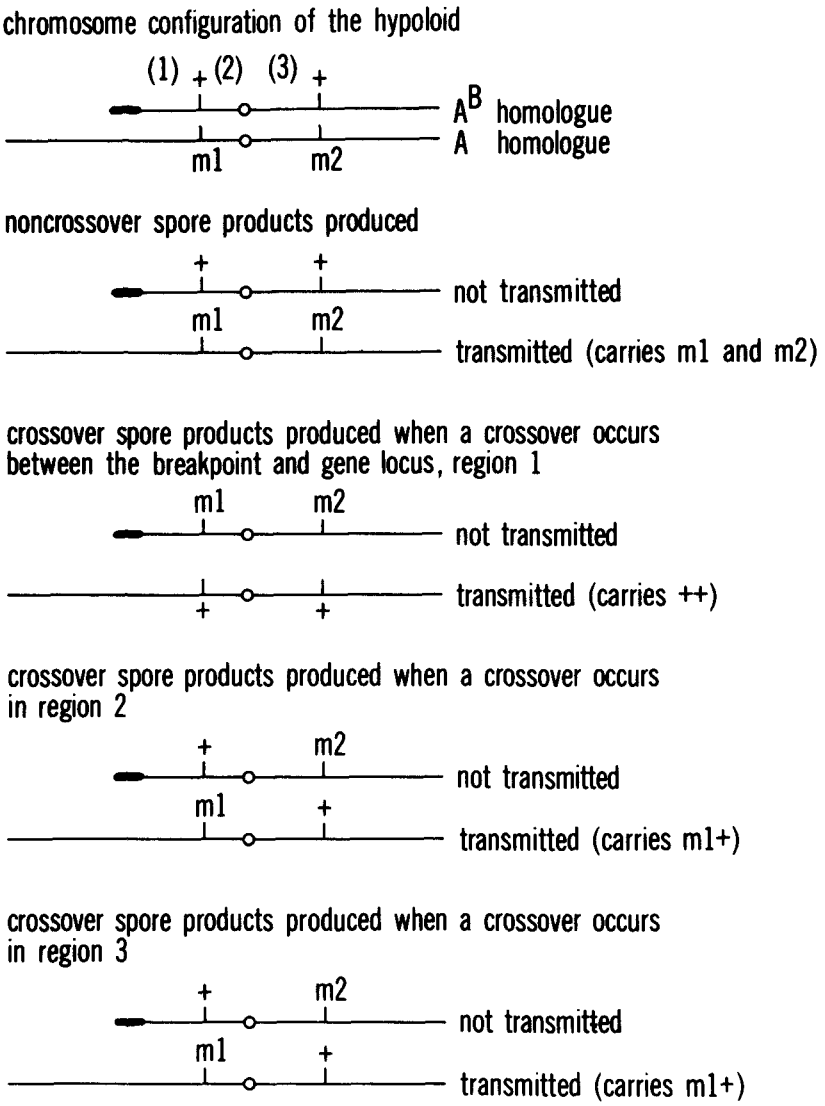

FIGURE 1.—The cytological configuration of a typical hypoploid heterozygous for mutants proximal to the breakpoint and in which the dominant alleles are carried on the deficient (A^B) homologue and the expected noncrossover and crossover products.

cleus. These plants have the A^B element of the translocation and the normal A homologue. Such hypoploid plants show 50% pollen and ovule abortion because microspores and megaspores receiving the A^B chromosome abort. If a hypoploid plant carries a recessive mutant gene on the normal homologue proximal to the B-A breakpoint and the normal allele on the A^B chromosome, most of the functional gametes will carry the recessive allele. The occurrence of the dominant normal allele will be a function of the amount of crossing over that occurs between the gene locus and the breakpoint (Figure 1). ROMAN

and ULLSTRUP (1951), using plants hypoploid for TB-1Sb (breakpoint 1S.05), were able to map the position of the gene for *Helminthosporium carbonum* susceptibility (*hm*) with respect to the translocation breakpoint. ROBERTSON (1967) BIANCHI and BORGHI (1966) and BIANCHI (1968) also determined the *wx*–breakpoint distance in plants hypoploid for TB-9Sb.

This report demonstrates that, in six different B-A translocations, the crossing over between the breakpoint in hypoploids and genes carried on their respective chromosomes is always greater in plants crossed as males than when plants are crossed as females. The term "hypoploid effect" will be used throughout this paper purely as a descriptive term for the higher percentage of crossover products observed in the male gamete of hypoploid plants and is not meant to imply a mechanism responsible for this condition.

MATERIALS AND METHODS

The translocations used in this study, along with the genes tested, are listed in Table 2. B-A translocation plants were crossed as males to marker gene stocks in which the genes are located proximal to the breakpoint. The F_1 populations were examined, and those with 50% abortive pollen grains (hypoploid) were used in exact reciprocal crosses (*i.e.*, the two plants involved in a cross functioned as both male and female parents with respect to each other) with lines homozygous for the marker gene.

Exact reciprocal test crosses were made of plants with normal chromosomes and heterozygous for two or more genes in the vicinity of the region tested for crossing over in the hypoploid plants. These tests were made to determine whether there was a difference in crossovers transmitted through microspores and megaspores of normal plants for the regions investigated.

To determine whether the different rates of crossing over observed when hypoploid plants were used as males and females were significant, a χ^2 test for independence was used utilizing fourfold contingency tables with 1 d.f. (SNEDECOR and COCHRAN 1967). A modification of this test was used when an entry was less than five in one cell, as found in LINDGREN (1968).

To determine whether there was a significant difference between the excess in male crossovers observed in the hypoploid tests and the excess in male crossovers found in the control (normal chromosome tests), the X^2 analysis proposed by STEEL and TORRIE (1960) for $2 \times 2 \times 2$ table was used.

TABLE 2

B-A translocations and their chromosome breakpoints and genes used in linkage tests with each translocation

Translocation	Breakpoint[a]	Genes tested	Phenotype
TB-4Sa	4S.25	*gl3*	Glossy seedling
		gl4	Glossy seedling
TB-5La	5L (breakpoint not located)	*bt*	Brittle endosperms
		a2	Colorless aleurone
TB-9La	9L.4	*sh*	Shrunken endosperm
TB-9Sb	9S.5	*v*	Virescent seedling
		wx	Waxy endosperm
TB-10La	10L.35	*y9*	Pale yellow endosperm
		bf2	Blue fluorescent seedling
		oy	Oil yellow plant color
TB-10Sc	10S (breakpoint not located)	*bf2*	Blue fluorescent seedling
		r	Colorless aleurone

[a] From BECKETT (1978).

RESULTS AND DISCUSSION

The crossover classes were significantly greater in all crosses when hypoploid plants were used as males than when they were crossed as females. This is true for all B-A translocations and all regions tested (Table 3). In seven instances the crossing over in males was two or more times greater than the crossing over in the females. Tests of crossing over in reciprocal crosses involving normal chromosomes for the regions involved in the hypoploid tests gave variable results, depending upon the region studied (Table 4). The region tested in chromosome 10 showed no statistically significant difference. In chromosome 9, for the *c-sh* distance, there were more crossovers in the female than in the male. The *sh-wx* distance, however, had more crossovers in the male-transmitted gametes. For the total *c-wx* crossing over, there may or may not be a difference in favor of male transmission at the 5% level of significance. The regions tested in chromosomes 5 (*a2-bt*) and 4 (*su-gl4*) both showed significantly greater crossing over in the male at the 1% level of significance.

There is no doubt that the transmission rate of crossovers through the male is higher than through the female of hypoploid plants. For chromosome 10, this rate differential is due to the hypoploid condition inasmuch as the control tests do not show a similar disparity between males and females. For chromosomes 9, 5 and 4, the role of hypoploidy in producing an excess of male-transmitted crossovers is not obvious because the control crosses also show an excess.

In most instances, the excesses seen in the control crosses have been reported before by others (see Table 1). There is, however, some disparity in the results obtained by various workers for some regions. For example, there are reports of more crossovers in male crosses for the *c-wx* region by some workers, whereas others indicate more crossovers in female crosses. Our data indicate more in the male. Also an excess of crossovers in plants used as males has been reported in the *c-sh* region by some, but again, others report more in the female. Our data indicate that more crossovers are recovered through the female. These discrepancies may be due to the status of knobs on these chromosomes. RHOADES (1978) has shown that plants with knobbed chromosomes have a higher crossover rate when crossed as males than when crossed as females. Plants missing the knobs do not show the male-female discrepancy in crossing over. Similar results were found by CHANG and KIKUDOME (1974). The variable results reported in Table 1 may reflect polymorphism only with respect to the knobs in the various lines tested.

Is the excess of male-transmitted crossovers observed in the plants hypoploid for chromosome 9, 5 and 4 just the result of the excess of male crossovers expected in these regions as demonstrated by the control crosses, or does the hypoploid excess represent something additional? In some cases, it would seem to be the latter. The data from Table 5 indicate that the hypoploid excess in males is significantly greater for all translocations than that observed for the controls crossed, with the exception of TB-10La-*oy* and *y9-bf2*. Thus, hypoploidy does seem to be consistently responsible for an excess of crossovers transmitted through the male.

TABLE 3

Transmission of crossover products through pollen and ovules in exact reciprocal crosses involving six hypoploid B-A plants heterozygous for various marker genes

Translocation	Gene locus	♀ Parent				♂ Parent				♂%C.O. / ♀%C.O.	% Difference ♂ ♀	χ^2
		C.O.	N.C.O.	Total	%C.O.	C.O.	N.C.O.	Total	%C.O.			
TB-10La	*y9*	143	1,100	1,243	11.5	358	1,352	1,710	20.9	1.8	9.4	44.7806**
TB-10La	*bf2*	288	3,929	4,217	6.8	1,042	6,085	7,127	14.6	2.1	7.8	154.6295**
TB-10La	*oy*	866	3,123	3,989	21.7	1,787	4,359	6,146	29.1	1.3	7.4	67.5402**
TB-10Sc	*bf2*	0	589	589	0.0	48	2,296	2,344	2.0		2.0	15.1358**
TB-10Sc	*r*	693	1,859	2,552	27.2	1,718	2,272	3,990	43.1	1.6	15.9	168.4553**
TB-9La	*sh*	233	489	722	32.3	341	400	741	46.0	1.4	13.7	28.4149**
TB-9Sb	*v*	169	1,277	1,446	11.7	601	1,433	2,034	29.5	2.5	17.8	155.4293**
TB-9Sb	*wx*	12	5,057	5,069	0.2	78	10,395	10,473	0.7	3.5	0.5	14.4435**
TB-5La	*a2*	37	812	849	4.4	603	2,592	3,195	18.9	4.3	14.5	105.0007**
TB-5La	*bt*	2	847	849	0.2	116	3,079	3,195	3.6	18.0	3.4	41.4289**
TB-4Sa	*gl4*	190	1,921	2,111	9.0	566	2,364	2,930	19.3	2.1	10.3	101.6397**
TB-4Sa	*gl3*	245	507	752	32.6	789	1,180	1,969	40.1	1.2	7.5	12.6460**

** Difference significant at the 1% level. C.O., crossover; N.C.O., noncrossover.

TABLE 4

Linkage studies of control plants using exact reciprocal crosses for genes in the proximity of the translocation breakpoints for B-A translocation involved in the hypoploid tests

Chromosome	Loci	♀ Parent				♂ Parent				% Difference ♂-♀	χ^2	*P*
		C.O.	N.C.O.	Total	%C.O.	C.O.	N.C.O.	Total	%C.O.			
10	*y9-bf2*	91	1310	1401	6.5	110	1317	1427	7.7	1.2	1.3974	0.20–0.30
10	*bf2-g*	221	1089	1310	16.9	211	1062	1273	16.6	−0.3	0.0220	0.80–0.90
10	*yg-g*	213	740	953	22.4	211	766	977	21.6	−0.8	0.1189	0.70–0.80
9	*c-sh*	145	3006	3151	4.6	58	1744	1802	3.2	−1.4	5.2328*	0.02–0.05
9	*c-sh*[a]	145	3006	3151	4.6	58	1929	1987	2.9	−1.7	8.6546**	>0.01
9	*sh-wx*	606	2545	3151	19.2	431	1371	1802	23.9	4.7	14.9248**	>0.01
9	*sh-wx*[a]	606	2545	3151	19.2	431	1556	1987	21.7	2.5	4.4226*	0.02–0.05
9	*c-wx*	751	2400	3151	23.8	489	1313	1802	27.1	3.3	6.4885*	0.01–0.02
9	*c-wx*[a]	751	2400	3151	23.8	489	1498	1987	24.6	0.8	0.3598	0.50–0.70
5	*a2-bt*	971	8370	9341	10.4	1044	7497	8541	12.2	1.8	14.7344**	>0.01
4	*su-gl4*	700	4596	5296	13.2	758	3540	4298	17.6	4.4	35.6008**	>0.01

* Difference significant at the 5% level; ** difference significant at the 1% level. C.O., crossover; N.C.O., noncrossover.

[a] Parental classes in this test were not in 1:1 proportions in the male cross. The *C SH Wx* class = 752, and the *c sh wx* class = 567 (a significant difference of 185, $\chi^2 = 25.95$, $P < 0.01$). In these tests, 185 was added to the male *c sh wx* class to compensate for this apparent deficiency. The reason for the male deficiency of this parental class is not known. There do not seem to be obvious deviations in the complementary crossover classes in the male crosses.

TABLE 5

χ^2 tests using 2 × 2 × 2 tables to determine whether the excess male crossing over in hypoploid tests is significantly greater than the excess male crossing over in control crosses

Hypoploid test	Control test	χ^2	*P*
TB-10La-*y9*	*y9-bf2*	7.942**	<0.01
	bf2-g	23.2582**	<0.01
	y9-g	23.695**	<0.01
TB-10La-*bf2*	*y9-bf2*	16.290**	<0.01
	bf2-g	47.228**	<0.01
	y9-g	46.823**	<0.01
TB-10La-*oy*	*y9-bf2*	1.591	0.20–0.30
	bf2-g	12.337**	<0.01
	y9-g	12.804**	<0.01
TB-10Sc-*bf2*	*y9-bf2*	8.577**	<0.01
	bf2-g	10.927**	<0.01
	y9-g	11.162**	<0.01
TB-10Sc-*r*	*y9-bf2*	10.722**	<0.01
	bf2-g	37.323**	<0.01
	y9-g	37.092**	<0.01
TB-9La-*sh*	*sh-wx*[a]	10.644**	<0.01
	sh-wx	5.184*	0.1–0.5
	c-sh[a]	30.0563**	<0.01
	c-sh	24.343**	<0.01
	c-wx[a]	17.449**	<0.01
	c-wx	9.793**	<0.01
TB-9Sb-*v*	*sh-wx*[a]	71.647**	<0.01
	sh-wx	54.034**	<0.01
	c-sh[a]	82.287**	<0.01
	c-sh	71.503**	<0.01
	c-wx[a]	92.215**	<0.01
	c-wx	70.690**	<0.01
TB-9Sb-*wx*	*sh-wx*[a]	9.806**	<0.01
	sh-wx	7.243**	<0.01
	c-sh[a]	22.787**	<0.01
	c-sh	19.724**	<0.01
	c-wx[a]	12.453**	<0.01
	c-wx	9.365**	<0.01
TB-5La-*a2*	*a2-bt*	72.079**	<0.01
TB-5La-*bt*	*a2-bt*	20.756**	<0.01
TB-4Sa-*gl4*	*su-gl4*	25.987**	<0.01
TB-4Sa-*gl3*	*su-gl4*	0.041	0.80–0.90

* Difference significant at the 5% level; ** difference significant at the 1% level.

[a] See Table 4 for explanation.

Why does this hypoploid effect occur? It could be due to some ordering of the chromatids in megasporogenesis following crossover so that crossover chromatids do not end up in the basal megaspore. RHOADES has established that crossing over can result in the directed orientation of chromatids to the basal megaspore in heteromorphic dyads produced by crossing over between knobbed and knobless (or less knobbed) homologue in the presence of abnor-

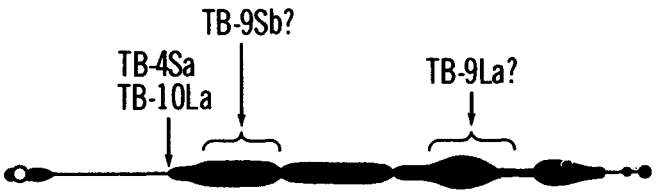

FIGURE 2.—Morphology of the B chromosome with the known breakpoints indicated for the B-A translocations used in this report. (Breakpoints from E. WARD, unpublished data.)

mal 10. This is due to the formation of neocentromeres on knobbed chromatids when abnormal 10 is present (see CARLSON 1977 for a review). Could a similar orientation be occurring in hypoploid plants? Crossovers between the breakpoint and the centromere will produce heteromorphic dyads. However, no neocentric activity is present to orient such dyads as in the case when abnormal 10 is present. Is there something else about such a crossover bivalent that might result in orientation of the chromatids? For those translocations in which the breakpoints are known, (Figure 2) the A^B chromosome will have a piece of B chromosome heterochromatin attached. If the B heterochromatin is sticky, a crossover bivalent in which heteromorphic dyads are produced would be oriented on the first metaphase spindle, with the normal chromatids toward the poles. However, when this happens, in most crossover situations, one intact outside chromatid will be a noncrossover chromatid, and one will be a crossover chromatid. Thus, this type of orientation would not result in the deficiency of crossovers observed in the female.

NOVITSKI (1951) showed in Drosophila that, if two homologues were of different lengths and a crossover occurred producing a heteromorphic dyad, the egg (the outside cell in a linear array of meiotic products) more often (67–72% of the time) received a shorter chromatid. In the hypoploid plants in maize, such a mechanism would result in a preferential incorporation of the A^B chromosome in the egg and a subsequent reduction in the recovery of crossover chromatids. Crossovers that are on the opposite chromosome arm to that in which the break is found, however, will not result in heteromorphic dyads, and thus, there would be no selection against crossover strands. Double crossovers in which one is in the breakpoint to centromere region and the other is between the centromere and a gene in the other chromosome arm will result in heteromorphic dyads and a subsequent loss of the A^B chromatids, if NOVITSKI's type of nonrandom disjunction is taking place. In three- and four-strand doubles this would result in the loss of the crossover strands resulting from exchange in the nontranslocation arm. Thus, crossover loss would be a function of breakpoint centromere distance and would uniformly decrease the recovery of the female crossovers for genes in the chromosome arm not involved in the translocation.

Such a uniform decrease in crossing over is not consistently found, as is seen from the percentage difference column of Table 4 (*e.g.*, 2.0% for *bf2* and 15.9% for *r* in the TB-10Sc cross). The 9.4% for *y9* and the 7.4% for *oy* with TB-10La and also the 7.5% for *gl3* and 10.3% for *gl4* with TB-4Sa, however, are similar values and might indicate a uniform affect of crossing over between

the breakpoints and centromeres. If the NOVITSKI type of nonrandom disjunction is occurring 100% of the time, the only way to recover a crossover for a gene in the female that is located in the region between the breakpoint and the centromere is by a double crossover (*i.e.*, one between the breakpoint and the gene and the other between the gene and the centromere). If NOVITSKI's type of nonrandom disjunction is something less than 100%, some single crossovers between the breakpoint and the gene can be recovered. In either case, there should be a reduction in the female transmission of these crossovers. For the most part, the recovery of fewer crossovers through the female than the male is in agreement with the transmission pattern due to the nonrandom type of disjunction found in heteromorphic dyads of Drosophila. However, there, could be other explanations.

It is possible that the piece of B heterochromatin attached to the deficient chromosome might be responsible for the differences in crossover rate. Studies by NEL (1973) and CHANG and KIDUDOME (1974) have shown that the presence of B chromosomes can affect crossing over. NEL (1973) found B's increased crossing over in selected regions of chromosomes 5 and 9. CHANG and KIKUDOME checked crossing over in three regions of chromosome 9 (*i.e.*, *yg2-sh*, *sh-bz*, *bz-wx*), in plants with zero to five B chromosomes and with homozygous small terminal knob or heterozygous small/large terminal knob on the short arm of chromosome 9. Although the number of B chromosomes influenced the amount of crossing over, they never resulted in a consistent increase of male crossovers as compared with female. Interestingly enough, the percentage of single exchanges in the short arm of chromosome 9 were consistently higher in the males that were heterozygous for the knobbed condition. In plants homozygous for the small knob, there were consistently more single crossovers for the same region in the female parent. Thus, the presence of the large knob or the heteromorphic condition with respect to the knobs, or both, result in more male crossing over. This observation is in agreement with RHOADE's observation (1978) that the presence of knobs increases male crossing over.

NEL (1973) found more crossing over in males than in females for two regions in chromosome 5. These differences were greater when one or two *B* chromosomes were present. Similar, but not as striking, increases in male crossing over were found for the *c-sh* and *wx-gl15* regions of chromosome 9 in the presence of B chromosomes. HANSON (1969) also found that, in the presence of B chromosomes, male crossing over in chromosome 3 relative to female crossing was greater. Thus, B chromosomes, in some instances, may enhance the difference between male and female crossing over. Such B enhancement may be responsible for the greater male crossing over in the deficient B-A translocation plants. The effects, however, may not be explained completely by B chromosomes. There may be something about the deficient condition that results in more male crossing over.

Another possible explanation, suggested by an anonymous reviewer of this paper, was that the B heterochromatin on the A^B homologue might inhibit synapsis in its vicinity and hence crossing over, and, for some reason, this effect (*i.e.*, the inhibition of synapsis) is stronger in the female than the male.

A second reviewer of this manuscript suggested that nondisjunction among noncrossover hypoploid tetrads could result in the observed higher male crossing over if there was a much lower rate of nondisjunction in the female than male sporocytes. The low rate of nondisjunction in the female is necessary because the nondisjunction products function in the megaspores and would result in wild-type phenotype (= crossover). If the nondisjunction rates are the same on the male and female sides, it would increase the frequency of crossover class in both sexes. Thus, equal rates of nondisjunction in both sexes will not explain the differences observed. If nondisjunction is responsible, there must be significantly more in males than females. Fortunately we have a genetic test that will tell us whether there is such a differential in male and female nondisjunction. In the reciprocal crosses with *wx* and TB9Sb, there are very few *wx* crossover products observed in either the male or female. Since the *wx* locus is so very close to the breakpoint, if nondisjunction is playing a *major role* in producing the difference, we should expect that the percentage of difference between males and females is due primarily to nondisjunction and not to some other phenomenon related to crossing over. If we assume that all of the difference is due to nondisjunction it must have reduced the effective population size by eliminating the noncrossover products so that there was an apparent 3.5-fold increase in the frequency of crossover (Table 3) in the transmitted male products. Since nondisjunction operates on the whole chromosome, it should affect all loci equally. Therefore, we would also expect a 3.5-fold increase in frequency for the TB-9Sb-*v* data. Similarly, if nondisjunction were the cause of the female-male differences the $\frac{\text{♂ \% crossover}}{\text{♀ \% crossover}}$ values should be nearly the same when dealing with a given translocation and different genes. This is not observed to be the case for TB-10La (four genes tested), TB-9Sb (two genes tested), TB-5La (two genes tested) or TB-4Sa (two genes tested). Thus, nondisjunction does not seem to be a valid explanation for the difference.

In summary, we are left with several alternative explanations for the "hypoploid effect." From the present data, however, it is impossible to determine whether one or more or, for that matter, any of the proposed alternatives account for increased transmission of crossovers through pollen of plants deficient for B-A translocations.

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