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Impact of different hosts and meridic diet on biology, reproductive fitness and demographic parameters of *Spodoptera litura* (Fabricius)

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ABSTRACT

S. litura is dreaded polyphagous insect pest in Asian tropics. The fundamental and applied research always requires laboratory rearing of insects. This study investigated the effects of natural hosts (castor, cauliflower, cabbage and tomato) and meridic diet on biological, reproductive physiology and demographic parameters of *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae). The castor and meridic diet gave better results in several parameters than other hosts. The total developmental period was shortest on castor. Though, it was longest on meridic diet, but the pupal weight and eupyrene sperm bundle counts were on par in both the cases. The fecundity was superior (1791.7 ± 65.64 per/female) in castor, followed by meridic diet (1718.3 ± 95.80). The demographic parameters and biotic potential were highest in castor, whereas the gross reproductive rate was highest on meridic diet. The study showed that the meridic diet may be an alternate choice in the absence of natural hosts for mass rearing of *S. litura* throughout the year. The demographic parameters calculated were linked to prediction of population structure on different hosts in developing life-table based simulations for use in pest management.

Key Words: Biology, Biotic potential, Demography, Hosts, Meridic Diet, Reproductive fitness, *Spodoptera litura*.

INTRODUCTION

The tobacco cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae) is major widespread polyphagous agricultural pests in Asia, Australasia and Pacific Islands (53,61). It feeds on 389 plant species from 109 families including field crops and vegetables (CABI, 2023). It's larvae feed on leaves, also damaging fruits and flowers. The older instars devour the leaves and other plant parts (52). This causes economic losses from 25.8 % to 100 % (57). The laboratory rearing of insects is essential for scientific research, pest management, disease control, conservation efforts, technological advancements and educational purposes (69). It provides a controlled environment for studying insects, manipulating variables and developing solutions to address various challenges related to insects and their interactions with the environment and human society (13).

The host affects insect survival and life cycle (18). Natural food resources are insufficient for extensive rearing (31). In entomological research, artificial diets are crucial for rearing and assays (15,16,46). Different hosts offer varying nutrition (82). Meridic diets with precise nutrients aid in understanding nutritional needs and optimizing rearing practices (43). Herbivore fertility is influenced by host plant quality [carbon, nitrogen and defense metabolites (58,80)]. This affects egg size, nutrient distribution, oviposition site selection

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and egg resorption hosts (5,29,54). Optimal dietary protein and carbohydrate ratios are crucial for insect adaptation (38). A suitable and accessible artificial diet (56) is crucial for year-round insect research, controlling environmental factors (30) and understanding insect biology, dietary needs, behaviors and population dynamics in a lab (18,21,49).

A life table is a useful tool for studying the dynamics of animal populations, particularly arthropods, as it can give crucial demographic data (40,76) and particularly the intrinsic rate of natural increase (*r*) (72). The host factor affects the gonadosomatic index, which governs gonadal development and maturity (50), as well as eupyrene (nucleated) and apyrene (anucleated) sperm counts, which are vital for healthy fertilization (22).

This research on reproductive physiology and demographics provides reasons to choose alternate hosts for insect rearing. It discusses the developmental parameters of *S. litura* on various hosts, essential for evaluating xenobiotics and creating effective integrated pest management techniques. Considering the above, a modest attempt was undertaken to document the impact of different hosts and meridic diet on reproductive fitness and demographic parameters of *Spodoptera litura*.

MATERIALS AND METHODS

I. Insect collection and rearing

The lab. experiments on the effects of larval diet on reproductive attributes and demographic parameters of *Spodoptera litura* were done at Division of Entomology, ICAR-IARI, New Delhi, under controlled conditions (27 ± 1ºC, 65 ± 5 % RH and photoperiod of 14:10 h of L: D). The larvae of *S. litura* were collected from capsicum crops cultivated in the fields of ICAR- IARI, New Delhi and reared on different hosts and chickpea-based meridic diet (56). On emergence, pair of adults were transferred to mating jars (20 × 15 cm) containing droplets of 10 % honey solution. Paper strips were placed in the mating jars for egg laying and the jars were covered by black muslin cloth. Egg masses were collected daily and transferred to the Petri plate containing the respective host for hatching. The larvae were fed on selected hosts for two generations (host conditioning).

II. Natural host and meridic diet

A total of four natural host plants *viz*., *Ricinus communis* (Castor), *Brassica oleracea var. capitata* (Cabbage), *B. oleracea var. botrytis* (Cauliflower) and *Solanum lycopersicum* (Tomato) and chickpea based meridic diet were used (56). A cohort of 150 eggs laid in a day were used for the study, the 100 neonates hatched were individually reared on each selected host plants (100 larvae/host) and meridic diet in small Petri plates (dia 4 cm, height :1 cm). To rear individual larva in respective natural hosts, the leaves of different host plants were collected from the field and rinsed with fresh water to remove contaminants and other impurities present on leaves and pat dried using fresh tissue paper. Afterwards the leaves were cut into small size and 3-pieces of cut leaf pieces were provided to larvae on alternate days until pupation. On the other hand, a meridic diet slice was given to the larvae every other day until they pupated (Plate 1).

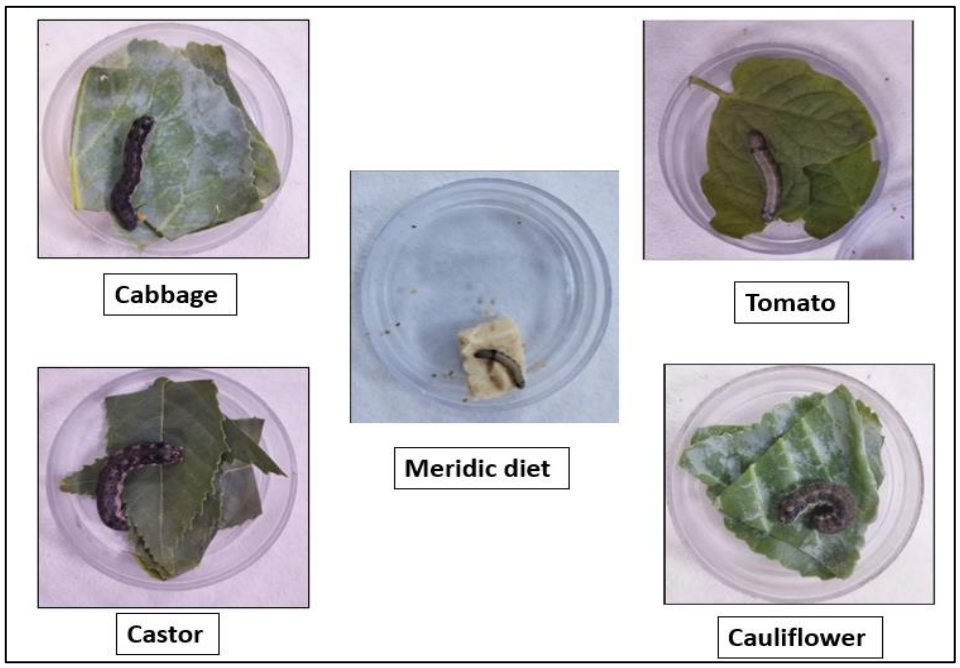

Plate 1. The different natural host (Cabbage, Tomato, castor and cauliflower) and Meridic diet

III. Reproductive fitness and demographic parameters of *Spodoptera litura* on selected hosts and meridic diet

The respective eggs collected from selected hosts and diet were inspected at 12 h intervals until they hatched to record the incubation period. Separately, 100 freshly hatched neonates from each host plant and diet were placed in 5 to 6 cm dia Petri plates. After every moulting, the period of each larval instar was recorded. The total larval period was determined based on the length of time required from egg hatching to pupation. Similarly, the pupal duration was documented from the start of pupation until adult emergence. The weight of the larvae and pupae was noted on the 10^{th} and 2^{nd} day of development,

Table 1. Formulae to calculate of growth indices

Sl. No	Growth indices	Formulae
1.	Larval Growth Index	Pupation (%) / Larval period (Days)
2.	Pupal Growth index	Adult emergence (%) / Pupalperiod (Days)
3.	Total developmental index	% Survival / Total developmental period (Days)
4.	Immature Growth Index	Adult emergence (%) Immaturestages period (larval + pupal period in days)
5.	Standardize growth index	Pupal weight (mg) / Larvalperiod (days)
6.	Fitness index	[Pupation (%) × Pupal weight (mg)] Larval period + pupal period (days) (25)
7.	Index of adequacy	(Female pupal weight / larval period) × % Adult formation (62)

respectively. The interval from the egg stage to active adult emergence was considered as total developmental period. The sex ratio was computed by dividing the number of females emerged by the total number of adults. Different growth indices were calculated for *S. litura* reared on different hosts and diets (Table 1).

Table 2. Formula for calculation of various demographic parameters

#	Demographic or population parameters	Formulae used
1.	Age-stage-specific survival rates (S_{xj}): the probability that a new born egg will survive to age x and stage j	$Sxj = \frac{nxj}{n_{01}}$
2.	Age-specific survival rate (lx): the probability that a new born egg will survive to age x	$lx = \sum_{j=1}^{m} sxj$
3.	**Age-stage-specific fecundity (f_{xj})**: It is the number of hatched eggs produced by the adult female at age *x* and *j* is the life stage number.	-
4.	Age-specific fecundity (mx): the number of eggs per individual at age x	$m_x = \frac{\sum_{j=1}^{m} S_{xj}\ f_{xj}}{\sum_{j=1}^{m} S_{xj}}$
5.	Age-specific maternity (lx*mx): the product of l_x and m_x	
6.	Age-stage-specific life expectancy (exj): the time that an individual of age *x* and stage *y* is expected to live. Where *S'ij* is the probability that an individual of age *x* and stage *y* will survive to age *i* and stage *j*.	$e_{xj} = \sum_{j=1}^{m}\sum_{j=1}^{m} S'_{ij}$
7.	Age-stage-specific reproductive value (Vxj): the contribution of individuals of age *x* and stage y to the future population	$v_{xj} = \frac{e^{-r\,(x+1)}}{S_{xj}} \sum_{i=x}^{n} e^{-r\,(i+1)} \sum_{j=y}^{m} S'_{ij}\, f_{ij}$
8.	Intrinsic rate of increase (r)	$\sum_{x=0}^{n} e^{-r\,(i+1)}\, l_x m_x = 1$
9.	Finite rate of increase (λ)	$\lambda = e^r$
10.	Net reproductive rate (R_0)	$R_0 = \sum_{x=0}^{\infty} l_x m_x$
11.	Mean generation time (T)	$T = \frac{lnR_0}{r}$
Here, *x* is the age of parental females, considered since the egg phase; *lx* is the specific survival rate of adult to age *x*; *mx* is the number of females off springs per female produced at age *x*; and *lx.mx* is the age-specific maternity.		

To study the reproductive parameters, the adults that emerged from all food sources were released into mating jars. The adult emergence percentage was calculated by dividing the number of adults emerged by the total number of pupae formed. To document the different reproductive attributes [pre-oviposition, oviposition and post-oviposition period, fecundity (eggs/female), fertility (%) and longevity of male and female adults], 15-pairs of male and female moths (<24 h of age) emerged from each food source were paired independently for each diet in a ratio of 1:1. To count eupyrene sperm bundles the procedure of (63) was followed, where the eupyrene sperm bundles will take up the stain, while apyrene sperm bundles do not take up the stain upon staining with lacto-aceto-orcein (LAO) stain. Conversely, gonadosomatic index (GSI*)* was calculated using the formula (50).

$$\text{GSI} = \frac{Weight\ of\ the\ wet\ ovary\ (g)}{Total\ weight\ of\ adult\ female} \times 100$$

The life history data of individual *S. litura* reared on selected hosts and meridic diet was analyzed using 'TWOSEX-MS Chart' 2022 software (14) for the computation of different demographic parameters (Table 2) and the age-stage, two-sex life tables of *S. litura* on the different hosts and diet were established. The biological characteristics were used to determine the biotic potential of *S. litura* on different hosts and diet according to the equation developed by (67).

$$\text{Biotic potential (BP)} : (sr * d)^{n} - e^{r},$$

Where, *Sr* : Number of females divided by members, *d* : Viable individual per females, *n* : Number of generation and e^{r} : Environmental resistance. Since insects were reared under laboratory conditions, the e^{r} was considered as zero.

IV. Statistical analysis

The significance of biological and reproductive parameters of *S. litura* reared on different diets was analyzed through one-way ANOVA in SPPS 20.0 and data was represented as mean ± SE. The probability of an individual of age *x* and stage *y* surviving to age *xj* and stage *j* and the age-specific fecundity curve (*mx)* were calculated using the TWOSEX-MS Chart program (version 12.24.2022) available at http://140.120.197.173/ Ecology (National Chung Hsing University).

RESULTS AND DISCUSSION

Biology and biotic potential of *Spodoptera litura* on different natural hosts and meridic diet

Castor leaves were best for rearing because of potent host but in the lab, mass-rearing of *S. litura* on castor leaves (*Ricinus communis*) was difficult because it necessitates the supply of fresh leaves throughout the insect's feeding stage, sometimes forcing a change of leaves twice daily. In addition, larva infection results in a poor harvest of any of the stages (20). The biology of any organism depends upon the host on which they feed. *S. litura*, like any other lepidopteran insects, depends upon multitudinous hosts for its larval development.

The development, ability to reproduce and general fitness of any insect was determined by the nutritional value and palatability of the host plants that insects feed upon. By thoroughly analyzing the life tables derived from cohorts raised on certain host plants under laboratory circumstances, the compatibility of the host plant may be determined (47).

In this regard, the experiment was performed to study the effects of different hosts (cauliflower, cabbage, tomato and castor) and potency of meridic diet on biology, biotic potential, reproductive fitness and demographic parameters of *S. litura* to get a host for rearing of *S. litura* in laboratory and it resulted into different wondering results.

Biology of *Spodoptera litura*

Started from biology, the incubation period of the eggs was longest on the meridic diet (4.0 ± 0.0 days) followed by tomato (3.2 ± 0.0 days), however on cabbage, cauliflower and castor it was 3.0 ± 0.0 days. These differences might be attributed to changes in the nutritional quality and amount of the host plants ingested by the larvae. Many studies have identified variations in the larval hatching phase of *S. litura* feeding on host plants (45).

(i). Larval Period

Similarly, the total larval period was significantly variable among the different diets. The larval period was longest on meridic diet (17.56 ± 0.53 days) followed by tomato (15.3 ± 0.155 days) and quicker in castor (12.33 ± 0.11 days) (p= <0.0001). The results were supported by different work that the larval period in tomato lasted for 24-26 days on tomato host (34,65). It was found that the mean larval period of *S. litura* on castor was 13.50 days (52) and 20.7 days in artificial diet (27).

To make up for the low nutritional content of their hosts like tomato, insects may extend their feeding period (71). Mortality in neonate stage of larvae was due to hardiness of the meridic diet (39), but the post neonate development rate is very fast in meridic diet (27,56). Castor leaves have long been employed as a host for the multiplication of *S. litura*, but the availability of castor in all seasons is a limiting factor.

On the other hand, the low survival rates of *S. litura* on cauliflower and cabbage are mainly attributed to the higher moisture content in the host. All the host are having their own nutritional and biochemical contents which interfere with development period of any organism. It was found that black soldier fly borer larvae survived on the substrate moisture contents of 90-97.5 % but with lower survival rates and reduced body weights than at 75-88 % substrate moisture (35). On the other hand, the low survival rate of larvae on tomato was due to pubescence and trichomes.

(ii). Pupal Period and Total Developmental Period

The total pupal period was prolonged on tomato (9.2 ± 0.21 days) and it was quickest in the castor (7.6 ± 0.13 days)**.** In corroboration to above results, it was found that the pupal period was 8 days in castor (45) and 9.7 days on artificial diet (27). It was found that the pupal period was 8.8 days on tomato (75). The total developmental period (TDP) was longest on meridic diet (29.6 ± 0.73 days) followed by tomato (28.5 ± 0.44 days) and the fastest developmental period was recorded in castor (23.10 ± 0.52 days) (p =<0.0001)**.** According to these findings, the best host plants for larval-pupal development were determined to be castor and meridic diet, whereas tomato and cabbage were shown to be less suited. The above results were supported by earlier reports, that the total developmental period was 22.4 days (6) in *S. litura*. In artificial diet the total developmental period of *S. litura* was 30.5 days (27).

To support their growth, development and reproduction, insects require food sources that are rich in the nutrients as per requirement. To support these activities, insect herbivores need food plants and they must forage in a variety of ecological niches to locate suitable

hosts plants (26). Insect herbivores often rely on plant-produced signals that provide details about pertinent plant features to discover and evaluate the quality of possible host plants. The interactions between plants and herbivores and microbes add another level of complexity to herbivore feeding (85).

It was also noticed that some plants possess trichomes, which regulate the development of organism. Similarly, it was observed that some genotypes of tomato with predominant trichrome recorded relatively more larval mortality, prolonged larval period and pupal duration with reduced adult emergence of also observed that the glandular trichomes were also playing a vital role in insects' biology and host preferences because they are negatively associated with pests (e.g., mortality, survival and entrapment) (70).

(iii). Adult period

The adult emergence percentage was highest in castor that was 95.83 % and 94.73, 93.84, 91.37 and 92.30 % in cauliflower, cabbage, Meridic diet and tomato respectively. The results said that larvae can be survived on all host but number will be varied (<0.0001). Similarly, it was recorded in *S. litura* that the adult emergence rate was 93.11 % cabbage (1), 86.67 % survival rate of *S. litura* on castor (45). In another work on *S. litura*, the adult emergences were 96.8 % and 96 % on castor (4) and 97.2 % when *S. litura* fed on artificial diet (27) (Table 3).

Table 3. Influence of different hosts and diet on biological attributes of *Spodoptera litura*

Parameters	**Meridic diet**	**Cauliflower**	**Cabbage**	**Tomato**	**Castor**	***p***
Incubation period (Days) n=10	4.0 ± 0.0^{a}	3.0 ± 0.0^{c}	3.0 ± 0.0^{c}	3.2 ± 0.0^{b}	3.0 ± 0.0^{c}	<0.0001
Total Larval period n=10	17.5 ± 0.539^{a}	13.2 ± 0.147^{d}	14.3 ± 0.138^{c}	15.3 ± 0.155^{b}	12.3 ± 0.110^{e}	<0.0001
Total Pupal period n=10	7.9 ± 0.187^{bc}	8.1 ± 0.127^{b}	8.0 ± 0.155^{bc}	9.2 ± 0.218^{a}	7.6 ± 0.132^{c}	<0.0001
Total developmental period n=10	29.6 ± 0.733^{a}	24.6 ± 0.221^{b}	25.1 ± 0.314^{b}	28.5 ± 0.448^{a}	23.1 ± 1.663^{c}	<0.0001
Larval weight (g) (10 days old) n=20	0.117 ± 0.021^{c}	0.617 ± 0.055^{b}	0.544 ± 0.063^{b}	0.245 ± 0.049^{c}	0.989 ± 0.022^{a}	<0.0001
Pupal weight (g) n=25	0.348 ± 0.0089^{b}	0.301 ± 0.0061^{c}	0.310 ± 0.0071^{c}	0.247 ± 0.0067^{d}	0.369 ± 0.0082^{a}	<0.0001
Adult emergence (%) n=100	92.30 ± 1.444^{bc}	94.73 ± 1.127^{ab}	93.84 ± 1.149^{abc}	91.37 ± 0.124^{c}	95.83 ± 0.912^{a}	<0.013
Sex ratio n=100	0.46	0.48	0.54	0.37	0.43	-
Male longevity n=10	8.6 ± 0.452^{c}	10 ± 0.365^{ab}	9.5 ± 0.268^{b}	10.4 ± 0.266^{ab}	10.6 ± 0.221^{a}	<0.0001
Female longevity n=10	8.4 ± 0.305^{b}	9.8 ± 0.416^{a}	9.6 ± 0.305^{a}	9.6 ± 0.476^{a}	9.8 ± 0.249^{a}	<0.043
Total life cycle (Male) n=10	37.3 ± 1.20^{a}	33.6 ± 0.61^{b}	32.1 ± 0.60^{b}	37.4 ± 0.28^{a}	33.0 ± 0.424^{b}	<0.0001
Total life cycle (Female) n=10	37.9 ± 0.874^{a}	34.4 ± 0.561^{b}	34.7 ± 0.472^{b}	39.0 ± 0.388^{a}	33.4 ± 0.653^{b}	<0.0001

Means ± SE within a row represented by different lowercase letters are significantly different for a particular trait

The nutritional reserves developed as larvae play a crucial role in determining insects' adult fitness. Many lepidopteran species' early larval instars are frequently sessile and the circumstances these larvae encounter are frequently greatly influenced by the mother's choice of oviposition (58). The pre-oviposition period was longest in cauliflower (2.70 ± 0.15 days) (p =<0.003). The oviposition period was found in different diets were 5.100 ± 0.233, 4.900 ± 0.339, 5.600 ± 0.221, 5.500 ± 0.233 and 4.600 ± 0.179 days in Meridic diet, cauliflower, cabbage, tomato and castor respectively (p=0.033). Similarly, the oviposition period on castor was 7.33 ± 0.24 days and in artificial diet 7.62 ± 0.31 days (62). The above finding on oviposition were evident from research on *Agrotis epsilon* that reproductive variables were also impacted by hosts plants. The preoviposition duration, oviposition period and number and lifespan of *A. ipsilon* adults were all significantly influenced by the hosts (37). It has been observed in *Spodoptera exigua* that the amount of soluble carbohydrates to crude protein in host plants was shown to have a beneficial impact on oviposition and a negative link with the length of the larval stage and the duration of the insect's life cycle (83).

Reproductive Parameters

The fecundity of herbivorous insects is significantly influenced by the quality of the host plant, which also influences insect reproductive processes, egg size and quality, the distribution of nutrients to eggs and the choice of oviposition locations and adult emergence. The fecundity was highest when reared on castor (1791.7 ± 65.64/ female), followed by meridic diet (1718.3 ± 95.80/ female) compared to other hosts (p =<0.0001). Similarly, it was recorded the fecundity up to 2486.2 eggs per female in the larvae fed on artificial diet (27). It was found the fecundity up to 2088 ± 49 and 2155 ± 74 eggs per female on castor and artificial diet (63). The higher fecundity in castor and meridic diet is due to the difference in different biochemical contents viz., fatty acids, protein and other biomolecules.

To support our above results, it was found the fecundity of potato tuber moth was shown to be strongly impacted by host plant species, with the most eggs placed on potatoes and the fewest on wolfberry because of high nutritional contents (79). Similarly, adult onion maggots fed on onion survived longer, had the highest fecundity and reproduction rates and the lowest immature developmental time (47). It was observed that linoleic and linolenic acid are precursors of prostaglandin, which is known to regulate ovarian development and ovipositional behavior (9). Throughout the reproductive cycle, monounsaturated fatty acids palmitoleic acid (16:1) and oleic acid (18:1) predominate, as do polyunsaturated fatty acids linoleic acid (18:2) and linolenic acid (18:3) (60).

The fertility (%) was quite similar on all diets *viz.*, meridic diet, cauliflower, cabbage, tomato and castor (84.15,84.8, 83.21,85.2 and 87.7 %) respectively (p =<0.039). It was found that fertility % was 88.9 % on castor (64). The varied nutrients may have varied effects on insect fertility (66). The artificial diet greatly increased the fertility of *S. litura* in our study. Similarly, when grown on an artificial diet versus host plants, *Spodoptera eridania* (42) and *Bradysia odoriphaga* (Zhang) demonstrate better fertility but reduced lifespan. As a result, it appears that there is a trade-off between fertility and lifespan in female adults.

Overall, our research indicates that *S. litura's* growth, fecundity, survival and mating preferences are significantly influenced by its food. Populations fed an artificial diet mature quickly and lay large number of eggs, two traits that are extremely helpful for the mass raising of *S. litura* (19). The varying nutrition of the various host plants that insects feed on

throughout their larval stages affects the life history features of insects, such as growth, reproduction, survival, etc. The dynamics of population and the status of pests in the field are significantly influenced by demographic research on *S. frugiperda* (3).

Biotic potential of *Spodoptera litura*

Because of nutritional content of the different host the biotic potential was highest in the group of *S. litura*, which fed on castor ($1.85*10^{31}$ individuals per year), followed by cabbage, cauliflower, meridic diet and tomato $1.93*10^{29}$, $2.53*10^{28}$, $1.29*10^{27}$ and $3.82*10^{24}$ individuals per year respectively (Table 4**).** It was found the biotic potential of *S. frugiperda* was estimated at 2.086×10^{29} individuals/female/year on artificial diet (41). It was also recorded that the biotic potential of *S. frugiperda* reared on artificial diet was 5.104×10^{28}, which is more than natural diet (5.740×10^{26}) (56), the reason was host factor. It was also demonstrated in the aphids that feeding on various host plants can have an impact on the population growth rate of aphids. These findings apply to variations in the immature stage of development, female fecundity and oviposition time on *Myzus persicae* (2). This will lead to the availability, low cost and easy preparation of meridic diet proved to be the preferable host for mass production as an alternate host.

Table 4. Reproductive traits and growth indices of *Spodoptera litura* on five different diets

Parameters	**Meridic diet**	**Cauliflower**	**Cabbage**	**Tomato**	**Castor**	***p***
Pre-oviposition period n=10	2.2 ± 0.133^{bc}	2.7 ± 0.152^{a}	2.1 ± 0.100^{c}	2.5 ± 0.166^{ab}	2.2 ± 0.133^{bc}	<0.003
Oviposition period bn=10	5.1 ± 0.233^{abc}	4.9 ± 0.339^{bc}	5.6 ± 0.221^{a}	5.5 ± 0.223^{ab}	4.6 ± 0.179^{c}	<0.033
Post-oviposition period n=10	1.1 ± 0.179^{c}	2.4 ± 0.371^{ab}	2.0 ± 0.365^{ab}	1.8 ± 0.249^{bc}	2.8 ± 0.249^{a}	<0.003
Fecundity (eggs/female) n=10	1718.3 ± 95.80^{a}	1130.8 ± 108.78^{c}	1374.0 ± 50.55^{b}	1240.9 ± 46.42^{c}	1791.7 ± 65.64^{a}	<0.0001
Fertility (%) n=10	84.15 ± 3.132^{b}	84.8 ± 1.980^{b}	83.21 ± 3.940^{b}	85.2 ± 1.991^{ab}	87.7 ± 1.505^{a}	<0.039
Biotic Potential	$1.29*10^{27}$	$2.53*10^{28}$	$1.93*10^{29}$	$3.82*10^{24}$	$1.85*10^{31}$	-
Gonad somatic Index n=5	46.6 ± 3.880^{b}	41 ± 3.162^{b}	44.4 ± 2.227^{b}	50.22 ± 4.532^{ab}	57.8 ± 3.246^{a}	<0.029
Eupyrene sperm bundles n=5	3070.0 ± 56.811^{a}	2989.0 ± 166.428^{a}	2880.0 ± 157.114^{a}	2037.0 ± 87.258^{b}	3086.0 ± 48.455^{a}	<0.0001
Larval growth index n=4	2.96 ± 0.047^{e}	5.75 ± 0.084^{b}	4.53 ± 0.075^{c}	3.77 ± 0.043^{d}	7.78 ± 0.087^{a}	<0.0001
Pupal growth index n=4	11.68 ± 0.162^{b}	11.60 ± 0.193^{b}	11.681 ± 0.131^{b}	9.93 ± 0.013^{c}	12.60 ± 0.150^{a}	<0.0001
Total development indexn=4	1.75 ± 0.014^{e}	3.08 ± 0.003^{b}	2.58 ± 0.028^{c}	2.03 ± 0.022^{d}	4.15 ± 0.015^{a}	<0.0001
Fitness Index n=4	5.41 ± 0.00^{d}	11.19 ± 0.118^{c}	8.80 ± 0.056^{c}	8.73 ± 0.053^{c}	12.509 ± 0.072^{a}	<0.0001
Standardize growth index n=4	0.019 ± 0.0001^{d}	$0.022 \pm 2.99E\text{-}05^{b}$	0.021 ± 0.0003^{c}	0.016 ± 0.00019^{e}	$0.029 \pm 8.88E\text{-}5^{a}$	<0.0001
Immature growth index n=4	3.60 ± 0.040^{d}	4.38 ± 0.0327^{b}	4.17 ± 0.0567^{c}	3.54 ± 0.056^{d}	4.76 ± 0.0064^{a}	<0.0001
Index of adequacy n=4	1.90 ± 0.0129^{d}	2.46 ± 0.020^{b}	2.16 ± 0.0022^{c}	1.52 ± 0.0046^{e}	2.90 ± 0.012^{a}	<0.0001

Means ± SE within a row represented by different lowercase letters are significantly different for a particular trait ($P<0.05$; Tukey's posthoc test)

In lepidoptera the eupyrene sperm bundle plays crucial role in efficient fertilization (68). The eupyrene sperm bundle count was 3070.0 ± 56.811 and 3086.0 ± 48.455 and gonadosomatic index was 46.6 ± 3.880 and 57.8 ± 3.246 in castor and meridic diet, respectively, which were quite similar that defines similar reproductive fitness of the insect. Similarly, the number of eupyrene sperm bundle count were 3169 ± 162, 3364 ± 93 and 4893 ± 546 in *S. litura* on artificial diet (64, 62 and 51 respectively). The results were supported by previous workers, it was observed that the effects of food competition and dietary stress on sperm production in *Plodia interpunctella* that production of sperm counts was greatly reduced, although neither sperm type's size is much affected (23). It was clear from experiment on *Euscepes postfasciatus* that natural host will be having always better reproductive traits compared to artificial diet. However, the sweet potato treatment group had considerably more sperm in the testis-seminal vesicles complex compared to artificial diet (28).

The spawning season is defined by a correlation between the Gonadosomatic Index (GSI) and the frequency distribution of the gonadal maturation stages since the GSI is an excellent predictor of reproductive activity (55). The GSI were 46.6 ± 3.88, 41 ± 3.162, 44.4 ± 2.22, 50.22 ± 4.53 and 57.8 ± 3.24 in meridic diet, cauliflower, cabbage, tomato and castor respectively ($p =<0.029$) (Table 3,4).

Development attributes

The mean larval weight (on the 10^{th} day) varied significantly among different hosts with the highest larval weight recorded on castor (0.989 ± 0.022 g) and lowest on meridic diet (0.117 ± 0.021 g) ($p =<0.0001$). Similarly, it was observed that the mean larval weight on the 11^{th} day of age was highest (941.26 mg) on castor followed by sunflower, okra and groundnut (24). Due to the high moisture content of cabbage, larval length and weight were found to be greater on cabbage, followed by alfalfa and sesbania. The moisture supply and content had a substantial impact on the larvae's weight increase in *Tenebrio monitor* (33)**.** The high moisture content of larvae and host plant affect the artificial rearing of any insect. Larval mobility, feed consumption, growth and survival are all impacted by the substrate moisture content along with that different substrate moisture contents have also been connected to variations in microbial activity (7).

Similarly, the mean pupal weight (2^{nd} day) was highest in castor (0.369 ± 0.0082 g) followed by Meridic diet (0.348 ± 0.0089 g) and lowest was recorded in tomato (0.247 ± 0.0067) ($p =<0.0001$). Accordance with present work it was found that the pupal weight cauliflower, cabbage and castor were 0.372, 0.361.66 and 0.301.33 g respectively (4). It was because of host nutritional content; it was found that the protein present in the diet influenced the duration of larval and pupal periods and pupal weight in *S. frugiperda* (74). The specific composition of the diets plays vital role in gaining pupal weight and it was clearly supported by workers that when plant-based and artificial diets have been compared, larval development, pupal weight and female fecundity were enhanced in lepidopteran species on artificial diet. These results represent an impact on life-history traits and fitness (17).

The sex ratios were found to be 0.46, 0.48, 0.54, 0.37 and 0.43 in meridic diet, cauliflower, cabbage, tomato and castor respectively. It was found the sex ratio on castor 1:0.98 and on artificial diet 1:1.02 (62) and it was similar in case of *S. frugipreda* (56). The sex ratio of insects was undoubtedly influenced by post-settlement environmental variables such the host plant, season and genetic composition (77).

Growth indices of *Spodoptera litura*

The larval growth index was significantly differing highest on the castor and lowest on the meridic diet (p =<0.0001). Interestingly, the pupal growth index was quite similar on all hosts *viz.* meridic diet, cauliflower, cabbage, tomato and castor respectively (p =<0.0001). It was due to similar survival rate. Total development index and fitness index were highest on castor (4.15 ± 0.015) (p =<0.0001). Immature growth index did not vary significantly among the population reared on different host (p=0.0001). The index of adequacy was highest in the case of castor followed by cabbage and cauliflower with 2.90 ± 0.012, 2.16 ± 0.0022 and 2.46 ± 0.020 respectively (p =<0.0001), but it was quite similar in the case of meridic diet (1.90 ± 0.0129) and tomato (1.52 ± 0.0046). Index of adequacy was recorded 1.54 on meridic (63). All the above indices were varying because of host factor which had already been affected the larval, pupal and total developmental period. In *Spodoptera cosmioides* larvae fed on leaves of Barbados nut and tung oil tree, the larval and pupal stages and lifecycle were longer, suggesting that secondary metabolites or non-nutritional chemicals present in the host may alter insect growth and development (11).

Insects' rates of growth and development, reproduction and survival are correlated with the types and amounts of ingested nutrients when environmental conditions are favorable. Insect growth, development and reproduction are supported by a balanced and plentiful supply of nutrients (48). It has been suggested that protein, amino acids and carbohydrates play crucial roles in the growth and development of phytophagous insects. The energy required by insects for growth and development can be provided by carbohydrates was seen in *Henosepilachna vigintioctopunctata* (79). The host plants' amino acids and proteins mostly influence how larvae consume and develop, with sugars having just a little stimulatory effect (10).

Correlation of fecundity and mean pupal weight

Fecundity is an essential life history feature in understanding population dynamics since it is one of the foundations on which population changes are governed by environmental conditions. Female fecundity of *Streblote panda* has been discovered to be related to weight in a variety of insects (8). It was evident that the fecundity is decided at the larval stage and higher larval weight produces a bigger adult, offering increased reproductive success (73). The correlation analysis revealed that fecundity was positively correlated (0.863) to the pupal weight of *S. litura* (Fig. 1). Similarly, observation was made by other researchers on *S. frugiperda* (25). Again, it was proved that the host plays vital role in fecundity that any biotic or abiotic factor that slows larval development will also affect pupal weight and hence reproduction. Their findings imply that food plant and temperature may have an impact on fertility by changing pupal weight (12). For female insects, *Cylas formicarius elegantulus*, body size is correlated positively with the number of offspring produced and often is described as a principal constraint in potential fecundity (59).

Life table analysis of *Spodoptera litura*

The life table is the way to predict population biology of any pest in support of our work asserted that unless the mean generation length is the same, comparing the reproductive rates of two or more populations could be extremely deceptive. The reproduction rate of two or more populations may be identical, yet intrinsic factors will vary. Because generations vary in length, rates of rise may be substantially varied. It is regarded

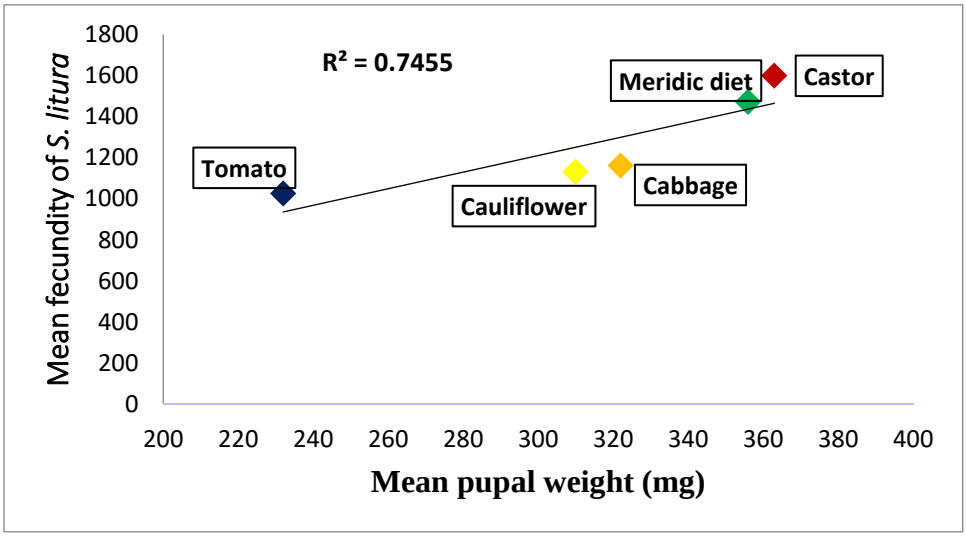

Figure. 1. Correlation between mean fecundity and mean pupal weight of *Spodoptera litura*

as a potent ecological tool that facilitates a thorough comprehension of insect populations' growth, survival and reproductive factors (44), which also facilitates the forecast of the population dynamics of insects. It was quoted that the different host plant nutrient compositions significantly impact the life cycles of herbivorous insects and the shifting trends in their populations, including those of *S. frugiperda* (81). In this study, it was found that the net reproductive rate, population doubling time and biotic potential of *S. litura* was lower on the proposed meridic diet (56) but the gross reproductive rate (GRR) was higher on meridic diet (1095.16 ± 33.17) as compared to castor (772.00 ± 15.84) which proves that the diet can be utilized for the mass production of *S. litura*. When compared to moths raised on castor leaves, fecundity of *S. litura* was modestly increased in moths fed a chickpea diet (up to 2,155 eggs per mated female) (64).

Age-stage-specific survival Rate (S_{xj})

Sxj of *S. litura* on the different hosts like castor, cauliflower, cabbage, tomato and meridic diet are shown in figure (Fig. 2). The values differed across developmental stages, which was attributable to variable growth rates among individuals. *S. litura* quickly completed the larval stage on the castor at 14 days and emerged quickly at 20 days. It slowly completed the larval stage in the meridic diet at 21 days and adult emergence in 27 days. However, there were no differences in the survival of adults between the two hosts. This result suggested that it significantly delayed the development of *S. litura* on a meridic diet.

Population survival rate and fecundity

It was shown that the influence of hosts on the survival rate and fecundity of *S. litura*: *lx*, *fx*, *mx* and *lx***mx* on the different natural host and meridic diet showed a downward trend with increasing age; based on the estimated values, the death of the last adult on all hosts occurred at different interval of days *viz.*, 40, 35, 33, 36 and 38 days in

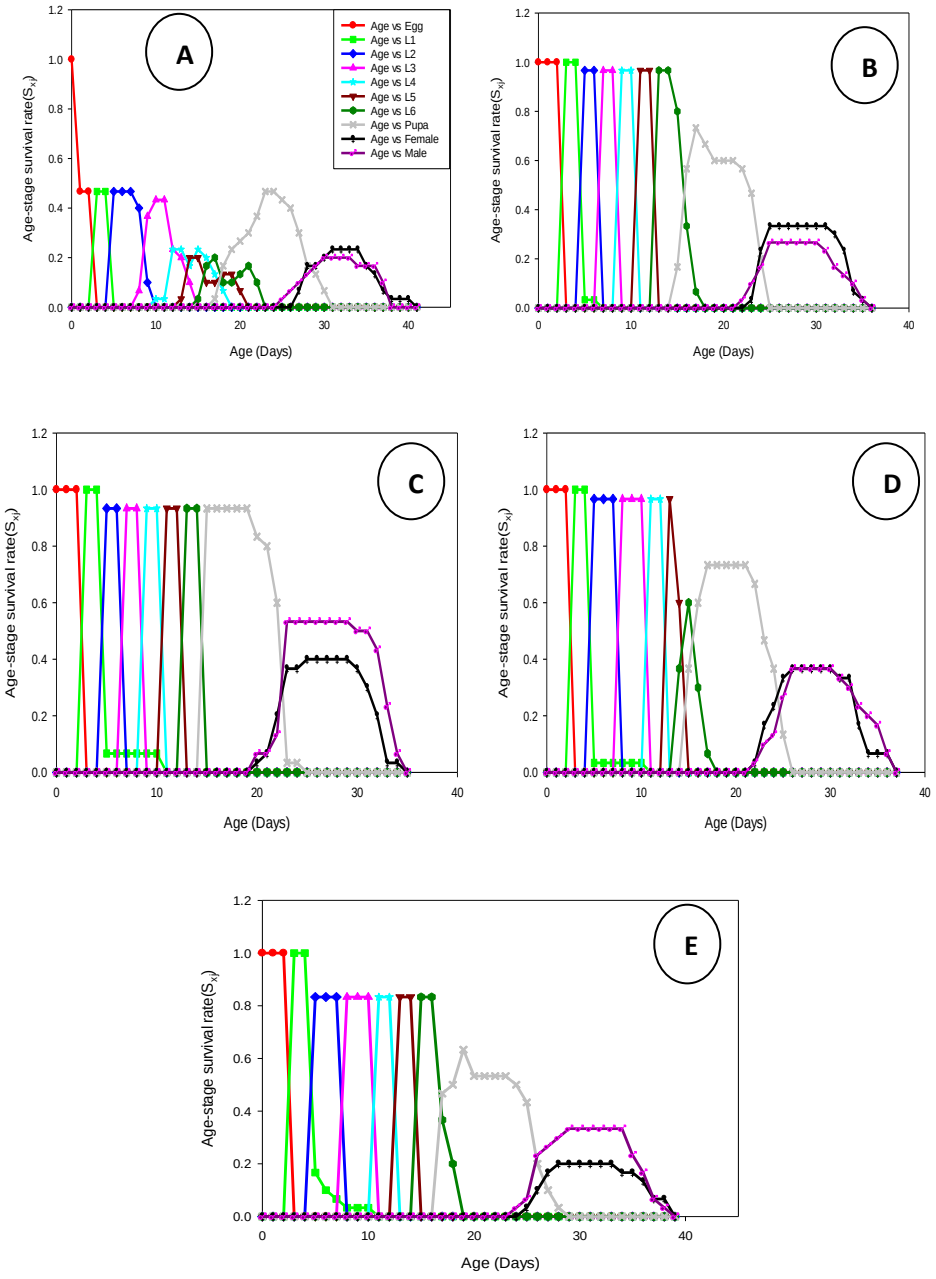

Figure 2. Age-stage-specific survival rate (S_{xj}) of *Spodoptera litura* on natural and artificial diets (A: Meridic diets (AD); B: Cabbage; C: Castor; D: Cauliflower; E: Tomato)

meridic diet, cabbage, castor, cauliflower and meridic diet respectively. *fx, mx* and *lx*mx* reached maximum at 30 days on meridic diet (668.33, 286.42 and 133.66, respectively) and 25 days on castor (392.166, 168.07 and 156.86 respectively) compared toother hosts; each of these maxima (*lx, fx, mx* and *lx*mx)* was minimum compared to meridic diet except *lx.mx*, which was higher in castor compared to other hosts. Thus, meridic diet was more conducive to the development and reproduction of *S. litura*. Additionally, the fluctuations in the fecundity curve suggested that the emergence and oviposition of *S. litura* did not occur at specific ages (Fig. 3).

Life expectancy

The value of Age-stage life expectancy (exj) showed a downward trend on all the natural hosts (castor, cabbage, cauliflower and tomato) and meridic diet, with maximum average longevity values of 34, 35, 36, 38 and 40 days, respectively, at age 0 (*e0,1*) (Fig.4). The value of Age-specific life expectancy (*ex*) was higher on meridic diet than other natural hosts, indicating that *S. litura* developed more slowly on meridic diet (Fig. 5). Age-stage reproductive value (v_{xj}) of *S. litura* on natural (castor, cauliflower, cabbage and tomato) and meridic diets at age zero (*v*, 0,1) was 1.28, 1.244, 1.240, 1.19 and 1.20, respectively, which were close to λ (Fig. 6). The peak value of the *vxj* curve showed an upward trend with advancing age and developmental stage, with the highest value at 30, 28, 26, 26 and 24 days on meridic diet (1267.095), tomato (747.48), cabbage (927.183), cauliflower (774.992) and castor (1073.801) respectively. The highest *vxj* was in female adults reared on a meridic diet. The reproductive value (v_x) of *S. litura* was found to be highest in the meridic diet compared to the other hosts, showing that reproductive fitness is higher on meridic diet (Fig. 7).

Fertility demographic parameters

The intrinsic rate of increase (r) and Finite rate of increase (λ) values of *S. litura* populations were > 0 and> 1, respectively, for all hosts and meridic diet, indicating that the *S. litura* were able to survive on all hosts. On the other hand, mean generation time (T) was quickest on the castor (26.43 ± 0.039) and longest on the meridic diet (32.25 ± 0.053) than other hosts (p =<0.0001). It was found that the net reproductive rate (R_0) was significantly highest on castor (712.75 ± 14.26 females/female/generation) compared to other natural hosts *viz*., cauliflower, cabbage, tomato and meridic diet 476.40 ± 12.20, 447.08 ± 11.54, 240.72 ± 9.54 and 402.74 ± 13.73 (p =<0.0001) respectively. The intrinsic rate of increase (r) was also highest on castor (0.25 ± 0.0001females /female/day) followed by cauliflower, cabbage, meridic diet and tomato with 0.22 ± 0.001, 0.21 ± 0.001, 0.18 ± 0.001 and 0.17 ± 0.0015 respectively (p =<0.0001). The finite rate of increase (λ) was significantly highest on castor (1.28 ± 0.001) followed by cauliflower, cabbage, meridic diet and tomato with values 1.24 ± 0.0014, 1.24 ± 0.001, 1.20 ± 0.001 and 1.19 ± 0.001 respectively (p =<0.0001). The population count doubled in 2.80 days when reared on castor; however, it took 4.06 ± 0.041 when reared on tomato. Most importantly, the gross reproductive rate (GRR) was found to be highest in the meridic diet (1095.16 ± 33.17) and lowest in tomatoes (466.11 ± 16.80) (p =<0.0001) (Table 5).

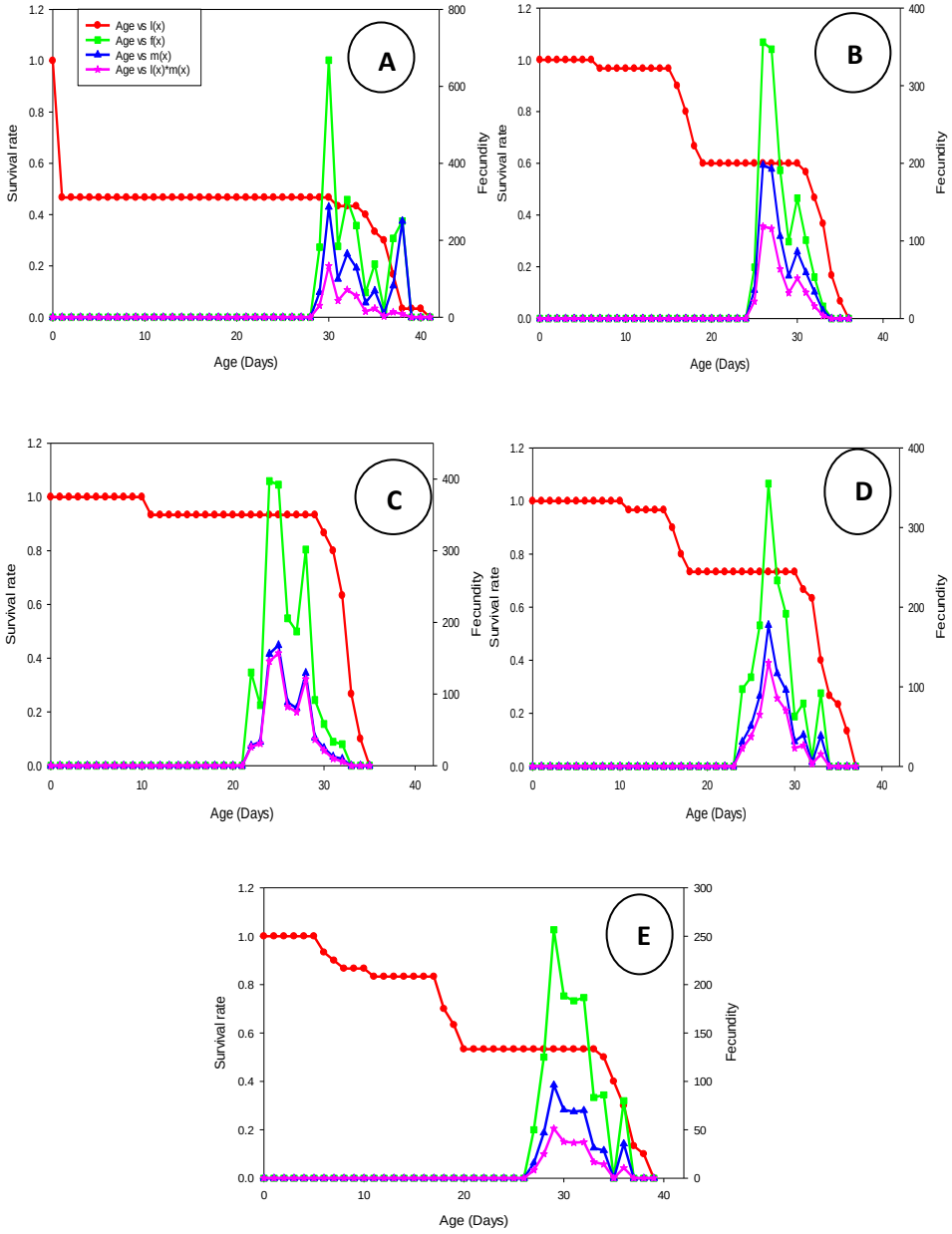

Figure 3. The age-specific survival rate (*lx*), female age-specific fecundity (*fx*), age-specific fecundity (*mx*) and age-specific maternity (*lx.mx*) of *Spodoptera litura* on natural and artificial diets (A: Meridic diet (AD); B: Cabbage; C: Castor; D: Cauliflower; E: Tomato)

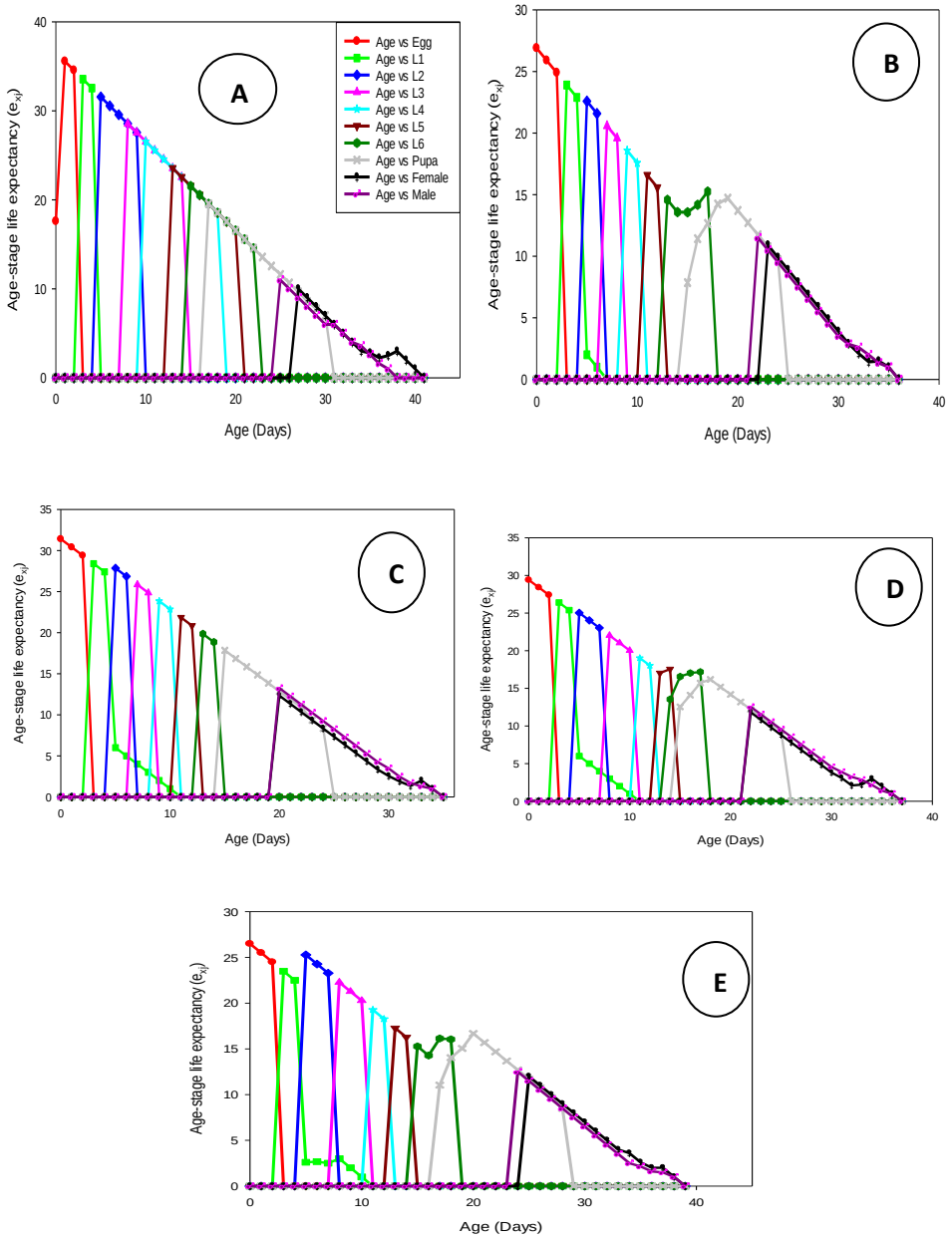

Figure 4. Age-stage life expectancy (e_{xj}) of *Spodoptera litura* on natural and artificial diets (A: Meridic diet (AD); B: Cabbage; C: Castor; D: Cauliflower; E: Tomato)

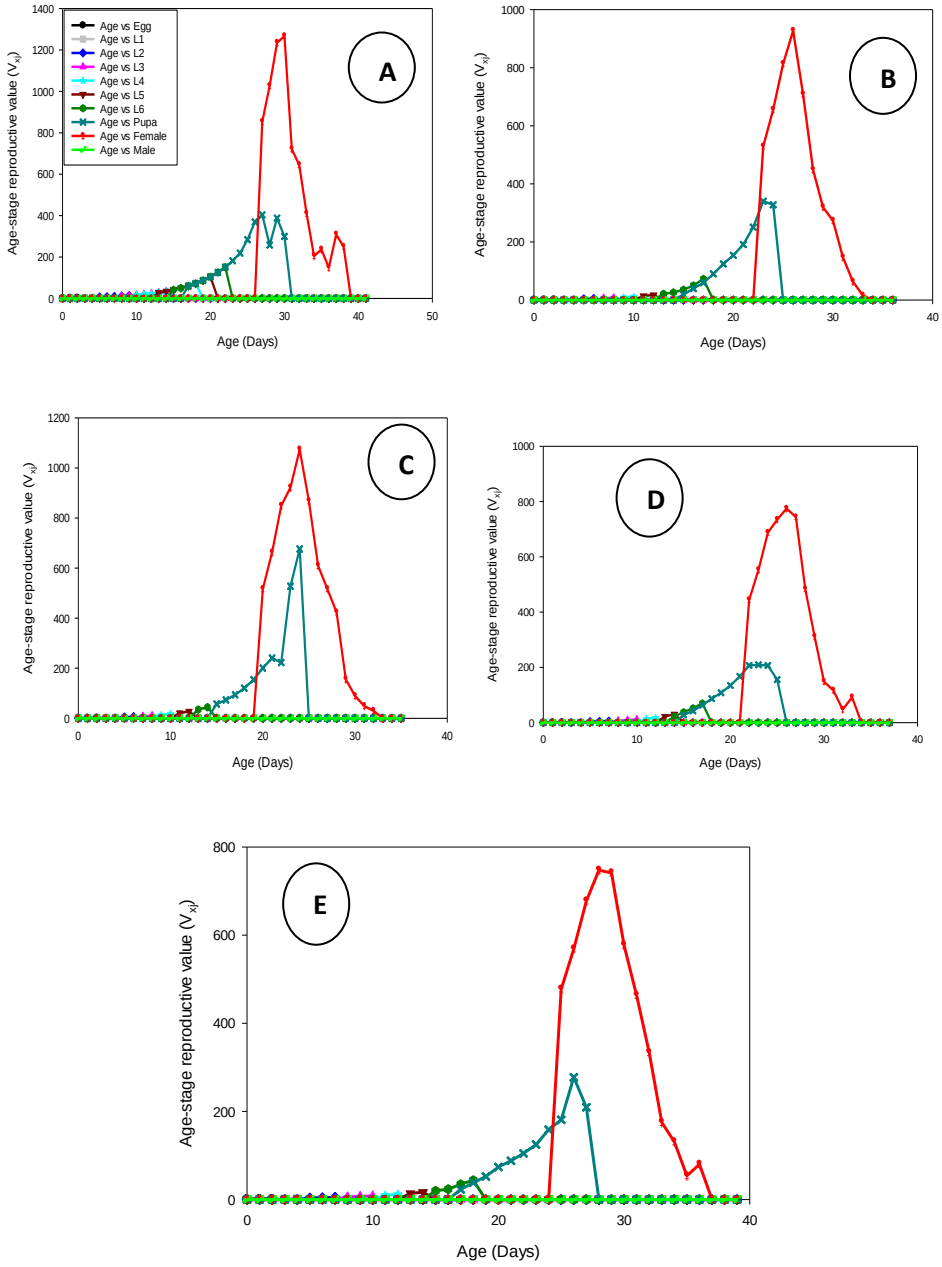

Figure 5. Age-stage reproductive value (V_{xj}) of *Spodoptera litura* on natural and artificial diets (A: Meridic diet (AD) ; B: Cabbage; C: Castor; D: Cauliflower; E: Tomato)

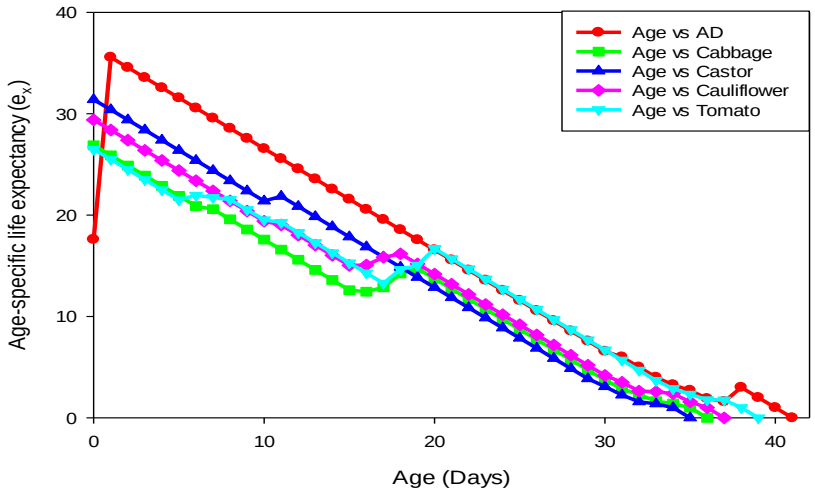

Figure 6. Age-specific life expectancy (e_x) of *Spodoptera litura* on natural and artificial diets

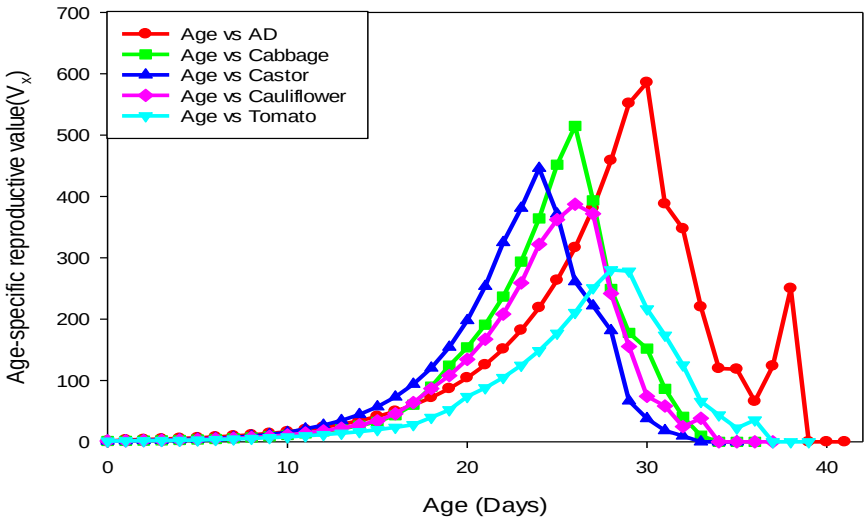

Figure 7. Reproductive value (v_x) of *Spodoptera litura* on natural and artificial diets

Table 5. Population parameters of *Spodoptera litura* on five diets

Host	r	λ	R_0	GRR	T	DT
Meridic diet	0.18 ± 0.0011^{d}	1.20 ± 0.0013^{d}	402.74 ± 13.73^{c}	1095.16 ± 33.17^{a}	32.25 ± 0.053^{a}	3.78 ± 0.024^{b}
Cabbage	0.21 ± 0.001^{c}	1.24 ± 0.001^{c}	447.08 ± 11.54^{b}	759.64 ± 15.16^{b}	28.38 ± 0.027^{c}	3.25 ± 0.016^{c}
Castor	0.25 ± 0.0001^{a}	1.28 ± 0.001^{a}	712.75 ± 14.26^{a}	772.38 ± 15.84^{b}	26.43 ± 0.039^{d}	2.80 ± 0.01^{d}
Cauliflower	0.22 ± 0.0011^{b}	1.24 ± 0.0014^{b}	476.40 ± 12.20^{b}	679.12 ± 16.44^{c}	28.19 ± 0.04^{c}	3.20 ± 0.017^{c}
Tomato	0.17 ± 0.0015^{e}	1.19 ± 0.0018^{e}	240.72 ± 9.54^{d}	466.11 ± 16.80^{d}	31.38 ± 0.06^{b}	4.06 ± 0.041^{a}
P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Means ± SE within a row represented by different lowercase letters are significantly different for a particular trait (P <0.05; Tukey's posthoc test).
r: Intrinsic Rate of Increase, λ: Finite Rate of Increase, R_0 : Net Reproductive Rate; GRR : Gross Reproductive Rate; T ; Mean Generation Time and DT: Doubling Time

In corroboration to the present work on *Spodoptera litura* was subjected to a life table assay was similar to (66) on castor, cabbage and cauliflower. The results revealed a 35-days survivability on castor and 38-day survivability on cabbage and cauliflower. Castor had the highest net reproduction rate (476.92 females per female per generation) compared to cauliflower's 340.61. Castor had a higher intrinsic rate of rise than cauliflower (0.1836 versus 0.2069 female/female/day). For castor, cabbage and cauliflower, the finite rate of increase was 1.23, 1.21 and 1.20 females/female/day, respectively. Castor's mean generation length was substantially longer on cauliflower (31.94 days). In a short amount of time (3.35 days), the population of *S. litura* will double on castor, compared to cabbage (3.71) and cauliflower (3.78), respectively.

Biological parameters of *S. litura* reared on meridic diet, *viz*., incubation period and total larval period was late compared to castor because castor is a natural host and was most preferred by *S. litura* (45). However, in present study, non-significant differences were observed in specific reproductive parameters, like eupyrene sperm count, fecundity and fertility. It was recorded the fecundity of up to 2486.2 eggs per female in the larvae fed on meridic diet (27). The index of adequacy is an empirical factor for determining the suitability of a diet for insect maintenance by incorporating parameters like growth, fecundity and survival. It was 1.90 ± 0.013 on the meridic diet and 2.90 ± 0.012 on the castor.

Based on the biological and reproductive characteristics of *S. litura* reared on a meridic diet, such as a higher gross reproductive rate (GRR), eupyrene sperm count, optimum GSI, optimum BP and higher fecundity compared to natural diets, the current study concludes that the meridic diet in the present study will be the best alternative in absence of natural host for the rearing of *S. litura* year-round in laboratory conditions and along with that the intermittent rearing on castor plants improve the biotic potential of the insect.

The alternate-rearing host-like meridic diets allows for the mass production of insects in an easier, more tightly controlled, economical and practical manner than growing them on native foods like plants or natural prey (30) and it can be utilized as a food source in absence of natural host alternate host. It substantially impacts insect biology and is essential

for insect development, a prepared diet should supply all of an insect's nutritional needs (32). In host plants, secondary metabolites, proteins and carbohydrates regulate insect growth and development (36). Low-cost and effective artificial diets are selected to meet the demand for the desired number of insects raised in laboratories. Proteins, carbs, lipids, vitamins, minerals and preservatives are the main elements of any artificial diet that aid in the growth and development of insects (8).

CONCLUSIONS

This study understood the reproductive fitness and demographic parameters of insects. Our results also demonstrated that different host plants had variable influences on the life table parameters. We concluded that meridic diets are comparatively better. However, rearing on natural hosts like castor is cost-effective and it improves the biotic potential of *Spodptera litura*. Further studies on the holistic nutritional analysis of the insects reared on different host plants in comparison with meridic diet may help in improving the quality of the meridic diets. For this polyphagous folivorous pest, further information on the life table and population factors may help in anticipating the dynamics of the population, which will further aid in planning an efficient integrated pest control and insect resistance management programme.

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DECLARATION

D. Sagar and Keerthi M.C. designed and planned experiment. Hemant Kumar and Reshma did experiments. Hemant Kumar, D. Sagar and Keerthi M.C wrote article. D. Sagar and Subramanian S corrected the manuscript. The authors have declared that no competing interests exist.

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the author(s).

ETHICAL APPROVAL

The authors declare that the study was carried out following scientific ethics and conduct.

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