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The effects of X-rays on quantitative characters

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1. INTRODUCTION

Serebrovsky (1935) and Rokizky (1936) were probably the first to examine the effects of X-rays on the genetic variation affecting a quantitative character—numbers of sternopleural *chaetae* in *Drosophila melanogaster*. They obtained an increase in variance after irradiation but little response to selection. But the high level of inbreeding which was practised during the selection would have reduced their chances of fixing genetic variation produced by the treatment. Scossiroli (1953) and Buzzati-Traverso (1953) obtained appreciable responses to selection following irradiation and their results, if proved to be general, would be of considerable scientific and economic importance. On the other hand, Clayton & Robertson (1955) obtained some increase in variance but little response to selection in a quantitative trait in *D. melanogaster* following irradiation of an inbred line. Scossiroli & Scossiroli (1959) published further evidence in support of their earlier thesis that X-rays are an efficient tool for the induction of additive genetic variance in polygenic traits in *D. melanogaster* in populations which have reached the limits of selection.

Yamada & Kitagawa (1961) obtained an increase in variance in bristle characters following irradiation of *Drosophila*. They were mainly concerned to estimate the X-ray doubling dose for genetic variance of quantitative traits, but in some of their experiments they obtained responses to selection attributable to irradiation. They worked with both isogenized and hybrid populations. The derived nature of the results they present makes it difficult to assess the significance of these responses but they apparently intend to publish fuller details in the future.

In this paper we shall present the results of a series of experiments on the irradiation of 'plateaued populations', whose realizable genetic variance for the trait in question appeared to have been exhausted by selection, and on other populations which had previously been made isogenic. This is an extension of work previously published (Clayton & Robertson, 1955), and appeared necessary in view of the contradictory nature of the results which have been reported thus far.

The numbers of bristles on the fourth and fifth sternites and on the sternopleura in *Drosophila melanogaster* were the two 'characters' used. Techniques of culture and selection have been fully described elsewhere (Clayton, Morris & Robertson, 1957). Details of methods employed in particular experiments are given with the results. The various selection experiments are summarized in Fig. 1.

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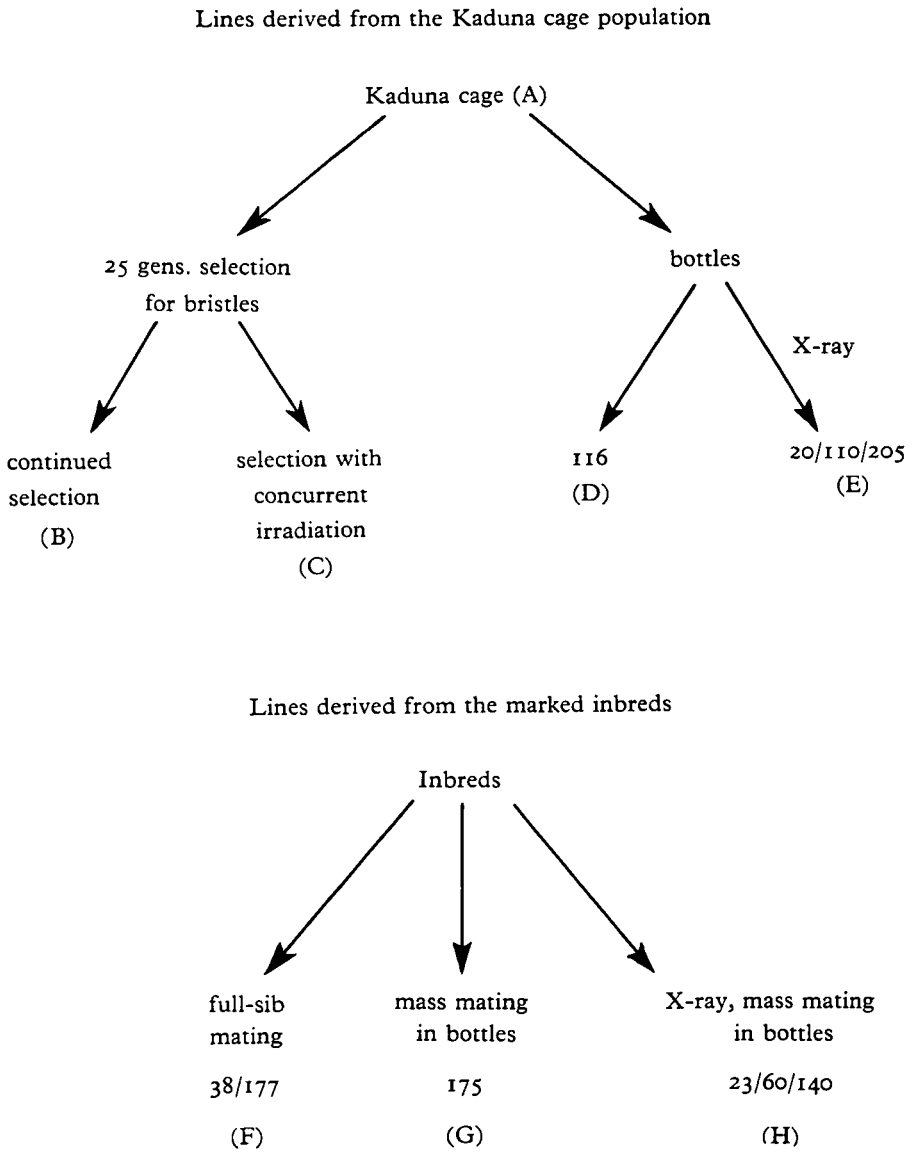

Fig. 1. A summary of the experimental lines. The figures give the number of generations after which divergent selection was applied.

2. RESULTS

(i) *The plateaued populations*

The stimulus to investigate methods of shifting the means of apparently plateaued populations comes from agriculture where many strains of economic animals and plants appear resistant to further improvement. Such strains usually have a long history of selection behind them and the use of laboratory material with a similar history appears logical. Moreover, the successful results reported by Scossiroli (1953)

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were obtained from such a selected plateaued line. Scossiroli gave a dose of 3000 r. to about 100 virgin females and 100 males, pair mated the treated flies and then scored three male and three female progeny from each fertile single pair culture. The scored members of the five families with the most extreme total count, i.e. fifteen males and fifteen females, were pooled to produce a mass culture. From the progeny of this mass culture, a sample of about 100 pairs was drawn to be irradiated and commence the next cycle. Each cycle was then of two generations, with selection alternating with irradiation.

We used a technique similar to Scossiroli's on two distinct sets of plateaued populations. It differed slightly in that only 1800 r. was administered to adults each cycle and the irradiated flies were mass mated rather than pair mated. Both sets of plateaued populations derive from the Kaduna cage stock (A) maintained in this laboratory. The first set consisted of four lines, two of which had been selected for increased and two for decreased numbers of sternopleural bristles. All had been mass selected previously for twenty-five consecutive generations and were showing little, if any, further response to selection. Selection intensity had been 10/25 in each sex. The second set was kindly made available by Dr B. D. H. Latter, who had been selecting for sternital bristles and three of whose four lines appeared to have reached a limit after twenty generations of selection at an intensity of 10/50. The other low line had been lost from infertility at the thirteenth generation of the original selection.

From each plateaued line two sub-lines were made, one of which was irradiated while the other acted as a control. In the generation in which the X-ray line was irradiated but not selected, the controls were mass mated without selection in numbers similar to those in the X-ray lines, so that the control lines also have alternate generations of selection and relaxation. The intensity and direction of selection

Table 1. *The response of plateaued populations to concurrent irradiation* (1800 *r./gen.*) *and selection* (*B and C in Fig.* 1)

			Change after 8 cycles of selection	
Sternopleural lines:		'Plateau'	X-ray	Control
High	1	28·82	+1·15	+1·58
	2	27·24	+1·35	+1·25
Low	1	12·65	−1·08	−0·33
	2	12·42	−1·15	−0·87
Base population (A)		17·80		
Sternital lines:			After 7 cycles	
High	1	53·76	+3·35	+0·03
	2	53·64	+3·06	+1·97
Low	1	21·65	−0·25	−0·61
Base population (A)		34·50		

used in reaching the plateau was continued in both control and X-ray lines. Eight cycles of selection were carried out in the sternopleural lines and seven in the sternital lines. The results are summarized in Tables 1 and 2. Table 1 gives the mean score of the two sexes in the various lines. The figures for the X-ray and control lines are averages of the measurements for the last three generations of selection. Each is therefore based on 150 individuals in the sternopleural lines and on 300 individuals in the sternital lines.

These results are certainly in general contradiction with those of Scossiroli in that, although in some lines the irradiation appears to have produced some new variation utilizable by selection, the responses to selection are all very small. The sternopleural high lines show a response, both control and X-rayed. In the two low lines the controls have responded but the X-ray lines appear to have shown a small though significantly greater response. In the sternital high-1, the X-ray line has responded and the control line has not, though the absolute change is small. The response is also greater than the control in the other X-rayed high line though here the control has responded as well. In the one low sternital line the selection had little effect in both control and X-ray lines.

No consistent picture emerges from the figures on variability in the sternopleural lines (Table 2). In the sternital lines the variability in high-1 seems to be significantly

Table 2. *Variance within sex at beginning and end of selection of lines in Table* 1

			At end of selection period	
Sternopleural lines:		Plateau	X-ray	Control
High	1	6·42	5·10	5·79
	2	4·91	5·66	5·08
Low	1	1·87	0·95	1·07
	2	1·47	1·21	0·82
		(each based on 150 individuals)		
Sternital lines:				
High	1	10·44	15·17	10·94
	2	12·04	12·76	16·01
Low	1	4·85	4·40	4·37
		(each based on 300 individuals)		

greater in the X-ray line than in the control, in agreement with the greater response. The greater variability in the control line in high-2 appears from that in other generations to be an accident of sampling.

Although we have not achieved the spectacular results that Scossiroli got in his high lines, it would appear that in some lines the irradiation has given us a greater response to selection.

(ii) *The irradiation of genetically invariant populations*

Plateaued populations of the kind we used are obviously in a very special genetic situation. They have ceased to respond much to selection but may nevertheless still contain some genetic variation. In view of the wider implications of the rate of production of new variation by mutation, it seemed desirable to examine as well the effect of irradiating populations which might be expected to contain very little genetic variation. Here it is essential to reduce the possibilities of contamination to a minimum and to use stocks in which contamination, if it occurs, can easily be detected. This was not necessary in the work on the plateaued populations in that any contaminant of those lines is likely to have a bristle count close to that in wild populations and neither it nor its progeny will be selected.

For all the work with genetically invariant material, we have used three lines in which the sex-linked genes white, vermilion and yellow respectively, were introduced into a standard inbred line, Oregon R, by Dr J. Schultz. The lines were then isogenized by him and then subsequently kept by full sibbing. Although the lines are marked by different genes, they are probably genetically similar to one another at other loci. In the work on the plateaued populations the irradiation was carried out during the selection but in the work on inbreds, irradiation was carried out for a varying number of generations before selection and ceased during the selection period. Each inbred line then gave rise to three populations, whose treatment prior to selection had been

(i) Continuously full-sib mated in vials without irradiation (F).

(ii) Mass-mated in bottles without irradiation (G).

(iii) Mass-mated in bottles with 1800 r. each generation (H).

Table 3. *The divergence after 5 generations of selection for sternital bristles of intensity 10/50. The two figures given in some cases are replicates carried out by different workers*

			Divergence		
Non-irradiated:			White	Yellow	Vermilion
Full-sib:	38 gens.	(F)	0·10*	1·06*	0·53*
	177 ,,	(F)	1·31/−0·36	−0·31/0·56	lost
Mass-mated:	175 ,,	(G)	0·24/0·81	0·81/0·94	2·52/0·63
Irradiated in bottles, 1800 r./gen.:		(H)			
23 gens.			3·54*	4·06*	1·54*
60 ,,			3·98	3·63†	2·62
140 ,,			8·03/4·87	12·42/12·77	2·23/3·73
Outbred population:		(A)		19·62	

* Selection 10/25.

† Selected for 4 generations only.

Selection was then imposed for high and low sternital bristle number. In most lines the selection intensity was 10/50 with two replicates though in one set it was 10/25. The divergent selection was carried on for five generations. Table 3 shows the divergence between the selected lines, the two replicates being given separately. Table 4 shows the variance in the lines in the early generations of selection.

The lines kept by continued full sibbing show very little response to selection and a consistent low level of variability. The non-irradiated bottle control populations all show positive but small divergences, though the phenotypic variability is, if

Table 4. *The phenotypic variance of sternital bristles at the start of selection in the lines in Table 3*

			Phenotypic variances			
Non-irradiated:			White	Yellow	Vermilion	d.f.
Full sib:	38 gens.	(F)	6·20	4·67	5·24	144
	177 ,,	(F)	4·12	4·63	lost	588
Mass-mated:	175 ,,	(G)	3·81	4·24	3·99	588
Irradiated in bottles, 1800 r./gen.:		(H)				
23 gens.			6·04	6·62	5·92	144
60 ,,			5·21	6·08	5·44	294
140 ,,			6·21	9·76	7·80	588
Outbred population:		(A)		11·35		1980

anything, below that of the inbreds. The selection applied to the irradiated populations at various times has undoubtedly produced a response, which was somewhat greater after the longer periods of irradiation. The three differently marked stocks behaved differently, though the agreement between replicate selections within stocks is good. This picture is confirmed by the variance results. The irradiated populations are more variable than the inbreds, and the yellow population, which showed the greatest response to selection, has the highest value. But it should be remembered that even this response, after a total of some 200,000 r., is only about one-half of that expected from our standard outbred population, which is given in the table, and correspondingly the yellow irradiated population does not approach the variance of the outbreds. We have here a definite indication that variation has been produced in this character by irradiation, but at a comparatively low rate.

Two points would seem to be relevant to the interpretation of these results. They are:

(i) The irradiation will undoubtedly produce deleterious recessive genes and chromosomal abnormalities. These may well interfere with the response to selection by enforcing heterozygosity in some sections of the chromosome. This is probably not important for such short periods of selection but it seemed well to pay some attention to this point.

These stocks have certainly accumulated lethal recessives as a result of the irradiation. Sixty-one third chromosomes were made homozygous using standard techniques at the 150th generation of irradiation and only eleven then produced viable individuals (Table 5). Some chromosomal abnormalities have also been accumulated; details will be published elsewhere.

Table 5. *The homozygous viability of third chromosomes taken from the irradiated bottle populations* (H) *at gen.* 150

	White	Yellow	Vermilion
Viable	8	2	1
Lethal	17	16	17

It seemed to us that the practical answer to this question was to give equivalent doses of radiation to outbred populations in which we knew that there was considerable genetic variance at the start and see whether this reduced the selection response. To do this, a large sample was withdrawn from the Kaduna cage population, mass cultured in bottles and irradiated in the same way as the marked inbreds, giving population (E). After twenty generations of irradiation, divergent selection for sternital bristles was carried out. At this time a lethal test showed that 75% of second chromosomes were lethal when homozygous. The response to this divergent selection was immediate and of almost the same magnitude as we were accustomed to obtain from the cage population. Contemporary controls, selected without irradiation, were not considered necessary, as the same intensity of selection had already been applied to this population at various times with consistent results. One such set of lines have already been referred to (the plateaued populations selected for sternital bristles described in the earlier section). The divergence after five generations of selection and the phenotypic variances are given in Table 6.

Table 6. *The irradiation of the standard outbred population. The divergence is after* 5 *generations of selection for sternital bristles of intensity* 10/50

		Diver-gence	Pheno-typic variance	d.f.
Kaduna population (no irradiation):	(A)			
Average of 5 reps. 20/100		19·87	11·35	1980
2 reps. 10/50		16·71	9·40	588
After 20 gens. of 1800 r./gen. in bottles:	(E)			
2 reps. 10/50		19·62	13·79	588

Selection of the irradiated lines was in fact continued for a much longer period though we have not presented the detailed results. The two high lines became increasingly difficult to culture and one eventually failed completely. The interpretation of the further changes was complicated by the occurrence of a major gene,

'scabrous', in one of them. This gene is known to increase sternital bristles by 15–20, but the homozygous females proved to be highly infertile. As the same gene has also been found in another line derived without irradiation from the same base population (McBride & Robertson, 1963), this occurrence cannot be ascribed to the irradiation. On the other hand the two low lines were continued without difficulty for twenty-eight generations when response appeared to have ceased at a level much lower than the surviving 10/50 line without irradiation and at the same level as the 20/100 lines.

It would seem from these results and from some related ones, given in the next section, that large doses of irradiation do not reduce the capacity of an outbred population to respond to selection although some lines became much less vigorous. In none of the X-ray lines did the early response much exceed that in other lines selected from the same stock without irradiation.

(ii) The population size under these culture conditions may be rather small and the increase of genetic variation by mutation may be rapidly balanced by its loss through chance fixation. Here it should be remembered that, if individual mutation rates are low and selection forces small, the final balance between mutation and chance fixation is reached, for genes acting additively, when the genetic variance in the population is $2N$ times that arising *de novo* each generation, where N is the effective population size. Further, it should take about $1{\cdot}4N$ generations to reach half this level starting from a genetically invariant line.

We therefore needed an estimate of the effective population size under these culture conditions. To get this, we used a stock originally used by Buri (1956) in his work on drift in gene frequency in small populations. The stock is homozygous for the gene *scarlet*, *st*, and is segregating for two alleles at the *brown* locus, *bw* and bw^{75}. Buri showed that all three genotypes at the *bw* locus can then be distinguished and that selective forces are small. We therefore set up fourteen replicate bottle populations with an initial gene frequency of 50% and our laboratory assistants were instructed to turn these over in the usual manner. When this had been done for fourteen generations, samples of eggs were taken and reared to emergence under uncrowded conditions. Estimates of gene frequency were made on an average of 150 individuals per replicate. The gene frequencies in the different replicates proved to be widely different and the drift is summarized in Table 7.

Table 7. *The gene frequency of* bw (*segregating with* bw^{75} *in an* st *background*) *after* 14 *generations in bottles. Initial frequency* 0·50

Gene frequency range	No. of lines
0–0·10	4
0·10–0·20	3
0·20–0·30	3
0·30–0·40	3
> 0·40	1

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The mean frequency of the more extreme *bw* allele had been reduced to 0·29, suggesting that its homozygote is at a selective disadvantage compared to the other homozygote of approximately 10%. We can make an estimate of the effective population size from the drift in gene frequency as follows.

If the population size is N, then the variance between lines in gene frequency is expected to increase by $q(1\text{-}q)/2N$ each generation in the early generations, where q is the average frequency. In later generations, the expression $q(1\text{-}q)(1\text{-}e^{-t/2N})$ is more accurate for the increase in variance, where t is the number of generations. The component of variance of gene frequency between our replicate lines is 0·0255. If we use an average value for q of 0·40, we then get an estimate for N of 60. This estimate is, of course, subject to considerable error because it is based only on the 13 degrees of freedom for the estimate of variance in gene frequency between replicates, and rough confidence limits for it would be 50 to 100. It does at least give the order of magnitude of the effect. We see that the population size in these bottles is so small that in some of our experiments the genetic variation may well be reaching the equilibrium point between mutation and fixation.

We can measure the effect of maintaining populations for many generations in bottles rather more directly, as we have two such populations, derived from our Kaduna base population. One (D) was maintained in bottles without irradiation as a control. The effect of divergent selection on the contemporary irradiated population (E) after twenty generations has already been dealt with. Divergent selection was applied to both populations after more than 100 generations in bottles and the results are given in Table 8, comparable figures for the base population being in Tables 3 and 4. It is clear that the genetic variance has been reduced in the non-irradiated population by continued maintenance in bottles and that irradiation has had little effect on this reduction.

Table 8. *The effect of continued maintenance in bottles on genetic variability for sternital bristles*

		Divergence	Phenotypic variance	d.f.
Non-irradiated:	(D)			
In bottles for: 116 gen.		9·48/9·42	8·39	588
Irradiated, 1800 r./gen.:	(E)			
In bottles for:				
110 gen.		13·89/9·15	9·70	588
205 ,,		10·19/11·45	8·04	588

3. DISCUSSION

The interpretation of these results is complicated by two factors. The first we have mentioned already—that in some of the experiments the restriction in population size in the ordinary culture bottles may have caused a balance between mutation and chance loss from the population so that the rate of accumulation of new mutation is not linear with time. We have made some efforts to estimate the population

size and our results obviously have to be discussed in this light. This, of course, only applies to populations which we have kept in bottle conditions for 100 or so generations and is therefore not relevant to the experiments on plateaued populations.

The second complication concerns the fate of new mutations produced by irradiation, in the absence of any selection for bristle characters. This again is mainly relevant to the discussions of the populations which have been maintained for very many generations. It is arguable that most genetically invariant populations are less fit than wild-type populations and that some new mutations may therefore be at an advantage. The expressions for the rate of accumulation of new genetic variation would then be incorrect. This is obviously an extremely controversial point and can merely be mentioned as a disturbing complication. Reference to the controversy on the effect of small doses of radiation, of which the papers of Wallace (1958) and Falk (1961) may serve as opposing examples, will indicate that this is not an argument to be entered into lightly.

The results from the irradiation of the plateaued lines are fairly clear-cut. Of the seven lines looked at, three showed a greater response after irradiation than did the controls, three showed a smaller response and in one the responses were approximately equal. In those lines in which the response was definitely greater under irradiation, it was rather small in absolute terms. The general trend of our results is therefore opposite to those of Scossiroli. On the irradiation of the plateaued high lines, he found in one line a very rapid response from the mean level of twenty-six bristles to a level of over forty bristles after ten cycles of selection. The other replicate under irradiation also responded rapidly at the start but reached a new plateau at a level of thirty-two bristles. In the low lines he found that the response was very much smaller. After seventeen cycles of selection, one of the irradiated lines was about 1·5 bristles lower than the controls and the other about 0·2 bristles lower. Since the publication of Scossiroli's results, attention has naturally centred rather more on the spectacular effects of irradiation of the high lines, but from our own work on seven different plateaued populations we must conclude that some phenomenon peculiar to Scossiroli's line itself must be the explanation rather than a general effect of irradiation.

The irradiation of the genetically invariant populations raises more general problems; the interpretation of the results is correspondingly more difficult. There can be little doubt from the results presented in Tables 6 and 8 that the population size in laboratory culture bottles is sufficiently small to be important in the interpretation of our results. The apparent effective population size deduced from Table 6 would suggest that any approach to equilibrium between mutation rate and chance fixation, whether it be from a genetically variant or an invariant population, should have a half-life of the order of 100 generations. This is borne out in Table 8 in which the genetic variance determined from the selection divergence in the non-irradiated population which had been in bottles for 116 generations was about half that in the original population. The results on the irradiation of genetically variable populations presented in Table 6 would suggest that we need not, in the context of short-term selection experiments, worry greatly about the effect of any deleterious

genes produced by irradiation on our ability to utilize the quantitative genetic variation. The irradiation would also be expected to increase somewhat the amount of genetic recombination but the importance of this would depend on the extent to which the population was in linkage equilibrium at the beginning. There is a further more mundane point which must be mentioned before we deal with the experimental results themselves. This work was done in marked inbred populations. Is it possible that genetic variation could have been introduced by contamination from outside without our detecting it? Some experiments to be presented elsewhere on population cages containing these stocks would suggest that any contamination of the inbred populations by wild-type flies will be detected as segregation at the marker locus in a very high proportion of cases even though the initial contamination may be only the introduction of one pregnant female into a population of some thousand individuals.

From the detailed results presented in Tables 3 and 4, it is quite clear that the continued irradiation has produced genetic variation which is utilizable by selection, though perhaps the response is rather small in relation to the high dosages given before selection. In general the increase in response to selection is paralleled by an increase in the phenotypic variation, but we shall concentrate our attention on the estimates of genetic variation derivable from the divergence produced by the selection.

The estimate is obtained as follows. If a selection differential of i standard deviations is imposed, then the expected response is equal to iV_A/σ_P, where V_A is the additive genetic variance and σ_P the phenotypic standard deviation. If divergent selection is applied for several generations, then the expected divergence is $\sum i\ V_A/\sigma_P$, i being summed over directions and generations. Now $\sum i$ may be calculated from the selection intensity (assuming the character is normally distributed) so that V_A may be estimated from the observed divergence and phenotypic standard deviation. If this genetic variance has accumulated over t generations with an input of V units per generation, and an effective population size of $2N$, it may be equated to $2NV(1\text{-}e^{-t/2N})$. This expression takes the value tV, when t is small, and $2NV$, when t is large.

If we take the results for the three separate sets of selection experiments on irradiated lines, i.e. after 23, 60 and 140 generations in bottles, we find estimates of the accumulated genetic variance in sternital bristles at the start of the selection of 0·75, 0·6 and 1·4 units respectively. Assuming that the population size is 60 and that natural selection is playing no part, we obtain estimates for the rate of production of new variation each generation of $1{\cdot}8 \times 10^{-5}$, $0{\cdot}6 \times 10^{-5}$ and 1×10^{-5} units per roentgen for the three experiments.

This is smaller by a factor of 3 than the result obtained in our earlier paper and by a factor of 10 than that obtained by Yamada and Kitagawa. They give two figures, one based on the analysis of the homozygous effect of chromosomes deriving from a dose of 4000 r. given to a homozygous line and another based on selection experiments. Unfortunately the details of the latter are not given. In view of the variation between replicates in our own experiments and the slight

heterogeneity in Yamada and Kitagawa's work, these discrepancies are perhaps not very surprising.

We can express our results in a more understandable way by calculating the dosage which is required to produce *de novo* as much variation as is present in our standard wild-type population for which the selection results are also given in Table 3. The stable genetic variance in sternital bristles in this population is then of the order of 5 units. If we take a mean of our three estimates of the rate of production of new variation we get a value of 500,000 r. but if we take Yamada and Kitagawa's figures this is reduced to about 60,000 r. In either case these are extremely high figures and would certainly suggest that in the context of the exposure of human and other mammalian populations to extra irradiation from nuclear sources of various kinds, any effects on quantitative traits would be so small as to be probably quite undetectable.

SUMMARY

1. The rate of production by X-rays of new genetic variation in two quantitative characters in *Drosophila melanogaster* (sternital and sternopleural bristles) has been investigated, using 'plateaued' populations which had reached the limit under artificial selection and, for sternital bristles only, populations which had been made genetically invariant by inbreeding. The genetic variation was always measured by the response of the population to selection. The X-rays dose given in any generation was always 1800 r. to adults.

2. Seven plateaued lines had eight cycles of alternate irradiation and selection, each with its non-irradiated control. All the responses were small but in three lines they were significantly greater after irradiation.

3. Selection was applied to three different inbred lines, genetically marked to detect contamination, after varying periods of irradiation. At the same time, the inbred lines and lines derived from them which had been mass mated in bottles were selected. The irradiated populations showed a greater response. The new genetic variance produced by the irradiation was approximately 10^{-5} units/r. The estimate of the dose required to introduce new variation equal to that in a standard outbred population was 500,000 r.

4. The effective population size was an important factor in the interpretation of some of these results on the long-term effects of radiation. By observing the variation between replicate lines in the frequency of a gene with a visible effect under these culture conditions (i.e. in a single culture bottle) the effective population size was estimated at sixty. Outbred populations kept under these conditions for many generations showed a reduction of genetic variability in agreement with this value.

5. To investigate the possibility that the deleterious genes produced by irradiation would interfere with the response to artificial selection, a standard outbred population was irradiated and selected. In spite of the observed high frequency of recessive lethals produced, the response to selection was very similar to that of the standard population.

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