AN ANALYSIS OF RADIATION-INDUCED VARIATION ON BODY-WEIGHT OF *HABROBRACON JUGLANDIS*¹

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THE use of irradiation has long been proved to be effective in inducing new genetic variability in a quantitative trait. SCOSSIROLI (1954) irradiated *Drosophila melanogaster* populations that had ceased to respond to selection for sternopleural bristle. The irradiated populations now responded to further selection: the response to upward selection was remarkably high, while that to downward selection was not as striking. Reverse selection always brought back the selected lines to the original levels. CLAYTON and ROBERTSON (1955) irradiated two inbred lines of *D. melanogaster* and applied upward and downward selection pressures on abdominal bristle counts. At the same time, the lines without irradiation were also subjected to the same selection scheme as the control of the experiment. The response to selection indicated an increase in genetic variability in the irradiated selection lines. However, selection was not as effective as reported by SCOSSIROLI.

In plants, GREGORY (1955) submitted dry seeds of a cultivated peanut to X rays. The yield observations made on phenotypically normal plants of the third generation after irradiation revealed an estimate of genotypic variance that was four times as large as that of the control. Upward selection on this material enabled GREGORY to produce new lines with significantly superior yield to that of the original variety. Subjecting a line of spring barley to X rays, GAUL (1961) was able to isolate 56 "earliness mutants" for which the heading time was from 10.1 to 0.2 days shorter than that of the original line over several years of observations. The same author also reported a significant induced variation with respect to 1000-kernel weight in spring and winter barley varieties.

The present paper deals with a quantification of radiation-induced genetic variability in *Habrobracon* in terms of genetic and environmental variances in two phases. The first phase is devoted to a survey of the empirical relationship between the radiation dose and the increase in variance, and the second phase represents a more detailed analysis of induced genetic variance.

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MATERIALS AND METHODS

Experimental material: The materials used were two inbred lines of *Habrobracon juglandis* Ashmead, a parasitic wasp. This organism can be raised in the laboratory, using caterpillars of the flour moth *Ephestia* as the feed. Yellow enriched cornmeal was used to rear a large number of *Ephestia* larvae. The two lines used will be denoted as Line No. 76 and Line honey. Line No. 76 is a phenotypically wild-type inbred line made available through a number of generations of inbreeding, and Line honey is another inbred line carrying recessive mutation "honey" that changes the wild-type body color (black) of wasps to a honey-colored body. After care was taken to insure a high level of inbreeding, each line was maintained in 15 replicates, each started with five males and five females on ten *Ephestia* caterpillars. They were placed in a modified chick incubator with constant temperature (29.5°C) and constant relative humidity (55%). These temperature and humidity conditions were kept throughout the entire study.

The traits chosen for the study were female and male wasp body weights. The female body weight was always measured as family means, while the male body weight was given in terms of family means and individual wasp weights.

Sources of radiation: Two different machines of cobalt 60 were used, Gammacell 220 and Gammacell 150, manufactured by Atomic Energy of Canada Ltd. The two machines were considered to be equivalent and delivered gamma rays at the maximum rate of about 250 kr per hour. The necessary calibration was made to use the two machines for the same purpose.

Basic experimental design: In *Habrobracon*, the female is diploid and develops from a fertilized egg, while the male is haploid and produced parthenogenetically from an unfertilized egg under the normal condition. The choice of the experimental design was based on the fact that a group of male offspring from an irradiated female would provide a sample of "gametic" arrays containing mutations in the form of adult males. This is a definite advantage of *Habrobracon* over a regular diploid organism for an induced-mutation study.

The basic experimental design is given in Figure 1 which illustrates a much simplified but fundamental scheme common to all the experiments performed in this study. The top two females in Figure 1 were virgins taken from Stock No. 76; one was assigned to the control

FIGURE 1.—Scheme of the experiments.

run, and the other to the irradiation run. The irradiated female was exposed to a dose of gamma rays at a given rate. Then, each female was placed in a shell vial with caterpillars. The sons were collected from each vial. The males from the control female were expected to be as identical as gametes from an inbred line, but those from the irradiated female should be "segregating" with respect to any mutations induced in the gametes of their mother.

Individual male progenies were separately mated to virgin females from an inbred line (No. 76 for the test with the homozygous genetic background and Line honey for the test with heterozygous genetic background). The mated females were placed individually into vials with two pre-stung caterpillars for 24 hours, and then transferred into new vials. After 24 hours in the new vials, each female was transferred a second time into another vial. All females were removed from the caterpillars after 24 hours from the second transfer. When the progeny began to emerge, the daughters were collected from each vial in each transfer. Thus there were three replicates of each family.

The measurements on female body weight were taken on these daughters. The females of each replicate were mass-weighed. Young wasps (one to two days old) were anaesthetized under CO_2 and placed on the tray of an analytic balance for weighing. Then, a pair of females from each replicate were saved for the production of the next generation of males (grandsons). The male body weight was scored on these grandsons, each family tracing back to one single grandfather. The males in a given family were mass-weighed for the preliminary dosage-response study, while individual male weights (4 or 5 males/replicate) were taken for the detailed investigation.

At this point, it may be helpful to consider a set of simple statistical quantities measuring the amount of variation due to the presence of radiation-induced mutations. The variance among means of families of daughters in the control, $\sigma_{c\phi}^2$ in Figure 1, is the measure of nongenetic variation associated with the family means. This is obvious, since all the daughters in the control group are of an identical genotype: in the homozygous genetic background test, they are members of the inbred Line No. 76, and in the heterozygous genetic background test, they are identically heterozygous with respect to the genes different between Line No. 76 and Line honey.

The daughters of any one male family in the irradiated group are genotypically identical, but the daughters belonging to different families in this group may differ in their genotypes, since male parents may carry different induced mutations. The effects of such mutations will be included in the variance of family means in the irradiated group, $\sigma_{r\phi}^2$, if these mutations express their effects in heterozygous conditions. When there is no mutation induced or if all induced mutations are completely recessive for the character considered, then the magnitude of $\sigma_{c\phi}^2$ is the same as that of $\sigma_{r\phi}^2$.

In the homozygous genetic background test, the variance among grandson families for the control, $\sigma_{c\sigma}^2$, is a measure of nongenetic variation, since all families are of an identical genotype, namely that of Line No. 76. The corresponding variance, $\sigma_{r\sigma}^2$, calculated for the irradiated group, includes the variation due to differences existing among grandfathers with radiation-induced mutations. The average variance within families of the control, $\Sigma_{c\sigma}^2$, is due to nongenetic causes, for all grandsons of any family are obviously of an identical genotype (Line No. 76), while the average variance within families in the irradiated group, $\Sigma_{r\sigma}^2$, includes the variation due to the segregation of heterozygous loci in daughters carried from single grandfathers.

In the heterozygous genetic background test, the variance among grandson families for the control, $\sigma_{c\sigma}^2$, measures the nongenetic variation among the means of families segregating for the same genetic difference, while $\sigma_{r\sigma}^2$ measures the variation similar to that accounted for by $\sigma_{c\sigma}^2$ plus that due to differences among radiation-mutated loci carried in grandfathers. The average variance within families of the control, $\Sigma_{c\sigma}^2$, is not due to only nongenetic causes any

FIGURE 2.—Increase in genetic variability measured by F-ratios of variances between families in the irradiated material to the corresponding variances in the control material. Female body weight.

more, since segregation and recombination occurred between the genomes of Lines honey and No. 76. The average variance within families in the irradiated group, $\Sigma^2_{r\sigma}$, contains the variance similar to $\Sigma^2_{c\sigma}$ plus that due to segregation of the radiation-altered genes of Line No. 76 and genes of Line honey.

RESULTS

Dosage-response relationship: Responses to gama-irradiation were investigated at five dose levels (0, 1.0, 1.5, 2.5, 4.0 kr) in three different runs. Each run contained the 0 dose level as control. In all three runs, females from Line No. 76 were irradiated, and their sons were mated to virgins from Line honey. Thus,

FIGURE 3.—Increase in genetic variability measured by F-ratios of variances between families in the irradiated material to the corresponding variances in the control material. Male body weight.

this phase of the study was conducted with a "heterozygous genetic background." The responses were represented by "F-ratios": $s_{r\sigma}^2/s_{c\sigma}^2$ for the female body weight data and $s_{r\sigma}^2/s_{c\sigma}^2$ for the male body weight data (s^2 stands for the estimate of σ^2). Figures 2 and 3 represent a graphic summary of the F-values obtained in this manner. It is clear that gamma radiation, in general, increased the variability between families with respect to male and female body weights. Furthermore, there seems to be an optimum dose for the increase of variability in female body-weight data at about 1,500r of gamma-irradiation.

There seems to be no simple explanation for observing quite different dose-response patterns between the female and male data. However, a likely cause for the difference may be that a mass of segregation expected in the grandson generation of the heterozygous background test can damp rather sharp response observed in the female data.

Detailed analysis—female body weight: Two experiments (A and B) were carried out in order to evaluate the amount of increase in genetic variability due to induced mutations under the homozygous (No. 76 irradiated $\times$ No. 76 unirradiated) and heterozygous (No. 76 irradiated $\times$ honey unirradiated) genetic background conditions. Thus, the factors to be considered in this phase of the study are replications (Experiments A and B), doses (control and 1,500r) and genetic backgrounds (homozygous and heterozygous). For each combination of the factors, there are male families (families descended from different male progeny of irradiated females, see Figure 1) and transfers within male families. The variance among transfers within male families represents a measure of environmental variation, while that among male families contains the environmental variance plus variance due to induced mutations. The results of analysis of variance of female body weight data were summarized in Table 1.

An inspection of Table 1 shows that the within- and among-family mean

TABLE 1
Analysis of variance on female body weight

Genetic background	Source of variation	df	Control MS	df	1,500 r MS	Expected MS
Experiment A						
Heterozygous	Among male families	15	40.07	37	390.17	$\sigma^2 + k_1 \sigma_{g1}^2$
	Within male families	12	55.75	28	35.27	σ^2
Homozygous	Among male families	18	27.90	36	676.68	$\sigma^2 + k_2 \sigma_{g2}^2$
	Within male families	15	64.13	26	63.44	σ^2
Experiment B						
Heterozygous	Among male families	18	27.66	32	617.29	$\sigma^2 + k_3 \sigma_{g3}^2$
	Within male families	16	52.44	26	151.75	σ^2
Homozygous	Among male families	18	54.54	35	459.49	$\sigma^2 + k_4 \sigma_{g4}^2$
	Within male families	16	55.81	26	90.06	σ^2

$k_1 = 1.74$ and 1.73 for the control and the treated material, respectively. Likewise, $k_2 = 1.78$ and 1.70 ; $k_3 = 1.84$ and 1.78 ; $k_4 = 1.84$ and 1.72 .

TABLE 2

Estimated genetic variance components for female body weight in Experiments A and B

Nature of the genetic background	Estimated genetic variance component s_g^2	Mean
Heterozygous	$s_{g1}^2 = 205.14 \pm 51.37$	233.34 ± 50.57
	$s_{g3}^2 = 261.54 \pm 87.12$	
Homozygous	$s_{g2}^2 = 360.73 \pm 91.86$	287.75 ± 55.88
	$s_{g4}^2 = 214.78 \pm 63.65$	
Arithmetic mean, $\overline{s_g^2} = 260.55 \pm 35.59$		

The distributions of family means around the general means in homozygous genetic background are shown in Figures 4 and 5.

squares (MS) are not different in the control data, indicating there was no additional variation attributable to family differences. On the contrary, with 1,500r irradiation there are always significant increases of among-family mean squares over the level of within-family mean squares.

In order to ascertain the amount of genetic variability induced, the four genetic components of variance (σ_{g1}^2 , σ_{g2}^2 , σ_{g3}^2 and σ_{g4}^2) were estimated from the data of 1,500r with the use of the expected mean squares in the table. For example, the estimate of σ_{g1}^2 , s_{g1}^2 , is given by $s_{g1}^2 = (390.17 - 35.27)/1.73 = 205.14$. The four estimates of induced genetic variation are listed in Table 2 with their appropriate standard errors. The four estimates are all close to each other and their magnitude is significantly different from zero (none of them deviates from the *over-all* mean with statistical significance). Thus, it may be concluded (a) that genes in Lines No. 76 and honey do not exhibit complete dominance over their mutated alleles, and (b) that there is no indication of differential interactions of mutated genes with the two different genomes of Lines No. 76 and honey.

Figure 4 (control) and Figure 5 (1,500r) are histograms showing the distribu-

FIGURE 4.—Distribution of family means for control female body weight in homozygous background. Data from Experiments A and B were pooled. Grand mean 1.10 mg.

FIGURE 5.—Distribution of family means for body weights of females, each carrying one genome from irradiated grandmothers. The dose was 1500r. Homozygous background. Data from Experiments A and B were pooled. Grand mean 1.08 mg.

tions of female mean body weights in milligram units for the homozygous background data. The comparison of the two figures reveals an obvious increase of variability in the irradiated group and only a slight shift of the general means (1.10 for control *vs.* 1.08 for irradiated). This enables one to hypothesize that some mutated alleles increase body weight, and others decrease, but mutations to increasing alleles occur just as often as those to decreasing mutations on the average. However, the extension of the range of the distribution with irradiation is somewhat greater toward low weight than toward high weight.

Detailed analysis—male body weight: An analysis of grandson family means was made in a similar manner to the analysis of female (i.e. daughter) family means (see Figure 1). If the hypothesis of equally frequent mutations to increasing (+) and decreasing (−) alleles in the preceding paragraph is correct, one expects that there should not be highly significant components of variance among grandson families of the irradiated runs over the within family variance of the same runs. This assertion was proved: $s_{g1}^2 = 1.49 \pm 66.26$, $s_{g2}^2 = 23.32 \pm 58.86$, $s_{g3}^2 = 22.10 \pm 35.52$ and $s_{g4}^2 = 11.36 \pm 40.77$.

On the other hand, the variance among grandsons within families is expected to be considerably greater in the irradiated runs than in the control runs. In Experiment A, the data were taken only for the families with the homozygous genetic background, while in Experiment B, the data were gathered with both homozygous and heterozygous genetic backgrounds. Individual wasps were weighed, and the variances were computed within vials within families. The within-vial variances were pooled to give estimates of within-family variances. The arithmetic means of the within-family variances are presented in Table 3 for the irradiated (subscript *r*) and control (subscript *c*) groups.

For a given experiment with a given genetic background, the difference was computed between the mean variance for the irradiated group and that for the control group (Table 4). This difference, *D*, is considered to measure the increase in variability due to irradiation of the original (great-grandmothers) females.

TABLE 3

Analysis of variance on individual male body weight

Genetic background	Arithmetic mean of variance among individuals within grandson families
Experiment A	
Homozygous	$\overline{s^2_{c1}} = 21.18 \pm 7.35$ $\overline{s^2_{r1}} = 203.58 \pm 44.32$
Experiment B	
Heterozygous	$\overline{s^2_{c2}} = 246.55 \pm 68.29$ $\overline{s^2_{r2}} = 286.44 \pm 54.53$
Homozygous	$\overline{s^2_{c3}} = 35.89 \pm 6.93$ $\overline{s^2_{r3}} = 244.31 \pm 49.51$

The two estimates of D in the homozygous genetic background are close to each other, and they clearly indicate a definite evidence of increased genetic variability due to segregation of mutated genes. However, the situation is not as clear for the heterozygous genetic background data. In the latter case, mutated genes as well as genes that originally differed between the Lines No. 76 and honey are jointly segregating. Consequently, a part of the variation due to the induced mutations may have been covered up by predominant segregation of the other genes. A more detailed discussion will be made later on this point.

Finally, histograms of individual body weights for the control (Figure 6) and the irradiated (Figure 7) groups of the homozygous background tests are presented in terms of the deviations of individual weights from the respective family means. Again, an increase of variability in the irradiated group over the control is clearly seen, and the increase seems to be symmetrical to an increase (+) and decrease (−) in mean body weight.

DISCUSSION

Range of doses in relation to mutation yields: Most radiation-induced visible

TABLE 4

Differences between mean variances for the controls and for the irradiated groups

Nature of the genetic background	Differences
Heterozygous	$\overline{s^2_{r2}} - \overline{s^2_{c2}} = D_{\text{het}} = 39.89 \pm 87.39$
Homozygous	$\overline{s^2_{r1}} - \overline{s^2_{c1}} = D_{\text{homo}} = 182.40 \pm 44.93$ $\overline{s^2_{r3}} - \overline{s^2_{c3}} = D_{\text{homo}} = 208.42 \pm 49.99$

The distribution of individual deviations around the mean within family for a given dose in homozygous genetic background is shown in Figures 5 and 6.

FIGURE 6.—Distribution of individual male body weights in terms of deviations from mean within family. Control data. Experiments A and B were pooled. Homozygous background.

point mutants known in *Habrobracon* were obtained with doses smaller than 4.5 kr (MARTIN 1947). Therefore, the set of doses investigated in the dose-response study was chosen between 0.0 and 4.0 kr. This was based on the assumption that the sensitivity of factors in "polygenic systems" is similar to that of genes responsible for visible mutations which have been shown to have a maximum response in this range. The results, summarized in terms of F-values, seem to indicate a fairly definite relationship between the radiation dosage and mutation yield, at least for the female trait. In this case, the relationship can be described by a single-peaked curve (Figure 2), the peak occurring at 1.5 kr. Thus, this dose level was used later for the detailed study.

However, the description of the dosage-yield relationship by the definite pattern found in the first-phase study can be disputed on the basis of the detailed

FIGURE 7.—Distribution of individual male body weights in terms of deviations from mean within family. Males were segregating for induced mutations. The dose used for irradiating their great grandmothers was 1500r. Data from Experiments A and B were pooled. Homozygous background.

investigation (Experiments A and B). The reason for this dispute comes from the finding that the F-ratio in the first investigation is only 3.81, while, in the detailed study, the ratio has much higher values ($F = 9.74$ in Experiment A and $F = 22.32$ in Experiment B) at $r = 1,500$. This indicates a possible existence of a far greater range of variation in F-ratio than was observed in the first-phase experiments, and this casts some doubt upon the definitive nature of the dosage-yield relationship found and presented in Figure 2.

Insofar as male body weight is concerned, there is not much to be said about the dosage-yield relationship as such, since there was no adequate information on this point in the results of the preliminary study.

Variance within grandson families: The results in Table 3 show that the average variation within families of grandsons is greater for the irradiated than for the control material. However, this increase is less marked when the grandsons are derived from females with the heterozygous background than for those derived from females with the homozygous background. Why should this occur? The four pertinent values for the comparison of the average variances among grandsons within families are found in the bottom half of Table 3, designated as Experiment B.

One might expect to observe approximately the same increment in genetic variance due to induced mutations in both genetic backgrounds if the latter did not interact with the induced mutations. However, such an expectation is not necessarily true, as can be illustrated from the following simple genetic model schematically presented in Table 5. The basic underlying assumptions in this model are: (i) in the polygenic system responsible for the expression of the character under consideration (male body weight), the genes either increase the expression of the trait (+ action) or decrease this expression (— action); (ii) the magnitude of gene action in either direction is about equal for all loci; (iii) the effect of a mutation is to change a “+” gene into a “—” gene and vice-versa; (iv) the two lines crossed are sufficiently unrelated and divergent; (v) no serious linkage phase imbalance exists among “+” and “—” genes; (vi) no epistatic gene interaction takes place. Under these assumptions, the amount of genetic variability found among grandsons within families becomes proportional to the number of heterozygous loci (+/—) in their respective mothers' genotype.

The model in Table 5 includes two female genotypes (II and IV in the Table) obtained when a particular male carrying mutations at loci 1, 3, 5 and 9, originally from Line No. 76, is mated to virgins from Line No. 76 (homozygous background) and from Line honey (heterozygous background). The other two female genotypes (I and III) are the two control materials (Line No. 76 $\times$ Line No. 76 and Line No. 76 $\times$ Line honey). Lines honey and No. 76 possess different sets of “+” and “—” genes, but any particular locus may have an identical allele in both lines (e.g. locus 1). The total number of loci included in the model is arbitrarily set at ten.

In the homozygous background, the female with the genotype represented by Female No. I in Table 5 (control) has a uniform gametic output. The genetic variability among males representing this gametic output is zero since none of

TABLE 5

Diagram of four female genotypes obtained by mating virgins from the Line honey and Line No. 76 to a male produced by irradiated (females II and IV) or nonirradiated (females I and III) mother from Line No. 76

Female No.	1	2	3	4	5	Locus 6	7	8	9	10	Number of segregating loci
Homozygous background											
I No. 76	+	—	—	+	+	—	—	+	—	+	0
No. 76	+	—	—	+	+	—	—	+	—	+	
II No. 76	+	—	—	+	+	—	—	+	—	+	4
No. 76*	—*	—	+	+	—*	—	—	+	+	+	
Heterozygous background											
III honey	+	—	+	—	+	+	—	—	+	—	6
No. 76	+	—	—	+	+	—	—	+	—	+	
IV honey	+	—	+	—	+	+	—	—	+	—	6
No. 76*	—*	—	+	+	—*	—	—	+	+	+	

+* means that a "—" gene mutated to "+". —* means that a "+" gene mutated to "—". No. 76* means that the male parent was produced by an irradiated female from Line No. 76.

the loci is to be segregating. In Female No. II, four genes have mutated; therefore, the genetic variance, proportional to the number of segregating loci, is 4. The difference between 0 and 4 corresponds to the amount of increased genetic variability.

In the heterozygous genetic background, six loci are segregating in the control run (Female No. III) as well as in the irradiation run (Female No. IV). Consequently, no difference in genetic variance could be observed.

Thus, the simple model presented can explain the results in Tables 3 and 4. However, it should be noted that linkage between segregating loci could influence the amount of genetic variance. For example, it can be shown that, with two linked loci in coupling condition with respect to gene action (i.e. ++ *vs.* —— combination), the genetic variance in the male progeny will be inflated proportionally to the factor $(1-r)$ to $\frac{1}{2}$, where r is the recombination fraction between the two loci. This holds true even when no epistasis is involved. Epistasis among loci could also influence the magnitude of the genetic variance in either direction. However, the experiments performed in this study were not designed to distinguish the increments in genetic variance due to such different factors.

The model just presented was made so restrictive that the point to be argued could be explained in a simple fashion. However, the relaxation of some of the assumptions does not impair the key point for explaining the discrepancy between the amounts of increased genetic variability in the two backgrounds. For example, assumptions (ii) and (iii) can be replaced by the assumption that mutant alleles exhibit positive and negative effects in random directions with random magnitudes.

Expected response to selection: The amount of genetic variance created in

body-weight genes of an inbred population by ionizing radiations was large as compared to the magnitude of environmental variance in such a population. In the case of individual male body weight, in homozygous genetic background, the estimate of heritability (i.e. the ratio of genetic variance to the total variance) is 0.87 for individuals within an average family. In reference to heritability values in diploid organisms, however, this figure is misleading insofar as the effectiveness of selection is concerned.

When selected males are mated to unselected females, there will not be any gain whatsoever among the male progeny, since males are produced parthenogenetically from female parents. Female progenies, however, will carry genes, in heterozygous states, which were selected in the male parents. The magnitude of the gain observed in the female progeny depends upon the kinds of gene action in diploid genotypes. For example, if all induced mutations are completely recessive, then the average female body weight is expected to be the same as that of unselected females.

The males in the next generation will contain one half of the genes selected in their grandfathers. This is obvious, since the mothers of the grandsons had only one half of their genes originating from the selected grandfathers. Hence, the appropriate heritability for the selection response expected between grandfathers and grandsons is one half the ratio of genetic variance to the total variance among grandfathers. When the heritability is to be expressed on a per-generation basis, the value obtained from the grandfathers must be further reduced by another factor of one half. Therefore, the expected response per generation in the homozygous genetic background material in this study is $S \times (\frac{1}{2})(\frac{1}{2})(0.87) = 0.22S$, when the selection is performed only on male body weight and S is selection differential.

Another point of interest is the kind of response expected under the pressure of a two-way (heavy and light body) selection. The kind of response which is referred to here is the degree of asymmetry which may be observed between the upward and downward selection lines. In order to obtain some judgement on this point, the frequency distributions of grandson body weight under the homozygous background were plotted in Figures 6 (for the control) and 7 (for the treated material). A difference between the two distributions is observed primarily in the magnitude of variance; the distribution for the irradiated group reveals much more variation than that for the control. Another important feature of these distributions is their symmetry. This indicates that, in the irradiated material, "+" mutations occurred as often as "-" mutations in a random fashion. When a two-way selection is performed on such a material, the response in the two directions are expected to be symmetrical.

The situation expected under selection for female body weight is more confusing than that for male body weight. The reason for this is primarily coming from the state of diploidy in the female genotype. As seen in RESULTS, there was a large increase in genetic variance from the control to the material carrying induced mutations in heterozygous conditions under the homozygous background. This contrast is observed in terms of the actual distributions of family means in Fig-

ures 4 and 5. The increase of variance from Figure 4 (control) to Figure 5 (irradiated) is obvious, but also noted is a fair degree of asymmetry in Figure 5. Such asymmetry can be caused primarily by varying degrees of dominance in gene action between the original alleles in Line No. 76 and their mutants. It seems, from Figure 5, that many mutations are partially recessive to their wild-type alleles, so that the resulting heterozygotes show body weights inferior to those of the wild-type homozygotes. On the other hand, there must be another group of mutants, perhaps not so large as the previous group, which increase the body weight when in heterozygous conditions.

All these observations lead to the conclusion that it is not possible to determine an adequate value of heritability on female body weight from the data collected in this study. However, it is clear that there will be a response to downward selection. The same or somewhat less degree of response to an upward selection pressure is also expected.

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SUMMARY

A quantification of the genetic variability induced by gamma-irradiation was carried out with quantitative characters of *Habrobracon juglandis*. Adult female (diploid) and male (haploid) body weights were studied in homozygous and heterozygous genetic backgrounds. The dose-response relationship was determined with respect to body weights of females that might be heterozygous for induced mutations. The responses to 0, 1.0, 1.5, 2.5 and 4.0kr irradiations were measured using the F-ratio between the variances among family means in the irradiated material and in the control. The maximum response was obtained at 1.5kr.

Induced genetic variability was studied in detail with 1.5kr irradiation. (1) A striking increase of genetic variance was observed for induced-mutation-heterozygote females in either homozygous or heterozygous genetic background. (2) A great increase of genetic variance was also observed among males segregating for induced mutations in an otherwise homozygous line (i.e. males produced by mutation-heterozygote females with the homozygous genetic background). However, there was no significant increase of genetic variance among males produced by mutation-heterozygote females with the heterozygous genetic background.—These findings suggest that (a) induced mutations can increase or decrease body weight, (b) induced mutations affecting body weight are not necessarily recessive to their wild-type alleles, and (c) there are little or no nonallelic interactions between induced mutations and the rest of the genes affecting body weight.

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