Study on a Suppressor System for Segregation-Distorter Action in Natural Populations of *Drosophila melanogaster* in Korea

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한국산 초파리의 자연집단에 있어서의 SD 요소에 대한 억제요인에 대하여

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摘 要

Hiraizumi, Sandler, Crow(1960)는 미국의 Wisconsin 주 Madison 의 *D. melanogaster* 의 자연집단을 분석하여 다수의 제 2 염색체가 SD 작용에 대한 억제 요인을 지니고 있음을 발견하였으며 최근에는 Hiraizumi 와 Nakajima(1965)가 일본의 자연 집단도 그러한 억제요인을 가지고 있다고 하였으며 Hiraizumi 와 Kataoka(1965)는 그 억제요인이 주로 X 염색체에 있다고 보고한 바 있으며 Kataoka(1967)는 그 억제 요인의 X 염색체상의 좌위를 결정하였고 억제요인을 지니고 있는 염색체의 빈도와 그 행동등 광범위한 연구를 한 바 있었다.

본인은 *D. melanogaster* 의 한국 자연집단에도 이러한 억제요인이 SD 작용에 관여하고 있는지 (1) 그리고 있으면 어떤 염색체에 들어 있는지 (2)를 연구하기 위하여 한국 9 개 지역으로 부터의 자연집단(춘천, 여수, 남해, 신촌, 광주(경기도), 군산, 광주, 제주, 부산)을 대상으로 하여 두가지 SD Stock[R—1, R(SD^{NH}—1)—1]을 사용하여 분석한 결과 다음 결론을 얻었다.

1. 9 개 집단은 모두 억제 요인을 지니고 있었다.
2. 억제 요인은 대개 X 염색체에 들어 있으며 그중 3 집단에서는 그 요인이 제 Ⅲ 또는 제 Ⅳ 염색체에 그리고 제 Ⅱ 염색체에 있는 경우도 있었다.
3. 기원이 다른 SD[R—1, 미국; R(SD^{NH}—1)—1, 일본]에 대한 억제 요인의 반응은 큰 차이를 볼 수 없었다.

INTRODUCTION

A meiotic drive is defined as the situation where by a heterozygote produces gametes containing an excess of one allele, rather than the expected equality(Sandler and Novitski 1957). Such aberrant segregations give rise to alter the gene frequencies with a population. Hence the meiotic drive can be one of the factors for evolution.

The first instance of meiotic drive in *Drosophila melanogaster* has been reported by Sandler, Hiraizumi and Sandler(1959). The phenomenon was termed as segregation-distortion and is caused by a locus designated SD.

Since SD was discovered in a natural population of *Drosophila melanogaster*, extensive studies on this element have been carried out by many investigators(Sandler, Hiraizumi and Sandler 1959; Sandler and Hiraizumi 1959, 1960a, b, 1961a, b; Hiraizumi, Sandler and Crow 1960; Mange 1961, 1968; Sandler 1962; Crow, Thomas and Sandler 1962; Hiraizumi 1962; Greenberg 1962; Peacock and Erickson 1965; Hiraizumi and Nakajima 1965, 1967; Hiraizumi and Kataoka 1965; Chung 1966, 1967; Watanabe 1967; Kataoka 1967; Denell and Judd 1968; Hiraizumi and Hartl 1968).

The main conclusions from these studies relevant to the present study will be briefly given below.

(1) SD is a locus, complex in nature, located on the right arm of chromosome 2, between the markers purple and cinnabar. With only rare exceptions, a male heterozygous for SD and a structurally normal SD^+ chromosome produces progeny among which almost all possess the SD chromosome. The k value is defined as the proportion of SD-bearing sperm. Thus, when the segregation is normal, $k=0.5$ and if distortion is complete, $k=1$.

(2) Segregation-distortion is operative only in SD heterozygous males, but not in SD homozygous males and females. Heterozygous females show normal 1 : 1 segregation ratio, but their heterozygous sons will again exhibit abnormal k values with certain exceptions.

(3) The SD region consists of at least two elements. One of these is the SD locus itself and closely linked to, and to the right of SD, there is an activator of SD, symbolized Ac(SD). The coupling of these two elements is necessary for SD to operate.

(4) An SD chromosome is insensitive to distorting action of another SD chromosome.

(5) There is stabilizer of SD, symbolized St(SD) at or near the tip of the right arm of chromosome 2. In the presence of St(SD), the SD action is stable and the segregation ratio is constantly high; in its absence the distorting effect of SD becomes somewhat variable, resulting in a reduced value of k.

(6) It is postulated that SD operates by nonrandomly orienting toward the "functional pole" during meiosis I in male, thus being included in most of the functional sperm.

(7) When a male carries segregation-distorter, the second and the sex chromosome do not assort randomly. SD tends to the functional pole together with the Y chromosome.

(8) Segregation-distortion is widespread in nature and is not of recent origin. Since SD was first discovered in a natural population from Baja California, Mexico and from a few United States. And the occurrence of SD is highly probable in Korean natural populations even though not conclusive.

(9) Temperature sensitivity of SD depends on the stage of meiosis which a particular sperm is undergoing, rather than the developmental stage of the individual fly. No effect is found following treatment of larvae, which contain no meiotic cells, and temperature effect on the SD action is not heritable.

Hiraizumi, Sandler and Crow(1960) analyzed a natural population of *D. melanogaster* from Madison, Wisconsin and found that many of the second chromosomes carried suppressor.

Hiraizumi and Nakajima(1965) found that the population from Japan contained a genetic system which suppressed the SD action. Hiraizumi and Kataoka(1965) reported that the main carrier of the suppressor for the SD action was the X chromosome.

Kataoka(1967) analyzed a system of suppressor for the SD action in natural population of *D. melanogaster* in Ojate, Japan and found that most of the suppressors were located on the X chromosome (1), the effect of the suppressor was different for the SD originated from different populations (2), and the suppressor was located somewhere between the v(vermillion) and f(forked) loci on the X chromosome(3).

The present study was undertaken in an attempt to see if any suppressor system for the SD action was involved in natural populations of *Drosophila melanogaster* in Korea.

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MATERIALS AND METHODS

The following stocks were used in the present study:

1. Standard stocks: *cn bw* standard laboratory stocks marked by cinnabar and brown on chromosome 2, which gives white eye color; *yf*:=/yi; *cn bw* stocks marked by yellow and forked on the reversed acrocentric compound X chromosome and by cinnabar and brown on chromosome 2. These stocks have been kept in small cultures

in the laboratory and have none of modifiers for the SD system, that is they are sensitive for the SD action.

2. SD stocks: *Original-SD chromosome* lines, isolated from natural populations include SD−72 [SD, Ac(SD), St(SD)] and SD^{NH}−2[SD, Ac(SD), St(SD)] which were collected from a natural population of Madison, Wisconsin, United States and from a population in Odate, Japan, respectively. These original-SD bearing chromosomes carry St(SD), so that the SD action is stable and the segregation-distortion is invariably strong. *Recombinant-SD* lines, R−1 [SD, Ac(SD), -bw], R(SD^{NH}−1) −1 [SD, Ac(SD), -bw] were obtained as recombinant from the original-SD/*cn bw*. The former line was derived from Madison and the latter, from Odate. These recombinant-SD lines carry the SD the Ac(SD), but the St (SD) was removed by crossing over and therefore the SD action is unstable and the average values of *k* were somewhat reduced. Both of original-SD and recombinant-SD lines have been kept by backcrossing to the stanpard *cn bw* females so that their genetic background is that of standard *cn bw* stock.

3. Wild type stocks: These are sources of suppressors and were collected from natural populations of nine localities in Korea; Choonchun, Yusoo, Namhai, Shinchon (Seoul), Kwangjoo(Kyunggi province), Koonsan,Kwangjoo(Chunnam province,), Jejoo and Pusan at different times from 1965 to 1967 and have been kept in mass culture in the laboratory.

During the experiment flies were kept in constant temperature room(25°±1°C). The food used was a standard corn meal, yeast, agar type with 0.5% propionic acid as a mold inhibitor.

RESULTS

The mating scheme shown in figure 1 was done to examine the existence of the suppressor system and to determine the bearing chromosome of it.

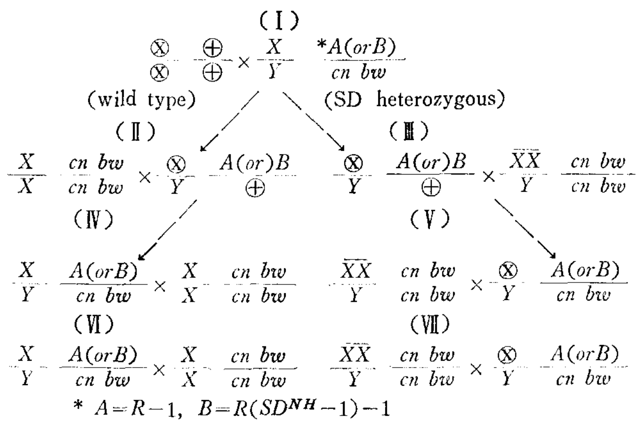

Fig. 1. The mating scheme done in the present experiment.

In mating I, two virgin females sampled from each wild type line of nine natural populations in Korea were mated individually with a R−1(symbolized A in Fig.1) male or R(SD^{NH}−1)−1(symbolized B) male. One half of the sons from mating I were mated with free-X; *cn bw* females in mating II, and the other half were mated with *yf:=/Yi; cn bw* females in mating III. Therefore males used in mating II and III were siblings. The sons from mating II were mated again with free-X; *cn bw* females in mating IV and the sons from mating III were mated with *yf:=/Yi; cn bw* females in mating V. The mating VI and VII are repeats of the mating IV and V, respectively.

The index of *k* values shown in Table 1 was used for examination of the existence of suppressor system and for determination of the suppressor-bearing chromosome. If a female in mating I carries any suppressing factor in any chromosome, then some or all of the males in mating II and III will show a greatly reduced amount of distortion(for simplicity, let k=1 and k=0.5 refer to the distorting and the non-distorting segregation ratio, respectively). Therefore, when males in mating II and III do not show a greatly reduced amount of distortion, it is suggested that no suppressing factor is involved in the population so that the further experiments(mating IV, V, VI, and VII) are not necessary. The comparison between mating IV and V will show in what chromosome pairs that suppressing factor is located as inferred from the mating scheme: if all of the males in mating IV and V show $k=1$ and $k=0.5$, respectively, the suppressor must be located on the X chromosome. If all of the males in both of mating IV and V show $k=1$, it must be located on the second chromosome. If half of the males in both of mating IV and V show $k=0.5$ and remaining half show $k=1$, it must be located on the third or the fourth chromosome. The mating VI and VII were made for the confirmation of the results of the mating IV and V.

Table 1. The k values used for the examination of the suppressor system and determination of bearing chromosome of the suppressor.

Mating No. (II)	(III)	(IV)	(V)	(VI)	(VII)	suppressor Bearing chromosome
0.5	0.5	1	1	1	1	II
0.5	0.5	1	0.5	1	0.5	X
0.5	0.5	0.5, 1	0.5, 1	0.5, 1	0.5, 1	III or IV
1	1					None

Since males in mating II and III in the present experiment showed a greatly reduced amount of distortion($k=0.5$) in all lines of populations from nine localities of Korea, it is certain that suppressing factor is involved in any chromosome in nine populations in Korea.

The results of the determination of bearing chromosome of the suppressing factor are shown in Table 2. The suppressing factors were found to be located on the X chromosome in all lines from Choonchun, Yusoo, Shinchon(Seoul), Kwangjoo(Chunnam), Jejoo, and Pusan, in most lines from Namhai, Kwangjoo(Kyunggi) and Koonsan populations. A few lines from Namhai showed to have a suppressing factor on the third or the fourth chromosome and Kwangjoo(Kyunggi), on the second chromosome. It was necessary to set up arbitrary border line for k to determine whether or not the male was distorting. In the present experiment a k value of 0.75 was adopted; values lower than 0.75 were scored as low k(non-distorting) and those higher than 0.75 as high k (distorting). This border line was based upon the distortion of k values in the mating of homozygous *cn bw* females to male heterozygous for the *cn bw* chromosome and the chromosome from the localities.

The results of the present experiment also showed that the response of the supperessor for differently originated SD, R−1 and $R(SD^{NH}-1)-1$ was found to be not different in lines from Choonchun, Yusoo, Shinchon(Seoul), Kwangjoo(Chunnam), Jejoo and Pusan populations, all of which carried the suppressing factor in the X chromosomes. In lines from three populations,

Table 2. Bearing chromosomes of the suppressor in nine natural populations in Korea.

Populations	SD lines	suppressor Bearing chromosome X	II	III or IV
Choonchun	*A	0		
		0		
	B	0		
		0		
Yusoo	A	0		
		0		
	B	0		
		0		
Namhai	A			0
		0		
	B	0		
		0		
Shinchon(Seoul)	A	0		
		0		
	B	0		
		0		
Kwangjoo (Kwunggi)	A	0		
		0		
	B	0		
			0	
Koonsan	A	0		
		0		
	B			0
		0		
Kwangjoo (Chunnam)	A	0		
		0		
	B	0		
		0		
Jejoo	A	0		
		0		
	B	0		
		0		
Pusan	A	0		
		0		
	B	0		
		0		

* A=R−1, $B=R(SD^{NH}-1)-1$

Namhai, Kwangjoo(Kyunggi) and Koonsan, the situation was somewhat peculiar. In Namhai population, all lines when $R(SD^{NH}-1)-1$ was used in mating showed to have the suppressing factor on the X chromosome but half of lines when $R-1$ was half, on the X chromosome. In Kwangjoo(Kyunggi) population, all lines when $R-1$ was used, was found to have it on the X chromosome but one half of lines when $R(SD^{NH}-1)-1$ was used, was found to have it on the second chromosome and the other half, on the X chromosome. In Koonsan population, all lines in the case of $R-1$ showed to carry the suppressor on the X chromosome but one half of lines in the case of $R(SD^{NH}-1)-1$ was found to carry it on the X chromosome and the other half, on the third or fourth chromosome. These peculiar results may be due to the only accidental or due to the other factors than the suppressor for the SD action. These must be investigated in further experiment so that the situation will be made clear. However, the response of the suppressor for differently originated SD was found to be not different in most populations in Korea.

DISCUSSION

Hiraizumi, Sandler and Crow(1960) analyzed a natural population of *Drosophila melanogaster* from Madison, Wisconsin and found many of the second chromosome carried suppressor, while samples of flies collected from five natural populations in Japan did not carry suppressors. Hiraizumi and Kataoka(1965) reported that the main carrier of the suppressor for the SD action was the X chromosome. Kataoka(1967) analyzed a system of suppressor for the SD action in natural population of *D. melanogaster* in Odate, Japan and found that most of the suppressors were located somewhere between the *v* and *f* loci on the X chromosome with quite a small frequencies but none of the third or fourth chromosome were found to carry the factor. The results of the present experiment showed that most of the suppressors were found to be located on the X chromosome and only a few lines showed that the suppressors located on the second and on the third or fourth chromosome. The results that the X chromosome is carrying suppressors in the present study is agreed with Kataoka's. However, the location of the suppressor on the third or fourth chromosome is disagreed with the reports of Hiraizumi *et al.* (1960) and with Kataoka's(1967).

Kataoka(1967) reported that the effect of the suppressor was slightly but significantly different for the different SD lines: the Japanese recombinant-SD line was suppressed more strongly in comparison with the American SD. This different response of the suppressor for differently originated SD, $R-1$(the American line) and $R(SD^{NH}-1)-1$ (the Japanese one) was not found in the present experiment with only few exceptional cases.

Hiraizumi, Sandler and Crow(1960) constructed population cages with SD under a non-suppressor background and found after one year passage that the cages became to carry a suppressor system for the SD action. Based on this result, they concluded that insensitivity appears to be concommitant with having SD in populations. Kataoka(1967) reported that the frequency of the suppressor-X was relatively low in a population when SD was present and this suggested the process of elimination of SD, which had been found to be associated with deleterious elements from the natural population. Chung (1966, 1967) reported that the occurrence of SD was highly probable in natural populations of *D. melanogaster* from Korea even though not conclusive. If SD will never found in the Korean natural populations then the results of the present experiment that the suppressing factor was found to be located on the X chromosome is against the conclusion of Hiraizumi *et al.*(1960). In order to make clear the above situation the occurrence of SD in the Korean natural populations should be examined to be conclusive.

During the process of locating the suppressor on chromosome pairs, somewhat peculiar cases were found that the locations of suppressor showed the inter-line differences in the populations: Namhai, Kwangjoo(Kyunggi) and Koonsan. To clarify this point the extensive study will be necessary.

SUMMARY

In order to see if any suppressor system for the SD action was involved in natural populations of *D. melanogaster* samples from the populations of nine localities in Korea, Choonchun, Yusoo, Namhai, Shinchon(Seoul), Kwangjoo(Kyunggi), Koonsan, Kwangjoo(Chunnam),

Jejoo and Pusan were analyzed by using the mating scheme for locating the suppressor on chromosome pairs. And also two kinds of recombinant SD lines R−1, the American line and R(SD^{NH}−1)−1, the Japanese one were used in order to see any difference of the response of the suppressor for differently originated SD.

The results of the experiment are given below.

(1) The suppressor system was involved in all lines of natural populations from nine localities of Korea.

(2) Most of the suppressors were found to be located on the X chromosome and only a few lines from three populations showed to carry the suppressors on the second chromosome and on the third or fourth chromosome.

(3) The response of the suppressor for differently originated SD lines showed no significant difference.

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