THE DEPENDENCE OF SEGREGATION-DISTORTION ON CHROMOSOME PAIRING IN *DROSOPHILA MELANOGASTER*

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Since the discovery of Segregation-distorter (*SD*) a series of studies on the genetics of *SD* have been reported by the *Drosophila* group at Wisconsin and others (see review by Zimmering et al. 1970).

This paper is concerned with the nature of the segregation distortion phenomenon and, particularly, with the dependence of *SD* activity on chromosome pairing. Sandler and Hiraizumi (1959) reported that chromosome pairing particularly in the region of the *SD* complex, is essential in order for the *SD* gene to operate. Novitski and Ehrlich (1966, 1970) reported in D.I.S. that the action of *SD* was drastically changed when *SD*⁺ homologues were involved in a Y translocation. They suggested that a more general effect than simple pairing of homologues must be invoked. In the present work different mutations including chromosome aberrations were produced by irradiating the *SD* bearing chromosome with high dose of X-rays, and the resulting changes in *SD* activity and its relation to chromosome aberrations, which were detected by recombination tests and cytological observations, were studied.

MATERIALS AND METHODS

To investigate the mechanism of the segregation distortion phenomenon one *SD-bw* stock was used exclusively during the whole course of these experiments. The origin of this stock is *SD-72*, which was collected from natural populations by Hiraizumi and Crow (1957). This chromosome was obtained by recombination from the cross of *SD-72/cn bw* females to *cn bw* males, and maintained as a homozygous stock by conventional transfer methods for more than one year. Presumably it lacks the stabilizer of the 2R tip, as well as the lethal inversion of 2R (Sandler and Hiraizumi 1960). A single *SD-bw* chromosome was sampled from the *SD-bw* stock and its *SD* activity was tested to confirm the high *SD* activity of this stock: males of the constitution *SD-bw/cn bw* were crossed to homozygous *cn bw* females and the two classes of phenotypes (*bw* and *cn bw*) were counted in the progeny. These tests were continued for three generations. The average K value of this stock was 0.9837, a very high value considering the lack of the stabilizer at the tip of the right arm of the second chromosome. K is the proportion of *SD* bearing progeny resulting from the cross of *SD* heterozygotes to normal homozygotes (Sandler, Hiraizumi, and Sandler 1959). For an investigation

of the dependence of *SD* activity on chromosome pairing, such a stock lacking the original large inversion, but with high and stable activity, was considered to be most suitable. For this reason, the *SD-bw* stocks was used throughout these experiments.

In order to obtain chromosome rearrangements, *SD bw/cn bw* males were irradiated with 5000 r of X-rays (dose rate: 92 r/min.). *SD* activity and recombination tests were conducted soon after irradiation. The mating scheme of all the experiments was as follows (the diagrammatical explanation is in Fig. 1):

Fig. 1. Mating scheme of all the experiments in this paper.

SD ACTIVITY TESTS

SD bw males were irradiated with x-rays at a dose of 5000 r and immediately crossed to *cn bw* females (Gen. 1). All the irradiated male flies were discarded from the bottles four days after the matings. Thus, only irradiated sperms were utilized. The *SD* activity of each *SD bw/cn bw* F_1 male was tested in Gen. 2 by counting two types of progeny, *bw* and *cn bw*.

In Gen. 3, 4 and 8 six males of constitution *SD bw/cn bw* from the progeny of previous generations were sampled from each line and were put in a bottle. The *SD* activity was tested with two (Gen. 3, 4) or four (Gen. 8) replications.

RECOMBINATION TESTS

b pr stw c sp

For this recombination test the recessive markers of the second chromosome, black (*b*), purple (*pr*), straw (*stw*), curve (*c*), and speck (*sp*) were used. The description of these markers is given in Bridges and Brehme (1944). These markers cover almost all the right arm and the proximal region of the left arm of the second chromosome. The map distance on the standard map (Bridges 1944) is: *b* 6 *pr* 0.6 *stw* 20.4 *c* 31.5 *sp*. The centromere is located between *pr* and *stw*. The *SD* locus is somewhere around the centromere region.

The male progeny of Gen. 4 were crossed to *cn bw* females in order to determine the genotype of these males (*cn bw/b pr stw c sp* individuals produce progeny of the phenotypes *cn bw* and wild type, whereas *SD bw/b pr stw c sp* males produce *bw*, and wild type progeny) and these same males were crossed to *b pr stw c sp* females.

The progeny of the cross in Gen. 6 were counted and recombination values were obtained.

Throughout the experiments all flies were cultured on the standard Pasadena medium (Lewis 1960) with Wagner's Y-2 yeast. A laboratory temperature of $22^{\circ}\pm 1^{\circ}\text{C}$. was maintained for all phases of the experiment, except recombination tests. The recombination experiments were carried out at $25^{\circ}\pm 1^{\circ}\text{C}$.

pr cn

For the second recombination test, the recessive markers, purple (*pr*) and cinnabar (*cn*) (map distance 3.0) were used. These markers cover only the centromere region of the second chromosome, in which the *SD* locus is believed to be located. Most of selected lines had reduced activities or reduced values in the previous recombination tests. The test was done in Gen. 9 and 10 (see Fig. 1).

Cytological observation

Induced chromosome rearrangements of the second chromosome were observed cytologically by mounting the salivary gland chromosome. The salivary glands were dissected in 0.7% NaCl and transferred to lactic-aceto orcein for squashing after fixation by acetic alcohol. Observation of the preparations was made with phase optics. Only 22 lines which showed low *SD* activity or different recombination values from nonirradiated lines were selected for this observation.

EXPERIMENTAL RESULTS

SD Activity Test

The *SD* activity of 560 irradiated *SD-bw* chromosomes was tested for three successive generations (Gen. 2, 3, and 4) and again at Gen. 8, as shown in Fig. 1. However, the data for *SD* activity were obtained from only 410 progeny because the other 150 were sterile. The control was conducted in exactly the same manner except without irradiation. The summary of the first *SD* activity test (Gen. 2) after X-irradia-

Table 1. The effects of X-irradiation to *SD* activity

	No. of chromosomes tested	Mean K values	Variance
Treated	410	0.9360**	0.012253175**
Control	116	0.9823	0.001125078

**Significant at the 1% level.

Fig. 2. The effect of X-irradiation on distribution of *SD* activities.

tion is shown in Table 1 and diagrammatically in Fig. 2. From Table 1 it can be said that the mean K value of the irradiated lines decreased compared with the control and that the variance in the irradiated group increased significantly. An approximate method was used for the test of significance (Cochran and Cox 1957). The average K value of the irradiated lines was 0.9360, whereas the K value of the nonirradiated lines was 0.9823. According to the K values of the first *SD* activity test, 40 irradiated lines were selected for further experiments. At this point it was not known whether the

Table 2. The results of *SD* activity test at four different generations and of two recombination tests in the 40 irradiated lines

Line number*	K values**				Recombination values (%)					Cytological observations***
	Gen. 2	Gen. 3	Gen. 4	Gen. 8	b-pr	pr-stw	stw-c	c-sp	pr-cn	
9(S)	0.8000	0.8878	0.7397	0.8780					27.24	2 para. inv., trans. (25D of 2L-61E of 3L) normal
16(S)	0.7021	0.5476	0.6301	0.5444						
45	0.7846	0.8860	0.9835	0.9781	3.8	0	13.1	28.5		0.38 normal
58	0.8831	0.8951	0.8905	0.9806	3.9	0	14.3	31.6		
60	1.0000	0.9857	0.9987	0.9917	3.5	0	14.2	29.0		
75	0.8247	0.8825	0.9946	0.9512	3.0	0	12.7	29.6		
78	0.8115	0.8525	0.9454	0.9732	3.5	0	12.9	27.9		
92(S)	0.9077	0.9670	0.9809	0.9445					0.91	trans. (42 of 2R-Y)
115	1.0000	0.9874	0.9955	0.9850	3.2	0	12.6	28.1		
125	0.8696	0.8489	0.9639	0.9722	2.9	0	14.0	32.1		0.14 trans. (31 of 2L-Y)
127	0.7290	0.9130	0.7775	0.9446	4.0	0	13.4	31.9		
132(S)	0.4310	0.3172	0.4485	0.4933						
144	0.8883	0.9235	0.8929	0.9817	2.9	0	12.3	30.6		
146	0.9375	0.8365	0.8949	0.9240	3.1	0	12.7	29.0	0.19	
150	0.6887	0.8255	0.8168	0.9084	3.9	0	13.0	32.5	0.40	normal
175	0.8000	0.7358	0.9835	0.9748	4.1	0	12.2	30.3		
180	0.6364	0.6475	0.7208	0.6282	4.0	0	13.3	31.7	0.52	normal
182	1.0000	0.9964	0.9906	0.9954	5.3	0	3.9	0.6	0.26	
183	0.8219	0.9239	0.9032	0.9508	3.4	0.06	14.9	30.4		0 peri. inv. (26 of 2L-56F of 2R)
186(S)	0.7778	0.5630	0.4885	0.6159						
202	0.4444	0.4446	0.4635	0.4585	6.7	0	16.1	32.3	42.59	normal
236	0.8791	0.8537	0.9929	0.9906	0.4	0	14.8	32.8		
239	0.8534	0.7856	0.8353	0.6823	4.1	0	14.6	29.9	0.18	para. inv. (35 of 2L-39 of 2L)
240	1.0000	0.9362	0.9871	0.9881	5.5	0.05	0.1	1.0	0.12	
256(S)	0.6818	0.7286	0.7414	0.6507						normal
257	0.7273	0.7445	0.9925	0.9814	4.4	0	17.0	33.5		
258	0.8700	0.8895	0.9753	0.9636	1.1	0	15.1	32.7	0.37	para. inv. (22F of 2L-30B of 2L)
291	0.8793	0.8568	0.9990	0.9593	4.0	0.03	13.2	29.7		
296	1.0000	0.9666	0.9897	0.9939	2.8	0	16.4	28.1	0.35	0.10 normal
297	0.7029	0.7838	0.8193	0.7555						
338	0.7273	0.8891	0.7522	0.7588	4.2	0	22.1	33.1	0.99	normal
343(S)	0.5000	0.5502	0.5768	0.5565					19.82	
356	0.9932	0.9944	0.9707	0.9882	3.4	0	14.9	29.9	0.27	trans. (37 of 2L-Y)
366	0.5887	0.7169	0.5993	0.6258	3.6	0	12.1	31.1	0.20	
379	0.5778	0.8092	0.9924	0.9824	3.3	0.05	12.5	32.8	0.38	normal
387	0.8319	0.8549	0.9140	0.9810	2.8	0	14.7	31.3	0.35	
392	0.7089	0.7292	0.8235	0.8385	3.2	0	15.0	32.1	0.57	trans. (centro of 2-97 of 3R) trans. (3R-2R)

Table 2. (Continued 2)

Line number*	K values**				Recombination values (%)					Cytological observations***
	Gen. 2	Gen. 3	Gen. 4	Gen. 8	b-pr	pr-stw	stw-c	c-sp	pr-cn	
398(S)	0.7143	0.4679	0.7318	0.6978						trans. (57 of 2R-Y)
405(S)	0.6016	0.4556	0.7068	0.3919						normal
407	1.0000	0.9904	0.9938	0.9613	3.4	0	13.6	28.6	0.23	
Average	0.7894	0.7968	0.8474	0.8461	3.6		13.4	28.8		
Control	0.9823	0.9213	0.9543	0.9492	3.3	0.01	14.0	30.6	0.49	

*(S) indicates the sex deviant line.

**The K values about the progeny from the cross specified.

***para. inv. = paracentric inversion

peri. inv. = pericentric inversion

trans. = translocation

low *SD* activities obtained were due to meiotic events or zygotic ones. However, it was confirmed later that these effects were mostly meiotic by counting the number of eggs and adult flies emerged using several low activity lines. Among the 40 lines selected, 32 lines showed low *SD* activity ($K < 0.9$), and most of the other 8 lines had a very high *SD* activity ($K > 0.9$). These high *SD* activity lines were selected as a kind of irradiated control. Nine lines out of the 410 lines tested in the first *SD* activity test showed a strikingly different sex ratio among the progeny counted; most of the *bw* phenotype progeny were males. These were given "S" designations: 9 (S), 16 (S), 92 (S), 132 (S), 186 (S), 256 (S), 343 (S), 398 (S), 405 (S). All these 9 lines were included in the 40 lines selected for further tests. The results of four *SD* activity tests, including the first *SD* activity test of 40 selected lines, are shown in columns 2-5 of Table 2. In this table, only the average K values are listed. The findings from the above tests are as follows. It would appear that the average K values increase with increasing generation number until they reach a maximum and then remain constant. The average K value of generation 2 was 0.7894; that of generation 4 was 0.8474 and that of generation 8 was 0.8461. The recovery of *SD* activity of the irradiated lines might have been caused by the replacement of irradiated third and fourth chromosomes by nonirradiated chromosomes. Thus it is very likely that the replacement of irradiated chromosomes by nonirradiated chromosomes was almost completed by generation 4 and that the only effect on *SD* activity after generation 4 was due to irradiated second and Y chromosomes, which were automatically selected by the mating scheme. Out of the 40 irradiated lines selected, lines 60, 92 (S), 115, 146, 182, 240, 296, 356, and 407 maintained high *SD* activity for eight generations. These lines apparently do not have any *SD* modifier (suppressor) in any irradiated chromosome. Among the other 31 lines which showed rather low *SD* activity at the first activity test, lines 9 (S), 16 (S), 132 (S), 180, 186 (S), 202, 239, 256 (S), 297, 338, 343 (S), 366, 392, 398 (S), and 405 (S) continued to have low *SD* activities for eight generations. It is almost certain that some kinds of mutations or chromosome rearrangements which affect *SD* activity occurred in the Y or the *SD*-bearing second chromosome of these lines. In the other 16 lines (45, 58, 75,

78, 125, 127, 144, 150, 175, 183, 236, 257, 258, 291, 379, 387) high *SD* activity was almost completely recovered by generation 8. It is quite reasonable to think that the recovery of *SD* activities in these lines is due to the replacement of irradiated background chromosomes with induced modifiers by normal, nonirradiated chromosomes. Among the 15 stable low activity lines, lines 9 (S), 16 (S), 132 (S), 186 (S), 256 (S), 343 (S), 398 (S), and 405 (S) showed a deviant sex ratio: in all these eight lines, almost all of the *SD*-bearing progeny were male flies. It was considered that the deviant sex ratio was caused by a translocation between the Y chromosome and the second chromosome.

Recombination Tests

b pr stw c sp

Recombination values for the intervals between *b*, *pr*, *stw*, *c*, and *sp* were measured in the irradiated *SD-bw* lines and the original *SD-bw* line. The results of this test are presented in Table 2. In this test only the 30 lines which had a normal sex ratio in the previous *SD* activity tests were examined, because sufficient numbers of *SD-bw/b pr stw c sp* females were not obtained in the deviant sex lines. The control (non-irradiated) line, which shows consistently high *SD* activity, showed the following results in this recombination test: 3.3% between *b* and *pr*, 0.01% between *pr* and *stw*, 14.0% between *stw* and *c*, 30.6% between *c* and *sp*. The values for *b-pr-stw-c* are lower than standard map values (especially *pr-stw*); this may reflect the presence of the small pericentric inversion associated with *SD-72* (Lewis 1962). Among the 30 irradiated lines tested, 23 lines (45, 58, 60, 75, 78, 115, 125, 127, 144, 146, 150, 175, 180, 183, 239, 291, 296, 356, 366, 379, 387, 392, 407) showed a more or less similar recombination value to that of the control line. This may indicate that they do not have any major chromosome rearrangements in the regions covered by markers. Among the lines which showed normal recombination values, 19 lines (45, 58, 60, 75, 78, 115, 125, 127, 144, 146, 150, 175, 183, 291, 296, 356, 379, 387, 407) had fairly high *SD* activity at least, in generation 8, whereas the *SD* activity of the other 4 lines (180, 239, 366, 392) was low. Four lines (182, 236, 240, 258) showed very low recombination values in some regions; lines 182 and 240 between *stw* and *sp*, lines 236 and 258 between *b* and *pr*. However, all these four lines showed very high *SD* activity in generation 8. It is clear from the reduction of recombination values that some kinds of chromosome rearrangements occurred in regions of the second chromosome. The fact that all four lines showed a very high *SD* activity may indicate that chromosome pairing in the region of *b-pr* and *stw-sp* is not essential for *SD* to operate. The other three lines (202, 257, 338) showed, in every region tested, somewhat higher recombination values than the control. One of these three lines (257) showed a high *SD* activity, but the other two lines (202, 338) had very low *SD* activities.

In order to know the relation, in general, between *SD* activity and recombination values, correlation coefficients between the *SD* activities of generation 8 and the recombination values of each region were obtained. For this calculation the data of line 202 were excluded from consideration because of the peculiar results of the *pr-cn*

recombination test. The correlation coefficients of *SD* activity with the recombination values of the regions, *b-pr*, *stw-c*, and *c-sp*, were -0.17, -0.21, and -0.21, respectively, and are not significantly different from zero.

pr cn

In the previous *b pr stw c sp* recombination test, the size of the experiment was too small for reliable recombination values between *pr* and *stw* to be obtained, due to the short map length of this region and probably also to the presence of the small pericentric inversion described below. In fact, in many lines, no recombinants were obtained. The *SD* locus is located in the centromere region of the second chromosome. Thus, as the second recombination experiment, the markers, *pr* and *cn*, were used in order to get more information concerning recombination in this region. Twenty-four irradiated lines, including 5 sex deviant lines, were examined by this recombination test. The results of this experiment are shown in column 10 of Table 2. The recombination value of the nonirradiated line was 0.49%. Canton S wild stock, which is completely free of the *SD* complex, showed a recombination value of 1.61%. The difference in recombination values between Canton S and the *SD-bw* line clearly indicates the existence of a pre-existent chromosome rearrangement of the *SD* region in *SD* lines. However, two sex deviant lines, 9 (S) and 343 (S), out of five tested, showed surprisingly high recombination values (27.24% and 19.82% respectively) and almost exclusively produced *cn* recombinants. In addition, one other line (202) showed a very high value (42%), but this line produced both recombinants (*pr* and *cn*) in almost equal frequency. The recombination values of these three lines are too high to explain from the point of crossing over. The mechanism of this phenomenon appears to be as follows: if a small segment which includes the *pr*⁺ gene of the *SD*-bearing chromosome is transferred to another autosomal chromosome, let us say the third chromosome, the *SD*-bearing chromosome can become deficient for the *pr*⁺ gene and the third chromosome will contain this segment as an addition. As the *SD* gene is not operative in females, all the chromosomes segregate at random in meiosis. Thus, *SD*-bearing females heterozygous for *pr cn* produce four kinds of gametes in equal frequency: (1) the *pr*⁺-deficient second and the *pr*⁺-bearing third chromosomes; (2) the *pr*⁺-deficient second and normal third chromosomes; (3) the normal second and *pr*⁺-bearing third chromosomes; (4) the normal second and normal third chromosomes. When the above females are crossed to *pr cn* homozygous males, the phenotypes of the progeny produced are wild type, *pr*, *cn*, and *pr cn* in equivalent frequency. It is quite reasonable to assume that *pr* progeny are lethals because of the deficiency in the *pr*⁺ region. In this case only one recombinant type, *cn*, is recovered and the frequency of recombination is 33%. The above assumption can fit well with the results of lines 9 (S) and 343 (S). Slightly lower recombination values in these two lines are easily explained if the *cn* progeny have decreased viability due to the duplication of the *pr*⁺ region. The results of line 202 are explained if *pr* progeny have almost normal viability.

The correlation coefficient between *SD* activity and the recombination values of the *pr-cn* region, omitting the sex-deviant lines and line 202 was -0.17 and insignificant. These results may indicate that the *SD* gene is located within the pericentric inversion and that crossing over between *pr* and *cn* occurs outside of this inversion.

Cytological Observation

The markers used for the recombination tests did not cover most of the left arm and the tip of the right arm of the second chromosome. In addition, little can be said from these tests as to what kind of chromosome rearrangements are involved. In order to obtain this information and to confirm the results of the recombination tests, the salivary gland chromosomes were observed cytologically. Twenty-two lines which showed reduced *SD* activity, and those which showed a reduction in recombination values, were mainly used for these observations. Lewis has reported (1962) that the centromeric rearrangement present in *SD-72* was a small pericentric inversion, with one breakage point in sections 39 or 40 of 2L and the other in section 42A of 2R. The lines which have only this rearrangement are described as being normal in type in this paper, because it was found in all the irradiated lines and in the original *SD bw* stock. Out of the 22 lines tested, lines 16 (S), 58, 150, 180, 202, 239, 256 (S), 297, 338, 366, and 405 (S) did not have any detectable chromosome rearrangement as far as microscopic observation is concerned. In lines 9 (S), 92 (S), 132 (S), 182, 186 (S), 236, 240, 258, 343 (S), 392, and 398 (S) at least one chromosome rearrangement was found. In all four lines (182, 236, 240, 258) which showed reduced recombination values, rearrangements were confirmed by cytological observations. Euchromatic breaks of Y-2 translocations were actually observed in only four lines out of 9 sex deviant lines.

The summary of the cytological observations in each of the lines are shown in column 11 of Table 2.

DISCUSSION

The results from the activity tests, following X-irradiation, clearly indicate that some kind of genetic change effecting *SD* activity was induced in the *SD*-bearing second and/or Y chromosome since lines 9 (S), 16 (S), 132 (S), 180, 186 (S), 202, 239, 256 (S), 297, 338, 343 (S), 366, 392, 398 (S), and 405 (S) still showed quite low activity in generation 8.

Other lines recovered their original high *SD* activity within a few generations. It is clear, therefore, that the *SD*-bearing second and/or Y chromosomes of these lines were not changed significantly with respect to *SD* activity. The reduced *SD* activity in these lines during early generation is, then, the result of genetic changes in the other chromosomes. In every generation, only *SD* heterozygous males, from the progeny of the previous matings, were selected for further crosses. Thus, irradiated X chromosomes are not included in the lines studied, and the third and fourth chromosomes must be considered the source of temporary effects disappearing after the early generations.

The location or number of modifiers cannot yet be evaluated. In order to locate these modifiers it will be necessary to replace the irradiated background chromosomes with marked normal chromosomes and then test the *SD* activity. Throughout the experiments the irradiated *SD-bw* chromosomes were transmitted through males only. Therefore, both the irradiated second chromosome and the irradiated Y chromosome

have been kept in the irradiated lines, and either (or both) might be responsible for instances of consistently low activity.

Sandler and Hiraizumi (1960) suggested on the basis of their results that all the *SD* genes including modifiers or stabilizers might be located in heterochromatic regions. If their suggestion is true, it is quite probable that the effects of the Y chromosome on *SD* activity are more important than would be expected from its size and general inactivity (Novitski and Ehrlich 1970). This might be related to its high heterochromatin content. The degree of importance of the Y chromosome to *SD* activity should be ascertained by replacing the irradiated Y chromosome of the low *SD* activity lines with a normal Y chromosome. There are data which suggest that the Y chromosome might be involved in the action of the *SD* gene; eight lines out of nine which have Y-2 translocations show significantly low *SD* activity. There is another possibility which might explain low *SD* activity in Y-2 translocated lines. In this assumption an *SD* modifier in the Y chromosome is not necessary. Rearrangement may cause competition in centric pairing and change the pairing situation in the *SD* region, thus influencing the action of the *SD* gene. This explanation may be applicable also to the effects of the third and fourth chromosome on *SD* activity.

The *SD* activity tests have revealed that X-irradiation reduces *SD* activity permanently in specific lines. The next problem is to discover what kind of genetic changes or chromosome rearrangements have occurred in the low *SD* activity lines. For this purpose two recombination tests, as well as cytological observation of the salivary gland chromosomes, were conducted. In the recombination tests the distal region of the left arm and the extreme tip of the right arm were not covered by markers. Cytological observations of the salivary gland chromosomes can detect any chromosome rearrangements except those in the region of the centromere (all the chromosomes adhere to each other in the centromeric regions and details of pairing cannot be seen). Thus, the entire analysis of chromosome rearrangements is restricted to the regions covered by the recombination tests and cytological observations.

Out of 40 lines tested, no major abnormality was found in 25, even though 5 lines (180, 239, 297, 338, 366) had reduced *SD* activities with a range in K value between 0.63 and 0.76. The other 20 lines (45, 58, 60, 75, 78, 115, 125, 127, 144, 146, 150, 175, 183, 257, 291, 296, 356, 379, 387, 407) had fairly high *SD* activities ($K > 0.9$). Fifteen lines were found to have some kind of chromosome rearrangements or genetic changes.

Out of 15 lines which have some kind of rearrangement, lines 92 (S), 182, 236, 240, and 258 showed fairly high *SD* activity, while the activity was lower in lines 9 (S), 16 (S), 132 (S), 186 (S), 202, 256 (S), 343 (S), 392, 398 (S), and 405 (S). Eight out of ten low activity lines are Y-2 translocated lines. Only one Y-2 translocated line had high *SD* activity. The two lines (202, 392) which have low *SD* activities and show normal sex ratios seem to have some rearrangements in the centromeric regions. It is worth noting that all 4 lines (182, 236, 240, 258) which do not have the Y-2 translocation, but have noncentromeric rearrangements, showed very high *SD* activity. Considering the resolving power of the tests conducted, it cannot be said that these four lines do not have any change in the centromeric regions. But the fact that all four lines showed high *SD* activity indicates that chromosome pairing of the regions covered by these

Fig. 3. The relation between *SD* activity and the position of rearrangements. Only the proximal breakpoint is shown. (?) indicates the possibility of point mutation elsewhere. The thick line around centromere indicates the position of pericentric inversion in which *SD* is located.

rearrangements is not essential for *SD* to function. The chromosome rearrangements of these four lines cover most of the second chromosome except the immediate centromeric region. Thus, it can be said that chromosome pairing in all regions of the second chromosome, except the *SD* region itself, is not necessary for the normal function of the *SD* gene. The positions of rearrangements and K values in the lines tested are shown in Fig. 3. Low *SD* activity was obtained not only from rearrangement-containing lines, but also from apparently normal lines. Very possibly these "normal" lines have some rearrangements in the centromeric region because the weakest point of the tests conducted is in this region. Thompson has demonstrated (1964), for example, that translocation breaks very near the centromere do not reduce crossing over as they do more distally.

These results suggests *in toto* that pairing of most of 2L and 2R is irrelevant to the action of *SD*. While *SD* does in fact seem to require pairing of its own immediate region for high activity, there seems to be little effect of distal breaks (or even of euchromatic breaks in general) on the pairing of the *SD* region.

The independence of *SD* pairing from euchromatic pairing may relate in part to the increasing likelihood that *SD* is *within* the small pericentric inversion of these lines and that the inversion acts as an independent pairing segment (Sandler, Hiraizumi and Sandler 1959).

SUMMARY

The *SD-bw* line, which was produced by recombination of *SD-72* with a *cn bw* stock, shows fairly high *SD* activity ($K > 0.9$). This line was irradiated with a high dose of X-rays and many chromosome rearrangements were produced. The *SD* activity was significantly reduced in many of the irradiated lines: in some cases, the original high activity was recovered in a few generations, while, in other cases, the reduction was permanent. The nature of the chromosome rearrangements was determined through recombination tests and cytological observation of the salivary gland chromosomes, and the results compared with the *SD* activity. The findings from these experiments are as follows:

1. Only chromosome pairing in the *SD* region corresponding to the small pericentric inversion of *SD* lines is essential for the normal function of the *SD* gene.
2. The Y chromosome may possess some function necessary for the *SD* gene to operate.
3. There may be modifiers of *SD* activity on the third chromosome and/or the fourth chromosome.

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