

## LINKAGE DISEQUILIBRIUM BETWEEN CHROMOSOMAL INVERSIONS OF *Drosophila mercatorum pararepleta* (DIPTERA, DROSOPHILIDAE)

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### ABSTRACT

Linkage disequilibrium (LD) in a lab population of *Drosophila mercatorum pararepleta* was analyzed through an investigation of the recombination rate between inversions. Inversions  $5a^2$  and  $5b^2$  of chromosome five were in total LD, with a null rate of recombination, as has been found for natural populations. The inversions of chromosome 2-3F presented a low rate of recombination between arrangements,  $2s^3-3n$  (0.89%) and  $2s^3-3g$  (2.5%) and null between  $3n-3g$  and  $3g-3h$ . The data suggest that casual adaptation of inversions are a consequence of disequilibrium and not a cause of it.

### INTRODUCTION

*Drosophila mercatorum pararepleta* is a subspecies of *D. mercatorum* (Patterson and Wheeler, 1942). It is part of the *mercatorum* subgroup, which belongs to the *repleta* group (Wasserman, 1962) and is found to the east of the Andes mountains in some types of open vegetation (chaco, pantanal, cerrado, dunes and caatingas), and in forests (Wasserman, 1982; Carson, 1965; Pereira, 1979; Sene *et al.*, 1981a; Vilela *et al.*, 1983; Sene, 1986; Tidon-Sklorz and Sene, 1992).

Sene (1986) studied the chromosomal polymorphism of some natural populations of *D. m. pararepleta*. He observed that marginal populations are different from the central ones, in terms of the frequency of inversion  $2s^3$  (chromosome 2-3F) and of the two inversions of chromosome 5 ( $5a^2$  and  $5b^2$ ). He showed that the inversions of

chromosome 2-3F ( $2s^3$ , 3n, 3g and 3h) are in linkage equilibrium, but those of chromosome 5 ( $5a^2$  and  $5b^2$ ) are in strong linkage disequilibrium (LD).

LD is a non-random association between alleles (or chromosomal markers) of different loci (Levitan, 1955). This phenomenon, also called gametic excess, is expressed by the deviation in the expected gametic frequency, estimated by its individual frequencies and the observed frequencies. LD may be established by selective or stochastic factors. Its maintenance in nature may be due to natural selection or intrinsic limitations of recombination (Levitan, 1955, 1958; Levitan and Salzano, 1959; Brncic, 1961; Turner, 1967; Zouros and Krimbas, 1973; Hedrick *et al.*, 1978).

The objective of this study was to analyze the LD for the chromosomal inversions of *D. m. pararepleta* under laboratory conditions. These conditions theoretically provoke a reduction in selection pressure on the associations, making possible the verification of the forces that maintain them.

## MATERIAL AND METHODS

For verification of the recombination rate we used females from four polymorphic isofemale lines of *D. m. pararepleta*: D33F43 and D33F55 (Cristalina, GO), polymorphic for the inversions  $5a^2$  and  $5b^2$ ; and D38N27 and D38N67 (Luiz Antônio, SP) polymorphic for inversions  $2s^3$ , 3n, 3g and 3h (chromosome 2-3F). A monomorphic strain of *D. m. mercatorum* RT15 (Univ. Texas Lab. no. 1529; from Lima, Peru) was used as a standard.

The inversion distances, estimated as number of bands, based on Wharton (1942) and Sene *et al.* (1981b) are:  $5a^2$  to  $5b^2$ , 26 bands; 3h to 3g, 12 bands; 3g to 3n, 4 bands;  $2s^3$  to 3n, 229 bands; and  $2s^3$  to 3g, 274 bands.

RT15 males were mated with 35 heterozygous virgin females, for the inversions of chromosome 5 ( $5a^25b^2/++$ ) and with six heterozygous virgin females for the inversions on chromosome 2-3F. The polytene chromosomes of the larvae resulting from these crosses were analyzed. This procedure allowed us to infer the genome of the egg provided by the parental female, and consequently the recombination frequency between the inversions.

The polytenic salivary gland chromosomes of third instar larvae were prepared by means of squashing in 2% lacto-acetic-orcein.

## RESULTS AND DISCUSSION

An analysis of 2,152 descendants of females heterozygous for inversions of chromosome 5 ( $5a^25b^2/++$ ) showed that the frequency of recombination between inversions is null (Table I).

Table I - Recombination frequency between inversions of chromosomes 2-3F and 5, in *D. m. pararepleta* heterozygous females.

Linkage (chromosome)	Parental type	Recombinant type	Recombination frequency (%)
s <sup>3</sup> -n (2-3F)	782	7	0.89
s <sup>3</sup> -g (2-3F)	897	23	2.50
n-g (2-3F)	1,173	0	0.00
g-h (2-3F)	2,070	0	0.00
a <sup>2</sup> -b <sup>2</sup> (5)	2,152	0	0.00

We suggest that inversions 5a<sup>2</sup> and 5b<sup>2</sup> stay together because of an absence of recombination between them. Apparently, this association is not maintained by selective mechanisms. This does not mean that the association is neutral.

We found a low recombination frequency between the more distant inversions and null between the closer ones in 2,070 descendants of females heterozygous for inversions of chromosome 2-3F (Table I). In spite of being low, this recombination rate may justify the linkage equilibrium found in nature by Sene (1986).

The low chromosomal recombination rate between different inversions of *D. m. pararepleta*, in heterozygotes, suggests a possible effect of the inversions on the adjacent regions in the chromosome. Low recombination rate seems to be related to geographic distribution of the chromosomal polymorphisms as described by Sene (1986). This reinforces the homoselection and heteroselection hypothesis proposed by Carson (1955, 1956). Marginal populations exposed to strong selective pressures would suffer a reduction in chromosomal polymorphism, provoking an increase in the recombination rate. At the same time, it would provoke an increase in the probability of the appearance of more favorable genetic rearrangements.

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### RESUMO

Analisamos o desequilíbrio de ligação (DL) em *Drosophila mercatorum pararepleta*, através da taxa de recombinação entre inversões. As inversões 5a<sup>2</sup> e 5b<sup>2</sup> do cromossomo cinco estão em total DL, com

taxa de recombinação nula, como o encontrado para populações naturais. As inversões do cromossomo 2-3F apresentam baixa taxa de recombinação entre os arranjos  $2s^3-3n$  (0,89%) e  $2s^3-3g$  (2,5%) e nula entre  $3n-3g$  e  $3g-3h$ . Os dados sugerem que a eventual adaptação das inversões deve ser consequência do desequilíbrio e não uma causa dele.

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