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ORIGINAL ARTICLE

# Does exposure of male *Drosophila melanogaster* to acute gamma radiation influence egg to adult development time and longevity of $F_1$–$F_3$ offspring?

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## Abstract

Two- to three-day-old male *Drosophila melanogaster* flies were irradiated with 1, 2, 4, 6, 8, 10, 20, 25, 30, 40 and 50 Gy doses of gamma radiation. The longevity and rate of development were observed for three successive generations to assess the impact of irradiation. The mean lifespan of irradiated flies was significantly increased at 1, 2 and 8 Gy, while it was vice versa for high doses at 30, 40 and 50 Gy. Paternal irradiation had an impact on $F_1$ generation, with significantly increased mean longevity at 2 (female), 4, 6, 8 and 10 and decreased mean longevity at 40 and 50 Gy (male and female). Significant increase in the longevity was observed in the $F_2$ generation of the 8 (male and female) and 10 Gy (male) irradiated groups, while decreased longevity was observed in $F_2$ female progeny at 40 Gy. In the case of $F_3$ progeny of irradiated flies, longevity did not show significant difference with the control. Paternal exposure to radiation had a significant impact on the mean egg to adult developmental time of the $F_1$ generation; it was shortened at 2 Gy and extended at 25, 30, 40 and 50 Gy compared to the control. Mean development time at 30, 40 and 50 Gy was significantly increased in the $F_2$ generation, while there were no significant changes in the $F_3$ generation. The present study concludes that the effect of acute gamma irradiation on longevity and "egg to adult" development time of *D. melanogaster* may persist to following generations.

**Key words:** eclosion, generation, hormesis, ionizing radiation, lifespan.

## INTRODUCTION

The protection of the environment from the effects of ionizing radiation has become a key subject for all relevant international organizations in the field of radiation protection (Keum *et al.* 2010). Any system for assessing the impact of a contaminant on the environment requires an analysis of the possible effects on the organisms and ecosystems concerned (Copplestone *et al.* 2008). Longevity is the most appropriate measure of the health effects of radiation (Cameron 2003). Longevity is an important component of fitness. It is an expression of the entire organization of an individual under a sequence of environments. Both genetic and environmental aspects are involved; the latter may be either internal or external (Malick & Kidwell 1966).

The effects of gamma radiation on the development and longevity of different insects have been studied by numerous researchers. Various studies have shown that developmental time and longevity are highly influenced by factors like the amount and duration of exposure throughout the developmental stage. High-dose irradiation led to prolongation of the prepupal period and chronic low-dose irradiation resulted in shortening of the larval development period in wild type Oregon R and mutant strain mus209 *Drosophila melanogaster* (Shaposhnikov *et al.* 2009). The irradiated eggs and larvae of the red flour beetle exhibited a dose-dependent developmental delay (Mehta *et al.* 1990). In *Anopheles*

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*arabiensis* the longevity of irradiated males was similar to the controls in the adult stage, while when irradiated in the pupal stage, overall similar or higher survival was observed compared to the control for the tested doses ranging between 0 and 100 Gy (Helinski *et al*. 2006). The life-prolonging effect of gamma irradiation was observed when the flour beetle *Tribolium confusum* was exposed to a single exposure of dosage of 30 Gy or chronic daily dosages of about 1 Gy (Cork 1957). There were no significant differences observed in male longevity of Guava fruit fly *Bactrocera correcta* when pupae were irradiated with 5, 10, 15 and 30 Gy doses of gamma radiation (Puanmanee *et al*. 2010).

*Drosophila melanogaster* is a well-established model organism for genetic studies on development, aging (Parashar *et al*. 2008) and longevity (Paaby & Schmidt 2009), and its genes share extensive homology with vertebrate counterparts (Bier 2005). Various environmental aspects like ultraviolet and ionizing radiation, temperature, nutrition, antioxidants, humidity, oxygen tension, population density and larval crowding have been shown to affect longevity in *Drosophila* (Yoon *et al*. 1990). In light of this information, an attempt has been made to assess whether the effects of radiation persist in the successive generation in terms of rate of development and longevity in *D. melanogaster*.

## MATERIALS AND METHODS

### Experimental stock

Wild *D. melanogaster* were collected by keeping banana baits at the fruit and vegetable stalls at KR Market, Bangalore, India. Once collected, flies were transferred to a wheat cream agar media culture bottle and maintained in the laboratory at 25 ± 2°C, 70 ± 5% relative humidity under conditions of 12 h light : 12 h dark (LD 12:12). Isofemale lines were maintained and male flies were used for the identification of species by using the guide of Markow and O'Grady (2006). Pure lines were prepared by continuous selection and inbreeding to eliminate naturally occurring recessive lethal by using the modified protocol of Shetty (1983). Further pure line stocks were used for experiments.

### Irradiation and mating of flies

Virgin females and unmated males were isolated within 4 h after eclosion and sexed separately for two to three days according to the modified protocol of Moriwaki and Tobari (1960). Fifty males were irradiated with 1, 2, 4, 6, 8, 10, 20, 25, 30, 40 and 50 Gy gamma rays. Co-60 gamma radiation (Theratron 780-C Telecobalt unit; AECL, Ontario, Canada) with a dose rate of 146.75 centiGray (cGy)/min (for 1, 2, 4 and 6 Gy), 135.73 cGy/min (for 8 and 10 Gy), 134.22 cGy/min (for 20, 25 and 30 Gy) and 303.13 cGy/min (for 40 and 50 Gy) was used as the radiation source. Exposure periods of 40.89 s, 1 min 21.77 s, 2 min 43.54 s, 4 min 5.31 s, 5 min 53.64 s, 7 min 22.05 s, 14 min 54.05 s, 18 min 37.57 sec, 22 min 21.1 s, 13 min 11.74 s and 16 min 29.67 s were used for 1, 2, 4, 6, 8, 10, 20, 25, 30, 40 and 50 Gy doses, respectively. Dosimetry confirmed that the doses delivered were within the 5% error range. Irradiated males were immediately mated with non-irradiated virgin females of the same age as single pair mating in vials measuring 75 mm × 25 mm. Non-irradiated males and females were used as controls. Further, the $F_1$ generation was obtained from the same vials. Inbreeding achieved $F_2$ and $F_3$ generations (Fig. 1). Fifty replicates were used for each generation.

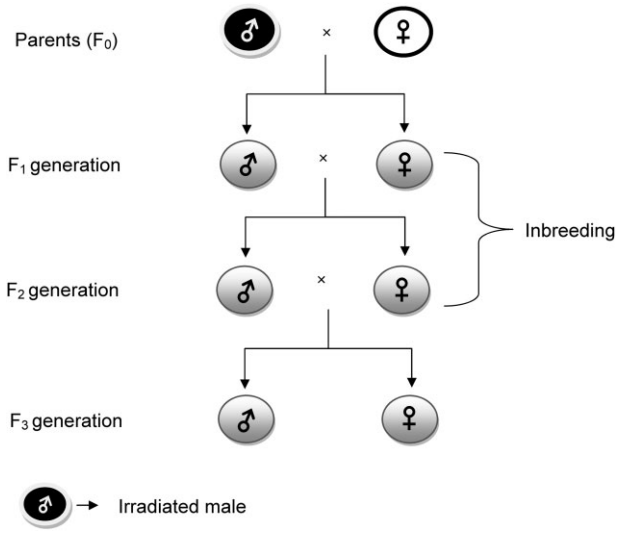


**Figure 1** Symbolic representation of cross between irradiated male with non-irradiated female ($F_0$) and inbreeding between their progeny ($F_1$–$F_2$).

### Egg to adult development time

The *D. melanogaster* life cycle consists of four stages: egg, larva, pupa and adult (imago). Single pair mated females (mated with irradiated males) were allowed to lay eggs for 4 h in media vials. Later, when pupae emerged in these vials, 105 pupae were selected randomly from 30 to 50 replicates. Vials were monitored for eclosion of adult flies at 6 h intervals after the pupae became dark. The observations were continued until no flies eclosed for three consecutive days. Times taken for egg to adult emergence of $F_1$, $F_2$ and $F_3$ generations for the test and control samples were recorded.

**Table 1** Developmental time of *D. melanogaster* $F_1$ generation

| Sample | *n* | Developmental time (mean ± SE) (days) | ANOVA | Tukey HSD |
|---|---|---|---|---|
| Control $F_1$ | 105 | 9.49 ± 0.05 | F = 9.249 | |
| 1 Gy $F_1$ | 104 | 9.42 ± 0.04 | d.f. = 2310 | $P = 0.484$ |
| 2 Gy $F_1$ | 104 | 9.21 ± 0.06 | $P = 0.000$ | $P = 0.000$** |
| Control $F_1$ | 104 | 9.54 ± 0.03 | F = 0.269 | |
| 4 Gy $F_1$ | 103 | 9.55 ± 0.03 | d.f. = 2307 | $P = 0.946$ |
| 6 Gy $F_1$ | 103 | 9.57 ± 0.03 | $P = 0.765$ | $P = 0.745$ |
| Control $F_1$ | 104 | 9.61 ± 0.05 | F = 0.430 | |
| 8 Gy $F_1$ | 103 | 9.58 ± 0.04 | d.f. = 2306 | $P = 0.900$ |
| 10 Gy $F_1$ | 102 | 9.64 ± 0.05 | $P = 0.651$ | $P = 0.875$ |
| Control $F_1$ | 104 | 9.51 ± 0.05 | F = 19.040 | |
| 20 Gy $F_1$ | 102 | 9.69 ± 0.04 | d.f. = 3403 | $P = 0.063$ |
| 25 Gy $F_1$ | 101 | 9.79 ± 0.05 | $P = 0.000$ | $P = 0.001$** |
| 30 Gy $F_1$ | 100 | 10.04 ± 0.06 | | $P = 0.000$** |
| Control $F_1$ | 104 | 9.50 ± 0.04 | F = 521.405 | |
| 40 Gy $F_1$ | 98 | 11.51 ± 0.07 | d.f. = 2295 | $P = 0.000$** |
| 50 Gy $F_1$ | 96 | 11.93 ± 0.06 | $P = 0.000$ | $P = 0.000$** |

*n*, numbers of flies used; SE, standard error; **$P \leq 0.01$.

### Longevity of mated flies

Longevity was assessed using the modified protocol of Harini and Ramachandra (2007). Fifty virgin females and males of $F_1$, $F_2$ and $F_3$ generation of *D. melanogaster* were aged separately for three days from the day of emergence. On the third day, a male and a female fly were placed in fresh food vials (75 mm × 25 mm culture vials) seeded with yeast grains and allowed to mate. Once in two days, each pair was transferred to fresh vials and the changes were continued till the flies were alive for the assessment of longevity.

### Data analysis

To test the difference in mean time taken for egg to adult development of irradiated and control flies for three generations, one-way analysis of variance (ANOVA) was conducted. Significant differences were determined by Tukey's honestly significant difference (HSD) post hoc test at $P \leq 0.05$. The effects of gamma irradiation on the longevity of irradiated males and their progeny were calculated with log-rank statistical analysis. $P \leq 0.05$ was considered as statistically significant. SPSS v17 software (SPSS, Chicago, IL, USA) was used for analysis.

## RESULTS

### Egg to adult development time

Mean egg to adult development times of $F_1$, $F_2$ and $F_3$ generations are given in Tables 1–3, respectively. There were no significant differences in the mean egg to adult development time of $F_1$, $F_2$ and $F_3$ progeny of males irradiated with doses of 1, 4, 6, 8, 10 and 20 Gy when compared to that of the control. Significant reduction in the development time was observed in the $F_1$ generation of the 2 Gy-irradiated group, while there were no significant changes in $F_2$ and $F_3$ generations compared to control. Significant increases in the development time were observed in $F_1$ progeny of the 25 Gy-irradiated group and the $F_1$ and $F_2$ progeny of the 30, 40 and 50 Gy-irradiated groups when compared to that of control.

### Longevity of mated flies

Tables 4–7 present the mean longevity of irradiated males and their non-irradiated female partners and that of the $F_1$, $F_2$ and $F_3$ progeny, respectively. Data revealed that the longevity of the 1, 2 and 8 Gy irradiated male flies increased significantly, while longevity was significantly reduced in the 30, 40 and 50 Gy irradiated males with corresponding male controls. There were no significant differences between the longevity of the control and 4, 6, 10, 20 and 25 Gy irradiated flies. Significant increases in the longevity of the $F_1$ generation (both male and female progeny) were noticed in the 4, 6, 8 and 10 Gy-irradiated groups, while for 2 Gy only female progeny longevity was increased. Male and female longevities of the $F_1$ generation were significantly reduced in the 40 and 50 Gy-irradiated group. A significant increase in longevity was observed in the $F_2$ male and female progeny of the 8 Gy-irradiated group and the $F_2$ male progeny of the 10 Gy-irradiated group. A

**Table 2** Developmental time of *D. melanogaster* $F_2$ generation

| Sample | *n* | Developmental time (mean ± SE) (days) | ANOVA | Tukey HSD |
|---|---|---|---|---|
| Control $F_2$ | 104 | 9.52 ± 0.04 | F = 0.756 | |
| 1 Gy $F_2$ | 103 | 9.46 ± 0.04 | d.f. = 2307 | *P* = 0.688 |
| 2 Gy $F_2$ | 103 | 9.44 ± 0.05 | *P* = 0.471 | *P* = 0.453 |
| Control $F_2$ | 105 | 9.59 ± 0.03 | F = 2.625 | |
| 4 Gy $F_2$ | 104 | 9.50 ± 0.04 | d.f. = 2309 | *P* = 0.180 |
| 6 Gy $F_2$ | 103 | 9.48 ± 0.04 | *P* = 0.074 | *P* = 0.084 |
| Control $F_2$ | 103 | 9.53 ± 0.06 | F = 1.435 | |
| 8 Gy $F_2$ | 103 | 9.48 ± 0.05 | d.f. = 2306 | *P* = 0.772 |
| 10 Gy $F_2$ | 103 | 9.61 ± 0.05 | *P* = 0.240 | *P* = 0.579 |
| Control $F_2$ | 103 | 9.52 ± 0.05 | F = 4.242 | |
| 20 Gy $F_2$ | 103 | 9.58 ± 0.05 | d.f. = 3405 | *P* = 0.866 |
| 25 Gy $F_2$ | 102 | 9.63 ± 0.05 | *P* = 0.006 | *P* = 0.463 |
| 30 Gy $F_2$ | 101 | 9.76 ± 0.05 | | *P* = 0.004** |
| Control $F_2$ | 103 | 9.69 ± 0.04 | F = 32.672 | |
| 40 Gy $F_2$ | 100 | 10.00 ± 0.04 | d.f. = 2299 | *P* = 0.000** |
| 50 Gy $F_2$ | 99 | 10.23 ± 0.06 | *P* = 0.000 | *P* = 0.000** |

**$P \leq 0.01$.

**Table 3** Developmental time of *D. melanogaster* $F_3$ generation

| Sample | *n* | Developmental time (mean ± SE) (days) | ANOVA | Tukey HSD |
|---|---|---|---|---|
| Control $F_3$ | 103 | 9.49 ± 0.04 | F = 0.727 | |
| 1 Gy $F_3$ | 103 | 9.51 ± 0.05 | d.f. = 2306 | *P* = 0.942 |
| 2 Gy $F_3$ | 103 | 9.43 ± 0.05 | *P* = 0.484 | *P* = 0.678 |
| Control $F_3$ | 104 | 9.49 ± 0.05 | F = 0.307 | |
| 4 Gy $F_3$ | 104 | 9.51 ± 0.05 | d.f. = 2309 | *P* = 0.933 |
| 6 Gy $F_3$ | 104 | 9.54 ± 0.04 | *P* = 0.736 | *P* = 0.714 |
| Control $F_3$ | 103 | 9.54 ± 0.05 | F = 1.965 | |
| 8 Gy $F_3$ | 104 | 9.63 ± 0.06 | d.f. = 2307 | *P* = 0.428 |
| 10 Gy $F_3$ | 103 | 9.49 ± 0.05 | *P* = 0.142 | *P* = 0.757 |
| Control $F_3$ | 105 | 9.59 ± 0.05 | F = 0.431 | |
| 20 Gy $F_3$ | 103 | 9.57 ± 0.05 | d.f. = 3409 | *P* = 0.994 |
| 25 Gy $F_3$ | 103 | 9.61 ± 0.06 | *P* = 0.731 | *P* = 0.993 |
| 30 Gy $F_3$ | 102 | 9.65 ± 0.05 | | *P* = 0.841 |
| Control $F_3$ | 104 | 9.57 ± 0.04 | F = 2.672 | |
| 40 Gy $F_3$ | 101 | 9.69 ± 0.05 | d.f. = 2303 | *P* = 0.185 |
| 50 Gy $F_3$ | 101 | 9.72 ± 0.05 | *P* = 0.071 | *P* = 0.078 |

significant decrease in longevity was observed in the $F_2$ female progeny at 40 Gy. There were no significant differences in the longevity of $F_3$ generation progeny with the corresponding control.

## DISCUSSION

Shaposhnikov *et al.* (2009) reported that high-dose irradiation (30 Gy) lengthened the prepupal period in wild type (Canon S and Oregon R) and mutant strains (DNA damage sensing (mei-41), DNA repair (mus209, mus210, mus309, rad54) and free radical detoxification (sod)). Chronic low dose (20 cGy) irradiation, on the other hand, was found to shorten the larval development period of Oregon R and mutant (mus209) strains and prolongation of the prepupal period on sod and rad54 mutant strains of *D. melanogaster*. Dose-dependent increases in the developmental periods of red flour beetle (Abbas & Nouraddin 2011), saw toothed grain beetle (Hosseinzadeh *et al.* 2010) and Indian meal

**Table 4** Longevity of parental ($F_0$) stock of *D. melanogaster*

| Sample | Male† | | Female | |
|---|---|---|---|---|
| | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) |
| Control $F_0$ | 41.62 ± 0.33 | | 43.58 ± 0.51 | |
| 1 Gy $F_0$ | 45.76 ± 0.52 | $\chi^2 = 39.316$, $P = 0.000$** | 43.90 ± 0.50 | $\chi^2 = 0.338$, $P = 0.561$ |
| 2 Gy $F_0$ | 45.60 ± 0.50 | $\chi^2 = 37.136$, $P = 0.000$** | 44.08 ± 0.47 | $\chi^2 = 0.510$, $P = 0.475$ |
| Control $F_0$ | 43.38 ± 0.50 | | 44.08 ± 0.55 | |
| 4 Gy $F_0$ | 44.66 ± 0.46 | $\chi^2 = 1.500$, $P = 0.221$ | 44.86 ± 0.51 | $\chi^2 = 0.683$, $P = 0.409$ |
| 6 Gy $F_0$ | 44.44 ± 0.50 | $\chi^2 = 1.048$, $P = 0.306$ | 45.02 ± 0.63 | $\chi^2 = 1.237$, $P = 0.266$ |
| Control $F_0$ | 43.04 ± 0.43 | | 44.24 ± 0.59 | |
| 8 Gy $F_0$ | 44.72 ± 0.75 | $\chi^2 = 4.036$, $P = 0.045$* | 45.02 ± 0.69 | $\chi^2 = 0.542$, $P = 0.462$ |
| 10 Gy $F_0$ | 44.34 ± 0.66 | $\chi^2 = 3.466$, $P = 0.063$ | 44.82 ± 0.79 | $\chi^2 = 0.826$, $P = 0.363$ |
| Control $F_0$ | 43.16 ± 0.44 | | 43.68 ± 0.45 | |
| 20 Gy $F_0$ | 42.96 ± 0.58 | $\chi^2 = 0.072$, $P = 0.788$ | 44.42 ± 0.68 | $\chi^2 = 1.241$, $P = 0.265$ |
| 25 Gy $F_0$ | 42.16 ± 0.60 | $\chi^2 = 0.231$, $P = 0.631$ | 44.34 ± 0.58 | $\chi^2 = 1.210$, $P = 0.271$ |
| 30 Gy $F_0$ | 40.74 ± 0.57 | $\chi^2 = 6.044$, $P = 0.014$* | 43.82 ± 0.52 | $\chi^2 = 0.130$, $P = 0.719$ |
| Control $F_0$ | 41.80 ± 0.58 | | 43.18 ± 0.63 | |
| 40 Gy $F_0$ | 35.44 ± 0.62 | $\chi^2 = 39.103$, $P = 0.000$** | 42.88 ± 0.59 | $\chi^2 = 0.137$, $P = 0.711$ |
| 50 Gy $F_0$ | 33.78 ± 0.51 | $\chi^2 = 73.307$, $P = 0.000$** | 42.60 ± 0.56 | $\chi^2 = 0.752$, $P = 0.386$ |

†Only male flies were irradiated; *$P \leq 0.05$, **$P \leq 0.01$.

**Table 5** Longevity of $F_1$ generation of *D. melanogaster*

| Sample | Male | | Female | |
|---|---|---|---|---|
| | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) |
| Control $F_1$ | 41.06 ± 0.62 | | 43.24 ± 0.64 | |
| 1 Gy $F_1$ | 42.18 ± 0.56 | $\chi^2 = 1.003$, $P = 0.317$ | 44.02 ± 0.67 | $\chi^2 = 1.346$, $P = 0.246$ |
| 2 Gy $F_1$ | 41.36 ± 0.64 | $\chi^2 = 0.112$, $P = 0.737$ | 45.26 ± 0.56 | $\chi^2 = 4.168$, $P = 0.041$* |
| Control $F_1$ | 42.34 ± 0.74 | | 45.18 ± 0.70 | |
| 4 Gy $F_1$ | 45.10 ± 0.61 | $\chi^2 = 4.918$, $P = 0.027$* | 48.04 ± 0.86 | $\chi^2 = 6.420$, $P = 0.011$* |
| 6 Gy $F_1$ | 46.40 ± 0.61 | $\chi^2 = 10.553$, $P = 0.001$** | 49.82 ± 0.90 | $\chi^2 = 17.000$, $P = 0.000$** |
| Control $F_1$ | 43.68 ± 0.55 | | 43.98 ± 0.61 | |
| 8 Gy $F_1$ | 48.24 ± 0.55 | $\chi^2 = 29.430$, $P = 0.000$** | 49.02 ± 0.56 | $\chi^2 = 29.726$, $P = 0.000$** |
| 10 Gy $F_1$ | 46.04 ± 0.54 | $\chi^2 = 9.701$, $P = 0.002$** | 47.02 ± 0.50 | $\chi^2 = 10.274$, $P = 0.001$** |
| Control $F_1$ | 42.98 ± 0.55 | | 44.32 ± 0.48 | |
| 20 Gy $F_1$ | 43.94 ± 0.51 | $\chi^2 = 1.459$, $P = 0.227$ | 45.16 ± 0.51 | $\chi^2 = 1.233$, $P = 0.267$ |
| 25 Gy $F_1$ | 43.52 ± 0.42 | $\chi^2 = 0.039$, $P = 0.844$ | 44.62 ± 0.55 | $\chi^2 = 0.404$, $P = 0.525$ |
| 30 Gy $F_1$ | 41.84 ± 0.55 | $\chi^2 = 1.750$, $P = 0.186$ | 43.56 ± 0.56 | $\chi^2 = 0.484$, $P = 0.487$ |
| Control $F_1$ | 41.74 ± 1.03 | | 43.88 ± 1.13 | |
| 40 Gy $F_1$ | 37.10 ± 0.83 | $\chi^2 = 13.525$, $P = 0.000$** | 38.14 ± 0.93 | $\chi^2 = 16.668$, $P = 0.000$** |
| 50 Gy $F_1$ | 34.44 ± 0.95 | $\chi^2 = 23.878$, $P = 0.000$** | 36.74 ± 0.89 | $\chi^2 = 24.067$, $P = 0.000$** |

*$P \leq 0.05$, **$P \leq 0.01$.

moth (Abbas *et al.* 2011) were also observed when eggs, larvae and pupae were exposed to gamma radiation. The present results revealed that paternal exposure to 2 Gy of gamma radiation triggered the rate of development of $F_1$ progeny, with no significant effect on $F_2$ and $F_3$ progeny. At higher doses, however, a decreased rate of development was noticed; that is, the time taken for egg to adult development of $F_1$ progeny was significantly increased at 25 Gy. Doses 30, 40 and 50 Gy caused a decrease in the rate of development of both $F_1$ and $F_2$ progeny. There were no significant changes in the rate of development of the $F_3$ progeny.

Single or multiple exposure to low doses of irradiation has a variety of anti-aging and longevity-extending

**Table 6** Longevity of $F_2$ generation of *D. melanogaster*

| | Male | | Female | |
|---|---|---|---|---|
| Sample | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) |
| Control $F_2$ | 42.40 ± 0.72 | | 44.82 ± 0.76 | |
| 1 Gy $F_2$ | 43.66 ± 0.57 | $\chi^2 = 0.654$, $P = 0.419$ | 43.96 ± 0.92 | $\chi^2 = 0.014$, $P = 0.907$ |
| 2 Gy $F_2$ | 43.92 ± 0.55 | $\chi^2 = 1.028$, $P = 0.311$ | 47.04 ± 0.50 | $\chi^2 = 2.029$, $P = 0.154$ |
| Control $F_2$ | 43.92 ± 0.48 | | 44.78 ± 0.51 | |
| 4 Gy $F_2$ | 44.94 ± 0.47 | $\chi^2 = 2.854$, $P = 0.091$ | 45.16 ± 0.57 | $\chi^2 = 0.614$, $P = 0.433$ |
| 6 Gy $F_2$ | 43.18 ± 0.49 | $\chi^2 = 1.230$, $P = 0.267$ | 44.80 ± 0.50 | $\chi^2 = 0.006$, $P = 0.938$ |
| Control $F_2$ | 43.64 ± 0.44 | | 44.78 ± 0.50 | |
| 8 Gy $F_2$ | 45.30 ± 0.57 | $\chi^2 = 7.112$, $P = 0.008$** | 46.16 ± 0.55 | $\chi^2 = 3.871$, $P = 0.049$* |
| 10 Gy $F_2$ | 45.22 ± 0.48 | $\chi^2 = 6.409$, $P = 0.011$* | 46.08 ± 0.52 | $\chi^2 = 3.097$, $P = 0.078$ |
| Control $F_2$ | 43.48 ± 0.43 | | 44.26 ± 0.52 | |
| 20 Gy $F_2$ | 43.90 ± 0.63 | $\chi^2 = 1.672$, $P = 0.196$ | 44.58 ± 0.56 | $\chi^2 = 0.243$, $P = 0.622$ |
| 25 Gy $F_2$ | 43.88 ± 0.38 | $\chi^2 = 0.310$, $P = 0.578$ | 44.34 ± 0.49 | $\chi^2 = 0.051$, $P = 0.821$ |
| 30 Gy $F_2$ | 42.94 ± 0.52 | $\chi^2 = 0.064$, $P = 0.800$ | 43.86 ± 0.56 | $\chi^2 = 0.283$, $P = 0.595$ |
| Control $F_2$ | 42.08 ± 0.56 | | 45.64 ± 0.80 | |
| 40 Gy $F_2$ | 41.44 ± 0.70 | $\chi^2 = 0.002$, $P = 0.967$ | 43.48 ± 0.67 | $\chi^2 = 4.950$, $P = 0.026$* |
| 50 Gy $F_2$ | 40.36 ± 0.79 | $\chi^2 = 0.792$, $P = 0.374$ | 43.88 ± 0.66 | $\chi^2 = 3.689$, $P = 0.055$ |

*$P \leq 0.05$, **$P \leq 0.01$.

**Table 7** Longevity of $F_3$ generation of *D. melanogaster*

| | Male | | Female | |
|---|---|---|---|---|
| Sample | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) | Longevity (mean ± SE) (days) | Log rank (Mantel–Cox) |
| Control $F_3$ | 40.68 ± 0.43 | | 45.84 ± 0.60 | |
| 1 Gy $F_3$ | 41.92 ± 0.40 | $\chi^2 = 2.263$, $P = 0.132$ | 46.16 ± 0.38 | $\chi^2 = 0.376$, $P = 0.540$ |
| 2 Gy $F_3$ | 40.96 ± 0.48 | $\chi^2 = 0.267$, $P = 0.605$ | 47.04 ± 0.43 | $\chi^2 = 0.612$, $P = 0.434$ |
| Control $F_3$ | 43.06 ± 0.50 | | 44.32 ± 0.58 | |
| 4 Gy $F_3$ | 42.84 ± 0.57 | $\chi^2 = 0.061$, $P = 0.805$ | 43.86 ± 0.61 | $\chi^2 = 0.307$, $P = 0.580$ |
| 6 Gy $F_3$ | 44.14 ± 0.42 | $\chi^2 = 1.495$, $P = 0.221$ | 45.12 ± 0.55 | $\chi^2 = 0.898$, $P = 0.343$ |
| Control $F_3$ | 43.50 ± 0.59 | | 44.36 ± 0.47 | |
| 8 Gy $F_3$ | 43.74 ± 0.56 | $\chi^2 = 0.056$, $P = 0.813$ | 44.42 ± 0.56 | $\chi^2 = 0.098$, $P = 0.754$ |
| 10Gy $F_3$ | 43.62 ± 0.49 | $\chi^2 = 0.234$, $P = 0.628$ | 44.44 ± 0.58 | $\chi^2 = 0.321$, $P = 0.571$ |
| Control $F_3$ | 43.70 ± 0.42 | | 44.34 ± 0.57 | |
| 20 Gy $F_3$ | 43.64 ± 0.53 | $\chi^2 = 0.493$, $P = 0.483$ | 44.20 ± 0.53 | $\chi^2 = 0.060$, $P = 0.806$ |
| 25 Gy $F_3$ | 43.10 ± 0.61 | $\chi^2 = 0.184$, $P = 0.668$ | 44.70 ± 0.57 | $\chi^2 = 0.198$, $P = 0.656$ |
| 30 Gy $F_3$ | 43.60 ± 0.47 | $\chi^2 = 0.037$, $P = 0.848$ | 44.22 ± 0.53 | $\chi^2 = 0.100$, $P = 0.751$ |
| Control $F_3$ | 43.18 ± 0.75 | | 43.52 ± 0.75 | |
| 40 Gy $F_3$ | 42.62 ± 0.76 | $\chi^2 = 0.058$, $P = 0.809$ | 43.64 ± 0.86 | $\chi^2 = 0.000$, $P = 0.985$ |
| 50 Gy $F_3$ | 41.94 ± 0.56 | $\chi^2 = 2.046$, $P = 0.153$ | 42.88 ± 0.74 | $\chi^2 = 0.412$, $P = 0.521$ |

hormetic effects (Rattan 2008). In the present study, 1, 2 and 8 Gy-irradiated males and $F_1$ progeny of 2 (only female), 4, 6, 8 and 10 Gy (male and female) doses showed a hormetic effect on longevity. Radiation-induced longevity hormesis in *D. melanogaster* has been reported by various researchers. Chronic low-dose irradiation with an accumulated dose of 0.6–0.8 Gy was reported to have increased the lifespan of male flies in wild-type strains Canton S, Oregon R, and GB-39 (Zainullin & Moskalev 2001). Longevity hormesis was observed in male flies when exposed to 0.5 and 0.75 Gy X-rays (Vaiserman *et al.* 2003) and 0.5 and 1 Gy gamma rays (Vaiserman *et al.* 2004b) at egg stage. X-irradiation with 1.2 and 2.1 Gy at the larval stage resulted in an

increase in the male maximum lifespan (Vaiserman *et al.* 2004a). Chronic low-dose gamma irradiation (60 cGy per generation) on the pre-imago stage increased the lifespan in strains with mutations in apoptosis genes *grim*, *hid*, *reaper*, *Dcp-1*, *dApaf-1*, *th* and *Sod* (Moskalev 2007). Preliminary exposure to chronic low dose (40 cGy) irradiation induced a hormetic effect and a radiation adaptive response to acute irradiation of 30 Gy (Moskalev *et al.* 2011).

Irradiation studies in *D. melanogaster* have given us an insight regarding the genes and factors involved in the radiation-induced hormetic effects of lifespan. Genes *Hsp*, *Hsf* (Moskalev *et al.* 2009), *FOXO*, *SIRT1*, *JNK*, *ATM*, *ATR* and *p53* (Moskalev *et al.* 2011) have been shown to play an essential role in hormesis and radiation-adaptive responses. Genome-wide analysis of low-dose irradiated male *D. melanogaster* with extended longevity has shown that approximately 13% of the genome exhibited changes in gene expression, and a number of aging-related genes were significantly regulated. Analysis of expression profiles showed that low-dose irradiation induced changes in transcript levels of genes in unique functional classes such as protein metabolism, energy production and oxidative stress responses (Seong *et al.* 2011). An increase in the lifespan of irradiated flies can be attributed to activation of the repair systems and other mechanisms of recovery (Zainullin & Moskalev 2001).

Moskalev *et al.* (2011) reported that acute gamma irradiation of 30 Gy led to a decrease in the median lifespan of *D. melanogaster*; in the present study mean longevity of 30, 40 and 50 Gy-irradiated male flies were reduced. Radiation shortens life by accelerating subsequent aging (Lamb & Smith 1969), while Helinski *et al.* (2009) reviewed that reduced longevity is often a result of radiation-induced somatic damage. Genome instability and apoptosis were reported in radiation-induced aging (Zainullin & Moskalev 2001). Golub and Chernyk (2008) studied the mutations induced by X-ray irradiation and certain chemical reagents that alter the lifespan of *D. melanogaster* and reported that transposition of mobile genetic elements in unstable loci of the X chromosome and mutations that induce neurodegenerative changes in brain structures are among the important causes for accelerated aging and shortened lifespan in *D. melanogaster*.

Moriwaki and Tobari (1960) studied the effect of parental irradiation for the doses 3, 6, 9, 12 and 15 Gy on progeny of *Drosophila*. Their results showed that longevity of the male offspring of irradiated parents were affected, while in the female offspring, no significant reduction in the lifespan was found when they lived with male flies. Contrary to this finding, in the present study it was observed that paternal exposure to radiation caused significant increase in the longevity of $F_1$ progeny of 2 (only female) and 4, 6, 8 and 10 Gy (male and female) irradiated flies, while the $F_1$ progeny of 40 and 50 Gy-irradiated flies showed significantly reduced longevity. Longevity hormesis was observed in the $F_1$ generation, when male *Drosophila* flies were exposed to 0.5 Gy gamma radiation at the egg stage. Cross-generational adaptive phenotypic plasticity may be the reason for such effects (Vaiserman *et al.* 2004b).

In the present study female longevity was higher than that of males in the control group as well as treated samples except in 1 and 2 Gy-irradiated $F_0$ males. Yoon *et al.* (1990) studied the longevity of 68 species of *Drosophila* including *D. melanogaster*; their results showed that, in general, females lived longer than males. Tower and Arbeitman (2009) reviewed that several possible and potentially overlapping genetic mechanisms have been suggested to explain differences in lifespan between genders, including asymmetric inheritance of sex chromosomes, mitochondrial genomes and other cytoplasmic genomes, differences in physiology, maternal effects and sex-specific selective pressures.

An insight into the effect of dose in correlation with ionizing radiation for non-human biota will equip us to draw radiological protection baselines of ecosystems (Nakamori *et al.* 2009). Lifespan alteration is the most general reaction to the influence of ionizing radiation (Moskalev 2007). Alteration in development rate and longevity not only determines the fate of the single organism but also may influence population dynamics. The present study gives an idea about the doses that have deleterious effect (decreased rate of development and longevity) and beneficial effects (increased rate of development and longevity) on the lifespan of *D. melanogaster*. It is shown that the effect of acute gamma irradiation on longevity and "egg to adult" development time of *D. melanogaster*, be it beneficial or deleterious, diminishes within the second or third generation.

Male exposure to gamma radiation at some doses had a significant impact on longevity and the rate development of $F_1$ and $F_2$ progeny. There were no significant changes observed in the longevity and rate development of $F_3$ progeny. The present study concludes that the effect of acute gamma irradiation on longevity and "egg to adult" development time of *D. melanogaster* may persist to the next generations.

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