

Recombination:

	<u>K 10/k 10</u>	<u>k 10/k 10</u>
g-r	13.5%	12.7%
r-sr ₂	0.9%	36.4%
g-sr ₂	14.4%	46.2%
Double crossovers	0.0%	1.6%

Percentage:

g	67.6*	49.8
R	73.6*	51.0
Sr	73.9*	50.0

* Statistically significant difference from a 1:1 ratio.

The data indicate that there is a drastic reduction in the recombination frequency between r and sr₂ in sibs having the abnormal chromosome 10. This reduction could be attributed to non-homology between abnormal 10 and normal 10 in the distal 1/6 segment of the long arm of normal 10. The absence of double crossovers in K 10/k 10 plants should not be surprising, since there is a great reduction in recombination between r and sr. (The frequency of expected double crossovers in the K 10/k 10 class is 1.2%.) The recombination value obtained for the r-sr region in k 10/k 10 sibs shows that there is considerable crossing over in the region distal to r. This is in agreement with crossing over data obtained by Joachim and Burnham.

In the g-r region, where there is homology between K 10 and k 10 chromatin, there exists no detectable difference between the recombination values obtained for the respective sib classes.

8. Preferential segregation in chromosome 9.

A. The effect of knob size.

(1) Heretofore it has been regarded that, in the presence of abnormal chromosome 10, preferential segregation of the other nine chromosomes occurs only when one homologue is knobbed and the other is knobless. When both homologues have the same sized knob there is no preferential segregation even when abnormal 10 is present. In a family segregating for $K^L 9S \underline{+} \underline{wx} / k 9S \underline{wd} \underline{+}$ and $K^L 9S \underline{+} \underline{wx} / K^M 9S \underline{+} \underline{+}$ plants (K^L = a large knob on chromosome 9 nearly the same length as the heterochromatin of abnormal 10; K^M = knob approximately 2/3 the size of K^L ; K^S = knob size approximately that found for chromosome 9 in "KYS" strain), the Wx:wx ratio was checked in plants of the K^L/K^M constitution. Statistically the Wx:wx ratio was found not to be a 1:1 ratio. Since this locus is quite removed from the knob of the short arm, the following set-up was used to determine whether this finding was apparent or real.

$$\frac{K^M}{K^S} \frac{+ + + +}{yg c sh wx} \frac{K 10}{k 10} \quad X \quad K^S yg c sh wx k 10$$

The results of the experiment are shown below:

(0)	(0)	(1)	(1)	(2)	(2)	(3)
$\frac{+ + + +}{2224}$	$\frac{yg c sh wx}{1028}$	$\frac{+ c sh wx}{401}$	$\frac{yg + + +}{202}$	$\frac{+ + sh wx}{133}$	$\frac{yg c + +}{56}$	$\frac{+ + + wx}{625}$
(3)	(1-2)	(1-2)	(1-3)	(1-3)	(2-3)	(2-3)
$\frac{yg c sh +}{230}$	$\frac{+ c + +}{8}$	$\frac{yg + sh wx}{4}$	$\frac{+ c sh +}{14}$	$\frac{yg + + wx}{11}$	$\frac{+ + sh +}{10}$	$\frac{yg c + wx}{4}$

Total population: 4950

Recombination:

% Yg = 69.0
 % C = 64.8
 % Sh = 63.2
 % Wx = 55.4
 % Doubles = 1.03

% yg-c = 12.9
 % c-sh = 4.3
 % sh-wx = 18.1
 % yg-sh = 16.8
 % c-wx = 21.8
 % yg-wx = 33.3

The results prior to classification of the yg marker were:

(0)	(0)	(1)	(1)	(2)	(2)	(1-2)	(1-2)	Σ
$\frac{+ + +}{2440}$	$\frac{c sh wx}{1716}$	$\frac{+ sh wx}{162}$	$\frac{c + +}{67}$	$\frac{+ + wx}{647}$	$\frac{c sh +}{280}$	$\frac{+ sh +}{10}$	$\frac{c + wx}{4}$	5336

Recombination:

% C = 61.1
 % Sh = 59.0
 % Wx = 52.2
 % c-sh = 4.6
 % sh-wx = 17.6
 % c-wx = 21.7

The post-germination percentages for the loci C, Sh, Wx are not the same as the percentages gotten for these respective loci in the pre-germination data. Approximately 6% of the seeds failed to germinate and most of the seeds that failed to germinate were the "shrunken" ones. The data were further analyzed to determine whether this seed loss introduced a bias into certain of the classes or whether, in spite of the loss, the post germination values were accurate reflections of the pre-germination values. Firstly the following type of comparison was made between the pre- and post-germination values:

	(0)	(0)	(1)	(1)	(2)	(2)	(1-2)	(1-2)	Σ
	<u>+++</u>	<u>c sh wx</u>	<u>+ sh wx</u>	<u>c ++</u>	<u>++ wx</u>	<u>c sh +</u>	<u>++ sh +</u>	<u>c + wx</u>	
Pre-germination	2440	1716	162	67	647	280	10	4	5336
Post-germination	2426	1429	137	64	636	244	10	4	4950

	<u>Pre-Germination</u>	<u>Post-Germination</u>	<u>Difference</u>
$\frac{+++}{(+++)+(c\ sh\ wx)}$	0.59	0.63	+ 0.04
$\frac{+ sh wx}{(+ sh wx)+(c ++)}$	0.71	0.68	- 0.03
$\frac{++ wx}{(++ wx)+(c sh +)}$	0.70	0.70	
$\frac{+ sh +}{(+ sh +)+(c + wx)}$	0.72	0.72	

This comparison shows that in the non-crossover and single crossover (c-sh) classes there is selection against "shrunken" and no apparent selection against "shrunken" in the other two crossover classes. This selection appears to be somewhat small. The 0.6-0.7-0.7-0.7 type of proportion is found in both the pre- and post-germination groups. When the recombination values for the c-sh, sh-wx, and c-wx regions are compared, they are very similar in the pre- and post-germination data.

	<u>Pre-Germination</u>	<u>Post-Germination</u>
% c-sh	4.6	4.3
% sh-wx	17.6	18.1
% c-wx	21.7	21.8

Since selection against "shrunken" has not seriously affected the relative proportions of Yg:C:Sh:Wx, the following correction procedure was taken to determine percentage of plants that would have had the Yg phenotype had all the seeds germinated.

	<u>Post-Germination</u>	=	<u>Pre-Germination</u>	
$\frac{\% Yg}{\% C}$	$\frac{69}{64.8}$	=	$\frac{x}{61.1}$	x = 65.1% Yg
$\frac{\% Yg}{\% Sh}$	$\frac{69}{63.2}$	=	$\frac{x}{59.0}$	x = 64.4% Yg
$\frac{\% Yg}{\% Wx}$	$\frac{69}{55.4}$	=	$\frac{x}{52.2}$	x = 65.0% Yg
				Av. x = 64.8% Yg

Had all the seeds germinated, approximately 65% of the plants would have been of the Yg phenotype. This corrected value is quite comparable to the percentage obtained for this phenotype in similar experiments where no selection against any particular class occurred. The ratios obtained for all of the loci studied were statistically significant deviations from a 1:1 ratio. These data definitely show that preferential segregation does occur even when both homologues are knobbed, but only when the knobs are of different sizes.

(2) In a family segregating for K^S 9/ k 9 and K^M 9/ K^S 9, the following backcross data were obtained:

		+	c	+	c	+	c	+	c		
		+	sh	sh	+	+	sh	sh	+		
		+	wx	wx	+	wx	+	+	wx		
a.	$\frac{K^S}{k} \frac{c}{+} \frac{sh}{+} \frac{wx}{+}$	$\frac{K}{k}$	10	1157	1828	41	101	344	677	2	5
b.	$\frac{K^M}{K^S} \frac{+}{c} \frac{+}{sh} \frac{+}{wx}$	$\frac{K}{k}$	10	2286	1398	134	79	827	418	4	5

a. $\Sigma = 4155$

% c = 62.6*
% sh = 61.3*
% wx = 53.4*

Recombination:

% c-sh = 3.6
% sh-wx = 24.7
% c-wx = 28.0

b. $\Sigma = 5136$

% C = 63.3*
% Sh = 62.2*
% Wx = 54.3*

Recombination:

% c-sh = 4.3
% sh-wx = 24.4
% c-wx = 28.4

*Statistically a significant deviation from a 1:1 ratio.

In this sib comparison, the degree of preferential segregation obtained in both groups for the respective loci is similar, although it is slightly higher in the K^M/K^S group. Even the recombination values are of the same magnitude. It seems, then, that K^M/K^S is equivalent to K^S/k . This finding further substantiates the previous finding (8A-1) that when both homologues are differentially knobbed, preferential segregation occurs in favor of the larger knobbed chromosome. Comparison of the data of the above K^M/K^S group with those of the K^M/K^S group discussed previously (8A-1) shows that both the recombination values and the percentage values obtained for the loci involved are in agreement.

(3) The effect of knobs of three different sizes upon the degree of preferential segregation of the wd and wx loci was studied. "wd" is actually a small terminal deficiency in the short arm of chromosome 9 and is pseudoallelic to yg.

					Percentage				
		<u>++</u>	<u>+ wx</u>	<u>wd +</u>	<u>wd wx</u>	Σ	<u>Wd</u>	<u>Wx</u>	<u>Recombination</u>
$\frac{K^S + +}{k \text{ wd wx}}$	$\frac{K \ 10}{k \ 10}$	1372	669	419	992	3452	59.1	51.9	31.5
$\frac{K^M + +}{k \text{ wd wx}}$	$\frac{K \ 10}{k \ 10}$	3994	1543	757	2272	8566	64.6	55.5	26.9
$\frac{K^L + wx}{k \text{ wd +}}$	$\frac{K \ 10}{k \ 10}$	1442	3463	1726	581	7212	68.0	56.1 (wx)	28.1

The percentage values shown for each locus are all statistically significant deviations from the 1:1 ratio one expects in normal (absence of abnormal 10) backcrosses. The source for each knob size is not the same, and the source of the small knob used here is different from that of the small knob used in the previous experiments. Statistical analyses were made to determine whether the percentage values obtained for the locus closer to the knob were truly an expression of the different levels of activity of the knob size, or whether knob size was inconsequential. It was found that K^L was different from K^M and K^S and that K^M was different from K^S . In other words, the larger the knob, the higher the degree of preferential segregation of the locus under study. Analyses have not been made for the Wx data as yet.

B. Comparisons were made of ratios obtained in the non-crossover classes and crossover classes for all knob combinations studied. The numerator in each instance is that reciprocal class containing the dominant marker nearest to the knob.

Examples: $\frac{+++}{(++++) + (yg \ c \ sh \ wx)}$; $\frac{++ \ sh \ wx}{(++ \ sh \ wx) + (yg \ c \ ++)}$

	<u>(0)</u>	<u>(1)</u>	<u>(2)</u>	<u>(3)</u>	<u>(1-2)</u>	<u>(1-3)</u>	<u>(2-3)</u>
$\frac{K^L + wx}{k \text{ wd +}}$	0.67	0.71					
$\frac{K^M + +}{k \text{ wd wx}}$	0.64	0.67					
$\frac{K^S + +}{k \text{ wd wx}}$	0.58	0.62					
(Control)	(0.51)	(0.51)					
$\frac{K^S + + +}{k \ c \ sh \ wx}$	0.61	0.71	0.66	0.71			

	(0)	(1)	(2)	(3)	(1-2)	(1-3)	(2-3)
$\frac{K^M + + +}{K^S c sh wx}$	0.62	0.63	0.66	0.56			
$\frac{*K^M + + + +}{K^S yg c sh wx}$	0.68	0.66	0.70	0.73	0.67	0.56 [†]	0.71
$\frac{**K^M + + + +}{K^S yg c sh wx}$	0.70	0.62	0.67	0.73	0.71	0.63	0.25 [‡]
$\frac{***K^M + + + +}{K^S yg c sh wx}$	0.73	0.62	0.68	0.73	0.73	0.67	1.00 [#]

*Post-germination data used here.

**Not summarized in this report since they show essentially the same results as the $K^M + + + + / K^S yg c sh wx$ group.

†0.56 ratio: due to 14:11 ratio obtained for the reciprocal crossover classes.

‡0.25: only 2 $++ sh +$ to 6 $yg c + wx$ ratio obtained.

#1.00 ratio: due to 3:0 ratio obtained for the reciprocal crossover classes.

C. Evidence that abnormal 10 alters the recombination frequency in chromosome 9.

The following sib comparison (backcross) data were obtained involving a small knobbed strain. The data for the sibs heterozygous for abnormal 10 are the same data reported under 8A-3. The loci studied were wd and wx.

	++	+ wx	wd +	wd wx	Σ	Percentage		
						Wd	Wx	Recom- bination
$\frac{K^S + +}{k wd wx} \frac{K 10}{k 10}$	1372	669	419	992	3452	59.1*	51.9*	31.5
$\frac{K^S + +}{k wd wx} \frac{k 10}{k 10}$	2034	733	716	1947	5430	51.0	50.6	26.7

*Statistically significant deviations from a 1:1 ratio.

It seems that abnormal 10 has the capacity of increasing the recombination frequency between the two loci studied. The \underline{Wd} and \underline{Wx} ratios obtained were found to be significant deviations from a 1:1 ratio. Since 59% \underline{Wd} is statistically different from 51% \underline{Wd} , and also 51.9% \underline{Wx} from 50.6% \underline{Wx} , the 4.8% difference between the two mean recombination frequencies could be statistically a significant one. Analyses ("t" test) have shown that the two means are different, although the difference is a small one.

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1. The enhancer factor--a fourth location.

In a previous Maize News Letter (1953) it was reported that Enhancer, (\underline{En}), the dominant mutator that causes \underline{pg}^m -mutable pale green- to mutate to \underline{Pg} -green - can be variously located. (Without \underline{En} , \underline{pg} is stable). It has been found (1) adjacent to \underline{pg} (the autonomous mutable condition), (2) on the same chromosome and 36 units from \underline{pg} , and (3) on an independent chromosome. \underline{En} has recently been found at a 4th location, on another independently assorting chromosome. This new location appeared among some F_2 progenies of a series of crosses of a non-segregating \underline{En} stock ($\underline{Pg}/\underline{Pg} \underline{En}/\underline{En}$) by \underline{pg}^s (stable pale green). Ordinarily, the self of this F_1 ($\underline{Pg}/\underline{pg} \underline{En}/+$) yields an F_2 with pale green seedlings segregating 3 \underline{pg}^m : 1 \underline{pg}^s . This ratio indicates that \underline{En} is segregating (\underline{pg} with \underline{En} is mutable and \underline{pg} without \underline{En} is stable). In one particular series of crosses, 2 or the 10 segregating progenies gave only 6% \underline{pg}^s among the \underline{pg} class which is significantly lower than the expected frequency of stables (25%). The expected genotype of the parents, F_1 and the segregation of these exceptional F_2 progenies are as follows:

$\underline{Pg}/\underline{pg} +/+ \times \underline{Pg}/\underline{Pg} \underline{En}/\underline{En} \text{ --- } F_1 \underline{Pg}/\underline{pg} \underline{En}/+$ (green)

<u>Exceptional F_2 progenies</u>				<u>% \underline{pg}^s</u>
1956	443-10	135 +	: 35 \underline{pg} (2 \underline{pg}^s : 33 \underline{pg}^m)	5.7%
1956	443-13	145 +	: 49 \underline{pg} (3 \underline{pg}^s : 46 \underline{pg}^m)	6.1%

These results suggest that \underline{En} must be in a heterozygous condition at two separate loci, each locus independent of \underline{pg} . The F_1 of the above cross would then be $\underline{Pg}/\underline{pg} \underline{En}/+ \underline{En}/+$. Of the resulting F_2 progeny, only 1/16 of the \underline{pg} genotypes would lack \underline{En} . These would therefore be stable: chromosome linkage of \underline{En} has not yet been established for either of the two independent locations.