Indian Journal of Entomology 85(1): 103-108 (2023) DoI. No.: 10.55446/IJE.2022.692

ASSESSING THE RADIATION HORMESIS ON THE REPRODUCTIVE BEHAVIOUR OF MALE *SPODOPTERA LITURA* (F.) TREATED WITH LOW DOSE IONIZING RADIATION IN THE PRE-IMAGINAL STAGES

Neha Vimal, Madhumita Sengupta, Nilza Angmo and R K Seth*

Applied Entomology and Radiation Biology Unit, Department of Zoology,
University of Delhi, Delhi 110007, India
*Email: rkseth57@gmail.com (corresponding author): ORCID ID- 0000-0001-7873-1362

ABSTRACT

The quality of the mass reared insects plays a crucial role in effective operation of radiation mediated inherited sterility (IS) programme, proposed to suppress the lepidopteran pest *Spodoptera litura* (F.). In this context, the low dose of ionizing radiation (LDIR) was assessed to have any stimulatory effect on the reproductive behaviour of male moths treated as 0-1 day old egg, third instar larva (L3) or 2-3 days old pupa. Radiation hormesis was observed in the mating success of males treated at 0.75 Gy and 1 Gy in both egg and L3 stages. Invitro sperm activation assay indicated more sperm activity during peak plateau phase in moths derived from treated egg (0.75Gy, 1 Gy) and treated L3 (1 Gy). These findings implicit beneficial effect on sperm activity and mating success of male *S. litura,* which might further improve mating competitiveness of male moths to be used in IS technique.

Key words: *Spodoptera litura*, male hormesis, low dose ionizing radiation (LDIR), sterile insect technique (SIT), F1 sterility, preimaginal stage, reproductive behaviour

Hormesis is characterized by the production of biological response in an organism or cell in response to low dose of physical or biologic agents whereas higher dose of the same agent has an inhibitory effect (Calabrese and Baldmin, 2003; Calabrese, 2008). This nonlinear/biphasic dose response can be seen from bacteria to vertebrates by various different stressors. It has now been observed in a wide range of organisms in response to many stressors like alkylating agents, thermal and oxidative stresses, ionizing radiation, chemical stressors, heavy metals etc. (Berry and López-Martínez, 2020). At low dose, a wide range of biological effects are induced which may modulate the physiological response (Luckey, 1999; Calabrese and Blain, 2005; Lefcort et al., 2008). *Spodoptera litura* (F.) is a polyphagous owlet moth that wreaks havoc on a variety of plants all around the world (Bragard et al., 2019). Sterile insect technique (SIT) is a unique radiogenetic strategy for controlling lepidopteran populations in an afflicted field and has been used to control these moths. The use of a high dose of ionizing radiation to produce sterile insects reduces the competitiveness of the irradiated moths (Seth and Reynold, 1993; Bakri et al., 2005). As a result, the F1 (inherited) sterility (IS) technique has been proposed to overcome this limitation of SIT, in which moths are exposed to a much lower dose of ionizing radiation and sub-sterile male insects are produced, and the progeny of these moths would be fully sterile.

Despite being an environment friendly and non-polluting method, it has some constraints like exposing an insect to sterilizing dose of gamma radiation can decrease the mating ability and reduce lifespan in comparison to wild or non-irradiated moths, and these factors can affect the fitness of insect pests (Shelly et al., 1994; Lance et al. 2000; Seth and Sharma, 2001). Lepidopteran insects have dichotomous spermatogenesis i.e. they have two concomitant types of spermatozoa which differ in their structure, DNA content and their differentiation. One form of sperm is nucleated (eupyrene) that can fertilize the egg (e.g., Baccerti, 1991). The other one, sometimes known as parasperm (Jamieson, 1987), is anucleated (apyrene) sperm that cannot fertilize the eggs. Apyrene sperms, on the other hand, play a role in sperm competition and proper functioning of eupyrene sperm (Silberglied et al., 1984; Gage and Cook, 1995). Sperm dynamics is considered as a crucial factor for insect's viability and mating competitiveness (Seth et al., 2016). Hence, it is important to maintain a reasonable level of the life span, insemination quality and mating competitiveness of the irradiated pest moths that would be employed in F1 sterility technique for pest suppression. Thus, the

purpose of this study was to investigate the stimulatory effect of low dose of gamma radiation on various male reproductive parameters, viz., mating success, mating frequency, sperm behaviour and fertility of *S. litura* treated with probable hormetic doses in early preimaginal stages, which might improve the male mating performance in radiogenetic IS technique.

MATERIALS AND METHODS

The adult *S. litura* of both sexes were collected from agricultural fields of Delhi, India and culture was maintained in an inhouse experimental facility at 27± 2ºC with 75± 5% RH, 12 hr:12hr (light: darkness) regimen. The adult moths were kept in humidified Perspex–nylon net cages in a size of 20x20x20cm for mating and provided with ad libitum supply of 10% honey solution. The adult moths were caged in 4 pairs and post mating and caster leave was put as ovipositional trap. The eggs were collected from the cage in a plastic container (10 cm diameter x 12 cm height) and freshly hatched larvae were reared on semi-synthetic diet until pupation, and the rearing cycle continued (Seth and Sharma, 2001). For the experiment, eggs (0-1day old), third instar larvae (L3) and pupae (2-3 days old) were exposed in different regimens to a range of 0.25-1.25 Gy low dose ionizing radiation (LDIR) in a Co^{60} Teletherapy unit (Bhabhatron-II) situated at Institute of Nuclear Medicine and Allied Sciences (INMAS) of Defense Research and Development Organization (DRDO), Delhi. In this experiment the non-irradiated insects in a particular preimaginal stage of the respective regimen were used as control. The dose rate of gamma radiation ranged from 0.746 Gy-1.099 Gy min^{-1} during the experimentation period.

The adult male exposed to LDIR at preimaginal stages were used for the sperm activation assay. An invitro sperm bioassay was performed by the procedure described by Seth et al. 2016 to assess the effect of LDIR on sperm motility. Sperm and activator were produced as described below for the in-vitro sperm assay. Duplex (ductus ejaculatorius duplex) was dissected out for sperms and secretions from the prostatic part (ductus ejaculatorius simplex) was used for activator preparation. 0.3 M HEPES-KOH buffer (at pH 7.0) containing 20 mg/mL bovine serum albumin (BSA) was used for sperm and 0.03 M ammonium bicarbonate-acetic acid buffer (at pH 7.0) was used for the activator (prostatic part secretions). The prostatic part was kept in 40 µL of ammonium bicarbonate-acetic acid buffer at pH 7.0. The secretion oozed out in this solution was centrifuged at 4°C for 10 min at 6000 rpm. Sperm activation was performed by mixing sperm from duplex and activator from prostatic part in 1:1 ratio at 27± 1°C to observe the temporal profile of sperm activity under compound microscope (at 400x). For this experiment, each replicate constituted a mean of 5 readings from each aliquot of sperm+ activator and the experiment repeated 10 times for each regimen.

Immediately after termination of mating (LDIR treated male x normal female), the spermatophore was isolated and the sperms were extracted. For sperm count, total number of apyrene sperm (loose sperm) and eupyrene sperm (sperm bundles) were examined under the phase contrast microscope. The content of the spermatophore was spread on a microscope slide for examination of eupyrene sperm bundles, whereas for apyrene sperm count, the content of the spermatophore was diluted with Belar's saline and 10 µl aliquots were examined in a haemocytometer. An average reading of these ten sample aliquots constituted one replicate. For this experiment, 6 replicates were taken for each regimen. The mating status of female was determined by dissecting the female immediately after death and examining the presence of spermatophore in bursa copulatrix. The mating success was determined by assessing the number of females mated out of total females under observation. The mating success was studied in ten replicates, each replicate comprising of 12-15 pairs in a cage (60x 60x 60 cm). The mating frequency was determined by observing the average number of spermatophores in the bursa copulatrix of experimental females that were mated (Seth and Reynolds, 1993; Makee and Saour, 2001).

After the emergence of the adult moths, the irradiated males were paired with virgin non-irradiated female moths and transferred to the mating cages. For control, the non-irradiated virgin males and females were paired. Each mating cage contained 4-5 pairs of insects and were provided with ab libitum supply of food (10% honey solution). Each mating cage was monitored, the egg masses were collected and counted daily during the oviposition period. For each experimental regimen, an average fertility of 10 batches of egg masses (comprising of 70-100 eggs per batch) constituted one replicate. This experiment was repeated 10 times for each regimen. One way ANOVA was performed to determine the evident effects of possible hormetic gamma doses on adult parameters (mating success, mating frequency, egg viability) followed by Tukey's test to confirm the statistically significant difference among the groups at $p<0.05$ level. All the

bio-statistics was carried out using GraphPad prism software program, version 9.3.1 (San Diego, USA).

RESULTS AND DISCUSSION

Dose response plays a central role in biological system as it helps in understanding the biology of a cell or organism by toxicologists, biologists, and pharmacologists (Calabrese, 2004). The term hormesis was given by toxicologists, Chester Southam and John Ehrlich in 1943. Hormesis is generally described as dose response phenomenon in which low dose of stressor elicits a response while high dose of the same stressor can inhibit the response. These stressors can be physical, chemical, radiation, heat stress, oxygen, overcrowding etc. (Sinclair and Howitz, 2005). Biphasic dose response is a fundamental feature of hormesis (Calabrese, 2005; Calabrese and Baldwin, 2001). A significant correlation between hormetic effects and the age of exposure in an organism has also been found in many experiments. It has been observed these hormetic exposures when applied at early life stages show long lasting and better results than at later stages of their lifetime (Le Bourg, 2005; López-Martinez and Hahn, 2014; López-Martinez, 2014; López-Martinez, 2016a; López-Martinez, 2016b; Visser, 2018).

Therefore, in the present study, the effect of low range ionizing doses (0.25 – 1.25 Gy) was evaluated in various preimaginal (egg, L3 and pupa) stages of *S.litura* in order to ascertain the hormetic effect of LDIR in reproductive behaviour of male moths, derived from these treated ontogenic stages. The male reproductive behaviour was assessed in terms of mating frequency, mating success and fertility. Interestingly, the mating success was apparently increased at 0.75 Gy and 1 Gy LDIR in egg stage ($F_{(5,54)}$ =10.95, p<0.001); 0.75 and 1.0 Gy LDIR in larval stage ($F_{(5,54)}$ =5.508, p=0.0002). In pupal LDIR treatment, the mating success of adult moths however did not show any significant difference at 1 Gy with respect to control (0 Gy), indicating that LDIR at 1 Gy didn't induce stressful impact on mating behaviour unlike its other range of doses tested (0.25-0.75 Gy) wherein the mating success was reduced with respect to control. The effect of LDIR investigated on mating frequency, oviposition and egg fertility could not exhibit any hormetic effect as compared to control (0 Gy) (Table 1 a,b,c). Thus, as per the present findings, the radiation hormesis was apparently observed on the mating performance of *S.litura* derived from LDIR treated egg and L3 stages. Similar result was observed by Lalouette et al. (2016) in *Spodoptera littoralis* when low dose of deltamethrin (~1/10 of the LD_{50}) resulted in improved mating success.

Further, the sperm activity of *S.litura* was observed at the probable hormetic doses, viz., 0.75, 1 Gy (egg), 1 Gy (L3) and 1 Gy (pupa), in view of the hormetic effects exhibited in terms of longevity and survivorship at these doses in our initial studies (Seth et al. unpublished). The sperm activity was ascertained as the proportion of sperms being active in *in-vitro* sperm activation assay during 5-135 min period. LDIR treatment at 1 Gy (egg), 1 Gy (larva) and 1 Gy (pupa) showed more sperm activity after 5 min of mixing sperm and activator in comparison to the control. After 15 min, the male moths derived from egg (0.75 Gy), egg (1 Gy) and L3 (1 Gy) were found to elicit more sperm activity with respect to non-irradiated moths. There were evidently more active sperms in the male moths derived from egg (0.75 Gy), egg (1 Gy) and L3 (1 Gy) during peak plateau phase of sperm activity (from 30 to 90 min after mixing sperm and activator) as compared to control (Table 2a). The effect of LDIR was also investigated on the apyrene and eupyrene sperm count but it did not exhibit statistically significant difference at any of the probable hormetic doses. Although, an increasing trend could be seen in moth sperm from 1 Gy treated egg stage but it was not statistically significant (Apyrene sperm $F_{(4,25)}$ =0.39, p=0.81) (Eupyrene sperm $F_{(4,25)}$ =0.48, p=0.75) (Table 2b).

These results suggested a positive role of low dose of ionizing radiation on *S. litura* when exposed in early preimaginal stages, which could be used in IS program because rearing of quality insects is a vital feature in this program. These results suggested that LDIR might increase the mating competitiveness of radiosterilized male moths which might be able to compete better with the wild male in comparison to the ones which were only irradiated with sub-sterilizing gamma irradiation. Thus, these probable hormetic doses might be used to enhance the efficiency and effectiveness of IS programme for this lepidopteran pest suppression.

ACKNOWLEDGEMENTS

The authors thank the Department of Zoology, University of Delhi for providing the necessary infrastructure. The authors acknowledge the International Atomic Energy Agency, Vienna (vide IAEA funded Research Project, RC-20565/RB) for the financial support. NV is grateful to CSIR for providing fellowship.

Table 1a. Effect of low dose ionizing radiation (LDIR) on reproductive parameters of male *S. litura* treated in egg stage

Reproductive parameters	Low dose ionizing radiation (LDIR) doses						
	Control (0Gy)	0.25 Gy	0.5 Gy	0.75 Gy	1 Gy	1.25 Gy	F value
Mating Success	83.130± 3.08a	83.02± 4.08a	77.43± 6.23a	87.98± 4.08ab	91.84± 2.5b	82.98± 4.08a	10.95 (5,54)*
Mating Frequency	1.6± 0.13a	1.6± 0.08a	1.6± 0.10a	1.5± 0.03a	1.8± 0.14a	1.5± 0.06a	2.55(5, 54)
Oviposition	1806± 56.52a	1694± 57.78a	1696± 52.84a	1771± 60.85a	1781± 41.36a	1623± 73.10a	1.64 (5,54)
Fertility (%)	82.6± 3.76a	80.3± 3.73a	78.8± 4.58a	78.7± 3.25a	80.2± 2.55a	78.5± 3.90a	4.09(5, 54)

Means followed by same letters within a row are not significantly different at $p<0.05$. One-way ANOVA followed by Tukey's multiple comparisons ($p<0.05$) was performed to test the significance among different regimens for a specific parameter. % data was arcsine transformed before ANOVA. n=10; 10-15 pairs constituted one replicate for mating success and average reading from a cohort of 4-5 pairs constituted one replicate for mating frequency, oviposition and fertility. Asterisks (*) signifies statistical significance at $p\leq0.05$

Table 1b. Effect of low dose ionizing radiation on adult parameters of *S. litura* treated as thirds instar larvae (L3)

Reproductive parameters	Low dose ionizing radiation (LDIR) doses						
	Control	0.25 Gy	0.5 Gy	0.75 Gy	1 Gy	1.25 Gy	F value
Mating Success	84.72± 2.88a	84.76± 2.59a	82.22± 5.52a	87.16± 3.52ab	92.99± 2.50b	82.95± 4.08a	5.51(5,54)*
Mating Frequency	1.8± 0.12a	1.7± 0.06a	1.6± 0.08a	1.8± 0.19a	1.8± 0.15a	1.7± 40.11a	2.12(5, 54)
Oviposition	1734± 49.81a	1625± 58.72a	1628± 42.7a	1590± 57.73a	1624± 48.8a	1583± 63.70a	1.49(5,54)
Fertility (%)	81.9± 2.49a	79.2± 2.62a	76.4± 2.63a	78.5± 2.63a	80.5± 1.70a	79± 2.55a	2.40(5, 54)

Means followed by same letters within a row not significantly different at $p<0.05$. One-way ANOVA followed by Tukey's multiple comparisons ($p<0.05$) was performed to test the significance among different regimens for a specific parameter. % data was arcsine transformed before ANOVA. n=10; 10-15 pairs constituted one replicate for mating success and average reading from a cohort of 4-5 pairs constituted one replicate for mating frequency, oviposition and fertility. Asterisks (*) signifies the statistical significance at $p\leq0.05$

Table 1c. Effect of low dose ionizing radiation on adult parameters of *S.litura* treated in pupal stage

Reproductive parameters	Low dose ionizing radiation (LDIR) doses						
	Control	0.25 Gy	0.5 Gy	0.75 Gy	1 Gy	1.25 Gy	F value
Mating Success	85.9± 2.08b	83.5± 3.08a	78.3± 6.24a	79.9± 4.08a	91.6± 2.5b	77.9± 4.08a	8.94(5,54)*
Mating Frequency	1.8± 0.08a	1.7± 0.07a	1.7± 0.12a	1.8± 0.15a	1.8± 0.18a	1.9± 0.13a	0.84 (5, 54)
Oviposition	1651± 61.95a	1541± 66.98a	1569± 38.84a	1586± 55.55a	1590± 48.19a	1509± 60.37a	0.74 (5, 54)
Fertility (%)	84.1± 2.07a	81.04± 3.80a	78.9± 2.94a	78.8± 2.69a	81.4± 2.04a	78.1± 2.89a	5.82 (5, 54)

Means followed by same letters within a row are not significantly different at $p<0.05$. One-way ANOVA followed by Tukey's multiple comparisons ($p<0.05$) was performed to test the significance among different regimens for a specific parameter. % data was arcsine transformed before ANOVA. n=10; 10-15 pairs constituted one replicate for mating success and average reading from a cohort of 4-5 pairs constituted one replicate for mating frequency, oviposition and fertility. Asterisks (*) signifies statistical significance at $p\leq0.05$

Table 2a. Effect of low dose ionizing radiation on sperm activation in male *S.litura* treated in probable hormetic doses (egg, larva, pupa- invitro assay)

LDIR exposure to preimaginal stage	% sperm active in moths derived from LDIR treated pre-imaginal stages (Time period after mixing sperm with activator)							
	5	15	30	45	60	90	105	135
Control (0Gy)	20.88± 1.6a	70.38± 1.8bc	89.69± 2.7ab	87.43± 2.8a	82.39± 2.8a	71.36± 3.2a	54.84± 3.1a	26.4± 1.1a
0.75Gy Egg	19.28± 1.5a	64.63± 2.4ab	86.57± 1.9a	89.21± 2.2a	88.78± 2.3ab	81.1± 3.7ab	53.41± 4.2a	23.26± 2.01a
1Gy Egg	24.62± 1.6ab	75.62± 1.8c	96.41± 1.5b	92.64± 1.9a	92.36± 2.01b	85.32± 2.1b	60.86± 4.5a	26.91± 2.6a
1Gy Larva	26.96± 1.2b	73.64± 2.1bc	93.92± 1.9ab	91.37± 2.8a	93.32± 2.5b	84.26± 3.2b	57.39± 3.2a	26.04± 1.6a
1Gy Pupa	23.03± 1.6ab	62.39± 2.2a	90.36± 1.8ab	90.75± 3.2a	87.83± 2.6a	73.13± 3.6a	55.28± 1.4a	25.37± 1.8a
F Value	4.03(4,45)*	7.69(4,45)*	2.67(4,45)*	0.86(4,45)	2.59(4,45)*	3.98(4,45)*	0.68(4,45)	0.56(4,45)

Means followed by same letters within a row not significantly different at $p<0.05$. One-way ANOVA followed by Tukey's multiple comparisons ($p<0.05$) was performed to test the significance among different regimens for a specific parameter. % data was arcsine transformed before ANOVA. n=10; sperms were derived from duplex and activator secretion from prostatic part of male reproductive tract. Asterisks (*) signifies the statistical significance at $p\leq0.05$

FINANCIAL SUPPORT

This work was a part of the FAO/IAEA Coordinated Research Project (D41026) on "Improved Field Performance of Sterile Male Lepidoptera to Ensure Success in SIT Programmes", and the financial support from International Atomic Energy Agency, Vienna (vide IAEA funded Research Project, RC-20565/RB) is gratefully acknowledged.

AUTHOR CONTRIBUTION STATEMENT

RKS conceived and designed research. NV conducted experiments. NV, MS and NA assisted in the conducting experiments and validation of data. RKS, NV analyzed the data and involved in writing, editing and reviewing the manuscript. All authors read and approved the manuscript.

CONFLICT OF INTEREST

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

REFERENCES

Baccetti B. 1991. Comparative spermatology 20 years after. Raven Press

Bakri A, Mehta K, Lance D R. 2005. Sterilizing insects with ionizing radiation. Sterile insect technique: Principles and practice in area-wide integrated pest management. pp. 233-268.

Berry III R, López-Martínez G. 2020. A dose of experimental hormesis: When mild stress protects and improves animal performance. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 242: 110658.

Bragard C, Dehnen-Schmutz K, Di Serio F, Gonthier P, Jacques M A, Jaques Miret J A, Justesen A F, Magnusson C S, Milonas P, Navas-Cortes J.A. 2019. EFSA Panel on Plant Health (PLH), Pest categorisation of *Spodoptera litura*. EFSA Journal 17(7): e05765.

Calabrese E J, Baldwin L A. 2001. U-shaped dose-responses in biology, toxicology, and public health. The Selected Works of Edward J. Calabrese, 1.

Calabrese E J, Blain R. 2005. The occurrence of hormetic dose responses in the toxicological literature, the hormesis database: an overview. Toxicology and Applied Pharmacology 202(3): 289-301.

Calabrese E J, Baldwin L A. 2003. Toxicology rethinks its central belief. Nature 421(6924): 691-692.

Calabrese E J. 2004. Hormesis: a revolution in toxicology, risk assessment and medicine: Re-framing the dose- response relationship. EMBO reports, 5(S1): S37-S40.

Calabrese E J. 2005. Paradigm lost, paradigm found: the re-emergence of hormesis as a fundamental dose response model in the toxicological sciences. Environmental Pollution 138(3): 378-411.

Calabrese E J. 2008. Neuroscience and hormesis: overview and general findings. Critical Reviews in Toxicology 38(4): 249-252.

Cook P A, Gage, M. J. 1995. Effects of risks of sperm competition on the numbers of eupyrene and apyrene sperm ejaculated by the moth Plodia interpunctella (Lepidoptera: Pyralidae). Behavioral Ecology and Sociobiology 36(4): 261-268.

Table 2b. Effect of low dose ionizing radiation (LDIR) on dichotomous sperm count of male *S. litura* treated with probable hormetic doses (egg, larva and pupa)

Type of sperm	Male moths derived from LDIR treated in preimaginal stages					
	Control (0Gy)	0.75 Gy- Egg	1 Gy- Egg	1 Gy- Larva	1 Gy- Pupa	F value
Apyrene sperm $x10^3$	279.7± 5.8a	276.9± 8.9a	287.9 ± 8.4a	275.5± 7.3a	276.6 ± 8.9a	0.39 (4,25)
Eupyrene sperm bundles	347.5± 8.9a	338.5± 15.9a	358.167± 9.9a	350.67± 8.5a	340.167± 12.6a	0.48 (4,25)

Means followed by same letters within a row are not significantly different at $p<0.05$ level. One-way ANOVA followed by Tukey's multiple comparisons ($p<0.05$) was performed to test the significance among different regimens for a specific parameter. n=6, Asterisks (*) signifies the statistical significance at $p\leq0.05$

Jamieson B G, Jamieson J B G. 1987. The ultrastructure and phylogeny of insect spermatozoa. CUP Archive.

Lalouette L, Pottier M A, Wycke M A, Boitard C, Bozzolan F, Maria A, Demondion E, Chertemps T, Lucas P, Renault D, Maibeche M, Siaussat D. (2016). Unexpected effects of sublethal doses of insecticide on the peripheral olfactory response and sexual behavior in a pest insect. Environmental Science and Pollution Research 23(4): 3073-3085

Lance D R, McInnis D O, Rendon P, Jackson C G. 2000. Courtship among sterile and wild *Ceratitis capitata* (Diptera: Tephritidae) in field cages in Hawaii and Guatemala. Annals of the Entomological Society of America 93(5): 1179-1185.

Le Bourg É. 2005. Hormetic protection of *Drosophila melanogaster* middle-aged male flies from heat stress by mildly stressing them at young age. Naturwissenschaften 92(6): 293-296.

Lefcort H, Freedman Z, House S, Pendleton M. 2008. Hormetic effects of heavy metals in aquatic snails: is a little bit of pollution good? EcoHealth 5(1): 10-17.

López-Martínez G, Hahn D A. 2014. Early life hormetic treatments decrease irradiation-induced oxidative damage, increase longevity, and enhance sexual performance during old age in the Caribbean fruit fly. PLoS One 9(1): e88128.

López-Martínez G, Carpenter J E, Hight S D, Hahn D A. 2014. Low-oxygen atmospheric treatment improves the performance of irradiation-sterilized male cactus moths used in SIT. Journal of Economic Entomology 107(1): 185-197.

López-Martínez G, Carpenter J E, Hight S D, Hahn D A. 2016a. Anoxia-conditioning hormesis alters the relationship between irradiation doses for survival and sterility in the cactus moth, *Cactoblastis cactorum* (Lepidoptera: Pyralidae). Florida Entomologist 99(sp1): 95-104.

López-Martínez G, Meagher R L, Jeffers L A, Bailey W D, Hahn D A. 2016b. Low oxygen atmosphere enhances post-irradiation survival of *Trichoplusia ni* (Lepidoptera: Noctuidae). Florida Entomologist. pp. 24-33.

Luckey T D. 1999. Radiation hormesis overview. Radiation Protection Management 16: 22-34.

Makee H, Saour G. 2001. Factors influencing mating success, mating frequency, and fecundity in *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Environmental Entomology 30(1): 31-36.

Seth R K, Reynolds S E. 1993. Induction of inherited sterility in the tobacco hornworm *Manduca sexta* (Lepidoptera: Sphingidae) by substerilizing doses of ionizing radiation. Bulletin of Entomological Research 83(2): 227-235.

Seth R K, Sharma V P. 2001. Inherited sterility by substerilizing radiation in *Spodoptera litura* (Lepidoptera: Noctuidae): Bioefficacy and potential for pest suppression. Florida Entomologist. 84(2): 183-193.

Seth R K, Khan Z, Rao D K, Zarin M. 2016. Appraisal of sperm dynamics as a crucial trait of radiosterilized *Spodoptera litura* (Lepidoptera: Noctuidae) and its F1 progeny for evaluation of the 'inherited sterility technique' for pest suppression. Florida Entomologist 99(sp1): 105-118.

Seth R K, Reynolds S E. 1993. Induction of inherited sterility in the tobacco hornworm *Manduca sexta* (Lepidoptera: Sphingidae) by substerilizing doses of ionizing radiation. Bulletin of Entomological Research 83(2): 227-235.

Shelly T E, Whittier T S, Kaneshiro K Y. 1994. Sterile insect release and the natural mating system of the Mediterranean fruit fly, *Ceratitis capitata* (Diptera: Tephritidae). Annals of the Entomological Society of America 87(4): 470-481.

Silberglied R E, Shepherd J G, Dickinson J L. 1984. Eunuchs: the role of apyrene sperm in Lepidoptera? The American Naturalist 123(2): 255-265.

Sinclair D A, Howitz K T. 2005. Dietary restriction, hormesis, and small molecule mimetics. Handbook of the biology of aging. Academic Press. pp. 63-104.

Visser B, Williams C M, Hahn D A, Short C A, López-Martínez G. 2018. Hormetic benefits of prior anoxia exposure in buffering anoxia stress in a soil-pupating insect. Journal of Experimental Biology 221(6): jeb167825.

(Manuscript Received: June, 2022; Revised: July, 2022;
Accepted: July, 2022; Online Published: July, 2022)
Online First in www.entosocindia.org and indianentomology.org Ref. No. e22572