FURTHER DATA ON THE GENETIC LOADS IN IRRADIATED EXPERIMENTAL POPULATIONS OF *DROSOPHILA MELANOGASTER*¹

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A study of the effects of genetic loads on the viability of irradiated and unirradiated experimental populations of *Drosophila melanogaster* has been published by SANKARANARAYANAN (1964). In contrast to the somewhat similar experiments of WALLACE (1956) and MOURAD (1962, 1964), the populations were maintained under conditions designed to minimize the natural selection due to larval competition and crowding. In every generation, numbers of eggs sufficient to produce between 50 and 70 adults were taken, and allowed to develop in uncrowded cultures with abundant food. The adult males received in every generation 2000r, 4000r or 6000r of X rays. The egg to adult viability in the respective populations fell rapidly for several generations, and then tended to decline very slowly or become stabilized at levels depending upon the radiation received. At various times subpopulations were derived from the chronically irradiated ones, and propagated without further irradiation. The egg to adult viability in such "relaxed" populations recovered rapidly, and in three to six generations arrived close to, but usually did not attain, the control level (i.e., the viability level in unirradiated populations).

The recovery of the relaxed populations is clearly due to the elimination of the components of the genetic loads with dominant and semidominant deleterious effects. The inquiry, the results of which are described in the present communication, concerns other components of the genetic loads influencing the viability, namely, the recessive, near-recessive and overdominant genetic variants. As will be shown below, the populations well on the road to recovery of their viability continue to harbor very large concealed genetic loads.

MATERIALS AND METHODS

Descriptions of the experimental populations used in the present work are summarized in Table 1. For more details, see SANKARANARAYANAN (1964). All the populations were maintained from generation to generation in half-pint culture bottles under near-optimal conditions. Females were allowed to oviposit in 6 inch glass vials with spoons containing cornmeal-molasses-agar medium darkened with charcoal. Eggs were counted 4 to 8 hours after deposition, and transferred to fresh culture bottles. The numbers of eggs taken for each experimental population varied depending on the radiation dose and the viability record. They were adjusted to yield approximately 40 to 60 adult flies per bottle. For instance, the number of eggs counted per replicate culture was 60 in the Control, 100 in II-EGR, 200 in IV-ER and 350 in VI-ER. In

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TABLE 1

Characteristics of the experimental populations

Population	X-ray treatment	Started	Ended
C-1	Control—no radiation	Sept 1962	continued
C-2	Control—no radiation	Nov 1962	Dec 1963
II-EGR	2000r in every generation	Feb 1962	Nov 1964
IV-ER	4000r in every generation	Nov 1962	Nov 1964
VI-ER	6000r in every generation	Nov 1962	Nov 1964
II-EGR-60	Derived from II-EGR after 60 generations; no radiation later	June 1964	continued
IV-ER-30	Derived from IV-ER after 30 generations; no radiation later	Dec 1963	continued
VI-ER-20	Derived from VI-ER after 20 generations; no radiation later	July 1963	continued

Abbreviations: C=controls; II, IV and VI indicate X-radiation administered in kiloröntgens. "ER" and "EGR" denote every-generation radiation. Arabic numerals indicate the number of generations after which radiation was discontinued.

later generations, these numbers were increased to 125 in II-EGR, 225 in IV-ER and 400 in VI-ER. In the subpopulations VI-ER-20, IV-ER-30 and II-EGR-60, at the generation of their relaxation from radiation, the numbers of eggs counted were, respectively, 150, 100 and 75. With increase in egg-adult viability, these numbers were progressively reduced to 60. Fifteen replicate cultures were maintained for each population, and the population size was in the range of 600 to 750 adults. In the populations where the males were to be irradiated, the females were isolated as virgins.

The second chromosomes from the experimental populations were analyzed genetically to detect genetic variants affecting the viability, which are carried in the population concealed in heterozygous condition. The technique of four-class tests devised by WALLACE has been used (for details see WALLACE 1956). Briefly, males from the experimental populations were crossed singly to Curly-Lobe-Plum analyzer (*Cy L/Pm*), carrying mutant marker genes and appropriate suppressors of recombination. Single *Cy L/+* males in the F_1 generation were backcrossed to the *Cy L/Pm* stock. Four *Pm/+* males and an equal number of *Cy L/+* females were selected in the progeny and intercrossed. To test chromosomes in the homozygous condition, brother-sister matings were used. To test the chromosomes in the heterozygous condition, *Pm/+* F_2 males of one line were outcrossed to *Cy L/+* females of another. Four classes appear in F_3 : (1) *Cy L/Pm*, not carrying the second chromosomes from the experimental populations, (2) *Cy L/+*, (3) *Pm/+*, and (4) *+/+*. Each chromosome or chromosome combination was tested in two replicate cultures.

RESULTS

1. *Egg-adult viability in the chronically irradiated populations*: Figure 1 summarizes the egg to adult viability recorded in the experimental populations. These data extend those reported by SANKARANARAYANAN, 1964, Tables 4a and 4b and Figures 4, 5, and 6. The viability of the Control population has remained steady at 87 to 90%. In the irradiated population II-EGR, which received 2000r per generation, the viability fluctuated between 40 and 60%, in IV-ER between 20 and 32%, and in VI-ER between 12 and 20%.

A regression analysis for the viability data has been made for all the populations (Figure 2). While all the generations are included for the Control, the first

FIGURE 1.—Egg-adult viability in the experimental populations. A = control; E = II-EGR; F = IV-ER; G = VI-ER; B = VI-ER-20; C = IV-ER-30; D = II-EGR-60.

FIGURE 2.—Regression of egg-adult viability on generations in the experimental populations. Triangles = control; squares = II-EGR; black circles = IV-ER; white circles = VI-ER (First four generations are excluded in all populations except the control. For explanation, see text.)

four are excluded for the chronically irradiated populations. This is because the decline in viability occurs during approximately this period, and thereafter the viability level fluctuates around an equilibrium. The regression values are as follows:

Control: Generation 1-60: $Y = 90.6 - 0.024X$, $\delta_b = 0.015$

II-EGR: Generation 5-70: $Y = 52.5 - 0.070X$, $\delta_b = 0.036$

IV-ER: Generation 5-54: $Y = 31.5 - 0.225X$, $\delta_b = 0.048$

VI-ER: Generation 5-54: $Y = 17.7 - 0.095X$, $\delta_b = 0.029$

The regression coefficients of the irradiated populations can be compared with that of the Control, using the Student's *t*-test. The results are as follows:

Control and II-EGR: $t = 1.13$, d.f.: 122, *P* between 0.20 and 0.30

Control and IV-ER: $t = 5.85$, d.f.: 106, $P < 0.01$

Control and VI-ER: $t = 2.55$, d.f.: 106, *P* between 0.01 and 0.02

While the viability of the population II-EGR did not significantly decline between Generations 5 and 70, the heavily irradiated populations show a slow decline. Although a simple rectilinear regression analysis may not be quite satisfactory, it is clear enough that the estimated decline in the viability is small relative to that which occurs in the first few generations. This is to be expected

if the populations are more or less at equilibrium with respect to the inflow of new harmful mutants and their elimination by natural selection.

2. *Egg-adult viability in irradiated and relaxed populations*: Most interesting is the behavior of the relaxed subpopulations, derived from the chronically irradiated ones and maintained without further irradiation. Some of the subpopulations described by SANKARANARAYANAN (1964) attained 90 to 95% of the Control viability in three to seven generations following the cessation of the irradiation. In the present experiments, the recovery patterns of three relaxed populations are compared. All these accumulated a radiation exposure of 120,000r before the relaxation. They differed in the number of generations during which this total exposure was accumulated. The population VI-ER-20 received 6000r in each of 20 generations, IV-ER-30 was getting 4000r in a series of 30 generations, and finally II-EGR-60 was given 2000r in each of 60 generations. The results are summarized in Figure 1 and Table 2. If generations 0 to 4 are excluded, the mean viability is 75.8% in VI-ER-20, 70.6% in IV-ER-30 and 71.5% in II-EGR-60. This viability level of 70 to 75% has persisted for 43 generations in VI-ER-20, 33 generations in IV-ER-30 and for 20 generations in

TABLE 2

Egg to adult viability in percent in subpopulations VI-ER-20, IV-ER-30 and II-EGR-60

Generation*	VI-ER-20	IV-ER-30	II-EGR-60	Generation	VI-ER-20	IV-ER-30
0	12.6	29.3	45.4	23	75.2	74.6
1	46.8	50.1	64.3	24	74.0	75.1
2	46.7	59.5	64.8	25	75.0	73.8
3	63.4	60.4	71.2	26	77.6	75.1
4	72.3	69.2	65.7	27	74.7	78.9
5	77.9	72.6	70.1	28	75.9	73.9
6	77.0	73.1	71.9	29	77.7	72.6
7	72.1	69.3	73.3	30	75.6	70.4
8	74.3	69.3	70.6	31	73.7	70.7
9	73.9	70.8	72.6	32	77.0	73.1
10	75.0	72.0	70.8	33	73.8	72.4
11	78.5	65.2	70.3	34	72.3	...
12	76.4	71.2	69.1	35	78.3	...
13	75.3	71.6	72.9	36	77.1	...
14	71.0	65.1	75.6	37	77.4	...
15	80.7	63.6	72.1	38	75.3	...
16	80.7	65.0	68.9	39	74.1	...
17	80.4	70.1	69.2	40	74.2	...
18	76.1	68.9	71.7	41	73.0	...
19	74.3	67.1	71.3	42	73.8	...
20	76.1	65.9	73.2	43	76.5	...
21	78.6	68.4	...	...	...	...
22	75.8	68.8	...	...	...	...
Mean†			71.5 ± .45		75.8 ± .37	70.6 ± .67

* Generations refer to generations of relaxation from radiation. i.e., Generation 0 = Generation 20 of Figure 1 for VI-ER-20, etc.

† Generations 0-4 are excluded.

TABLE 3

Frequencies of second chromosomes carrying lethals and semilethals in the experimental and control (C) populations

Population	Generation	Chromosomes tested	Lethals	Semilethals	Percent lethals and semilethals
C-1 and C-2	14 and 20	135	19	5	17.8 $\pm$ 3.3
VI-ER	20	108	90	5	87.9 $\pm$ 3.1
IV-ER	30	103	87	6	90.3 $\pm$ 2.9
II-EGR	60	107	61	.	57.0 $\pm$ 4.8
VI-ER-20	19	145	110	.	75.9 $\pm$ 3.6

II-EGR. The observation that the levels to which the viabilities rise are extremely similar in the three derived populations is perhaps not unexpected in view of the fact that each of them has received 120,000r, although at three different rates.

3. *Concealed genetic variability in the experimental populations:* The numbers and percentages of the second chromosomes which were found to be lethal or semilethal in double dose are presented in Table 3. A lethal is defined as a chromosome giving fewer than 2.3% wild-type flies in the cultures, a semilethal between 2.4% and 11.9% and a quasinormal more than 11.9%. The ideal Mendelian ratio of +/+ flies in the test crosses is 25%. Note should be taken of the fact that the chromosome analysis has been made at the 20th generation in VI-ER, at the 30th in IV-ER, at the 60th in II-EGR and at the 19th in VI-ER-20. Each of these populations has received an accumulated dose of 120,000r, as stated above, but delivered at different rates per generation. In the populations VI-ER and IV-ER roughly nine out of every ten second chromosomes are lethal or semilethal when homozygous, and the frequencies of such "drastic" chromosomes are not significantly different in the two populations. The population II-EGR shows, on the other hand, a much lower frequency, 57%. This is not significantly higher than the frequency, $50.0 \pm 6.6\%$, observed in the population II-ER, which received 28,000r in 14 generations (SANKARANARAYANAN 1964, Table 6). It appears, then, that the genetic loads may not be the same in populations with the same total accumulated radiation exposures.

One may, accordingly, expect that the genetic loads will also be reduced with time in the populations after the relaxation of the radiation treatment. This is what is actually observed. As shown in Table 3, the frequency of lethal and semilethal chromosomes in the population VI-ER-20 was reduced from 87.9% to 75.9% in 19 generations of relaxation from radiation. On the other hand, it should be emphasized that the 19 generations of relaxation have by no means reduced the genetic load to the Control level (17.8%).

The data on the viability of the tested chromosomes from the experimental populations are summarized in Table 4. The test-cross design was such that the +/+ class was homozygous for the second chromosomes in one series of crosses and heterozygous in others. The viability of all the classes is expressed in relation to that of the *Cy L/Pm* class (WALLACE 1956; HALDANE 1956).

When all the chromosomes—lethal, semilethal and quasinormal—are con-

TABLE 4

Estimates of the viability (relative to that of the standard class) of the homozygotes and heterozygotes for second chromosomes in certain populations

Population	Generation	<i>Cy</i> L/+		<i>Pm</i> /+	
		N	D	N	D
VI-ER	20	1.200 ± .041 (33)	1.182 ± .016 (244)	1.204 ± .061 (42)	1.308 ± .018 (235)
IV-ER	30	1.141 ± .040 (27)	1.157 ± .016 (174)	1.393 ± .106 (17)	1.399 ± .025 (184)
II-EGR	60	1.197 ± .021 (103)	1.138 ± .018 (115)	1.435 ± .029 (105)	1.387 ± .025 (113)
VI-ER-20	19	1.177 ± .022 (63)	1.192 ± .017 (198)	1.400 ± .036 (70)	1.433 ± .026 (191)
Population	Generation	Homozygous		Heterozygous	
		All	N		
VI-ER	20	0.118 ± .029 (108)	0.876 ± .079 (13)	1.356 ± .024 (169)	
IV-ER	30	0.120 ± .034 (103)	1.020 ± .155 (10)	1.290 ± .028 (92)	
II-EGR	60	0.491 ± .058 (107)	1.142 ± .044 (46)	1.376 ± .030 (109)	
VI-ER-20	19	0.243 ± .039 (145)	1.068 ± .054 (33)	1.358 ± .028 (109)	

N represents quasi-normal chromosomes; D, "drastic" (lethal and semilethal) chromosomes. The number of tested chromosomes or chromosome combinations is shown in parenthesis.

sidered together, the estimated mean viability of the +/+ homozygotes is extremely low relative to that of the homozygotes for quasinormal chromosomes alone. In populations VI-ER and IV-ER where about 90% of the second chromosomes are lethal or semilethal when homozygous, the mean viability of "all" homozygotes is the lowest, being only about one-eighth that of the quasinormal homozygotes. In II-EGR (with 57% lethal chromosomes) and in VI-ER-20 (with 75.9% of the chromosomes lethal in double dose) the viabilities of "all" homozygotes are, respectively, about one half and one quarter that of the quasinormal homozygotes.

The mean viability of the +/+ heterozygotes is always higher (significantly so, except in IV-ER) than that of the quasinormal homozygotes. It should be noted that the higher viability of the heterozygotes is obtained in spite of the fact that a vast majority of the heterozygous combinations, in all these populations studied, are between second chromosomes which are themselves lethal or semilethal in the homozygous condition (the few allelic lethal crosses are excluded from the computations). It will also be noticed that the viabilities of the *Cy* L/+ and *Pm*/+ heterozygotes are not significantly affected when the + chromosomes in question are drastic (lethal or semilethal) or when they are quasinormal.

4. *Productivity of the cultures:* Table 5 reports the mean number of the flies which hatched in the cultures in which the +/+ class was homozygous or heterozygous for the + second chromosomes, in different experimental populations. For

TABLE 5

Mean number of flies per culture in different crosses producing homozygous and heterozygous wild-type individuals

Population	Homozygous		Heterozygous
	Lethal and semilethal	Quasinormal	
C-1 and C-2	205.9 $\pm$ 12.3	251.7 $\pm$ 4.8	238.1 $\pm$ 3.2
II-ER	203.2 $\pm$ 7.2	234.0 $\pm$ 11.2	261.0 $\pm$ 6.6
II-EGR	182.7 $\pm$ 5.5	203.9 $\pm$ 6.8	210.5 $\pm$ 4.5
IV-ER	178.4 $\pm$ 3.0	180.8 $\pm$ 7.9	219.3 $\pm$ 4.5
VI-ER	186.0 $\pm$ 3.9	215.0 $\pm$ 10.5	199.1 $\pm$ 3.3
VII-OR	192.4 $\pm$ 8.4	248.8 $\pm$ 8.2	252.1 $\pm$ 5.7
VI-ER-20	172.7 $\pm$ 3.5	209.6 $\pm$ 8.6	226.8 $\pm$ 4.9

purposes of comparison, the populations C-1 and C-2, II-ER and VII-OR from the earlier studies are also included. The "homozygous" cultures are subdivided into those in which (1) the + chromosomes were quasinormal and (2) in which they were "drastic" (i.e., lethal and semilethal). The mean numbers of offspring per culture bottle in (1) does not significantly differ from those in "heterozygous" cultures. This is true in all the experimental populations. However, the productivity of the "quasinormal-homozygous" test cultures is greater, often significantly so (as in populations C-1 and C-2, II-ER, VII-OR and VI-ER-20) than in the "drastic-homozygous" test cultures. If the low viability (or inviability) of the homozygotes were producing their complete "replacement" by the mutant heterozygotes, as claimed by FALK and RAHAT (1963), then the mean productivity of the "drastic-homozygous" test cultures should be equal to that of the "quasinormal-homozygous" test cultures. The present data indicate that the replacement effect is small. WALLACE (1963a) observed a similar phenomenon in his experiments.

It is interesting to compare the mean productivity of the "quasinormal-homozygous" cultures in the different experimental populations. The unirradiated Controls have the highest productivity, as expected. The productivity of the cultures is reduced in the irradiated populations. In populations in which the radiation was discontinued, as in VII-OR, the mean productivity has risen considerably.

5. *Estimation of the frequencies of subvitals:* WALLACE and MADDEN (1953) have devised statistical techniques for the estimation of the frequencies of subvital and supervital chromosomes in populations. DOBZHANSKY and SPASSKY (1953) have used a slightly modified method which is applicable to the present data. The observed variances (σ_{ges}^2) of the viabilities of the chromosomes and chromosome combinations have at least three components, namely, the real or genetic (σ_g^2), environmental (σ_e^2) and sampling (σ_s^2) variances. The relevant estimates for the quasinormal homozygotes and the heterozygotes are given in Table 6. All the populations studied, including those described by SANKARANARAYANAN (1964), are included in the analysis. It is clear that the observed vari-

TABLE 6

Variance of the viability of homozygotes and heterozygotes in the experimental populations

Population	Generation	Nature of crosses	σ^2_{ges}	σ^2_{es}	σ^2_g	σ^2
Controls						
C-1 and C-2	14 and 20	Homozygous	.085638	.033910	.051728	.2275
		Heterozygous	.066272	.043463	.022809	.1510
Chronically irradiated populations						
II-ER	14	Homozygous	.086950	.039656	.053294	.2309
		Heterozygous	.090721	.045859	.044862	.2118
II-EGR	60	Homozygous	.080720	.022414	.058306	.2415
		Heterozygous	.100553	.055982	.044571	.2112
IV-ER and VI-ER	30 and 20	Homozygous	.145859	.046001	.099858	.3124
		Heterozygous	.074536	.044901	.029635	.1722
VI-ER	20	Heterozygous	.105770	.065511	.040259	.2006
Relaxed populations						
VII-OR	14	Homozygous	.081565	.031699	.049866	.2233
	14	Heterozygous	.072148	.060067	.012081	.1099
VI-ER-20	19	Homozygous	.094589	.024798	.069791	.2642
		Heterozygous	.088313	.062456	.025857	.1608

ances (σ^2_{ges}) of both the homozygotes and heterozygotes in the different populations are different. The σ^2_{ges} is higher in the homozygotes than in the heterozygotes in C-1 and C-2, in VI-ER and IV-ER, and in VI-ER-20; and it is slightly lower in II-ER and II-EGR. Unexpectedly, the environmental and sampling variances (σ^2_{es}) of the heterozygotes tend to be higher than in the homozygotes. However, the genetic variances of the homozygotes are invariably larger than that of the heterozygotes, as expected.

Following WALLACE and MADDEN (1953) and DOBZHANSKY and SPASSKY (1953), the subvital homozygotes are defined as those giving, under the conditions of the experiments, viabilities which deviate by more than two σ_g below the average viability of the heterozygotes. Estimates of the frequencies of subvital chromosomes are reported in Table 7. The frequencies of subvitals are higher in the heavily irradiated populations than in others. These estimates compare

TABLE 7

Estimated percentages of chromosomes in the experimental populations which produce subvital hemozygotes

Population	Percentage
C-1 and C-2	27.5
II-ER	28.1
II-EGR	21.8
IV-ER and VI-ER	
(A) Using IV-ER heterozygotes as standard	48.5
(B) Using VI-ER heterozygotes as standard	49.3
VII-OR	37.2
VI-ER-20	45.2

favorably with those obtained by WALLACE and MADDEN for the experimental populations, but are much lower than the figures obtained by DOBZHANSKY and SPASSKY for the natural populations of *D. pseudoobscura* and *D. persimilis*. (Table 7 in DOBZHANSKY and SPASSKY (1953) contains some mistakes in the computations. The frequencies of the subvital second, third and fourth chromosomes in *D. pseudoobscura* should be 93.5, 78.3 and 69.9% respectively, and in *D. persimilis*, 66.9 for the second, 79.8 for the third and 98.4 for the fourth chromosomes. The frequencies of supervitals in *D. pseudoobscura* second, third and fourth chromosomes are, respectively, 0.10, 0.02 and 0.04%, and for *D. persimilis*, the corresponding figures are 0.3, 2.7 and 0.4%.)

DISCUSSION

The genetic events that occur in natural and experimental populations of *Drosophila* exposed to ionizing radiations have been studied by several investigators (among them BONNIER, JONSSON and RAMEL 1958a,b, 1959; CARSON 1964; MOURAD 1962, 1964; STONE, WHEELER and WILSON 1962; WALLACE 1962 and earlier papers). One of the most important findings of all these studies is that the populations under irradiation accumulate enormous genetic loads. However, the dynamics of genetic loads, especially of the loads induced and/or modified by irradiation, is still not adequately understood.

MOURAD (1962, 1964) utilized the phenomenon of balanced chromosomal polymorphism to investigate the behavior of irradiated and unirradiated chromosomes in experimental populations of *D. pseudoobscura*. The Arrowhead (AR) and Chiricahua (CH) gene arrangements in the third chromosomes for which his populations were polymorphic were followed cytologically, generation after generation. In populations which were started with irradiated AR founders (no radiation later), the frequency of AR chromosomes declined sharply for the first few generations and then began to increase, eventually reaching an equilibrium level somewhat below that obtained in the unirradiated Controls. On the other hand, when the CH chromosomes were irradiated at the beginning, the AR chromosomes increased in frequency and the equilibrium level was slightly above that found in the Controls. In those populations in which, in addition to the initial irradiation of the AR chromosomes, freshly irradiated AR chromosomes were added in every generation, their frequency and equilibrium level was much lower than in the Controls.

These results are not unexpected, in view of the coadapted nature of the genetic system studied, where the chromosomal polymorphism is adaptive and balanced. Disruption or damage by radiation to any component of the adaptively integrated gene complexes, brings about concomitant changes in the gene pool. Natural selection is able to sort out the genetic changes induced by the irradiation, and to eliminate or to reduce the frequencies of the deleterious ones in the gene pool.

In the present investigation, the viability patterns in all the chronically irradiated populations—II-EGR, IV-ER and VI-ER—are qualitatively similar. A decline occurs in the first few generations, after which the viability levels ap-

proach equilibria, these being a function of the amount and the history of the irradiation and consequently, of the nature and magnitude of the induced genetic loads. The magnitude of the accumulated genetic loads is great. About 90% of the second chromosomes in populations IV-ER and VI-ER were lethal or semilethal when homozygous. As mentioned earlier, these populations, at the time the analysis was made had received a total dose of 120,000r. However, the population II-EGR, which also had received the same total dose but delivered over a period of 60 generations, had only 57.0% of the second chromosomes lethal or semilethal when homozygous.

In the population II-EGR the magnitude of the induced mutation pressure which is counteracted by natural selection, is considerably less than either in IV-ER or VI-ER. This, coupled with the fact that in II-EGR, at the 120,000r level, there were three times as many generations as in VI-ER (or twice as many as in IV-ER) indicates that natural selection has reduced the frequencies of the deleterious variants. The genetic loads that populations accumulate, under a given cumulative dose of irradiation, depend upon the numbers of the generations during which the radiation is administered.

The behavior of the relaxed subpopulations (VI-ER-20, IV-ER-30 and II-EGR-60) is extremely interesting. With the cessation of the irradiation, there is a steep rise in the egg-adult viability, presumably due to the elimination of gross chromosomal aberrations and other semidominant changes. After the initial rise for the first four generations, the viability levels of these populations remain between 70 and 75%. In population VI-ER-20 in which the second chromosomes were analyzed after 19 generations of relaxation from radiation, the frequency of lethal second chromosomes dropped from about 88% to 76.5%. A similar phenomenon was observed by WALLACE (1956) in the subpopulations 17 and 18. As will be noticed, the decline in lethal frequency is smaller relative to the steep rise in the viability.

The observation that the relaxed subpopulations have reached a kind of plateau as regards their egg-adult viability, poses some interesting questions. (1) It is conceivable that, after the major semidominant and deleterious changes have been eliminated in the first few generations of recovery, what are left in the populations are, perhaps, mutants that are mildly deleterious. Several of these, present in the population, collectively can reduce viability for several generations. Natural selection will presumably take a long time to reduce their frequencies to near-Control levels. (2) It is also possible that some of the radiation-induced mutants are heterotic (and hence multiplied by natural selection), although they might be lethal or otherwise deleterious in the homozygous condition. The viability in such a population will be consistently reduced, owing to the formation of lethal homozygotes in every generation. Evidence that some radiation-induced mutants can be adaptively incorporated into the gene pool of populations has been furnished by WALLACE (see WALLACE 1963b for references). A study of the allelism of lethals in the experimental populations may throw some light on this problem. Such a study is underway and the results will be published in due course.

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SUMMARY

The genetic consequences of exposure to X rays are studied in experimental populations maintained under conditions of relaxed natural selection. Three doses are used (2000r, 4000r and 6000r) to irradiate the males in every generation. The egg to adult viability is studied.

In all the populations, the viability decreased for the first few generations, and then fluctuated at equilibrium levels depending on the amount and the history of irradiation. Three subpopulations were derived, one from each of the chronically irradiated populations, at the total accumulated dose of 120,000r. When relaxed from radiation, the subpopulations rapidly recovered in about four or five generations to 70 to 75% viability level and remained there.

For a given total dose of radiation, the frequencies of accumulated lethals and semilethals vary depending on the number of generations during which the total dose is delivered. Thus, at the cumulative dose level of 120,000r administered at the rate of 6000, 4000 and 2000r per generation for 20, 30 and 60 generations respectively, the frequencies of second-chromosome lethals and semilethals in the first two populations were close to 90%, whereas in the third population, it was only 57%.

Using statistical techniques devised by WALLACE and MADDEN and by DOBZHANSKY and SPASSKY, estimates of the variances of the viabilities of the chromosomes and the chromosome combinations were made, and the frequencies of the subvitals computed. The genetic variances of the homozygotes were higher than that of the heterozygotes; the frequencies of subvitals were greater in the heavily irradiated populations than in the others.

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