THE EFFECT OF RADIATION-INDUCED MUTATIONS ON THE FITNESS OF DROSOPHILA POPULATIONS*

B. G. BLAYLOCK and H. H. SHUGART, JR.

Oak Ridge National Laboratory, Oak Ridge, Tennessee 37830

Manuscript received November 14, 1969
Revised copy received June 29, 1972

ABSTRACT

The change in frequencies of D. melanogaster and D. simulans in competition experiments was used to measure the effect of radiation on the fitness of a population. A dose of 250 or 500 rads given to the males of highly inbred lines of D. simulans at the beginning of competition and every three weeks thereafter increased the relative frequency of the irradiated population. If the dose was increased to 1000 rads, the deleterious effects of radiation became too great a burden on the population, and the frequency of the irradiated population decreased. From these results it was concluded that below certain doses the introduction of radiation-induced mutations into a highly homozygous population would increase the fitness of the population.

THE effect that newly induced mutations have on the fitness of an individual has received considerable attention during the past decade. However, there is still considerable controversy among outstanding workers in this area. Although the consensus of most geneticists is that newly induced mutations lower the fitness of an individual, a review of the literature by DOBZHANSKY (1964) found conflicting results and conclusions.

Notable exceptions were those of WALLACE (1958, 1963), BURDICK and MUKAI (1958) and MUKAI (1961). WALLACE (1958) found that under certain conditions radiation-induced mutations on the average were favorable in the heterozygous condition. CRENSHAW (1965) working with Tribolium confusum obtained similar results. When considering these results, it should be emphasized that in both cases radiation-induced mutations were introduced into a genetic background made homozygous by inbreeding. LERNER (1954) and MUKAI et al. (1965) observed an optimum level of heterozygosity. Until this level was reached a greater proportion of newly arising mutants have heterotic effects than after this level was reached or exceeded. MUKAI, YOSHIKAWA and SANO (1966) demonstrated that mutations, mainly polygenic, induced with 500 rads of X irradiation were heterozygously slightly beneficial in a homozygous genetic background. DOBZHANSKY and SPASSKY (1968) concluded that the effect of newly arising mutations on the fitness of an individual depended on the intrinsic properties of the mutation and the genetic background into which it was introduced.

* Research sponsored by the U. S. Atomic Energy Commission under contract with the Union Carbide Corporation.

In most experiments the fitness of an individual or a Mendelian population was measured by evaluating one or more components of the life cycle such as fecundity, longevity, hatchability, etc. The competitive displacement principle was employed by Claringbold and Barker (1961) and Barker (1963) to estimate the fitness of Drosophila populations. In the present study the rate of change in the frequencies of *Drosophila melanogaster* and *Drosophila simulans* in competition was used to estimate the relative fitness of the populations. Blaylock (1969) has shown that irradiation can change the outcome of competition between *D. melanogaster* and *D. simulans*.

The purpose of the present study was to determine whether the relative fitness of a highly inbred line of *D. simulans* in competition with *D. melanogaster* could be increased by irradiation. Fitness in this case refers to the relative frequency of *D. simulans* in the total adult population at a particular time.

**MATERIALS AND METHODS**

The strains of *Drosophila melanogaster* and its sibling species, *Drosophila simulans*, used in this experiment are the same ones used in previous competition experiments by Blaylock (1969). The *D. melanogaster* strain contained the "e" sooty marker in order to distinguish easily both sexes of *D. melanogaster* from *D. simulans*. Inbred lines of both species were established by sibling matings for more than 20 generations. Laboratory populations were usually started with 25 virgin females and males of each species.

The population cages and the technique for counting the total adult population were described by Blaylock (1967). The total number of adults of each species were counted every 21 days and transferred along with food cups containing larvae and pupae to another cage to continue the population. One of the three food cups containing 40 ml of a corn meal live-yeast medium was changed weekly. Population cages of this type will support from one to two thousand adult Drosophila.

The source of radiation was a 60Co Cobalt Gammacell 200 from the Atomic Energy of Canada Ltd. The adult males were given a dose of 250, 500 or 1000 rads at a dose rate of approximately 8 rads/sec. The male *D. simulans* receiving irradiation were treated immediately before the population was started and every 21 days thereafter when the population was counted. Inbred populations of *D. simulans* in competition with inbred *D. melanogaster* populations were given the following treatments:

1) Controls. (n=3)
2) 250 rads to *D. simulans* males (n=2)
3) 500 rads to *D. simulans* males (n=3)
4) 1000 rads to *D. simulans* males (n=1).

Data were analyzed using canonical correlation analysis (Seal 1964).

**RESULTS**

The effect of radiation on the fitness of the Drosophila populations is shown by plotting the average numbers of *D. simulans* in populations subjected to the different treatments against time (Figure 1). Clearly the responses of the control populations strongly resembled that of the population treated with 1000 rads to the *D. simulans* males. The 250- and 500-rad treatments were similar to one another, but were markedly different from the controls and the 1000 rad treatment (Figure 1).
Figure 1.—Mean numbers *Drosophila simulans* in competition with *Drosophila melanogaster* determined at 21-day sampling periods. The males of *D. simulans* were treated with 0 (control), 250, 500 or 1000 rads at the start of each experiment and every three weeks during competition.

Canonical correlation analysis (Seal 1964) using 95% “circles of uncertainty” indicated the total number of flies in the population cages were similar (under) the control and 1000 rad treatment (Figure 2). The 250- and 500-rad treatments were similar to one another in total number of flies, and both were significantly different from either the 1000-rad treatment or the controls (Figure 2). Cages in which the male *D. simulans* had been treated with 250 or 500 rads generally held more flies of both species.

Percentage of *D. simulans* and the population sites of *D. simulans* differed among all 4 treatments (Figure 2), but the 250-and 500-rad treatments were associated with an increase in percentage and numbers (Figure 1) of *D. simulans*. The numbers of *D. melanogaster* showed considerable overlap (Figure 2) and only the controls and the 250-rad treatments showed significant differences (Figure 2). The *D. melanogaster* in competition with *D. simulans* subjected to the 250-rad treatment were less numerous than in the control populations.

**DISCUSSION**

Most radiation effects studies concerning the fitness of populations have dealt with single species populations. Barker (1967) has reviewed some definitions of fitness and concluded that although it is still necessary to consider various meas-
Figure 2.—Results of competition experiments with treatments of 0 (control), 250, 500 or 1000 rads to male Drosophila simulans. Circles represent 95% “circle of uncertainty” (Seal 1964). Upper right: Percentage D. simulans. Lower right: Number of D. simulans. Lower left: Number of D. melanogaster. Upper left: Total numbers of flies of both species in population cages.
ures of fitness in single species of populations to understand a given genetic situation, the more complex model involving interspecific competition should provide a more realistic estimate of population fitness. In this study the use of interspecific competition between *D. melanogaster* and *D. simulans* proved to be a sensitive way to demonstrate the effects of radiation on the fitness of a population.

The fitness of the *D. simulans* populations was increased by doses of 250 and 500 rads (Figures 1 and 2). This demonstration of an increase in fitness agrees with the results of Wallace (1956) and Crenshaw (1965) and supports the hypothesis that in a homozygous genetic background radiation-induced mutations which would be deleterious in the homozygous condition can produce a heterotic effect.

Under the 1000-rad treatment, the difference in the frequency of *D. simulans* in the irradiated and control population decreased. At this level of irradiation, the frequency of recessive lethals and deleterious genes would accumulate most rapidly in the gene pool of the population (Wallace 1956; Mourad 1962; San-karanarayanan 1964). As the frequency of these genes increased, the deleterious effects on the fitness of the population would be expressed.

Carson (1961) and Cannon (1963) have shown that when varying amounts of foreign genetic material were introduced into inbred populations, a large increase in population size was observed. However, when the genetic diversity was introduced by irradiating the population, Carson (1964) concluded that new mutations introduced by irradiation did not appear to improve the fitness in experimental populations. Van Delden and Beardmore (1968) observed an increase in fitness when genetic variation produced by radiation-induced mutations was injected into inbred experimental populations. Their conclusion which disagrees with that of Carson's (1964) was explained by a difference in radiation dose. Van Delden and Beardmore suggested that heavy doses of radiation produced so many deleterious mutations that the chance of a favorable mutation being selected was very low. Our results (Figure 2) emphasized the different effects that doses of 250, 500 and 1000 rads can produce on the fitness of a population. Apparently the deleterious mutants produced by the dose of 1000 rads were too great a burden on the fitness of the population, and the effect of any favorable mutants was concealed. Thus, it appears that under these conditions the level of radiation determines whether the favorable effect of radiation-induced mutations will be expressed as an increase in the fitness of a population.

It was evident from these data that the fitness of a highly inbred population was increased by radiation; however, the increase in fitness was dependent upon the level of radiation. These results support a hypothesis that in a highly inbred population, heterozygosis for radiation-induced mutations is on the average favorable when the dose is below a certain level and will be expressed as an increase in fitness of the population. On the other hand, at doses above this level of radiation the frequency of deleterious mutants overshadows the favorable mutants, and the fitness of the population will decrease.

We are indebted to John Beauchamp for statistical consultation.


