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

II. TWO MODIFIERS FOR *SD* SYSTEM ON THE SECOND CHROMOSOME OF *D. MELANOGASTER*

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Segregation distorter (*SD*) was first found by Hiraizumi in a natural population of *D. melanogaster* in Madison Wisconsin (Sandler *et al.* 1959); it has subsequently been found in some natural populations (Mange 1961; Greenberg 1962; Hiraizumi *et al.* 1965; Watanabe 1967; Nicoletti *et al.* 1967). *SD* is a locus on the second chromosome close to centromere. *SD/SD*⁺ heterozygous males transmit *SD* to the next generation in a great excess over its theoretical frequency of 50%. Segregation distortion occurs in *SD* heterozygous males, but neither in *SD* homozygous males nor in females. The *SD* system consists of following three major elements (Sandler *et al.* 1959, 1960a, 1960b): (1) *SD* is the element causing segregation distortion; (2) an activator of *SD*, *Ac(SD)*, is the element which closely linked to the right of *SD*. It, in coupling with *SD*, is necessary for *SD* action; (3) a stabilizer of *SD*, *St(SD)*, is the element which is located at, or near the tip of the right arm of the second chromosome. In the presence of *St(SD)*, either in coupling or in repulsion phase, *SD* action is stabilized and enhanced; in the absence of it, distorting effect of *SD* becomes somewhat variable resulting in a relatively weak distortion.

There is a modifier of *SD* which was found in a natural population, Odate, Japan (Hiraizumi *et al.* 1965). The factor is located on the X chromosome and named as *SD-suppressor* according to the function of suppressing *SD* action (Kataoka 1967). *SD-suppressor* can suppress *SD* action almost completely in the heterozygous males for the *Recombinant-SD* chromosome which consists of *SD*, *Ac(SD)* and has lost *St(SD)* by recombination. On the other hand, the effect of *SD-suppressor* was incomplete for the *Original-SD* heterozygous males which have all of *SD* elements, *SD*, *Ac(SD)* and *St(SD)*. The facts suggest that *St(SD)* has enhanced the action of *SD* against *SD-suppressor*. In addition to *SD-suppressor*, two other modifiers which were located on the second chromosome were involved in Odate population (Kataoka 1967). One was a dominant suppressor of *SD*, another was an enhancer of *SD*. As the effects of these two modifiers were similar to *Ac(SD)* in repulsion phase with *SD* and *St(SD)* respectively (Hiraizumi *et al.* 1967), they were symbolized as *Ac(SD)-like* and *St(SD)-like* (Kataoka 1967). The present study was purposed to clarify whether the two modifiers were *Ac(SD)* and *St(SD)*, or not.

MATERIALS AND METHODS

Standard stocks:

- (1) *cn bw* and *cn vg bw* (*cn*=cinnabar eye: 2R-57.5, *vg*=vestigial wing: R-67.0, *bw*=brown eye: 2R-104.5) These stocks have none of modifiers for *SD* system.
- (2) *y f*:(XX)/Y; *Cy bw/cn bw* (*y f*:= =reversed acrocentric compound X chromosome marked by yellow and forked; *Cy*=inversion 2LR marked by curly wing. *Cy* chromosome was used as a crossing over suppressor). This stock has no modifier for *SD* except *Cy bw* chromosome. *Cy bw* chromosome is entirely insensitive for *SD* action (Sandler *et al.* 1959).

SD stocks:

Recombinant-SD chromosome lines (1) $R(SD^{NH})^{bw}$ and (2) $R(cn)-14$. These second chromosomes (abbreviated to RSD_1 and RSD_2 hereafter) consist of *SD* and $Ac(SD)$. The former was derived from *Original-SD* chromosome collected in Odate and the latter from that in Madison. They are marked by *bw* and *cn* respectively. Their genetic backgrounds were replaced by that of *cn bw*.

Odate stocks:

These stocks consist of many isofemale lines collected at different times in 1963 and 1964 in Odate population. The total 21 lines were used in the present study. Several wild second chromosomes were sampled from each line. For example, q-1-1 and q-1-2 were two chromosomes sampled from q-1 line. These second chromosomes have been kept by backcrossing to the standard *cn bw* females more than ten generations. Therefore their genetic backgrounds are that of *cn bw*.

SD-suppressor stock:

This stock has a special X chromosome on which *SD-suppressor* is located between *v* (vermillion eye: I-33.0) and *f* (forked: I-56.7) and the genetic background of *cn bw*.

Age of flies used was 2 to 5 days. In almost all matings, a single male was mated with 2 to 3 virgin females for 2 days, after that all adults were discarded. The *k* values (the transmission rate of *SD* from heterozygous male carriers) were calculated on a progeny size of at least 20.

RESULTS

Sampling Ac(SD)-like bearing chromosomes

Several $+/cn bw$ males from each Odate stock line were mated individually with two or three $\overline{XX}/Y$; *Cy bw/cn bw* females to sample the *Ac(SD)-like* bearing chromosomes (Fig. 1a). Several phenotypically *Cy* daughters were mated with a $RSD_1/cn bw$ male. Then $+/RSD_1$ sons were mated individually with two *cn bw* females, and *k* values were checked by counting their progenies (k_1). If a wild second chromosome tested carried *Ac(SD)-like*, *SD* action must be suppressed, *i.e.*, *k* value of the male will be nearly about 0.50. As a *k* value of the borderline between distortion and non-distortion, 0.75 was adopted (Kataoka 1967). On this criterion, all second chromosomes

Fig. 1. Mating scheme for sampling modifier bearing second chromosomes.

*: The genetic background of this male was replaced by that of *cn bw*.

+ : This wild second chromosome was sampled from Odate stock.

X^{sup} : The X chromosome which bore *SD-suppressor*.

which showed *k* values lower than 0.75 were regarded as *Ac(SD)*-like bearing chromosomes. As seen in *k*₁ values in Table 1, *Ac(SD)*-like bearing chromosomes were as follows: f-8-2, m-7-1, m-7-2, n-1-2, n-2-1, n-2-3, n-2-8, A-10-1 and B-7-1.

Sampling *St(SD)*-like bearing chromosomes

To sample the *St(SD)*-like bearing chromosomes, several *+/cn bw* males from each Odate wild line were mated individually with two or three $\overline{XX}/Y; Cy\ bw/cn\ bw$ females (Fig. 1b). Several *Cy* daughters from these matings were mated a $RSD_1/cn\ bw$ male which carried *SD-suppressor* on the X chromosome. Non *Cy* sons which bore *SD-suppressor* were mated with two *cn bw* females, then *k* values were checked (*k*₂). If this male carried *St(SD)*-like, its *SD* action must not be suppressed by *SD-suppressor* (i.e., the *k* value must be higher than 0.75), because of enhancing effect of *St(SD)*-like. As seen in *k*₂ values in Table 1, the chromosomes which were recognized to carry *St(SD)*-like were as follows: e-5-1, e-5-5, k-7-1, k-7-4, n-8-2, q-1-4, q-1-5, q-1-6 and q-3-3.

Each one of all second chromosomes tested was passed through females in heterozygous condition with *cn bw* chromosomes. Then associated inversions were examined for the chromosomes which produced no recombinant. There was no inversion except *In(2R)NS* (Table 1). As shown in Table 2, this inversion was associated significantly with *St(SD)*-like (*P*=0.024), but not with *Ac(SD)*-like (*P*=0.258).

Variation in modifying effects of *Ac(SD)*-like and *St(SD)*-like

For the wild chromosomes tested, it was revealed that one second chromosome possessed only one modifier, either *Ac(SD)*-like or *St(SD)*-like, but not both. In Tables

Table 1. The effects of suppression and enhancement for *SD* action by the second chromosomes of *cn bw* (standard chromosome) and 21 lines from Odate wild stock

2nd chromosome	Associated inversion	k_1	k_2
<i>cn bw</i>	—	0.995	0.508
d-7-1	<i>In</i> (2R) NS	0.940	0.485
● e-5-1	<i>In</i> (2R) NS	0.950	<i>0.878</i>
● e-5-5	<i>In</i> (2R) NS	0.968	<i>0.822</i>
f-6-2	—	0.999	0.570
○ f-8-2	—	<i>0.726</i>	0.500
g-2-2	—	0.900	0.448
j-8-1	—	0.900	0.448
● k-7-1	<i>In</i> (2R) NS	1.000	<i>1.000</i>
● k-7-4	<i>In</i> (2R) NS	1.000	<i>0.932</i>
m-2-1	—	0.931	0.491
m-2-2	—	0.917	0.498
○ m-7-1	—	<i>0.696</i>	0.531
○ m-7-2	—	<i>0.711</i>	0.464
m-7-4	—	0.839	0.538
○ n-1-2	<i>In</i> (2R) NS	<i>0.561</i>	0.499
○ n-2-1	—	<i>0.654</i>	0.500
○ n-2-3	—	<i>0.664</i>	0.513
○ n-2-8	—	<i>0.721</i>	0.516
● n-8-2	<i>In</i> (2R) NS	1.000	<i>0.843</i>
● q-1-4	—	1.000	<i>0.751</i>
● q-1-5	—	1.000	<i>0.889</i>
● q-1-6	—	0.999	<i>1.000</i>
● q-3-3	<i>In</i> (2R) NS	0.959	<i>0.920</i>
q-5-1	—	0.900	0.409
q-6-3	—	0.995	0.364
q-7-1	—	0.900	0.450
q-8-1	—	1.000	0.585
r-2-4	<i>In</i> (2R) NS	1.000	0.517
○ A-10-1	—	<i>0.492</i>	0.501
○ B-7-1	—	<i>0.676</i>	0.516

cn bw: This chromosome has none of modifiers for *SD* system.

k_1 and k_2 values represent suppressor and enhancer effects for *SD* action respectively.

*RSD*₁ was used as homologous of *cn bw* and the wild second chromosomes.

○ and ●: 2nd chromosomes which were recognized as *Ac(SD)-like* ($k_1 < 0.750$) and *St(SD)-like* ($k_2 > 0.750$) bearing chromosomes. Their k values were shown in italics.

Table 2. Association of *Ac(SD)-like* and *St(SD)-like* with *In(2R)NS* (exact probability in 2×2 table)

	NS	NS-free	Total	
<i>Ac(SD)-like</i>	1 (line)	5	6	P=0.258
<i>Ac(SD)-like-free</i>	6	9	15	
Total	7	14	21	
<i>St(SD)-like</i>	4	1	5	P=0.024
<i>St(SD)-like-free</i>	3	13	16	
Total	7	14	21	

3 and 4, the distributions of k values for suppression or enhancement of *SD* were shown for two groups of the second chromosome, *Ac(SD)-like* carriers and *St(SD)-like* carriers. Two lines (5 chromosomes) belonged to the former group and 4 lines (7 chromosomes) to the latter. As shown in Table 3, the effects of suppression by *Ac(SD)-like* were not so stable, which varied k values from 0.35 to 0.94. For both m-7-2 and n-2-8 chromosomes, the mean k values of $RSD_1/m-7-2$ and $RSD_2/m-7-2$, and of $RSD_1/n-2-8$ and $RSD_2/n-2-8$ were significantly different ($P \ll 0.01$).

Similar tendencies were observed in the case of the enhancement of *St(SD)-like* (Table 4) even the difference of $RSD_1/q-1-5$ and $RSD_2/q-1-5$ was not statistically significant ($0.05 < P < 0.10$). The distributions of k values of *St(SD)-like* bearing chromosomes were rather variable except $k-7$ line.

Mapping of *Ac(SD)-like*

For mapping of *Ac(SD)-like*, m-7-1 and m-7-2 chromosomes were used. The mating scheme was shown in Figure 2. Several $+|cn\ bw$ or $+|cn\ vg\ bw$ females were mated individually with a $RSD_1/cn\ bw$ or $RSD_2/cn\ bw$ male --- (P). Phenotypically $+$ sons (genotypically $RSD_1/+$, $RSD_2/+$, RSD_1/cn , $RSD_1/cn\ vg$, $RSD_2/vg\ bw$ or RSD_2/bw males) were collected and mated individually with two or three $cn\ bw$ or $cn\ vg\ bw$ females --- (F_1), then the k values and the genotypes of the male parents in F_1 generation ($+$ sons) were simultaneously checked by counting their progenies, *i.e.*, the location of *Ac(SD)-like* was estimated --- (F_2). If *Ac(SD)-like* is located near *cn* locus, RSD_1/cn or $RSD_1/cn\ vg$ male has to produce only or almost only RSD_1 progenies. And if it is located near *bw* locus, RSD_2/bw or $RSD_2/vg\ bw$ male has to produce almost only RSD_2 progenies. In the case in which *Ac(SD)-like* is located in an intermediate region between *vg* and *bw* loci, k values of $RSD_1/cn\ vg$ or $RSD_2/vg\ bw$ males may suggest the location of *Ac(SD)-like*. The results shown in Table 5, that is, RSD_1/cn or $RSD_1/cn\ vg$ males gave the k values very close to 1, while the k values of $RSD_2/vg\ bw$ or RSD_2/bw males were about 0.50, indicate that *Ac(SD)-like* was located between *cn* and *vg*, presumably close to *cn* locus. And it was also shown that the mean k value was dependent on the kind of *Recombinant-SD* chromosome used. For both m-7-1 and m-7-2, the mean k values of $RSD_1/+$ and $RSD_2/+$ males were significantly different ($P \ll 0.01$).

Table 3. Distributions of k values for SD suppression by X/Y ; $RSD/Ac(SD)$ -like and $St(SD)$ -like males

k	Male genotypes															
	$Ac(SD)$ -like bearing male								$St(SD)$ -like bearing male							
	RSD_1	RSD_1	RSD_2	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1
	m-7-1	m-7-2	m-7-2	m-7-2	n-2-1	n-2-3	n-2-8	n-2-8	RSD_1	RSD_2	RSD_1	e-5-1	e-5-5	k-7-1	k-7-4	q-1-4
																q-1-5
																q-3-3
1.00-0.95												3	6	2	4	12
0.94-0.90		1					1					4	3			3
0.89-0.85	1	1					2					1	1			
0.84-0.80		2		1			3									2
0.79-0.75		4					3									
0.74-0.70		6			1	3	2									
0.69-0.65	1	5			1	2	1	2								
0.64-0.60	1	4					2	1								
0.59-0.55	1	1	2		2		2	4								
0.54-0.50		1	1	1	1	1	1	1								
0.49-0.45			2													
0.44-0.40			2													
0.39-0.35			2													
Total no. of ♂ tested	4	25	9	6	6	6	18	9				8	10	2	4	17
Mean k	0.696	0.711	0.469	0.654	0.654	0.664	0.721	0.567	0.950	0.968	1.000	1.000	1.000	1.000	1.000	0.959

Table 4. Distributions of k values for SD enhancement by X^{sup}/Y ; $RSD/St(SD)$ -like and X^{sup}/Y ; $RSD/Ac(SD)$ -like males

k	Male genotypes															
	$St(SD)$ -like bearing male								$Ac(SD)$ -like bearing male							
	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_2	RSD_1	RSD_1	RSD_1	RSD_1	RSD_1	RSD_2
	e-5-1	e-5-5	k-7-1	k-7-4	q-1-4	q-1-5	q-1-5	q-1-5	q-3-3	m-7-2	m-7-2	n-2-3	n-2-8	n-2-8	n-2-8	n-2-8
1.00-0.95	5	3	31	1	14				10							
0.94-0.90	2	2	1		2	13			6							
0.89-0.85	1	3		1	3	6		1	2							
0.84-0.80					2	4		1	2							
0.79-0.75		2			4	5		3	2							
0.74-0.70	3	4			5			2	3							
0.69-0.65	1				2	3										
0.64-0.60	1				3	1			1				1			
0.59-0.55		1				1				1	1	1	2	1		
0.54-0.50		1			1					3	4	1		2		
0.49-0.45	1					1				1	3	1		2		
0.44-0.40										2	2		1			
Total no. of ♂ tested	14	16	32	2	22	49		7	26	6	10	3	4	5		
Mean k	0.878	0.822	1.000	0.932	0.751	0.889		0.785	0.920	0.464	0.488	0.513	0.516	0.517

Fig. 2. Mating scheme for mapping *Ac(SD)*-like.

+ : *Ac(SD)*-like bearing chromosome, in this expeliment m-7-1 and m-7-2 were used.

X^{sup}: The X chromosome which beared *SD-suppressor*.

Table 5. Distributions of *k* values for mapping *Ac(SD)*-like modifier

<i>k</i>	Male genotypes									
	RSD ₁	RSD ₂	RSD ₁	RSD ₁	RSD ₂	RSD ₂	RSD ₁	RSD ₂	RSD ₁	RSD ₂
	+*	+*	cn	cn vg	vg bw	bw	+**	+**	cn	bw
1.00-0.95	1		1 (10) ***	1					(6) ***	
0.94-0.90	2									
0.89-0.85	1									
0.84-0.80	3									
0.79-0.75	3						1			
0.74-0.70	6	2				1				
0.69-0.65	3	1				1	1			1
0.64-0.60	4	4						1		1
0.59-0.55	1	7				2	1			1
0.54-0.50	2	8			1	1		1		1
0.49-0.45	1	4				4	1	1		
0.44-0.40		1			1	1		1		
Total no. of ♂ tested	27	27	1 (10)	1	2	10	4	4	(6)	4
Mean <i>k</i>	0.712	0.568	0.991	0.986	0.482	0.536	0.623	0.510		0.586

* + : m-7-1
** + : m-7-2
*** Since these males transmitted only RSD₁ chromosomes to the next generation, it was not detected whether the genotypes were RSD₁/+ or RSD₁/cn. However it is very reasonable that almost all are classified as RSD₁/cn, because all these males showed *k*=1.000(RSD₁/+ males are non-distorted type).

Fecundity of RSD₂/*Ac(SD)*-like male

Hartl (1969) reported that the fecundity of *SD Ac(SD)/Ac(SD)* males was only 59.3% as much as that of *SD⁺ Ac(SD)⁺/Ac(SD)*. Then he hypothesized that “if *SD* were the element primarily responsible for producing whatever it is that predisposes a spermatocyte to give rise to dysfunctional sperms, and if *Ac(SD)* were the element which was responsible for determining which specific chromosome in a male would be rendered

Table 6. Fecundity and segregation ratio of three genotypes of males

Male genotypes (a/b)	Number of males tested	Segregation ratio (b/a + b)	Total number of progenies/male
<i>cn bw/RSD₂</i>	10	0.804	261.7 ± 29.0
<i>Ac(SD)-like*/RSD₂</i>	9	0.512	243.1 ± 38.5
<i>Ac(SD)-like*/Cy bw</i>	8	0.505	418.6 ± 16.1

* *Ac(SD)-like*; m-7-2

Ages of males and females tested were 6 to 9 days and 5 days old respectively (sexually matured well enough). Each male was mated with one *cn bw* female only once, then male was discarded. Each inseminated female was transferred to a fresh culture once everyday until the female produced no more progenies.

dysfunctional by the action of *SD*, then with two *Ac(SD)*'s of equal "strength" in a genotype, the segregation ratio would be expected to be normal, whereas the fecundity ration would still be reduced in accordance with the mutual dysfunctional model". If *Ac(SD)-like* were *Ac(SD)*, the same results would be expected irrespective as to whether his assumption is correct or not. As fecundity was easily influenced by rearing conditions, the three types of males which used as materials of this experiment were sibs from the identical parents: that is, *RSD₂/cn bw*, *RSD₂/Ac(SD)-like* and *Cy bw/Ac(SD)-like* sons were collected from the mating of *Cy bw/RSD₂* females and *Ac(SD)-like/cn bw* males and mated individually with one *cn bw* female. Results were shown in Table 6. The fecundity of *RSD₂/Ac(SD)-like* was only 58.1% as large as that of *Cy bw/Ac(SD)-like*. The ratio was almost the same as that of *RSD₂/cn bw* (62.5%). This result supported that *Ac(SD)-like* would be *Ac(SD)*.

Mapping of *St(SD)-like*

Mapping of *St(SD)-like* was done by the mating scheme of Figure 3 using the q-1 line which had no inversion. Several *+|cn bw* females were mated individually with a *cn bw* male --- (P). The sons (*+|cn bw*, *cn/cn bw* or *bw/cn bw*) mated individually with three $\overline{XX}/Y$; *Cy bw/cn bw* females --- (F₁). Each of *+|Cy bw*, *cn/Cy bw* and *bw/*

Fig. 3. Mating schem for mapping *St(SD)-like*.

$+$: *St(SD)-like* bearing chromosome, in this experiment *q-1-4* and *q-1-5* were used.
 X^{sup} : The X chromosome which beared *SD-suppressor*.

Table 7. Distributions of *k* values for mapping *St(SD)-like* modifier

<i>k</i>	Male genotypes						
	<i>RSD</i> ₁	<i>RSD</i> ₁	<i>RSD</i> ₂	<i>RSD</i> ₁	<i>RSD</i> ₁	<i>RSD</i> ₁	<i>RSD</i> ₂
	<i>+</i> *	<i>cn</i>	<i>bw</i>	<i>+</i> **	<i>+</i> **	<i>cn</i>	<i>bw</i>
1.00-0.95	2	2		1			
0.94-0.90				6			
0.89-0.85	2			4	1	1	
0.84-0.80	6	3		2	1	2	
0.79-0.75	5				2		1
0.74-0.70	2	1	1		1	4	1
0.69-0.65	2		2		4	6	2
0.64-0.60	7	2	3	1	1	6	
0.59-0.55	8	4	9	1	1	9	5
0.54-0.50		6	6	1		11	
0.49-0.45		3	8			5	
0.44-0.40			2			4	
0.39-0.35		2	2				
0.34-0.30		1	2				
Total no. of ♂ tested	34	24	35	16	11	48	9
Mean <i>k</i>	0.702	0.592	0.517	0.854	0.720	0.603	0.624

* *+*: q-1-4 ** *+*: q-1-5

Table 8. Distributions of *k* values for X^{sup}/Y; resynthesized-*+*/*RSD*₁ (a), X^{sup}/Y; *cn*/*RSD*₁ (b) and X^{sup}/Y; *bw*/*RSD*₁ (c) males

<i>k</i>	(a)	(b)	(c)
1.00-0.95	3		
0.94-0.90	5		
0.89-0.85			
0.84-0.80		3	
0.79-0.75	1		1
0.74-0.70		1	1
0.69-0.65		3	1
0.64-0.60		3	
0.59-0.55	1		1
0.54-0.50		1	
0.49-0.45		1	
Total no. of ♂ tested	10	12	4
Mean <i>k</i>	0.899	0.676	0.676

Cy bw daughters mated with a *RSD*₁/*cn bw* or *RSD*₂/*cn bw* male which beared *SD-suppressor* --- (F₂). *RSD*₁/*+*, *RSD*₂/*+*, *RSD*₁/*cn* and *RSD*₂/*bw* with *SD-suppressor* sons mated individually with two *cn bw* females --- (F₃), then *k* values were checked in the

F_4 generation --- (F_4). If *St(SD)-like* is located near *cn* locus, RSD_2/bw sons must show high k values. If it is located near *bw* locus, RSD_1/cn sons must show high k values, and if it is located somewhere in the central region of the right arm, these two types of sons must show high or low k values which depend on their gonotypes. The results shown in Table 7 were rather unexpected. In the case of q-1-5 chromosome, each mean k value of RSD_1/cn (0.603) and RSD_2/bw (0.624) was significantly lower than those of $RSD_1/+$ (0.854) and $RSD_2/+$ (0.720) males respectively ($P \ll 0.01$, $P < 0.03$). For q-1-4, the same tendency was obtained. From these facts it was suggested that *St(SD)-like* would not be single locus but more than two. To clarify this point, $+$ chromosomes were resynthesized by mating the flies carrying two types of recombinant chromosomes of q-1-5 chromosome, *i.e.*, *cn/cn bw* and *bw/cn bw*, then the effect of *SD* enhancement of these resynthesized $+$ was checked. The results were shown in Table 8. The mean k value of resynthesized $+$ (0.899) was significantly higher than those of both recombinants *cn* (0.676) and *bw* (0.676) ($P \ll 0.01$).

DISCUSSION

For the study of *SD* modifiers in a natural population, Odate, the author (Kataoka 1967) found the frequency of *SD* insensitive chromosomes was 3% in 1963 and 1964, and that of *SD* enhancement chromosomes was 4% (1963) and 11-16% (1964) (Table 9). Since *Ac(SD)* was found to be completely insensitive for *SD* action in repulsion condition (Hiraizumi *et al.* 1967), the *SD* insensitive element was named *Ac(SD)-like* modifier. As the effect of *SD* enhancement element was similar to *St(SD)*, that is, it suppresses the action of *SD-suppressor* on the X chromosome, it was named *St(SD)-like* (Kataoka 1967). The present study was purposed to clarify the two modifiers were *Ac(SD)* and *St(SD)*, or not by mapping tests.

According to the results of mapping experiment in the present study, *Ac(SD)-like* was located between *cn* and *vg* on the second chromosome, presumably close to *cn* locus. Therefore it can be reasonably assumed that the modifier might be *Ac(SD)* itself. Hartl (1969) reported that the fecundity (number of progeny) of *SD Ac(SD)/Ac(SD)* males was only about one half of normal males. By the same method, the fecundity of *SD Ac(SD)/Ac(SD)-like* males was revealed to be about one half of normal males. This fact also supported the assumption that *Ac(SD)-like* might be *Ac(SD)*.

Table 9. Frequencies of modifiers for *SD* action in natural populations, Madison and Odate. The Madison data from Hartl (1970).

Population	Year	Frequency		
		Sex-linked suppressor	Autosomal suppressor	Autosomal enhancer
Odate	1963	0.64	0.03 (0.08)	0.04 (0.06)
Odate	1964	0.84	0.03 (0.19)	0.11-0.19 (0.13-0.19)
Madison	1967	0.85	0.45	—

The parenthesized values are the corrected frequencies. See text for full interpretation.

Since four out of five *St(SD)-like* bearing chromosomes were linked with *NS* inversion, mapping test for the *St(SD)-like* modifier could be made for only one chromosome which was free from the inversion. By this experiment it was suggested that the *St(SD)-like* was not one element, but at least it consisted of two elements on the second chromosome. This assumption was confirmed by the facts that the second chromosome with only one of these two elements has little effect as *SD* enhancer, but resynthesized chromosomes which possess these two elements again recovered the efficiency as *St(SD)-like* modifier. As these two elements could be separated easily by recombination, it is hard to expect they could act effectively as *SD* enhancer in natural populations. The existence of the second chromosomes with two elements of *St(SD)-like* modifier in Odate populations, though with a low frequency, needs some explanations for the unknown mechanism for the maintenance of this type of chromosome.

Except for one chromosome described above, *St(SD)-like* modifiers found in the present analysis were associated with *NS* inversion. For these *St(SD)-likes* it was impossible to determine whether they were *St(SD)* itself or not, because any recombinant could not be obtained through the present study.

Hiraizumi *et al.* (1960) reported on *SD* insensitive elements in experimental and natural populations. In the experimental populations which originally consisted of *SD* and *cn bw* chromosomes (*SD* sensitive), they recovered some *SD* insensitive chromosomes after about 20 generations from starting time. For the natural populations they found *SD* insensitive element in Madison population which involved *SD*, but could not find the element in various local populations in Japan, none of which contained *SD*. Then they suggested that *SD* insensitivity appeared to be a concomitant of having *SD* in populations. It is very probably that *SD* insensitive element in populations might be *Ac(SD)* which was derived from *SD* chromosome by recombination.

Recently Hartl (1970) reported that *SD* insensitive chromosome was involved with a fairly high frequency (45%) in Madison population (Table 9). He also discussed about the difference in the frequency of *SD* insensitive elements between Madison and Odate population. Since the frequencies of *Ac(SD)-like* and *St(SD)-like* obtained by the method of Kataoka (1967) were underestimated by the frequency of *SD-suppressor*, some corrections are necessary to obtain their exact frequencies. The corrected frequencies of *Ac(SD)-like* and *St(SD)-like* are given by $a/(1-s)$ and b/s , where s , a and b are the frequencies of *SD-suppressor*, *Ac(SD)-likes* and *St(SD)-like*, in the report of Kataoka (1967). Observed and corrected frequencies of *SD* modifiers were shown in Table 9. Actual frequencies of *Ac(SD)-like* reestimated by above method were about 8% in 1963 and 19% in 1964. Those of *St(SD)-like* in 1963 and 1964 were about 6% and about 13-19% respectively. Hartl suggested the discordance in frequency of *SD* insensitive modifier between Madison and Odate populations caused by the different system developed in any locality in response to *SD*. In this regard, it has been known that the inversion structure of *SD* bearing chromosomes are different between these two populations. All *SD* bearing chromosomes, sampled from Madison population in 1957 beared inversions and were classified into two types, one has a small proximal inversion and *NS* inversion as seen in *SD-5*, and another has only *NS* inversion like *SD-72* (Sandler *et al.* 1959). For Odate population Hiraizumi *et al.* (1965) reported that eight

SD bearing chromosomes carried two overlapping inversions without exception, one of which was *NS* inversion. The different inversion types may result in the different rate of crossing over in these *SD* bearing chromosomes. This may lead to the discordance in frequency of *SD* insensitive element. Furthermore, if the time of appearance of *SD* were different, the discordance between two populations would be expected.

Through this study, the *k* values which represent the efficiency of *Ac(SD)-like* or *St(SD)-like* in modifying *SD* action were not so stable. However, it was observed that the *k* values of *RSD*₁/+ were always higher than those of *RSD*₂/+ in all corresponding experiments. Since *k* may vary depending upon the relative strength of suppressing effect of *Ac(SD)-like* or enhancing effect of *St(SD)-like* to distorting ability of *SD* allele, the difference of *k* values between *RSD*₁ and *RSD*₂ heterozygous for an identical second chromosome might be due to the different abilities of the *RSD*₁ and *RSD*₂ bearing chromosomes to the segregation distortion. Actually, the *k* value of *RSD*₁/*cn bw* stock (0.983) is significantly higher than that of *RSD*₂/*cn bw* stock (0.940).

SUMMARY

Two kinds of modifiers for *SD* system on the second chromosomes, *Ac(SD)-like* and *St(SD)-like* were examined on a natural population, Odate, Japan. Among 21 isofemale lines six lines carried *Ac(SD)-like* and five beared *St(SD)-like* modifiers. None of the second chromosomes examined beared both of these two kinds of modifiers simultaneously.

The effects of these modifiers as a suppressor or a enhancer of *SD* were not so stable and were differently affected by different *Recombinant-SD*, i.e., *RSD*₁ and *RSD*₂. In general, the *k* values of *RSD*₁/*Ac(SD)-like* or *RSD*₁/*St(SD)-like* males were higher than those of *RSD*₂/*Ac(SD)-like* or *RSD*₂/*St(SD)-like* males respectively. These results probably came from the different strength of distortion in these two *SD* strains.

From the results of mapping experiments, *Ac(SD)-like* was located near *cn* locus, and it was estimated to be *Ac(SD)* itself. The results of fecundity experiments also supported this conclusion.

A *St(SD)-like* modifier which was located on an inversion free second chromosome seemed to consist of at least two elements. Therefore this *St(SD)-like* was concluded not to be *St(SD)*. On the other *St(SD)-like* associated with *NS* inversion, any direct genetic analysis was impossible.

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