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ASPECTS OF LOW-TEMPERATURE-INDUCED MEIOTIC NONDISJUNCTION IN DROSOPHILA FEMALES

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Footnote

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Introduction

It has been shown that aging of females of *Drosophila melanogaster* at low temperature induces very high frequencies of meiotic primary nondisjunction of the X chromosomes (Tokunaga, 1970). This paper analyzes several aspects of such induced nondisjunction. It reports on (a) the stage during meiosis at which it occurs; (b) the finding that the nondisjunction is not restricted to the X chromosomes; and (c) the finding of a positive correlation between number of retained mature eggs in treated females and frequency of nondisjunction.

Materials and Methods

In the main experimental series, newly eclosed females were subjected to a "pretreatment" on minimal food at 25°C for 3 days (for composition of the minimal food see Tokunaga 1970). This pretreatment was followed by a "treatment" period of 1 or 2 weeks on minimal food at 10°C. After treatment, the females were placed on normal food at 25°C, and mated for 1 day to males that were at least 3 days old.

Beginning with the end of the treatment period, the females were transferred daily to new culture vials so that successive broods could be obtained. When only broods from the first 5 days were collected no second mating was initiated, but when later broods were collected a second mating was initiated on the sixth day after treatment. In some experimental series, the procedures just outlined were modified by using normal instead of minimal food during the pretreatment or during the treatment period.
In general, single treated females were used for each culture vial. However, since the progeny of the first-day brood is very limited, this brood was mostly obtained from mass matings of usually 15 females and 30 males per vial. In some cases, later broods were collected from random samples of the treated females from which the first-day brood had been collected.

**Results**

1. **Low-temperature-induced nondisjunction occurring at the first meiotic division:** According to earlier experiments (Tokunaga, 1970), the first-day brood from low-temperature-treated females derives mostly from retained mature oocytes which had been subjected to the low temperature. This is the only brood among the first- to 13th-day broods that shows an extremely high frequency of nondisjunction.

   In order to distinguish between the occurrence of nondisjunction at the first and at the second meiotic divisions, the following genetic procedures were employed. Treated females had one normal X chromosome marked by the recessive yellow (y, 1-0.0) and one abnormal X chromosome marked by yellow$^2$ (y$^2$) and by the possession of a short duplication of the tip of a y$^+$ X chromosome, very close to the kinetochore on the right arm. These females were mated to Bar (B, 1-57.0) males. [The normal X chromosome of the females also carried white. Only B and the y alleles will be considered further. In detail, the constitution of the abnormal X chromosome was In(1LR) sc$^V_1$, y$^2$ sc car, y$^+$ (Lindsley and Grell, 1968). It will be referred to as y$^+$ duplication X.] Treatment at low temperature followed 3 days of pretreatment and lasted 1 week.
The regular progeny of the cross consists of $B/+ \text{ females and } +$ and $y \text{ males.}$ Nondisjunction at the first meiotic division would result in exceptional $y^+ B^+,$ XXY females and $y^+ B,$ X0 males. Nondisjunction at the second division would result in the two kinds of exceptions referred to as well as $y, B^+ \text{ females, and } y^2, B^+ \text{ females occurring due to crossing-over between the kinetochore and the } y \text{ locus. Cross-overs between the kinetochore and the } y^+ \text{ duplication would occur very rarely if ever, and are not considered further.}$ The X-chromosome constitution of each exceptional female was tested by mating to $y$ males. If the female were the consequence of nondisjunction at the first division, her male progeny would be $y^+$ and $y;$ if from the second division, only $y^+$ males would be found.

The $F_1$ progeny of the treated females of the first series of experiments are listed in Table 1. There were no $y$ or $y^2$(XXY) daughters. A total of 212 $y^+$ (XXY) females was recovered, of which 210 were from the first day and 2 from later broods. Each of these females was crossed to $y$ males. Nineteen females were either sterile (12 cases, including one from a 9th-day brood), or died (four cases) or were lost before mating (three cases). All the remaining 193 fertile females produced $y^+$ and $y$ sons, thus proving that they had one $y^+$ duplication X and one normal X chromosome. Of the two exceptional daughters from later broods, one was sterile and the other proved to have resulted from nondisjunction at the first division.

The results show clearly that the low-temperature-induced nondisjunction occurred exclusively at the first meiotic division of the eggs retained by the P females during treatment. This finding is similar to
most of the studied cases of spontaneous nondisjunction (see Merriam and Frost, 1964) or nondisjunction induced by meiotic mutants (with one exception; see Sandler, Lindsley, Nicoletti and Trippa, 1968).

2. Low-temperature-induced nondisjunction of X chromosomes and autosomes: Table 1 shows that in addition to XXY and X0 exceptions, 79 flies—i.e., 2.4% of the total first day broods—were triploid intersexes. Seventy of these had a $B^+$ (XXY 3A) phenotype and nine were $B$ (XX 3A).

The recovery of the intersexes at this high frequency cannot be due to accidental presence of triploid females among the parents. If it were, then the intersexes should be found in various later broods instead of exclusively in the first brood.

The 70 XXY 3A intersexes apparently came from eggs which had two second and two third chromosomes, due to failure of reduction in meiosis before fertilization, and were fertilized by Y sperm. The 9 XX 3A intersexes came from eggs in which the X chromosomes had disjoined normally but the long autosomes had failed to do so.

As to the short fourth chromosomes, the situation is not fully clear. Perhaps the failure of disjunction of the long autosomes was accompanied by nondisjunction of chromosome 4; perhaps chromosome 4 had disjoined normally. No decision is offered by the phenotype of the intersexes, since diplo-4 and triplo-4 intersexes cannot be distinguished by mere inspection. There is, however, independent evidence for nondisjunction of chromosome 4, as is shown below.

As pointed out above, 70 out of the total of 79 triploid intersexes involved nondisjunction of the X chromosomes and fertilization by Y sperm. One would expect an equal number of 3X3A triploids originating
from 2X 2A eggs and X sperm. These triploids would have large, slightly B-type eyes due to the B constitution of the X sperm. Prior to the recognition of 2X 3A intersexes in the experiment no search for triploid females had been made, so that such females, if occurring, were lost among the regular F1 B females. If triploid females actually occurred with the same frequency as Y+ triploid intersexes, then the frequency of nondisjunction of the X chromosomes would be considerably higher than judged by the value of 14.44% that is based on recovered exceptions only. The 14.44% is a very much higher frequency than that reported in Table 3 in Tokunaga (1970), which was 5.13%.

In order to ascertain whether the high frequency of autosomal nondisjunction is a typical feature of low-temperature-treated eggs, the experiment was repeated (Table 2). In this second series, broods of the first 3 days were collected and a control series added in which the females were aged on minimal food at 25°C. As expected, there was a high frequency of nondisjunctional exceptions of the X chromosomes in the first day's broods and only one exceptional female in the later broods. Other nondisjunctional exceptions, all arising in first-day broods, included 1 triploid female, 9 intersexes, 5 haplo-4 females, and 1 male who was both X0 and haplo-4 (the haplo-4 flies are included but not listed separately in Table 2). Once again it is apparent that all autosomal exceptions occurred exclusively in the first-day broods, which is evidence against accidental involvement of triploid or haplo-4 P females. Additional evidence for this is the fact that no autosomal exceptions were found among the control flies.
The total number of X-chromosome exceptions among the 1023 first-brood progeny includes 21 $y^+$ females (XXY), 28 B Males (X0), the triploid female, and the 4 $B^+$ intersexes out of a total of nine intersexes. In summary the X nondisjunctional exceptions amounted to 5.2%. This value is not so high as that in the first series of low-temperature experiments, but is very similar to the earlier published value of 5.13% involving normal X chromosomes (Tokunaga, 1970).

The experiments presented so far involve the presence of the $y^+$ duplication X chromosome. In order to test for the possibility that the occurrence of autosomal nondisjunction was caused by the special X chromosome, a third low-temperature experiment was conducted simultaneously with the second; it differed from the second by involving only structurally normal X chromosomes in the P females. Specifically the females were homozygous $y^w$ and the males $++$. A total of 1599 progeny from first-day broods from 1250 treated females included 23 $y$ females (XXY), 34 $y^+$ males (X0), and 5 $y$ intersexes out of 10 intersexes (the other 5 intersexes were $y^+$. The presence of 10 intersexes among the progeny is evidence that autosomal nondisjunction has been induced by the treatment independent of the structural type of the X chromosomes in the P females. The frequency of X nondisjunctional exceptions was 3.17%, which is significantly lower than the 5.2% in the control series of experiments as well as significantly lower than the average 5.13% in the comparable experiments reported earlier.

In summary, the experiments demonstrate the occurrence of nondisjunction of a whole set of diploid chromosomes, or of a set of second
and third autosomes as well as of nondisjunction of the fourth chromosomes either alone or in combination with X-chromosomal nondisjunction.

3. **Factors influencing the frequency of induced nondisjunction:** The various experimental series discussed above yielded significantly different frequencies of X-chromosomal exceptions. It is possible that part of the variation is caused by genetic differences between the females treated. This, however, is not likely to be the sole cause. The very striking difference between the percentages of exceptions in the low-temperature experiments 1 and 2 (14.4 vs. 5.2%) concerned flies of very similar constitutions, including the possession of the \( Y^+ \) duplication X chromosome.

A. nongenetic factor known to influence the frequency of nondisjunction is the duration of the low-temperature treatment. The average frequency observed in earlier experiments with the 2-week treatment was significantly higher than after a 1-week treatment period. However, the frequency was **not** still higher after a 3-week treatment. In the experiments reported herein, duration of treatment was uniformly 1 week, so that this time factor could not account for the different frequencies of nondisjunction.

One possible source of the frequency variation observed could have been variations in the length of the interval from the last collection of newly eclosed females in the culture vessels to the next collection of females to serve as P females in the crosses. Usually, this interval spanned only from 1 to 2 hours; in some cases it was longer, although always less than 4 hours. During longer intervals, females would have
more opportunity to feed on normal food in the culture bottle before
being placed on minimal food for treatment. Such slightly older females
would have more mature eggs retained during pretreatment and treatment
than the younger females. In order to test the hypothesis that the fre-
quency of nondisjunctional exceptions among the first-brood flies can be
increased by increasing the number of retained mature eggs, a further
experiment was made.

Females with normal X chromosomes of the homozygous genotype
were low-temperature-treated for 2 weeks and then mated to wild-
type males. In series A, the females were placed on normal food during
the pretreatment period and on minimal food during treatment. In series
B the females were kept only on normal food. In both series, some eggs
were deposited during the pretreatment period, their number being
estimated as averaging 5.4 per female (650 eggs from 120 females).
After treatment 50 females in each series were separately mated to two
wild-type males each and the first-day broods collected. In addition, at
the end of the pretreatment period the ovaries of 25 females in each
series were dissected out in order to obtain a count of the number of
eggs. The ovaries of another 25 females were dissected out at the end
of the treatment period (the ovaries were fixed, stained by the Feulgen
method, and mounted on slides; see King, Burnett, and Staler, 1957).

The findings in this last series of experiments are given in Table 3,
lines 2 and 3. For comparison, data from previous studies using minimal
food throughout treatment and pretreatment are also presented (line 1).
In series A, there were 51 out of 307 or 16.6% F₁ flies which were X-
chromosomal exceptions; in series B 41 out of 205 or 20% exceptions.
These values are more than twice the value of 49 out of 604 or 8.1% exceptions obtained earlier after provision of minimal food throughout $\chi^2 P < 0.1\%$. Concomitantly, the mean numbers of treated mature eggs in the females in both A and B series are much higher than in the experiments with minimal food only. In the latter there were 7.4 mature eggs per female in contrast to 52.8 in A and 60.2 in B. Similarly, pretreatment with minimal food resulted in 6.0 eggs per female in contrast to 40.68 after pretreatment with normal food.

The results indicate that the greater the number of retained mature eggs in the treated females, the higher is the frequency of low-temperature-induced nondisjunctional exceptions among the first-day brood. This presupposes that all or most mature eggs are deposited during the first day after the end of treatment.

**Discussion**

Our experiments have shown that low temperature applied to aged mature eggs induces nondisjunction of not only the X chromosomes but also whole chromosome sets. This is not the first instance of induction of polyploidy in Drosophila. Mickey and Blount (1951) and Mickey (1958) were able by means of cold shock to produce mosaics for ploidy by affecting mitotic divisions during embryogenesis and larval stages. Whole triploid flies were obtained by Bauer (1946) after administering cold shocks of various intensities and durations to the polar cells of early embryonic stages. Mickey and Blount, however, failed to obtain the same results in an experiment with a different chromosomal constitution of the treated embryo.
In Bauer's experiment, the highest frequency of triploid was 0.75%. In our own series, the highest frequency of triploid intersexes was 2.1% (Table 1, line 1), and the number of triploid females may be assumed to have been similar. Actually, only a single such female was found; probably any other triploids were not recognized because their presence was not suspected. It seems likely that improvements in the technique of inducing triploidy by low-temperature treatment of mature eggs will make this a useful tool in the production of triploids.

It has been known since the work of Mavor (1922-1929) that X rays increase the frequency of nondisjunction of the X chromosome. Later, Patterson, Brewster, and Winchester (1932) showed that X rays applied to retained maturing eggs increase nondisjunction. It is of interest to compare the effects of low temperature with those of X-ray treatment. Although both types of treatment result in increased nondisjunction, there are distinct differences. It was pointed out earlier (Tokunaga, 1970) that the sex ratio of nondisjunctonal exceptions, XXY: X0, tends to be 1:1. This also holds true for all experiments reported in this paper. In contrast, the presence of many more X0 males than XXY females is characteristic for both spontaneous and X-ray-induced cases. The excess of X0 males over XXY females has been interpreted as due to meiotic loss of X chromosomes, a loss which is superimposed on nondisjunctonal events (Morgan, Bridges, and Sturtevant, 1925). When this interpretation is applied to the X-ray-induced exceptions of Patterson, Brewster, and Winchester, a substantial number of X0 males must be attributed to chromosome loss. This drastically reduces the frequency of true nondisjunction, in contrast to the very high frequency in low-temperature
induction. Thus the three authors found 51 males and 5 females among 1262 offspring of X-rayed, aged mothers, i.e., 4.43% exceptions. Adjusted for equality of sex ratio, only 0.79% of the flies were truly nondisjunctional. Similarly, among 3997 control offspring, of mothers aged without x raying, 5 males and 0 females were exceptional. The raw frequency of 0.11% nondisjunction decreases to an adjusted frequency of 0%.

Another difference is that low-temperature effect is restricted to the retained mature eggs. The X-ray effect is similarly very high with regard to the retained mature eggs (first-day brood), but the subsequent broods also indicate higher frequencies of exceptions compared with the control (see Tables IV and V, Patterson et al., 1932). In comparison, Mavor's original studies covered the effect of X-rays applied to females of ages ranging from pupal to adult stages without aging treatment (Mavor, 1924, 1929). In other words, the X-ray effect is not restricted to the retained mature eggs but is extended to the earlier stages of eggs.

Patterson et al. suggested that the susceptibility may be related to the condition of the chromatin in maturing eggs under aging conditions. More recently Mikamo (1968) has attributed the effect of overripeness of eggs in the amphibian Xenopus to faulty spindle formation. Furthermore, abnormalities of the spindle involved in nondisjunction have been observed in eggs from homozygotes for the "claret" nondisjunction gene in Drosophila simulans (Wald, 1936). In analogy to the situation in D. simulans, Davis (1969) suggested that nondisjunction in a homozygote for the "claret nondisjunctional" gene in D. melanogaster is also due to abnormal spindle formation. No cytological observations were made in this case.
It remains to be seen whether the high susceptibility of retained mature eggs to low-temperature induction is due to chromosomal or to spindle defects.

Summary

1. Low-temperature-induced nondisjunction of the X chromosome in retained mature eggs occurs exclusively at the first meiotic division.

2. In addition to X-chromosomal exceptions, other exceptions occur following nondisjunction of chromosome 4 and of chromosomes 2 and 3. Various combinations of exceptional types were found, including individuals nondisjunctional for chromosomes X, 2, 3, and possibly 4.

3. The frequency of exceptions induced among the first-day brood can be raised by increasing the number of mature eggs in the ovaries by feeding the females well, before the treatment.

4. The sex ratio of X-chromosomal exceptions induced by low temperature is approximately 1:1, in contrast to X-ray-induced exceptions, which contain a surplus of males.

5. The efficiency of inducing polyploidy by subjecting retained mature eggs and embryonic polar cells to low temperature is discussed.
Acknowledgment

The author is very grateful to Dr. Curt Stern for his constructive comments during the course of investigation and during the preparation of the manuscript. The outstanding technical assistance of Mrs. P. C. Ulrichs is especially appreciated, as is help by Miss T. L. Gregg. Thanks are also due to Dr. Collin Murphy and Mr. G. Williams for their helpfulness during preparation of the manuscript.

Literature Cited


1929 The effect on crossing-over and nondisjunction of X-raying the anterior and posterior halves of Drosophila pupae. Genetics 14: 129-159.


Tokunaga, C., 1970 The effects of low temperature and aging on nondisjunction in *Drosophila*. Genetics 65:

Wald, H., 1936 Cytologic studies in abnormal development of the eggs of the claret mutant type of *Drosophila simulans*. Genetics 21: 264-281.
Table 1. Progeny of the crosses between 1-week low-temperature-treated (10°C) females of \( \text{In(1LR) sc}^V_1, \ y^2 \text{ sc car} \cdot y^+ / y \ w \) and B males. Only the phenotypes \( y, y^2 \) and B alleles are described. (First-day brood is from 2085 treated females, and the remaining broods are from 142 females randomly selected from the 2085 treated females).

<table>
<thead>
<tr>
<th>Brood (day)</th>
<th>Females</th>
<th>Males</th>
<th>Females</th>
<th>Males</th>
<th>Triploid</th>
<th>Total</th>
<th>X-chromosomal exceptions (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>B</td>
<td>( y^+ )</td>
<td>( y \text{ (or } y^2 ) )</td>
<td>( y^+ )</td>
<td>( y \text{ (or } y^2 ) )</td>
<td>B</td>
<td>B^+</td>
</tr>
<tr>
<td>1</td>
<td>1420</td>
<td>620</td>
<td>734</td>
<td>210</td>
<td>0</td>
<td>190</td>
<td>70</td>
</tr>
<tr>
<td>6</td>
<td>4750</td>
<td>2447</td>
<td>2546</td>
<td>0</td>
<td>0</td>
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<td>0</td>
</tr>
<tr>
<td>7</td>
<td>4919</td>
<td>2338</td>
<td>2688</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>5132</td>
<td>2388</td>
<td>2883</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>4162</td>
<td>2016</td>
<td>2384</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>10-11</td>
<td>3525</td>
<td>1574</td>
<td>2090</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
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</table>
Table 2. Progeny of the crosses between 1-week low- (10°C) or control (25°C) temperature treated females of In(1LR) \( sc \) \( v^1 \), \( y^2 \) \( sc \) car \( v^+/y \) w and \( B \) males. Only the phenotypes \( y \), \( y^2 \) and \( B \) alleles are described. (First-day brood is from 525 (10°C) or 600 (25°C) treated females, and the remaining broods are from 125 females randomly selected from the treated females.

<table>
<thead>
<tr>
<th>Brood (day)</th>
<th>Regular Males</th>
<th>Regular Females</th>
<th>Exceptional Males</th>
<th>Exceptional Females</th>
<th>Triploid Triploid</th>
<th>Triploid Total</th>
<th>X-chromosomal exceptions (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>469 y+</td>
<td>294 y( or y^2)</td>
<td>201 y+</td>
<td>21 y( or y^2)</td>
<td>28 B</td>
<td>1 B</td>
<td>4 5</td>
</tr>
<tr>
<td>2</td>
<td>2349 y+</td>
<td>1372 y( or y^2)</td>
<td>1130 y+</td>
<td>1 y( or y^2)</td>
<td>0 B</td>
<td>0 B</td>
<td>0 0</td>
</tr>
<tr>
<td>3</td>
<td>3245 y+</td>
<td>2059 y( or y^2)</td>
<td>1684 y+</td>
<td>0 y( or y^2)</td>
<td>0 B</td>
<td>0 B</td>
<td>0 0</td>
</tr>
</tbody>
</table>

**10°C series**

<table>
<thead>
<tr>
<th>Brood (day)</th>
<th>Regular Males</th>
<th>Regular Females</th>
<th>Exceptional Males</th>
<th>Exceptional Females</th>
<th>Triploid Triploid</th>
<th>Triploid Total</th>
<th>X-chromosomal exceptions (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1026</td>
<td>636</td>
<td>571</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0 0</td>
</tr>
<tr>
<td>2</td>
<td>3408</td>
<td>1950</td>
<td>1734</td>
<td>0</td>
<td>0</td>
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<td>0 0</td>
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<tr>
<td>3</td>
<td>2984</td>
<td>1708</td>
<td>1430</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0 0</td>
</tr>
</tbody>
</table>

**25°C series**
Table 3. The effect of different food supply on the number of Stage 14 eggs in the ovary and on the frequency of X chromosomal nondisjunction in 2 weeks low temperature treated y w females. The sample size for the egg count is 25 females in each series.

<table>
<thead>
<tr>
<th>Food</th>
<th>Number of Stage 14 eggs</th>
<th>X exceptions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>After pretreatment</td>
<td></td>
</tr>
<tr>
<td>Pretreatment</td>
<td>After treatment</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Average per (%)</td>
<td>Range (%)</td>
</tr>
<tr>
<td>(3 days at 25°C)</td>
<td>Average per (%)</td>
<td>Range (%)</td>
</tr>
<tr>
<td>minimal</td>
<td>minimal</td>
<td>6.0±0.52</td>
</tr>
<tr>
<td>normal</td>
<td>minimal (A)</td>
<td>40.68±2.33</td>
</tr>
<tr>
<td>normal</td>
<td>normal (B)</td>
<td>60.2±3.05</td>
</tr>
</tbody>
</table>
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