キイロショウジョウバエのSD効果の変更因子 (1)

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GENETIC ANALYSIS OF MODIFYING SYSTEM OF SEGREGATION DISTORTION IN *DROSOPHILA MELANOGASTER*

I. ACTIVE STAGE OF THE *SD-SUPPSESSOR* AND THE RECONFIRMATION OF THE DYSFUNCTIONAL SPERM MODEL

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Since *Segregation-Distorter* (Symbol *SD*) was first discovered in a natural population in Madison, Wisconsin, many properties of the *SD* system have been discovered (Sandler, Hiraizumi and Sandler 1959; Sandler and Hiraizumi 1959, 1960a, b; Hiraizumi, Sandler and Crow 1960; Sandler and Hiraizumi 1961a, b; Hiraizumi and Nakazima 1967). Some of the properties, which are relevant to the present study will be briefly given below;

(1) When a SD/SD^+ heterozygous male is mated to normal females, among progeny of this mating, *SD* is recovered in great excess over its theoretical frequency of 50%, often 90% or more.

(2) The *SD* system consists of three major elements, *SD*, *Ac*(*SD*) and *St*(*SD*). *SD* is the element causing segregation distortion, which is located on the second chromosome close to the centromere. *Ac*(*SD*), activator of *SD*, is closely linked to the right of *SD* and is necessary for *SD* to operate in coupling phase. *St*(*SD*), stabilizer of *SD*, is located at or near the tip of the right arm of the second chromosome; it stabilizes and strengthens the *SD* action in either coupling or repulsion phase with *SD*. *Original-SD* chromosomes which were collected from natural population always carried these three elements while *Recombinant-SD* chromosomes having lost *St*(*SD*) by recombination, consist of *SD* and *Ac*(*SD*).

(3) *Segregation-Distortion* occurs only in *SD* heterozygous males, never in females.

(4) The temperature sensitive period of *Segregation-Distortion* is during meiosis 1 (Mange 1968). This may indicate that *SD* first acts at this period (Hartl, Hiraizumi and Crow 1967).

(5) For the mechanism of segregation distortion, the two models have been suggested so far. One was the functional pole hypothesis which was proposed by Peacock and Erickson (1965), i. e., *D. melanogaster* regularly forms two functional and two nonfunctional sperms from each primary spermatocyte. The determination of these two classes of sperms occurs at miosis 1, where an inequality of two spindle poles, one functional and the other nonfunctional, is proposed. They then suggested that the *SD*-bearing second chromosome tended to move to the functional pole, resulting in the production of two functional *SD*-carrying sperms. Another model, the dysfunctional sperm hy-

pothesis, was proposed by Hartl, Hiraizumi and Crow (1967). They concluded that the mechanism of segregation distortion is independent of such a polarity and the final effect of *SD* is to produce dysfunctional SD^+ sperm.

(6) A suppressor system of *SD* was found in a natural population of Japan (Hiraizumi and Kataoka 1965). The main suppressor was located somewhere between *vermilion* and *forked* loci in the X chromosome (Kataoka 1967), and suppressed almost completely the action of *SD* in the *Recombinant-SD*.

In this study, first concerning the item (4), the temperature sensitive stage of *SD-suppressor* was examined to judge its operation time. On the other hand, the mechanism for segregation distortion was investigated by means of test for progeny count combined with the effect of *SD-suppressor*.

MATERIALS AND METHODS

cn bw: A standard laboratory stock (*cn*=cinnabar eye; 2R, *bw*=brown eye; 2R) which carries, as far as has been tested, none of the modifiers for the *SD* action.

Original-SD chromosome lines: *SD*-72 and SD^{NH}-2. These chromosome lines were collected from a natural population in Madison, Wisconsin and in Odate, Japan respectively, and carry *SD*, *Ac*(*SD*) and *St*(*SD*).

Recombinant-SD chromosome lines: *R*(*cn*)-14 and $R(SD^{NH})$-1. These chromosome lines were obtained as a recombinant from *SD*-72 and SD^{NH}-2 respectively, they then consist of *SD* and *Ac*(*SD*).

SD-suppressor: An X-chromosome line carrying a *SD-supperessor*. This X-chromosome was isolated from a natural population in Odate, Japan.

The *SD* and *SD-suppressor* chromosome lines have been kept by back crossing to the standard *cn bw*, or to the $\overline{XX}$/Y, *cn bw* females for more than twenty generations. Therefore, their genetic backgrounds are those of the standard *cn bw* stock. Throughout the present study, the room temperature was maintained at 25±1°C.

For the convenience of the readers, a list of the genotypes of the males used in the present study were shown as follows:

(1) *SD*/*cn bw* heterozygous males (abbreviated as *SD* heterozygous males hereafter) without *SD-suppressor*. These males had the standard X chromosome of *cn bw* stock.

Original-SD heterozygous males; X/Y; *SD*-72 or SD^{NH}-2/*cn bw*

Recombinant-SD heterozygous males, X/Y; *R*(*cn*)-14 or $R(SD^{NH})$-1/*cn bw*

(2) *SD* heterozygous males with *SD-suppressor*: X^{sup}/Y; *R*(*cn*)-14 or $R(SD^{NH})$-1/*cn bw* (X^{sup} is an abbreviation of the X chromosome beaing *SD-suppressor*).

Test for temperature sensitivity: *SD* heterozygous males with or without the suppressor were treated at 17°C for two days at various stages of development (Tables 1 and 2). Treated males which eclosed (within one day old) were mated individually to two vigrin *cn bw* females for three days in culture vials, then, the adult flies were discarded. All of the progeny which emerged from these vials were counted and the *k* values (the proportion of *SD* progeny to total progeny) were estimated.

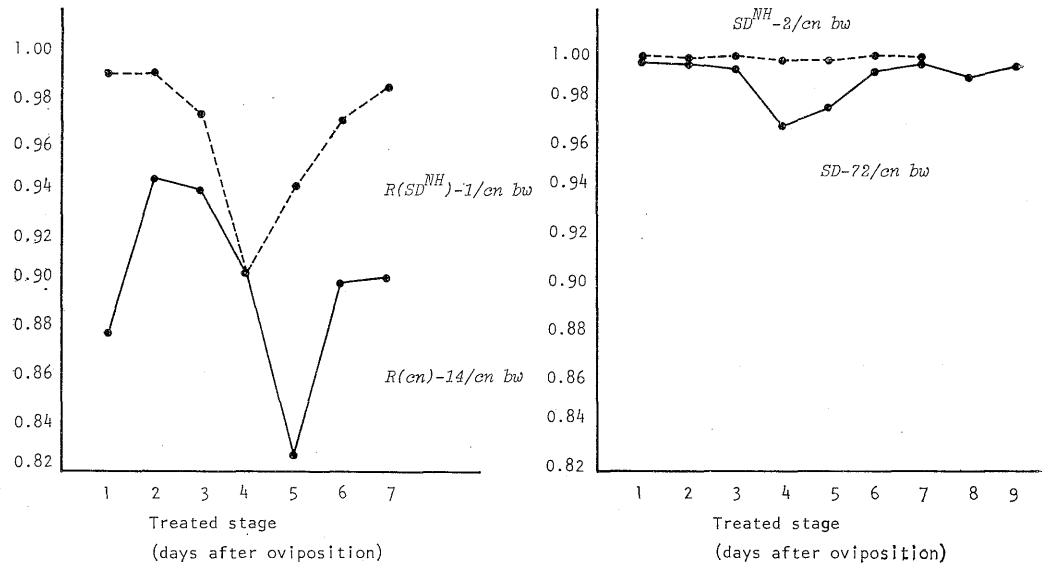
Test for progeny count: Standard *cn bw* homozygous males and the *SD* heterozygous males with or without the suppressor (within one day old) were mated individually

to two virgin *cn bw* females for two days (brood I), then, each of the males was aspirated when transferred to the fresh culture vials with two new *cn bw* virgin females for another two days (brood II). This procedure was repeated until all of the males became sterile. The inseminated females were transferred to fresh culture vials once every other day until none of the females were fecund.

RESULTS

The temperature sensitive stage of SD

The results of the experiment were summarized in Table 1 and in Figs. 1 and 2. The maximum reduction in k values was observed in *SD* heterozygous males treated



Figs. 1 and 2. The k values for *SD* males treated at various developmental stages at 17°C for 48 hours. Untreated k values of *R(cn)-14*, *R(SD^{NH})-1*, *SD-72* and *SD^{NH}-2* were 0.940, 0.984, 0.995 and 1.000 respectively.

at the fourth or fifth day after oviposition, even though the degree of decrease was heterogeneous among *SD* lines. With respect to *Recombinant-SD* lines, the reduction in k was observed at the fifth day in the *R(cn)*-14, and at the fourth day in the *R(SD^{NH})*-1. For *Original-SD*, it was observed at the fourth day in the *SD*-72, but practically no reduction was observed in the *SD^{NH}*-2 line.

The differences in k values between untreated males and the minimum values of treated males were 0.113, 0.080 and 0.026 in the *R(cn)*-14, *R(SD^{NH})*-1 and the *SD*-72 respectively. The *SD^{NH}*-2 might not be affected by temperature treatment. It was a general tendency that the *Original-SD* lines were rather stable to the treatment than the *Recombinant-SD*.

The light microscopic observation of testes at the fourth or fifth day after ovi-

position showed that the most advanced stage was at early spermatocyte.

For the *R(cn)*-14, the *k* value at the first day was rather low.

The temperature sensitive stage of SD-suppressor

These experiments were repeated twice (exp. A and exp. B in Table 2 and Fig. 3).

Table. 1. The *k* values for *SD* males treated at verious developmental stages at 17°C for 48 hours period

Treated stages (Day after oviposition)	X/Y; *R(cn)-14/cn bw*			X/Y; *R(SD^{NH})-1/cn bw*			X/Y; *SD-72/cn bw*			X/Y; *SD^{NH}-2/cn bw*		
	k	No. of males treated	No. of progeny	*k*	No. of males treated	No. of progeny	*k*	No. of males treated	No. of progeny	*k*	No. of males treated	No. of progeny
1	0.880	14	1130	0.992	17	1630	0.997	10	611	1.000	16	949
2	0.947	17	1610	0.992	18	1368	0.996	36	3841	0.999	30	2631
3	0.942	8	732	0.975	17	1619	0.994	33	3727	1.000	31	3239
4	0.904	11	939	0.904	15	1398	0.969	37	3922	0.998	37	3661
5	0.827	10	817	0.943	13	1366	0.977	37	4437	0.998	31	4380
6	0.901	15	1347	0.972	12	1162	0.993	20	1852	1.000	10	614
7	0.904	12	1138	0.986	13	1114	0.996	18	1383	0.999	16	1374
8	—	—	—	—	—	—	0.990	33	3349	—	—	—
9	—	—	—	—	—	—	0.995	30	2793	—	—	—
Untreated	0.940	69	6569	0.984	55	5459	0.995	44	4273	1.000	48	5287

Table 2. The *k* values for *SD* males bearing *SD-suppressor* treated at various stages at 17°C

Experiment	Treated stages (Days after oviposition)	X^{sup}/Y; *R(cn)-14/cn bw*			X^{sup}/Y; *R(SD^{NH})-1/cn bw*		
		k	No. of males treated	No. of progeny	*k*	No. of males treated	No. of progeny
A	1 (48 hrs*)	0.486	7	970	0.525	18	2797
	2 (96 hrs)	0.501	18	2115	0.506	10	1289
	3 (72 hrs)	0.538	18	1983	0.530	19	2237
	4 —	—	—	—	—	—	—
	5 (72 hrs)	0.515	16	3137	0.498	16	2493
	6 —	—	—	—	—	—	—
	7 (72 hrs)	0.562	14	2020	0.713	13	2061
B	1 (48 hrs)	0.513	28	2488	0.530	26	2817
	2 (48 hrs)	0.531	28	3212	0.529	22	2390
	3 (48 hrs)	0.544	24	2330	0.529	18	2055
	4 (48 hrs)	0.535	50	4897	0.496	17	2001
	5 (48 hrs)	0.520	18	2295	0.502	21	2476
	6 (48 hrs)	0.523	26	3232	0.528	12	1615
	7 (48 hrs)	0.536	47	5271	0.635	25	2403
	8 (48 hrs)	0.541	56	6760	0.542	25	2891
	9 (48 hrs)	0.530	33	5624	0.552	26	2325
	Untreated	0.501	36	6386	0.500	40	6796

*: the length of treatment

The effect of temperature was somewhat different between the *R(cn)*-14 and the *R(SD^{NH})*-1 lines. In *R(SD^{NH})*-1, it was observed that the temperature sensitive stage of the suppressor was at the seventh day. In *R(cn)*-14, however, the sensitive stage was obscure.

The light microscopic observation of testes at the seventh day showed that the most advanced stage was at early spermatid.

Total number of progeny of normal and Recombinant-SD heterozygous males with or without the suppressor

The results were summarized in Table 3. As is clearly seen in the table for the *Recombinant-SD* males without *SD-suppressor*, the length of fertile period was about one half of, and the total number of progeny was less than one half of the other genotype males, *cn bw* and *Recombinant-SD* with the suppressor.

In the *SD* heterozygous males which carried the suppressor, the length of fertile period and the total number of progeny were almost the same as those of the *cn bw*

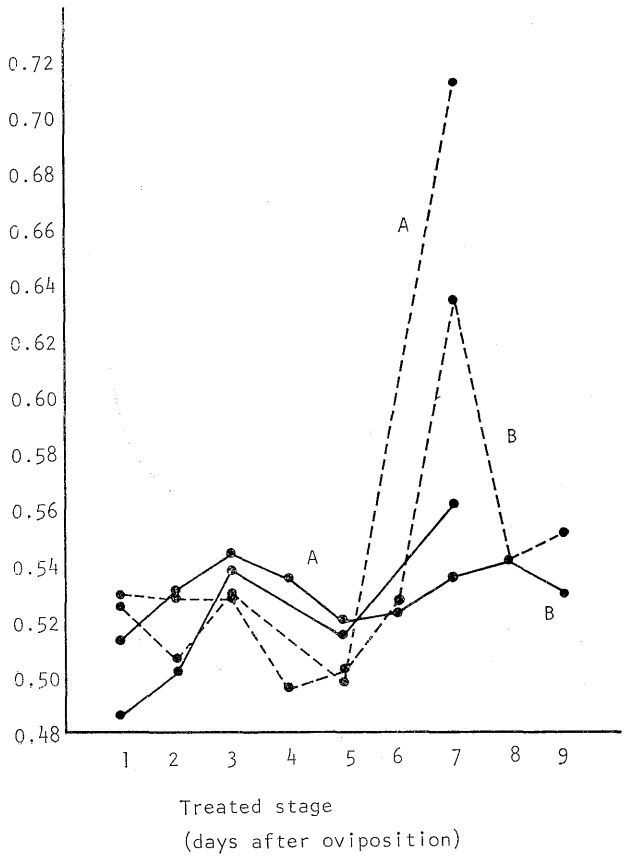


Fig. 3. The *k* values for *Recombinant-SD* males treated at various developmental stages at 17°C. A and B are duplications. Untreated *k* values of *X^{sup}/Y; R(cn)-14/cn bw* and *X^{sup}/Y; R(SD^{NH})-1/cn bw* were 0.501 and 0.500 respectively.

●———● X^{sup}/Y; *R(cn)-14/cn bw*

●-------● X^{sup}/Y; *R(SD^{NH})-1/cn bw*

Table 3. Total progeny production for *Recombinant-SD* and *cn bw* males with or without *SD-suppressor* (average number of progeny per male) and mean *k* values

	with *SD-suppressor*						without *SD-suppressor*			
Brood	*R(SD^{NH})-1*	Number of fertile ♂	*R(cn)-14*	Number of fertile ♂	*cn bw*	Number of fertile ♂	*R(SD^{NH})-1*	Number of fertile ♂	*cn bw*	Number of fertile ♂
I	452.1	10	396.3	9	394.6	8	301.4	7	340.0	10
II	318.7	10	362.3	9	557.8	8	210.2	7	261.8	10
III	374.1	10	464.3	9	512.1	8	287.7	7	386.7	10
IV	294.5	8	328.5	9	211.2	8	271.4	7	317.2	10
V	217.9	8	224.8	8	418.8	8	132.2	5	286.4	10
VI	396.7	8	424.7	8	261.3	8	189.8	4	380.6	10
VII	326.6	8	298.0	8	350.9	8	32.0	2	338.0	8
VIII	382.3	7	275.6	8	324.5	8	—	—	293.9	8
IX	331.2	7	331.2	8	196.6	6	—	—	309.4	7
X	191.1	6	226.8	8	141.0	3	—	—	246.3	7
XI	121.3	5	199.8	5	110.0	2	—	—	200.7	5
XII	151.5	4	167.3	3	409.0	1	—	—	117.2	5
XIII	—	—	36.0	2	74.0	1	—	—	82.0	4
XIV	—	—	148.5	2	—	—	—	—	75.0	2
XV	—	—	183.0	1	—	—	—	—	133.0	1
Total	3558.0		4067.1		3961.8		1424.7		3768.2	
k	0.516		0.496				0.985			

males, and the mean *k* value was reduced from 0.9 to about 0.5. For *cn bw* males, there was no difference between the males with and without the suppressor in both the length of fertile period and the total number of progeny.

DISCUSSION

The test for temperature effects of *SD-suppressor* clearly showed that the sensitive stage for the suppressor was different from that for *SD*.

The remarkable reduction in *k* value of *SD* heterozygous males, without the suppressor, was observed at the fourth or fifth day after oviposition. This result indicated that the most sensitive stage was around early meiosis, and this was in agreement with Mange (1968).

The considerable decrease in *k* values was observed in *Recombinant-SD* males, while *k* values were rather stable in *Original-SD* which consists of *SD*, *Ac(SD)* and *St(SD)* (Table 1, Figs. 1 and 2). The last element was lost in *Recombinant-SD*. *St(SD)* makes *SD* action strong and stabilizes the *k* values. In this case, *St(SD)* makes the *SD* action less sensitive to the temperature treatment.

Two *Recombinant-SD* lines with the suppressor responded to temperature treatment differently (Table 2, Fig. 3). This divergence might be caused by the origin of these *SD* lines.

In both of the two *Recombinant-SD* lines with the suppressor, almost all k values of the treated males were higher than those of the untreated ones except the first day in the *R(cn)*-14 and the fourth and fifth day in the $R(SD^{NH})$-1. Some physiological changes may occur by the temperature treatment through the spermatogenesis. The reduction in k values at the fourth and fifth day in both of the *Recombinant-SD* with the suppressor may be due to the effect of *SD* to temperature treatment.

The results of the progeny count showed that the number of progeny of *SD* heterozygous males was doubled by having the suppressor. Therefore the suppressor may operate in changing the polarity, if the mechanism for *Segregation-Distortion* can be interpreted by the polarity suggested by Peacock and Erickson (1965). And if the suppressor has such a function, the number of progeny of the normal (*cn bw*) males may be doubled by bearing the suppressor. However, the normal males produced almost equal number of progeny irrespective of the presence or absence of the suppressor. This result indicated that the suppressor did not function in changing the polarity and rather prevented the operation of *SD* element itself (or its production), or helped repair the "damaged" SD^+. These results seem to be in favour of the dysfunctional sperm model. Since many motile sperms could be found in the testes of both normal and *SD* males after the males became infertile, the method used in progeny counts casts some doubts on whether the total number of progeny really reflected the total number of sperm produced in the males.

SUMMARY

The study of the temperature treatment revealed that the sensitive stage of *SD* was at early meiosis 1. This was in agreement with Mange (1968). While the sensitive stage of *SD-suppressor* was at early spermatid. And also it was found that *St(SD)* made the *SD* action less sensitive to the temperature treatment.

On the results of the progeny counts, the mechanism for *Segregation-Distortion* was examined. It was concluded that the "dysfunctional sperm" hypothesis was reasonable.

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