THE INTERACTION OF KNOBS AND B CHROMOSOMES OF MAIZE IN DETERMINING THE LEVEL OF RECOMBINATION[1,2]

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ABSTRACT

Enhancement of recombination by B chromosomes is influenced by the kind of heterochromatic knob present in or near the tested region of the A chromosomes. In homomorphic chromosome 9 bivalents of K^s/K^s constitution, double exchanges were increased at the expense of singles, but in the K^*/K^s heteromorphs there was a gain in both single and double exchanges at the expense of no-exchange tetrads. Modification of the B chromosome enhancement in different knob compounds was observed only in the megasporocytes.——Different frequencies of recombination are found in plants with odd and even numbers of B chromosomes; this effect is especially striking in the megasporocytes. The modification in recombination produced by an odd or even number of B chromosomes is a function of the interaction of a particular region and the knob constitution. Odd numbers of B chromosomes were more effective than even numbers in causing increased recombination.——It is concluded that heterochromatic knobs and the essentially heterochromatic supernumeraries may interact in the process of crossing over, with the level of recombination determined in part by knob constitution.

THE ability of the B chromosomes of maize to promote recombination has been demonstrated by RHOADES (1968a, b), by HANSON (1969), by NEL (1969, 1973) and by WARD (1972). RHOADES, HANSON and NEL each observed a shift in the distribution of exchanges from the distal to the proximal region of the short arm of chromosome 9 in the presence of B chromosomes. NEL noted that it is the proximal region of the chromosome which responds to the presence of the supernumeraries and that the increase in recombination is either more pronounced in or confined to the microsporocytes. Moreover, the enhancement of recombination was accentuated when the abnormal chromosome 10 (K10) was also present. The K10 chromosome possesses an exotic piece of chromatin containing a large block of heterochromatin with unusual genetic properties. Not only does K10 interact with B chromosomes to affect crossing over, but it also is able to increase recombination in the absence of B's in certain regions of the genome (RHOADES and DEMPSEY 1957, 1966; NEL 1973).

Heterochromatic knobs on chromosome 9 have been shown to influence the crossover increment induced by the K10 chromosome (KIKUDOME 1959). Inasmuch as the B chromosome, like the exotic segment of K10, is essentially heterochromatic, we wished to ascertain if knobs would similarly modify the recombinational response induced by B chromosomes. The K^* and the K^s (s = small) terminal knobs of the short arm of chromosome 9 were selected for this study. The K^* knob is similar in size to the large heterochromatic element which characterizes the K10 chromosome and is the largest known knob terminating the short arm of chromosome 9. It has none of the genetic properties of K10, according to our tests. The K^s knob, on the other hand, is similar in size to that found on chromosome 9 in the inbred line KYS and is approximately one-seventh the length of the K^* knob.

MATERIALS AND METHODS

Evaluation of the interaction of the knobs of chromosome 9 with B chromosomes was made through analysis of reciprocal testcross data from heterozygotes in two partial sib classes with differing knob combinations and varying numbers of B chromosomes. Since recombination in a given chromosome or chromosomal region can vary, from season to season, the testcrosses were made in the same season to avoid invalid comparisons. The comparison that we would like to have made was between K^s/K^s and K^*/K^* homomorphs rather than between a homomorph and a heteromorph. The latter type of comparison introduces the problem of pairing difficulty in the heteromorphs. If pairing in the heteromorphs were severely affected by the dissimilarity in knob size, the comparison would be highly suspect. Inasmuch as the K^*/K^* homomorphs with varying numbers of B chromosomes are not available, we resorted to the comparison shown below, cognizant of the potential danger confronting such an undertaking.

A.

$$\frac{K^s \quad + \quad + \quad + \quad +}{K^s \quad yg \quad sh \quad bz \quad wx} \quad \text{with} \quad \text{0B,} \quad \text{1B,} \quad \text{2B's,} \quad \text{3B's,} \quad \text{4B's,} \quad \text{5B's}$$

B

$$\frac{K^s \quad + \quad + \quad + \quad +}{K^* \quad yg \quad sh \quad bz \quad wx} \quad \text{with} \quad \text{0B,} \quad \text{1B,} \quad \text{2B's,} \quad \text{3B's,} \quad \text{4B's,} \quad \text{5B's}$$

The genetic markers used in our study can be characterized as follows: "Yellow-green" (yg) is a seedling and mature plant trait while "shrunken" (sh) is an endosperm marker. "Bronze" (bz) and "waxy" (wx) can be used either as mature plant or endosperm markers but are more readily scored in the endosperm.

When heterozygotes are used as males in testcrosses, heterofertilization may occur, resulting in kernels with embryos and endosperms of non-corresponding genotypes. Thus, an error may be introduced into the calculation of recombination values when one character is scored in the endosperm and the other in the seedling or mature plant. Since the effect of heterofertilization on our data appeared to be negligible, no corrections were made on the recombination values in the (yg–sh) region of chromosome 9. Therefore, the values presented for this region obtained in the backcrosses of heterozygous pollen parents may be somewhat higher than the actual frequencies. Recombination between sh, bz, and wx is not affected by heterofertilization since these traits were scored in the endosperm.

RESULTS

During our attempt to ascertain whether there is interaction between knobs and B chromosomes in determining the level of recombination attained in the

TABLE 1

Recombination values from testcrosses of two classes of knob combinations with varying number of B chromosomes

No. B's		Megasporocytes					Microsporocytes				
		I	II	III	Total	Total progeny	I	II	III	Total	Total progeny
0B	A.	23.86	2.47	15.72	42.05	7934	25.58	2.46	18.11	46.15	2479
	B.	8.35	1.61	19.10	29.05	6038	20.48	2.82	25.17	48.47	3369
1B	A.	22.08*	2.32	17.27*	41.66	5658	23.32	1.79	20.56*	46.67	2344
	B.	10.92**	1.69	21.39**	34.00**	9539	18.16*	1.84	25.30	45.30*	2285
2B	A.	24.17	2.12	16.23	42.52	7444	26.50	1.44**	17.64	45.59	2494
	B.	8.12	1.43	21.05*	30.60	5121	15.94**	1.88*	25.48	43.26**	2973
3B	A.	21.77*	1.81	17.44*	41.06	2494	24.94	1.70	17.23	43.87	2530
	B.	10.41**	2.05	23.44**	35.80**	4430	19.23	1.96*	25.48	46.66	2814
4B	A.	23.47	1.86*	16.07	41.40	5587	24.48	1.74*	17.81	44.03	3734
	B.	8.97	1.48	21.94**	32.39**	4202	18.48	2.44	24.11	45.03*	1970
5B	A.	23.69	1.85	18.33*	43.87	971	25.83	1.84	19.80	47.48	1409
	B.	12.63*	1.86	22.77**	37.27**	966	16.67**	1.80*	23.94	42.41**	1278

*,** denote deviations, significant at the 5% and 1% levels, respectively, from the "0B" category of the same knob combination.

Crossover regions: K———yg———sh———bz———wx———O $K^s/K^s = A$
                              I   II   III $K^*/K^s = B$
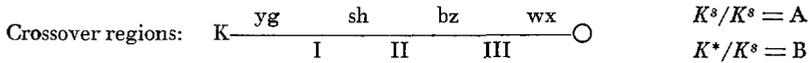
short arm of chromosome 9, we obtained the following information concerning the supernumeraries and the heterozygous K^* knob, respectively (see Table 1 and Figure 1): (a) In both the proximal (*bz–wx*) and the distal (*yg–sh*) regions, regardless of knob constitution, we observed an "odd-even" effect on recombination with increasing numbers of B's. Each of these regions is adjacent to heterochromatin. On the other hand, the interstitial (*sh–bz*) region showed little if any difference in recombination frequencies with odd or even numbers of B's. Unlike the distal and proximal regions, this region is far removed from heterochromatin. As can be seen in Figure 1, the "odd-even" effect is only weakly displayed in the microsporocytes. (b) Secondly, the supernumeraries were capable of promoting recombination in megasporocytes but appeared not to enhance it in microsporocytes. (c) Insofar as the heterozygous K^* knob is concerned, the data indicate that it acts as an effective suppressor of recombination in the distal region in megasporocytes and is relatively ineffective in microsporocytes. In addition, we have evidence that knobs of chromosome 9 participate in the B-chromosome effect.
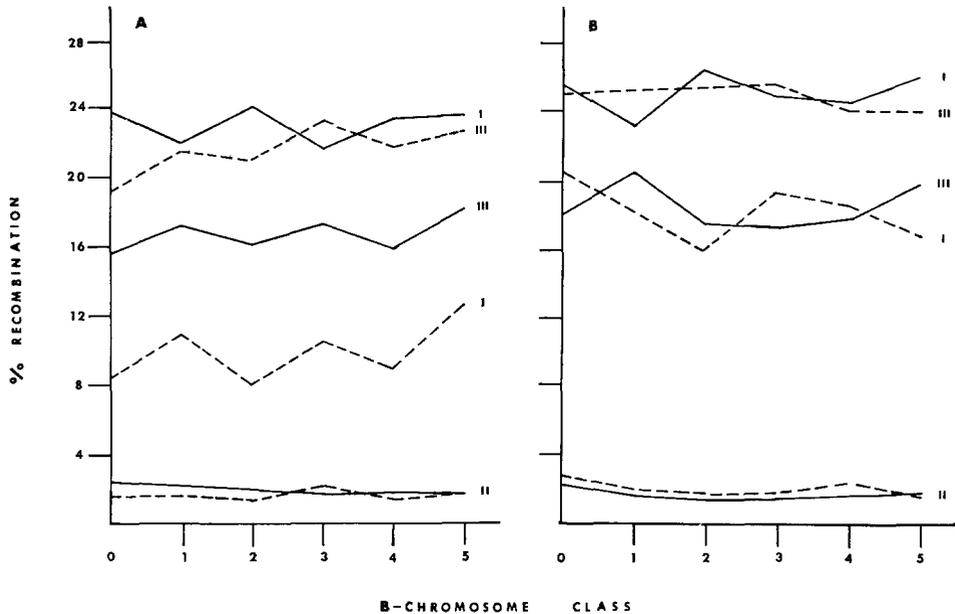
FIGURE 1.—Recombination percentages for three regions of chromosome 9 in megasporocytes (A) and microsporocytes (B) of K^s/K^s homomorphs (———) and K^*/K^s heteromorphs (– – –) with zero to five B chromosomes.

Involvement of knobs in the "odd-even" effect of B chromosomes

In megasporocytes of the homomorphs, an odd number of B's reduced the frequency of recombination in the distal region while an even number restored it to the original (0B) value (see Table 1). However, in the proximal region, an odd number of B's resulted in enhancement in recombination while an even number resulted in the restoration of the 0B value. The opposite effect was observed in megasporocytes of the heteromorphs. In the distal region, odd numbers of B's increased recombination while in the proximal region both odd and even numbers of B's resulted in enhancement, with an odd number being more effective than an even number. In contrast to the situation in megasporocytes, there is no clear-cut evidence for the involvement of knobs in the "odd-even" effect of B chromosomes in microsporocytes.

Another interesting observation was made in megasporocytes. In K^s/K^s plants with an odd number of B's, a decrease in the distal region was accompanied by an increase in recombination in the proximal region. When an even number of B's was present, the values obtained for these two regions were not significantly different from those obtained in the 0B plants. The extent of the change in recombination induced by an odd number of B's was about the same for the 1B, 3B, and 5B categories. However, in K^*/K^s plants, an increase in recombination was observed in both the proximal and distal regions when B chromosomes were present. The increase was more pronounced in plants with an odd number of B's. As in the homomorphs, the extent of the increase was approximately the same for the different B-containing categories.

Involvement of knobs in the modification of exchange frequencies induced by B's

The effect of the supernumeraries on double exchanges was similar in the two knob classes (see Tables 2 and 3). In both classes, increases in combined double exchanges for all regions were realized only in megasporocytes, and the rise in the doubles appears to be correlated with the increase in the number of B chromosomes. The increase in the double exchange frequencies induced by the supernumeraries was approximately the same in the two knobs classes (K^s/K^s: 1.4–4.2 times and K^*/K^s: 1.5–3.5 times). However, only the homomorphs show an enhancement of the I-III exchanges when those are considered separately, the enhancement being progressively more pronounced with increasing numbers of B's (Table 2). The calculated percentages of tetrad ranks presented in Table 3 reveal that in megasporocytes of the homomorphs the increase in the number of tetrads with double exchanges is at the expense of the single exchange tetrads with double exchanges is at the expense of the single exchange tetrads while in the heteromorphs the single and double exchange tetrads appear to be increased at the expense of the no-exchange tetrads.

When the percentages of single and double exchange tetrads are summed, there is no difference in the homomorphs either between megasporocytes and microsporocytes or among the six B-chromosome categories. In contrast to the homomorphs, megasporocytes of the heteromorphs exhibit an overall increase in the number of tetrads with one or more exchanges when B chromosomes are present;

TABLE 2

Coincidence values for double crossovers in the yg-sh *and* bz-wx *(I–III) regions*

No. B's		Megasporocytes		Microsporocytes	
0B	A.	0.07	(0.34%—27/7934)	0.47	(2.62%—65/2479)
	B.	0.10	(0.18%—11/6038)	0.44	(2.52%—85/3369)
1B	A.	0.11**	(0.48%—27/5658)	0.47	(2.39%—56/2344)
	B.	0.08	(0.28%—27/9539)	0.35*	(1.71%—39/2285)
2B	A.	0.14**	(0.59%—44/7444)	0.44	(2.20%—55/2494)
	B.	0.15	(0.37%—19/5121)	0.46	(2.19%—65/2973)
3B	A.	0.18**	(0.72%—18/2494)	0.51	(2.33%—59/2530)
	B.	0.08	(0.38%—17/4430)	0.43	(2.27%—64/2814)
4B	A.	0.09	(0.50%—28/5587)	0.36	(1.87%—70/3734)
	B.	0.18	(0.38%—16/4202)	0.39	(1.88%—37/1970)
5B	A.	0.29**	(1.44%—14/ 971)	0.47	(2.62%—37/1409)
	B.	0.07*	(0.62%— 6/ 966)	0.28**	(1.25%—16/1278)

*,** denote deviations, significant at the 5% and 1% levels, respectively, from the 0B category of the same knob combination and sex.

The percentages and numbers of combined double crossovers in regions I-II, II-III and I-III are given in parentheses.

$$K^s/K^s = A \qquad K^*/K^s = B$$

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TABLE 3

Calculated percentages of exchanges in meiocytes of two classes of knob combinations with varying number of B chromosomes

No. B's		Megasporocytes				Microsporocytes			
		None	Single	Double	Total progeny	None	Single	Double	Total progeny
0B	A.	17.28	81.36	1.36	7934	17.54	72.62	9.84	2479
	B.	42.64	56.63	0.73	6038	14.76	75.16	10.08	3369
1B	A.	19.64	79.49	1.91	5658	16.22	74.22	9.56	2344
	B.	33.20	65.67	1.13	9539	16.24	76.92	6.84	2285
2B	A.	17.32	80.32	2.36	7444	17.32	74.20	8.48	2494
	B.	40.40	58.12	1.48	5121	22.50	68.50	9.00	2973
3B	A.	20.76	76.43	2.81	2494	21.26	69.74	9.00	2530
	B.	29.94	68.53	1.53	4430	15.92	74.84	9.24	2814
4B	A.	19.30	78.70	2.00	5587	19.12	73.72	7.16	3734
	B.	36.74	61.83	1.43	4202	18.08	73.80	8.12	1970
5B	A.	18.02	76.22	5.76	971	15.96	73.54	10.50	1409
	B.	27.96	69.56	2.48	966	20.18	74.82	5.00	1278

$$K^s/K^s = A \qquad K^*/K^s = B$$

the "odd-even" effect is clearly evident in the single exchanges. The total percentages of exchanges in microsporocytes of heteromorphs are consistently higher than in the corresponding megasporocytes, but they show no consistent pattern of variation in the six B-chromosome categories. Further, in the homomorphs, double exchanges are decidedly higher in microsporocytes than in megasporocytes, but the single exchanges appear to be somewhat higher in megasporocytes. In the heteromorphs, both single and double exchanges are higher in microsporocytes than in megasporocytes. When one considers the recombination values obtained only in microsporocytes of the two knob classes, they are found to be quite comparable.

DISCUSSION

In maize and in other species, B chromosomes are capable of modifying chiasma formation (JOHN and HEWITT 1965; CAMERON and REES 1967; JONES and REES 1967; AYONOADU and REES 1968; VOSA and BARLOW 1970; SIMCHEN, ZARCHI and HILLEL 1971; EVANS and MACEFIELD 1972) and recombination (RHOADES 1968a, b; HANSON 1969; NEL 1969, 1973; CHANG and KIKUDOME 1971; WARD 1972). While in the majority of cases, B chromosomes act as promoters, in *Lolium perenne* (CAMERON and REES 1967), *Lolium temulentum × L. perenne* hybrid (EVANS and MACEFIELD 1972), and in *Triticum speltoides* (SIMCHEN, ZARCHI and HILLEL 1971), they behave as suppressors. The study of

EVANS and MACEFIELD is of particular interest in that the B's were observed to suppress pairing and chiasma formation between homoeologous chromosomes, thereby promoting these activities between homologs.

HANSON (1969) suggested that segments of maize chromosomes 3 and 9 possessing knob sites were the only regions which exhibited decreased crossing over in the presence of B's. However, he did not determine the knob constitution cytologically and the observed reduction in crossing over could well have been a consequence of interaction between B chromosomes and knobs. NEL (1973) reported that B chromosomes increase crossing over in centric or proximal regions of chromosomes 5 and 9 and that the response of these regions to the presence of B's was greater in microsporocytes than in megasporocytes. In his chromosome 9 study, NEL found that the distal (c–sh) region was unaffected by the presence of B's in both types of sporocytes. In addition, he obtained results indicating possible interaction between B's and the abnormal chromosome 10 (K10) in boosting recombination in the proximal (wx–gl) region of chromosome 9. NEL's studies indicate that qualitative differences may exist between centric heterochromatin of the various maize A chromosomes. Whether qualitative differences exist among knobs is still to be determined. Although we observed no obvious difference in pairing between the two knob classes, the modification of recombination observed in K^*/K^s individuals could still be a structural effect caused by dissimilarity in knob size and the resulting disturbance in effective pairing. Interaction of a somewhat difference type involving knobs and B chromosomes was described by RHOADES and DEMPSEY (1972a, b). They reported that B chromosomes could induce breaks in knobbed A chromosomes during the second microspore division and that modifying genes markedly affect the frequency of such breaks. They also showed that in knobbed heteromorphs it is the chromosome with the larger of the two knobs which experiences a higher frequency of breakage (RHOADES and DEMPSEY 1972a). Our data do not indicate that B chromosome-induced breaks occurred at a detectable level in the two knob classes. Nonetheless, we intend to determine the effectiveness of B chromosomes in inducing breaks in chromosomes 9 possessing the K^* knob.

AYONOADU and REES (1968) noted that the effect of maize B chromosomes on chiasma frequencies in microsporocytes was not consistent for all chromosomes and chromosomal segments. HANSON and NEL made similar observations in their recombination studies. While HANSON found the increase in total recombination to be due to a heightening of double exchanges at the expense of single exchanges, we found that the level of recombination can also be raised by an increase in both double and single exchanges at the expense of the no-exchange tetrads. The particular combination of chiasmata leading to an increase in recombination depends upon the knob constitution. In the homomorphs, double exchanges were enhanced at the expense of the single, while in the heteromorphs, single and double exchanges were increased at the expense of no-exchange tetrads. It is possible that at least a portion of the variability in response to B chromosomes found in different parts of the genome by AYONOADU and REES, by HANSON, and by NEL may be attributed to the presence of undetected knobs.

In his chromosome 9 study, Nel observed that the proximal (*wx–gl*) region was the only region to show a significant response to the presence of the supernumeraries and only in microsporocytes. This region includes a major portion of the centric heterochromatin. In our study, the proximal (*bz–wx*) region does not span the centromere and includes, at best, little of the centric heterochromatin. This region, however, showed an increase in recombination in megasporocytes of heteromorphs and of homomorphs with odd numbers of B's. The distal (*yg–sh*) region which we studied lies close to the terminal knob heterochromatin. It, too, showed an increase in recombination, but only in megasporocytes of heteromorphs with odd numbers of B's. In both studies, the region flanked by euchromatin (*c–sh* and *sh–bz*) showed no rise in recombination in the presence of B's. It appears from both studies that if a region is to show any significant increase in recombination in the presence of B's, it must lie sufficiently close to heterochromatin. A partial explanation of the difference between Nel's and our results lies in the fact that non-identical regions are involved and in the likelihood that the background genotypes involved in the two studies are different. This difference notwithstanding, both studies reveal that different chromosomes and chromosomal segments uniquely respond to the presence of B's and the manner in which they respond can be profoundly influenced by the "sex" in which crossing over is followed.

A finding of some interest is the difference in recombination frequencies observed in plants with odd and even numbers of B chromosomes. In the distal (*yg–sh*) region, an odd number of B's decreased recombination in the homomorphs but increased the level in the heteromorphs. An even number resulted in the reestablishment of the 0B value in both the homomorphs and the heteromorphs. In the proximal (*bz–wx*) region of heteromorphs, an odd number was more effective in enhancing recombination than was an even number, although both classes showed increased crossing over. In the homomorphs, on the other hand, only odd numbers of B's were effective, even numbers merely reestablishing the 0B value.

Kirk and Jones (1970) found that the relative amount of total nuclear protein and RNA in rye decreased with increasing numbers of supernumeraries, the values being consistently lower in plants containing odd numbers of these chromosomes. The amount of histones increased with additional B's, and again the plants with odd numbers of B's showed a greater effect than those with even numbers. They believe that histones produced by the supernumeraries inhibit genetic activity. However, Himes (1967) found no increase in the histone: DNA ratio when B chromosomes are added to the maize genome. While Jones and Rees (1969) postulate higher activity of rye B chromosomes when they occur in pairs, Rhoades and Dempsey (1972b) favor the idea that paired B chromosomes show less activity than unpaired ones. Our observations are in agreement with the suggestion of Rhoades and Dempsey. Table 4 lists the increases (+) and decreases (−) in recombination in the distal and proximal regions and the total recombination percentages for each of the six B-chromosome categories of both classes of knob-compounds.

TABLE 4

		0B	1B	2B	3B	4B	5B
	Distal region	....	1.78—	0.31+	2.09—	0.39—	0.17—
K^s/K^s	Proximal region	....	1.55+	0.51+	1.72+	0.35+	2.61+
	Total recombination:	42.05	41.66	42.52	41.06	41.40	43.87
	Distal region	....	2.57+	0.23—	2.06+	0.62+	4.28+
K^*/K^s	Proximal region	....	2.29+	1.95+	4.34+	2.84+	3.67+
	Total recombination:	29.05	34.00	30.60	35.80	32.39	37.27

The plants with even numbers of B's consistently show the least effect on recombination. Little or no change in total recombination was observed in K^s/K^s plants with increasing numbers of B chromosomes. In the homomorphs, the "permissible" level of recombination, it could be argued, is achieved in the absence of the supernumeraries and cannot be increased. Thus, the enhancement induced by B's in the proximal region is compensated by a decrease in the distal region. On the other hand, in the K^*/K^s plants, where the overall level of recombination is low due to the presence of the K^* knob, the activity of B chromosomes is more readily detected. Thus, in the proximal region, which is considerably removed from the K^* knob, both odd and even numbers of B's promote recombination, although even numbers are less effective than odd numbers. In the distal region, where the negative influence of the K^* knob is strongest, only odd numbers of B's are capable of partially overcoming the suppression of crossing over.

The data presented in this paper support the existence of an "odd-even" effect of B chromosomes in maize, similar to that described by JONES and REES (1969) and by KIRK and JONES (1970) in rye, and indicate that knobs also influence recombination. Although the *modus operandi* of B chromosomes, as well as of the heterochromatic knobs, still eludes us, it would appear that these elements are capable of interacting in highly specific ways.

We wish to dedicate this paper to PROFESSOR M. M. RHOADES, for whom we have deep affection and respect. To him and MISS ELLEN DEMPSEY, our gratitude, for their critical review of this paper.

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