MUTAGENIC SENSITIVITY OF MATURING DROSOPHILA SPERM

II. DELETED X's

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(With Five Text-figures)

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INTRODUCTION

Much evidence has recently accumulated that the early post-meiotic stages of Drosophila sperm are more sensitive than mature sperm to the mutagenic effects of X-rays. This has been demonstrated for dominant lethals (Lüning, 1952a), recessive lethals (Auerbach, 1954), deleted X's (Lüning, 1952b) and translocations (Oster, 1955).

The present author had endeavoured to study this phenomenon in greater detail and in a more quantitative way. For this, the dominant lethal response was chosen (Bateman, 1956) as the simplest genetic change available for study.

However, experiments on feeding 32P to larvae as a mutagen (Bateman, 1955) had indicated that the incidence of deleted X's was especially sensitive to maturation stage, and warranted special study parallel with dominant lethals. Hence this paper.

METHODS

In his study of deleted X's, Lüning mated irradiated males to yellow females and scored the frequency of hyperploid, non-yellow sons (hyperploid for an X fragment carrying the wild-type allele of the yellow locus at one end and the centromere at the other— a 'deleted' X). In the following experiments, attached-X yellow females were used and the frequency of non-yellow hyperploid daughters was observed. The second method gives a much better yield of deleted X's because the addition of an X fragment has a much less drastic effect on the viability of females than on males. Following 960 r. Lüning obtained a maximum of 0-1% hyperploid males. My maximum after 1000 r. was 4% hyperploid females.

A comparison of the viabilities of males and females carrying the same X fragment was provided as a by-product of the progeny testing of suspected hyperploid females. Fragments which produced no effect on viability in the female had a maximum viability in the male of 0-4. Fragments reducing the viability of females to two-thirds were lethal in the male.

One might expect that if reduced viability is one of the general consequences of hyperploidy, small variations in cultural conditions, such as degree of crowding, would produce big changes in the recovered frequency of hyperploids. If that were so, hyperploids from crowded cultures would show a mean viability higher than those from sparse cultures. Such an effect was not, however, detectable. It is inferred that any increase in size of the

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fragment above a certain critical value produces complete lethality under all the cultural conditions encountered in these experiments.

Two attached-X stocks were used: y and y vicro. The mated females were obtained by outercrossing in the previous generation to Muller-5 males. This gave improved vigour, while at the same time enabling the recognition of matings involving non-virgin females. At first the y stock was used as this had a higher fertility and a higher mating incidence. It was not, however, possible to distinguish with certainty, except by progeny tests, true hyperploids from non-yellow females which had arisen through detachment or the odd contamination, though a high proportion of the hyperploids showed characteristic phenotypes such as branched veins, rough eyes and notched wings. It was therefore necessary to progeny test many non-yellow daughters. When they proved completely sterile their sterility was attributed to hyperploidy.

Using y vicro females, on the other hand, progeny tests were unnecessary as the true hyperploids were identifiable as homozygotes for one or more of the marker genes not covered by the y-bearing fragment. A complication from using this stock however, was the difference in viability of the two sexes. The y vicro females had only three-quarters the viability of their wild-type brothers. Now in measuring the frequency of hyperploids one may use as standard the frequencies of euploid males or females. The males represent the frequency of treated X's recovered (that is, less recessive and dominant lethals and those entirely lost through damage to the centromere). The females represent the frequency of treated Y's plus the lost X's. In the y series the results were the same whichever standard was used, except for the most immature sperm, when the high frequency of X-borne lethals depressed the male standard.* In the y vicro series it was decided to use the females as the standard as the chromosome constitution of the females which depressed their viability was common also to the hyperploids. Consequently euploid sisters were used as the standard in both series.

Dose Dependence

The dose relationship of all second order responses is generally taken to be according to the $\frac{3}{2}$ power of the dose. This has been found to apply specifically to deleted X's (Muller, 1938). Whilst Muller has tended to regard this as a law, 'the $\frac{3}{2}$ power rule', more mathematically minded workers (Haldane & Lea, 1947; Baker, 1949) have pointed out that this is a purely empirical relationship due to the averaging out of various factors over the dose range used, which is limited by practical considerations. Owing to the non-linearity of the dose curve, below a dose of about 1000 r. for ripe sperm the frequency of rearrangements becomes too low for accurate measurements. Above a few thousand roentgen, sterility due to dominant lethals again leads to too low a yield of rearrangements.

For the purposes of this paper therefore it was necessary to reinvestigate the dose-dependence of deleted X's. The dose ranged from 1000 to 10,000 r., and sampling was confined to the first 3 days' mating of males emerging overnight before the irradiation and then mated immediately to two females per day. As will be shown later, there was no consistent variation in the rate of deleted X's over the 3 days, which were therefore pooled.

* There was one extreme case in the post-sterile matings of a male given 10,000 r. He produced only daughters. His spermatogonia must have all carried sex-linked lethals, presumably at one, or at most a few, loci. This is evidence that the number of primary spermatogonia responsible for the recovery of fertility can be very small indeed.