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# Alteration of sex ratio associated with the Segregation Distortion (SD) phenomenon in Drosophila melanogaster: Analysis of the segregation of first and second chromosomes of $Sd^{R-1}/Sd^{+}$ males, heterozygous for different $SD$ and $SD^{+}$ chromosomes

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# **Genetica.** — *Alteration of sex ratio associated with the Segregation Distortion* (SD) *phenomenon in* Drosophila melanogaster: *Analysis of the segregation of first and second chromosomes of* $Sd^{R-1}/Sd^{+}$ *males, heterozygous for different* SD *and* $SD^{+}$ *chromosomes.* Nota di ADA LOVERRE (*), ROSADELE CICCHETTI (*) e GIOVANNI TRIPPA (*), presentata (**) dal Socio G. MONTALENTI.

RIASSUNTO. — È stato esaminato il tipo di correlazione esistente tra segregazione dei primi e dei secondi cromosomi in maschi di *Drosophila melanogaster* eterozigoti per il cromosoma $SD^{R-1}$ (portatore del fattore $Sd^{R-1}$ = *Segregation distorter*$^{\text{Roma}-1}$ : 2–52.9) o alcuni suoi derivati e differenti cromosomi $SD^{+}$. I risultati ottenuti hanno dimostrato che una alterazione del rapporto sessi in favore delle femmine è presente nella sola progenie di tipo $SD^{+}$ e che l'intensità di questa alterazione è direttamente correlata con l'intensità della segregazione distorta dei secondi cromosomi.

Le presenti osservazioni vengono interpretate in base all'ipotesi che l'intensità dell'alterazione del rapporto sessi in relazione al grado di distorsione della segregazione dei secondi cromosomi, in maschi $SD/SD^{+}$, sia la conseguenza di un processo differenziale di disfunzione dei gameti $SD^{+}$ a seconda del tipo di cromosoma sessuale in essi presente durante la meiosi.

## INTRODUCTION

The Segregation Distortion (SD) phenomenon in *Drosophila melanogaster* is one of the most extensively studied examples of meiotic drive, as defined by Zimmering *et al.* (1970). A review by Hartl and Hiraizumi (1976) and a detailed study by Ganetzky (1977) have recently redescribed the main features of this phenomenon which consists essentially in the fact that males heterozygous for a second *SD* chromosome and a suitable $SD^{+}$ chromosome produce progeny which are almost exclusively of the SD type. Recovery of the second chromosomes in the progeny of these males is altered and the *k* values (= *SD* bearing progeny/total progeny) are generally closer to 1.00 than to the expected value of 0.50.

The effect of the *Sd* factor is to cause the degeneration of $SD^{+}$ gametes into heterozygous $SD/SD^{+}$ males (Nicoletti, 1968; Tokuyasu *et al.*, 1972).

In the present study the type of relationship existing between intensity of Segregation Distortion and the degree of alteration of the sex ratio in $Sd^{R-1}/Sd^{+}$ males is examined, using different *SD* and $SD^{+}$ chromosomes.

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For the nomenclature of the two main components of the *SD* system, in accordance with Ganetzky (1977), we report that the symbol *Sd* refers to the locus responsible for distortion, mapped on the second chromosome at locus 52.9 (Tanzarella *et al.*, 1972), while *SD* indicates the entire distorting chromosome. The symbol $Sd^+$ is used to indicate the alternative *Sd* allele, even though to date there has been no evidence that $Sd^+$ is other than the absence of *Sd*. It is convenient to accept the term Responder (*Rsp*) for the site of action of *Sd*. Two of the possible alleles will be referred to as $Rsp^{ins}$ (Responder insensitive to *Sd*) and $Rsp^{sens}$ (Responder sensitive to *Sd*).

## MATERIALS AND METHODS

For the construction of the different combinations of *SD* and $SD^+$ the following chromosomes were used (a complete description of the best known markers is given in Lindsley and Grell, 1968):

1. *SD chromosomes* ($Sd\,Rsp^{ins}$) : $SD^{R-1}$, recovered from a natural Italian population from Rome (Nicoletti and Trippa, 1967; Sandler *et al.*, 1968), has no recessive lethals or structural rearrangements. $SD^{R-1}$ *recombinant derivatives*: $SD^{R-1}\,L_1$, $SD^{R-1}\,L_2$ and $SD^{R-1}$ *Pin*, obtained from $SD^{R-1}$/*Sp Bl L Pin*, $SD^{R-1}$/*L Pin* females,

2. $SD^+$ *chromosomes*. These chromosomes in heterozygosis with the chromosome $SD^{R-1}$ have proved to be sensitive in a different degree to the distorting action of the factor $Sd^{R-1}$.

We have arbitrarily grouped them into two classes:

2 a. $SD^+Rsp^{sens}$ *chromosomes*, those which showed *k* values between 0.70 and 1.00 : *bw–5*, a second chromosome of an isogenic line marked by *y* ; *bw–5* ; *st–5*, selected for its high sensitivity to *SD* chromosomes and used in maintaining the *SD* stocks; $L_1$, a recombinant derivative from *Bl L/bw–5* females; $L_2$ and *Sp*, recombinant chromosomes from *Sp Bl L Pin/bw–5* females; *Pin*, from *L Pin/bw–5* females;

2 b. $SD^+Rsp^{ins}$ *chromosomes*, those with *k* values between 0.50 and 0.70 : *Bl L* , *Sp Bl L Pin* , *Sp b pr cn L Pin*, multimarked second chromosomes kept as balanced lethal strains in heterozygosis with the balancer chromosome *SM5* ; $Bl_1$ , *Sp Bl* and $Bl_2$, recombinant chromosomes from *Bl L/bw–5* and *Sp Bl L Pin/bw–5* females.

All the *SD*/$SD^+$ males of the different genotypes examined were singly crossed with females of the strain *y* ; *bw–5* ; *st–5*. The cultures were kept at a temperature of 24° ± 1 °C. The progeny were counted 14 to 18 days after crossing.

## RESULTS

The type of relationship between Segregation Distortion ($k$) and sex ratio ($sr$ = male progeny/total progeny) in the offspring of $Sd^{R-1}/Sd^{+}$ males, was examined for different $SD$ and $SD^{+}$ chromosomes.

Table I shows the different genotypes of the males examined and the relative equally weighted means of $k$ and $sr$ values, the latter for both $SD$ and $SD^{+}$ progeny.

TABLE I

*Distribution of* k *(SD progeny/total progeny) and* sr *values (male progeny/total progeny) in the offspring of* SD/SD$^{+}$ *males heterozygous for different* SD *and* SD$^{+}$ *chromosomes.*

| Genotype | Number of crossed males | $\bar{k}$ ± S.E. | $\overline{sr}$ (SD$^{+}$) ± S.E. | $\overline{sr}$ (SD) ± S.E. |
|---|---|---|---|---|
| $SD^{R-1}/bw\text{-}5$ . . . . . . . . | 42 | .98±.00 | .23±.07 | .47±.01 |
| $SD^{R-1}$ recombinant derivative/$SD^{+}$ $Rsp^{sens}$ chromosome | | | | |
| $SD^{R-1}L_1/bw\text{-}5$ . . . . . . . | 33 | .96±.01 | .10±.05 | .50±.01 |
| $SD^{R-1}Pin/bw\text{-}5$ . . . . . . . | 25 | .92±.02 | .24±.07 | .50±.02 |
| $SD^{R-1}L_2/bw\text{-}5$ . . . . . . . | 16 | .85±.03 | .33±.07 | .51±.02 |
| $SD^{R-1}/SD^{+}Rsp^{sens}$ chromosome | | | | |
| $SD^{R-1}/Pin$ . . . . . . . . | 22 | .98±.01 | .19±.11 | .53±.01 |
| $SD^{R-1}/L_1$ . . . . . . . . . | 112 | .91±.01 | .34±.03 | .50±.01 |
| $SD^{R-1}/L_2$ . . . . . . . . . | 41 | .88±.01 | .30±.02 | .49±.01 |
| $SD^{R-1}/Sp$ . . . . . . . . . | 51 | .86±.02 | .33±.03 | .52±.01 |
| $SD^{R-1}/SD^{+}Rsp^{ins}$ chromosome | | | | |
| $SD^{R-1}/Sp\ Bl\ L\ Pin$ . . . . . | 26 | .70±.02 | .44±.04 | .49±.02 |
| $SD^{R-1}/Bl\ L$ . . . . . . . . | 65 | .70±.01 | .46±.02 | .51±.01 |
| $SD^{R-1}/Sp\ b\ pr\ cn\ L\ Pin$ . . . | 39 | .68±.02 | .45±.02 | .52±.01 |
| $SD^{R-1}/Sp\ Bl$ . . . . . . . . | 30 | .66±.02 | .44±.02 | .48±.01 |
| $SD^{R-1}/Bl_1$ . . . . . . . . | 26 | .64±.02 | .46±.02 | .51±.01 |
| $SD^{R-1}/Bl_2$ . . . . . . . . . | 27 | .63±.02 | .44±.02 | .49±.02 |

As in each group males with identical *SD*/*SD*+ genotypes showed varying *k* values, it was investigated whether the trend of the intragroup *k* and *sr* values was of the same kind as that of intergroup values. Fig. 1 gives for each genotype studied the trend of the *sr* values in relation to the *k* values arbitrarily grouped into classes with an amplitude of 0.10 in the *SD* and *SD*+ progeny.

## DISCUSSION

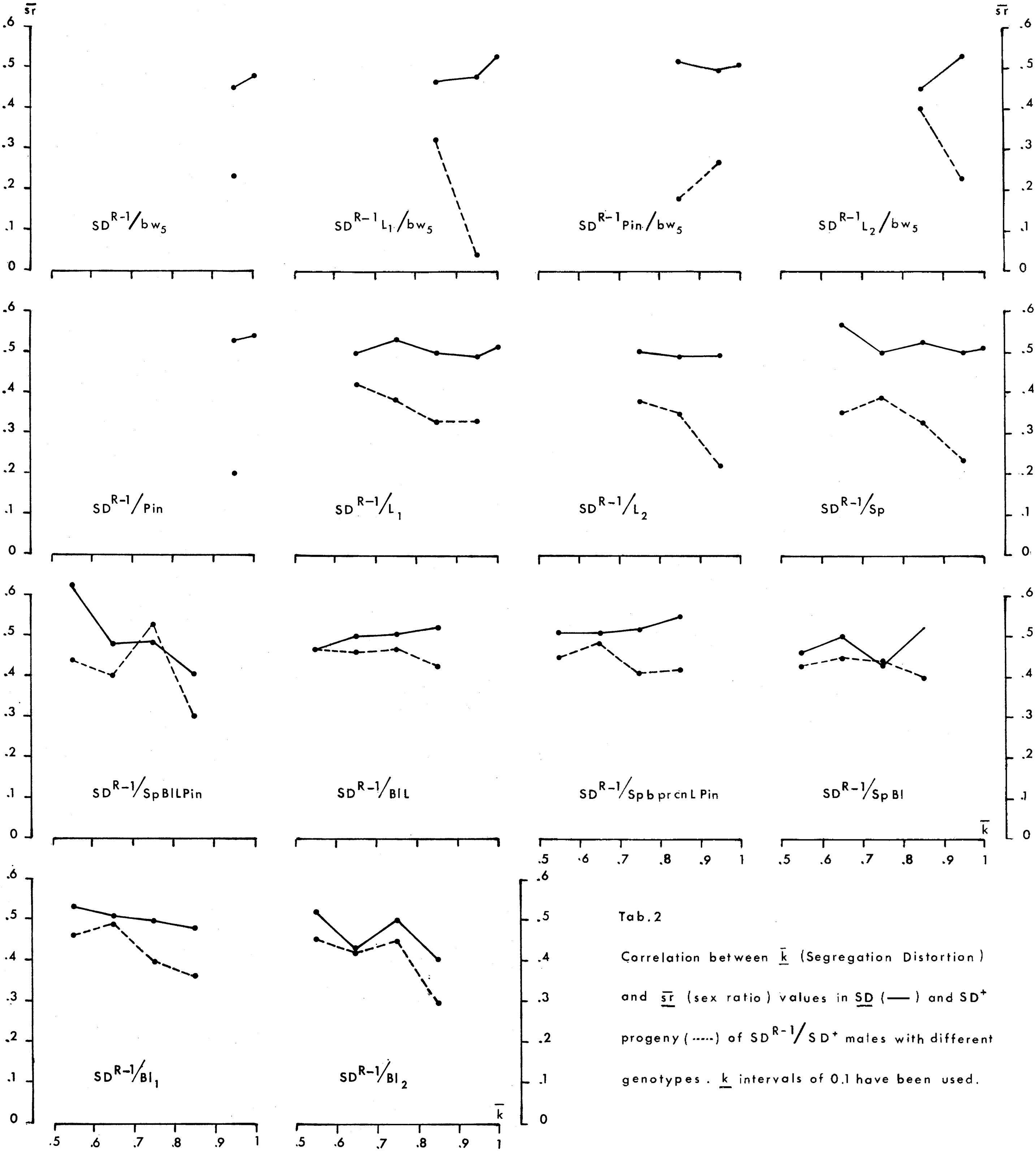
Alteration of the sex ratio in the progeny of *SD*/*SD*+ males was observed for the first time by Hiraizumi and Nakazima (1967). The *SD* progeny were preferentially males while the *SD*+ progeny were mainly females. Subsequently Denell *et al.* (1969) and Denell and Miklos (1971) extended these observations to the segregation of different combinations of sex chromosomes in relation to the intensity of the distorted segregation in *SD*/*SD*+ heterozygous males, using the *SD-72* and *SD-36* chromosomes. Their results made it possible to exclude the presence of a significant alteration of the sex ratio in the *SD* progeny, and to prove that this alteration does exist in the *SD*+ progeny and is related to the *k* values and, finally, to observe that the intensity of the sex ratio increases from *X*/*Y* males to *XY*/*Y* males to *XY*/*O* males.

Our data on the $SD^{R-1}$ chromosome and some of its derivatives and different *SD*+ second chromosomes in *SD*/*SD*+ heterozygous males made it possible to confirm some of the main characteristics of the sex ratio in relation to the *SD* phenomenon. Firstly, alteration of the sex ratio in favour of the females is present only in the *SD*+ progeny, while the sex ratio is normal in the *SD* progeny. Secondly, the intensity of alteration of the sex ratio is directly related to the intensity of segregation distortion of second chromosomes, due to the interaction between $SD^{R-1}$ and *SD*+ chromosomes.

Table I shows that the average values of *sr* relative to the *SD* progeny are generally 0.50 for all genotypes studied, while in the *SD*+ progeny they are always lower than the expected value of 0.50 even in those genotypes in which the intensity of the segregation distortion is relatively weak ($SD^{R-1}/SD^{+}\ Rsp^{ins}$ males).

The observations on the trend of the sex ratio in relation to the intensity of Segregation Distortion in each genotype (intragroup) parallel the intergroup observations, even if in the entire series of groups of males with genotype $SD^{R-1}/SD^{+}\ Rsp^{ins}$ the trend of the sex ratio is not always manifestly proportional to the *k* values (fig. 1).

Two different hypotheses can be put forth to interpret the observations made so far: the first, which would explain the data of Hiraizumi and Nakazima (1967), is based on the fact that there is a certain degree of homology between the *X* chromosome and the *SD* chromosomes, which would segregate at meiosis (non-random disjunction hypothesis) causing a differential distribution of sex chromosomes in the *SD* and *SD*+ gametes differently determined to meet the dysfunction process. The second hypothesis is based on the fact that the



Tab. 2

Correlation between $\underline{\bar{k}}$ (Segregation Distortion) and $\underline{\bar{sr}}$ (sex ratio) values in $\underline{SD}$ (——) and $SD^+$ progeny (-----) of $SD^{R-1}/SD^+$ males with different genotypes. $\underline{k}$ intervals of 0.1 have been used.

Fig. 1.

altered sex ratio in the class $SD^+$ and its intensity in relation to the intensity of the Segregation Distortion are the consequence of a differential process of dysfunction of the $SD^+$ gametes depending on the type of sex chromosome present in them.

This last hypothesis seems to us to be more plausible since it would explain both our present observations and the results of Denell *et al.* (1969) and Denell and Miklos (1971).

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