

progenies gave 1:1 ratios for Lg:lg while the remainder gave frequencies of Lg varying from 57-72%, but all significantly different from a 1:1. The six progenies with 1:1 ratios are presumably derived from plants of $\frac{\text{Lg Na k a}}{\text{lg na k a}}$ constitution resulting from a crossover between Na and K.

Progenies with excess Lg came from $\frac{\text{Lg Na K a}}{\text{lg na k a}}$ plants resulting from a crossover between K and A. If all six of the 1:1 progenies trace to Na k crossovers, the frequency of Na-K recombination in the total population would be 36% X 11% or about 4% and the frequency of K-A recombination would be 32%. The presence of K10 K10 in the original backcross may have increased these frequencies above their normal levels. Two of the six 1:1 progenies were borderline cases, whose occurrence would be expected with probabilities of 20% and 30%; if these are eliminated, Na-K recombination becomes 2.5% and K-A would be 33.5%.

The variation in frequencies of preferential segregation of Lg (from 57% to 72%) in the second backcross was greater than expected, even though the 54 populations sampled generally did not exceed 200 individuals. K10 is heterozygous in all cases and the same knob is present; some unidentified factor apparently influenced the rate of preferential segregation. Since preferential segregation occurs only after a crossover between the knob and its centromere, variations in crossing over may be responsible.

E. Dempsey

2. The effect of K10 on chromosome breakage and recombination.

In structurally normal bivalents, the enhancement of recombination produced by abnormal chromosome 10 (K10) is restricted to the proximal regions adjacent to the centromere. In general, these regions consist of heterochromatic, deeply staining chromomeres. Crossing over in k10 k10 plants within segments adjacent to centric regions is much lower per unit of pachytene length than in more distally situated euchromatic regions. It was suggested (Rhoades and Dempsey, 1966) that the proximal heterochromatic regions were not as tightly coiled in K10 plants and that this relaxation in coiling facilitated the intimate pairing

essential for exchanges to occur. If crossing over takes place by breakage and reciprocal reunion, might not the enhancement induced by K10 be caused by breaks occurring more readily in the relatively uncoiled proximal chromonemata of K10 plants than in the more contracted chromatin of k10 plants? Cytogenetic studies of inversion heterozygotes provide data which are pertinent to the above question.

Progenies were obtained from sib plants heterozygous for In3a and for the G1 Lg and A markers in the long arm of 3 which were testcrossed. The sibs differed by the presence and absence of K10. Both the N and the In chromosome possessed the large knob at position 0.6 in the long arm. Consequently, preferential segregation due to knob heterozygosity is not a complicating factor in interpreting the recombination data.

G1 A K Lg In3a
g1 lg K a N3 heterozygotes were used as female parents in backcrosses. The crossover regions are indicated in the leftmost diagram in Figure 1 and the constitution of the anaphase I bridge following a crossover between A and Lg is shown on the right. The backcross data from K10 N10 and N10 N10 sibs are given below (Families 29736-29753):

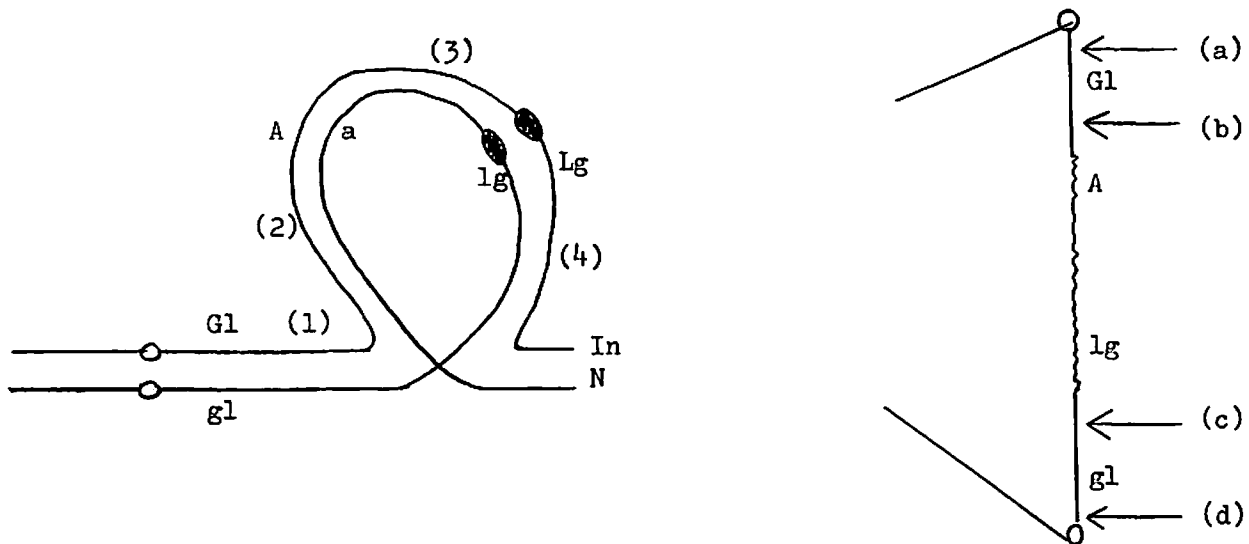
	(0)	(3-4)*	(2-4) (1)	(2-3)*	(2-3)	(2-4)** (1)	(3-4)	(0)	
	<u>G1</u>	<u>G1</u>	<u>g1</u>	<u>g1</u>	<u>G1</u>	<u>G1</u>	<u>g1</u>	<u>g1</u>	
	<u>Lg</u>	<u>lg</u>	<u>Lg</u>	<u>lg</u>	<u>Lg</u>	<u>lg</u>	<u>Lg</u>	<u>lg</u>	
	<u>A</u>	<u>A</u>	<u>A</u>	<u>A</u>	<u>a</u>	<u>a</u>	<u>a</u>	<u>a</u>	Σ
K10	1678	160	407	66	54	415	92	1549	4421
N10	3316	182	453	91	34	458	78	3282	7894

*Dp Df chromosomes from (3) and (1-3) exchanges included

**Dp Df chromosomes from (2) included

In the K10 data there are 160 G1 lg A and 92 g1 Lg a chromosomes. The g1 Lg a arise from (3-4) double exchanges and an equal number of G1 lg A are expected from the same doubles. The difference (160 - 92 = 68) is attributed to G1 lg A chromosomes which are Dp Df strands arising from singles in (3) and doubles in (1-3). They may come from breaks in regions represented by arrows (a), (c) and (d) in the diagram of the anaphase I bridge (Figure 1). The fraction stemming from breaks between g1 and the In (region c) can be estimated, if region c and region b breaks occur with the same frequency, by comparing the frequency of g1

Figure 1. Pachytene pairing and anaphase I bridge configuration (following a single crossover in region (3)) in $\frac{Gl\ A\ K\ Lg\ In\ 3a}{gl\ lg\ K\ a\ N3}$ heterozygotes.



Bridge breakage at AI between the Gl locus and the centromere is indicated by arrows (a) and (d). Breaks between Gl and the inversion occur in regions (b) and (c). A wavy line indicates the inverted segment. Breaks in (a) or (d) give Dp Df chromosomes with both the Gl and gl alleles while breaks in regions (b) and (c) give Dp Df chromosomes that are not redundant for the Gl locus.

Bridge breakage at (a)	gives a N Dp Df	<u>gl</u> <u>lg</u> <u>A</u> <u>Gl</u>	chromosome
"	"	" (b)	gives a N Dp Df <u>gl</u> <u>lg</u> <u>A</u> "
"	"	" (c)	gives an In Dp Df <u>Gl</u> <u>A</u> <u>lg</u> "
"	"	" (d)	gives an In Dp Df <u>Gl</u> <u>A</u> <u>lg</u> <u>gl</u> "

lg A and Gl Lg a classes. The 54 Gl Lg a chromosomes are derived solely from (2-3) doubles and an equal number of gl lg A is expected from the same doubles. The difference between 66 and 54 or 12 represents those Dp Df gl lg A chromosomes coming from bridges following single exchanges in region (3) or (1-3) doubles and they are formed only when the bridge breaks between the Gl locus and the inversion breakpoint (arrow b in the anaphase diagram). An equal number of Dp Df Gl A lg should come

following breaks at arrow c. It follows that 56 (68 - 12) Dp Df chromosomes arose from breaks in the proximal segments between G1 and the centromere. The ratio of breaks in the G1-centromere regions (a and d) to those in the G1-In regions (b and c) is 56 : 24 or 2.3 : 1.0. When a similar analysis is made of the N10 N10 data the calculations give 47 cases of breaks in the a and d regions and 114 in the b and c segments, a ratio of 0.4 : 1.0. It appears that, when breaks occur in an anaphase bridge, the chances of a proximal break (at a or d) are approximately six times greater in K10 than in N10 plants. In the above calculations the number of Dp Df chromosomes is an indirect estimate based on the assumption that complementary crossovers from double exchanges occur with equal frequencies in the population. Moreover, sampling errors would be high because of the small number of Dp Df chromosomes. However, the validity of the conclusions reached regarding a greater tendency for breaks to occur in segments a and d in K10 plants than in N10 plants was supported by an analysis of proven Dp Df chromosomes derived from both K10 and N10 parents. Among the Dp Df chromosomes from K10 plants there were twelve arising from breaks in the a or d regions and six from breaks in the b and c regions. The Dp Df chromosomes from N10 parents consisted of ten coming from breaks in the a and d regions and 58 from breaks in the b and c regions. The ratio of the Dp Df chromosomes coming from a and d breaks to those from b and c breaks is much higher in K10 than in N10 plants. The data are in agreement with the original conclusion.

It may be of more than passing interest to find that the K10 chromosome renders the proximal heterochromatin more susceptible to breakage and also enhances the frequency of recombination within the same chromosomal segment. If crossing over occurs by breakage and reciprocal reunion a greater susceptibility to breakage might be correlated with increased crossing over. Such appears to be the case although it should be kept in mind that enzyme induced breaks are presumably involved in crossing over while rupturing of the dicentric bridge is due to tension. Incidentally, all of the inversion heterozygotes in these experiments had several B chromosomes so any differential effect of B's on transmission or recovery of Dp Df chromosomes

(see Rinehart, MNL 1970) is not a factor.

An estimate of the amount of crossing over within the inversion loop in K10 and N10 plants can be calculated from the frequencies of G1 Lg a (2-3) and gl Lg a (3-4) double crossover chromosomes. These two recombinant types contain no Dp Df chromosomes, although their complementary crossover classes do. In K10 plants there were 146 such doubles in a population of 4421, or 3.3%. This value should be doubled (6.6%) to allow for the equal number of gl lg A and G1 lg A double crossover chromatids. The percentage of double crossover chromatids calculated in a similar manner is 2.8% in N10 plants. If the frequency of double crossover chromatids truly reflects the amount of recombination within the loop in K10 and N10 plants, there is 2.36 times as much inversion crossing over in K10 as in N10 sibs. This finding is in agreement with our earlier studies where K10 was shown to markedly increase crossing over in structural heterozygotes. Since the frequency of Dp Df chromosomes from dicentric bridges produced following a crossover between Lg and A is 2% in N10 plants (161 ÷ 7,894), the percentage of Dp Df chromosomes recovered from K10 plants should be 2% x 2.36 or 4.72%, if there is no preferential segregation to the functional megaspore of the intact member of a dyad consisting of a normal and a broken chromatid. The observed percentage of Dp Df chromosomes from K10 plants is only 1.8% (80 ÷ 4421) even though more frequent breaks in the proximal segments of the dicentric bridge in K10 plants might be expected to enhance the number of viable Dp Df chromosomes. These data support the hypothesis of Rhoades and Dempsey (1966) that a knobbed intact chromatid is preferentially recovered from deficient dyads in K10 plants and that random segregation of the intact and deficient chromatids occurs in N10 plants.

M. M. Rhoades
E. Dempsey

3. Evidence that ameiotic results in a substitution rather than an elimination of meiosis.

Preliminary evidence suggested to us that in the ameiotic plants meiosis did not occur and that it was not replaced by a modified form