

Duplex crossed as	#plants	# progeny with			total
		OK10	1K10	2K10	
male	2	11	74	6	91
female	5	9	93	13	115
No. observed		20	167	19	206
No. expected with random chromosome segregation		34.33	137.33	34.33	205.99
χ^2		5.98	6.42	6.86	19.26

The somewhat reduced ability of K10-carrying pollen to compete with k10 pollen in fertilization may account for the slight excess of male backcross progeny in the OK10 compared to the 2K10 class while the reverse imbalance noted in the female data might reflect the occurrence of preferential segregation of K10 (Rhoades, 1942, Genetics 27:395). Assuming that these two complicating factors would essentially cancel out each other, the male and female data were pooled for purposes of χ^2 calculations.

The observed distribution of K10 among the progeny does not fit ($\chi^2=19.26$, $P=0.005$, $df=2$) that expected on the basis of random chromosome 10 pairing and disjunction in the duplex parents. Rather, the data suggest the occurrence of a high frequency of homomorphic bivalents (K10/K10 and k10/k10) leading to the excess of 1K10 progeny. Cytological data on chromosome 10 pairing relationships at diakinesis support this contention. It was found that homomorphic bivalents occurred in 195 (56.7%) among a total of 344 microsporocytes while heteromorphic bivalents occurred in only 43 cells (12.5%). Quadrivalents and trivalents plus univalents were found in 98 (28.5%) and 8 (2.3%) cells, respectively. If pairing and chiasma formation were random among the four chromosomes 10 in duplex heterozygotes, the frequency of homomorphic associations among total bivalents scored should be only 33.3% whereas it was actually found to be 81.9%. This represents considerable preferential pairing.

Undoubtedly preferential synapsis will render the factors of double reduction and numerical non-disjunction considerably lower in this case than the estimates of 2.7% and 2.6% for chromosome 4 (Catcheside, 1956, Heredity 10:205) so that their elimination from the above considerations is warranted.

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2. The effect of abnormal chromosome 10 on numerical non-disjunction

Tetraploids carrying 0, 1, and 2 abnormal chromosomes 10 (K10) were derived from asynaptic diploids segregating for

K10 and crossed as females to established tetraploid stocks. The K10 constitution and chromosome number of the derived tetraploids were determined from examination of dividing root tip cells prepared by a modified Feulgen squash technique. The extent of numerical non-disjunction of chromosome 6 was determined by scoring the nucleolar constitution of quartets of balanced 40-chromosome plants. Quartets with 3 or 4 spores containing 2 nucleoli each were scored as having arisen from 2-by-2 anaphase I disjunction. Quartets with 2 spores containing 3 nucleoli each (or 3 and 2 nucleoli) and separated by the anaphase I division plane from 2 spores containing 1 nucleolus each were scored as having arisen from 3-by-1 disjunction. Numerical non-disjunction of chromosome 6 is recorded below as per cent of 3:1 quartets.

Chromosome 6 non-disjunction	OK10			1K10			2K10		
	A*	B	C	A	B	C	A	B	C
#plants	4	2	3	3	2	2	1	2	1
#quartets	618	520	473	517	364	364	360	229	327
%3:1 quartets	4.9	5.0	7.0	9.3	7.2	12.1	11.4	11.7	15.3
overall quad. freq. at metaphase I									
tot. #homologues	1540	1150	1340	1260	1090	1080	980	1010	810
quad. frequency	.853	.853	.893	.873	.853	.880	.895	.848	.874
X% quads. with free ends	41.7	46.3	42.6	42.3	35.7	40.6	37.2	36.2	38.8

*lines A and B had the same diploid but different tetraploid parentage while line C consisted of backcross progeny of 2K10 plants from line B

It is apparent that a striking increase in chromosome 6 non-disjunction is associated with the presence of K10 in all lines, especially in C. At least three explanations could be offered for this phenomenon: (1) K10 causes a significant increase in chromosome 6 quadrivalent frequency thereby increasing the possibility of numerical non-disjunction; (2) K10 alterations in chiasma frequency result in an increase in those quadrivalent configurations which lead to the more irregularly disjoining linear and indifferent centromere orientations (see Darlington, 1931, Jour. Gen. 24:65); (3) K10-induced neocentric activity overtakes true centromere activity resulting in greater disjunctive irregularity.

That explanation (1) is unlikely is suggested by the above data demonstrating that K10 has little or no effect on overall quadrivalent frequency as determined from whole-cell scoring. Furthermore, preliminary data reveal no difference in chromosome 6 quadrivalent frequency at diakinesis (.943 versus .938) between OK10 and 2K10 plants from line C.

If possibility (2) were tenable one might expect that the presence of K10 would result in an increase in those quadrivalents with free ends, that is, those configurations with one or more chromosome arms not involved in a chiasma. However, data reported in the above table show that such quadrivalent types scored at diakinesis actually decrease in the presence of K10.

Possibility (3) postulates a relationship between K10-induced non-disjunction and knob constitution. This prediction seems to be fulfilled at least for T6-9b/N heterozygotes. Dempsey (MNL 33:55, and personal communication) has obtained data which indicate, first of all, a substantial K10-induced increase in 3 to 1 segregation in these translocation heterozygotes and secondly, a greater increase in 3 to 1 segregation in those heterozygotes with two chromosome 9 knobs than in those with only one. Pachytene analysis of several line B plants in the present study revealed that chromosome 6 was quadriplex for one knob in the long arm and duplex for another more distal knob.

Limited data (Carlson, personal communication) suggest that non-disjunction may also be increased by K10 in T5-9c/N heterozygotes. Non-disjunction of chromosome 10 itself has been found to occur in K10 carrying diploids (Emmerling, 1959, Jour. Hered. 49:203; Ashman, 1964, MNL 38:122) and has been attributed by Emmerling to neocentric activity.

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3. The effect of abnormal chromosome 10 on female fertility in autotetraploids.

Autotetraploid sterility in maize, as well as in other plants, has been attributed to both genetic and cytological causes although its precise nature remains unresolved. In a new approach to this problem (suggested by Dr. Rhoades) abnormal 10 (K10) was introduced into three tetraploid lines A, B, and C, as described in the above report, to investigate the possibility of correlating K10-induced neocentric activity, or increases in crossing over and chiasma frequency, with effects on fertility. Forty-chromosome tetraploids were pollinated daily until fresh silks no longer appeared. Developed kernel and ovule counts were made on the resulting ears from which the tip and butt ends had been removed and fertility is expressed below as the per cent of ovules which successfully developed into mature kernels.

	line	OK10			1K10			2K10		
		A	B	C	A	B	C	A	B	B
#ears		6	2	4	7	4	5	-	9	2
tot. # ovules		2631	607	1188	2887	1610	2239	-	3434	633
% successful ovules		72.3	74.7	76.8	73.0	73.9	65.1**	-	70.7	54.8**

**significantly different from OK10 at P=0.001 (t test)