CHROMOSOMAL BASIS OF DOSAGE COMPENSATION IN DROSOPHILA

1. HYPERACTIVITY OF THE POLYTENE X-CHROMOSOME IN MALE DROSOPHILA MELANOGASTER AND DROSOPHILA PLUMERIAE

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ABSTRACT

The functional morphology and the transcriptional activity of the male X-chromosome in Drosophila melanogaster and D. plumeriae have been examined. In both these species of the melanogaster subgroup, the X-chromosome in the polytene glands of the male larva is enlarged and pale stained as in Drosophila melanogaster. Mitral cells in ascidians show that in both the species, the relative rate of RNA synthesis by the single X of the males is similar to that by the two Xs of female.

The results indicate that (a) the reduction and pale staining of the single X in the larval polytene glands of the male of a species contains a mutant male, and (b) despite the changes in the epigenetic organization of the X-chromosome in these species (that take place during their evolution), the hyperactivity of the male X, and therefore, dosage compensation for X-linked genes, has remained unaltered.

INTRODUCTION

In the course of evolution in the genus Drosophila there have been many chromosomal rearrangements involving the sex chromosomes. While in some cases the configuration of the original X-chromosome is changed, in several instances such rearrangements have modified the sex-determining mechanism (Southworth and Novitski, 1941; Pardee and Stout, 1955). Previous studies (Mukherjee, 1966; Mukherjee et al., 1968, 1969; Lakhotia and Mukherjee, 1968; 1970; Lakhotia, 1970, 1971) have indicated that in Drosophila melanogaster, dosage compensation operates by hyperactivity of the single X in the male, that this hyperactivity shows a cellular autonomy in sex months, and that it is functionally related to the replicative organization of the male X, and finally, that the hyperactivity of the male X is not a 'position effect' (Lakhotia, 1971).

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In view of these findings, a taxonomic and phylogenetic analysis of differences in specimens of Drosophila should be underway for a better understanding of the chromosome basis of dosage compensation in the genus.

In the present work, the functional morphology and transcriptive activity of the X chromosome of D. melanogaster (Nagao et al., 1954) and D. bicolor (Nagao et al., 1955) are presented. Two series of specimens have been selected because in the course of evolution of these species the original X chromosome has undergone various changes (Parkinson and Stonor, 1953). In D. melanogaster the X is more workable as that in D. bicolor. In the present work, the discoidal position in the original X chromosome of Y has been transposed to the 4th chromosome, and in D. bicolor in addition to this translocation the bristle X chromosome is in the 4th chromosome, which in this case has occurred in the formation of a subgenus called Hystrix in the X chromosome (Parkinson and Stonor, 1953). The present work aims at showing that these differences in dosage compensation are the basis of heterochromatin in the male and that despite the evolutionary compartmentation of the X, there are no differences in dosage compensation mechanisms.

MATERIAL AND METHODS

Functional morphology

Wild strains of Drosophila melanogaster (from Brazil) and Drosophila bicolor (from Colombia) were used for these studies. The flies and larvae were reared in the standard Drosophila food at 25°C. The salivary glands from the third instar larval head were dissected out on a slide at pH 9.5 (prepared according to Berendt et al., 1951) and squashed preparations made following the usual technique (Lakshmi and Mookherjee, 1960). From the preparations, the widths of the X chromosomes and a particular autosome (the details are in the manuscript) were measured in the male and female of these two species were measured by the technique described earlier by us (Mookherjee et al., 1960). Lakshmi and Mookherjee, 1960 and the autosomal X chromosome which ratios calculated to examine the enlargement of the X in the male.

Observations

1. Dosage compensation in two different species. The dosage compensation in D. melanogaster (Lakshmi and Mookherjee, 1960) and D. bicolor (Mookherjee, 1960) has been found to be identical. This is in agreement with the fact that the species is a close relative of D. simulans (Rambur, 1842).

2. The dosage compensation in the autosomal X chromosome in D. melanogaster (Mookherjee, 1960) and D. bicolor (Mookherjee, 1960) has been found to be identical. This is in agreement with the fact that the species is a close relative of D. simulans (Rambur, 1842).

3. The dosage compensation in the autosomal X chromosome in D. melanogaster (Mookherjee, 1960) and D. bicolor (Mookherjee, 1960) has been found to be identical. This is in agreement with the fact that the species is a close relative of D. simulans (Rambur, 1842).
Table 1. Autosomal-X chromosome ratio in polytene nuclei of male and female model of Drosophila melanogaster and D. bipunctata.

<table>
<thead>
<tr>
<th>Model</th>
<th>Mean autosomal-X chromosome ratio</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>1.00±0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>Male</td>
<td>1.00±0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>Drosophila</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>1.00±0.01</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>1.00±0.02</td>
<td>0.02</td>
</tr>
</tbody>
</table>

The test for significance of the autosomal-X chromosome ratios was carried out in the male and female model of Drosophila melanogaster and D. bipunctata.
Table 2. — Mixed tissue incorporation in male and female salivary gland nuclei of Drosophila yakuba and D. bicincta.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>M</th>
<th>T</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. yakuba</td>
<td>341</td>
<td>247</td>
<td>104</td>
<td>120</td>
</tr>
<tr>
<td>D. bicincta</td>
<td>382</td>
<td>258</td>
<td>105</td>
<td>106</td>
</tr>
</tbody>
</table>

This table shows the incorporation of mixed tissue in the salivary glands of males and females of Drosophila yakuba and D. bicincta.

In conclusion, the incorporation of mixed tissue in the salivary glands of males and females of Drosophila yakuba and D. bicincta indicates that the male and female nuclei are similar in the two species. The high incorporation rate in the male nuclei suggests that they are more active in DNA synthesis. The differences observed may be due to environmental factors or genetic variations.
D. melanogaster (Mather, 1898), D. subobscura and D. Meigelia, (Kaplan and Ploble, 1972) on D. melanogaster (Mather and Meigelia, 1972). The present work extends this observation to D. subobscura and D. intermedia. As mentioned in the introduction, the behavior of the three species of Drosophila differ in the configuration of their Y chromosomes, in the origin of the Y of D. subobscura and D. intermedia on male autosome region (in both cases not known) in relation to autosomes, is believed to have been by translocation. Since the dosage compensation in Drosophila is not a 'position effect' inasmuch as mutation, it is to be expected that the evolutionary rearrangements that have led to the present situation of the species would not disturb the presumptive regulatory system of dosage compensation in Drosophila. The single Y of the males of D. subobscura and D. intermedia serves as an hypoviril in D. melanogaster. Unfortunately, no genetic studies are available in these species to demonstrate the presence of dosage compensation at a phenotypic level. The results obtained in the present study in the males of D. subobscura in the male and female larval salivary glands in D. intermedia and D. subobscura is consistent with respect to RNA synthesis and comparing with the situation in D. melanogaster (Lange, Langemeyer, Lange, and Alexander, 1972) this would indicate that at a phenotypic level too, there would be, in general, a full compensation of the single Y chromosome in these species.

More detailed studies on different aspects of dosage compensation in three different species of Drosophila would be even more important to have a better understanding of the chromosomal basis of the dosage compensation mechanism. For extensive genetic studies in these species are required to show that at chromosomal level, there is a compensation in the phenotypic level too. So far, at the chromosomal level, a lack of sufficient analysis of RNA synthesis is necessary to show that all the information on the X are equally accessible in these species. Clearly this is the problem of the geneticists in the larval salivary glands, part of the original X, which now has become translocated to the very chromosome, it is necessary to find out the dosage relationships of the genetic loci based on this report, that the Y gene is represented in D. subobscura and D. melanogaster in three doses in the male, but only in two doses in the female. And so, a study of the dosage compensation at chromosomal level in D. subobscura and D. melanogaster with partial dosage compensation at genetic level. Moreover, it is expected to provide a better and clear idea of the dosage compensation mechanism in Drosophila.

LITERATURE CITED


