Association between temperature and life table development of Fall armyworm *Spodoptera frugiperda* under control condition

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Abstract

Fall armyworm *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) (FAW) is one of the devastating polyphagous pests having a wide range of host plants that contribute substantial losses to crop cultivation. For such pests, temperatures exert a significant impact on biology, distribution, and abundance. Hence the present study was executed with the aims of evaluating the effects of different temperatures on the growth and development of fall armyworm. FAW larvae collected from the infested field and were reared in three different temperatures regimes viz. $25\pm 1^{\circ}\text{C}$ (T25), $30\pm 1^{\circ}\text{C}$ (T30) and $35\pm 1^{\circ}\text{C}$ (T35) incubator provided with 12:12 photo period. Life table and fecundity tables were calculated using growth parameters. The results indicated that the mean duration of each stage of lifecycle at three different temperatures were significantly different from each other. The accumulated mortality at the adult stage was 95%, 61% and 64% at T35, T30 and T25 respectively. The net reproductive rate (R_o) was 132.17, the average period of generation time (T_c) was less in T30 (32.31) with the daily finite rate of increase in number (λ) was 1.1702 females/female/day and a population doubling time of 3.004 days. Similarly, the intrinsic rate of natural increase in number (r_m) was 0.1511 females/female/day and hypothetical female population in the F2 generation was found to be higher at T30 (17468.20) thus the results indicated that T30 favors the growth and development of FAW compared to the other tested temperatures. Our findings could be useful for the implication in pest management and forecasting.

Introduction

The environmental, economic, and social impacts of invasive alien species are jeopardizing the livelihoods and food security of small-scale farmers in developing countries. (Early et al., 2016; Paini et al., 2016; Pratt et al., 2017). Among them, the *Spodoptera frugiperda*, also known as the fall armyworm (FAW), is a polyphagous lepidopteran pest native to tropical and subtropical America and mainly associated with maize crops (Cruz et al., 1999; Sarmiento et al., 2002). It is a member of the genus *Spodoptera*, of the Noctuidae family, which is responsible for the world's highest monetary losses to agriculture (Groote et al., 2020) due to the nature of highly mobile insect pests infesting with a wide range of host crops. However, this tropical pest cannot survive in cold temperatures for long periods (Westbrook et al., 2015). Hence high variations in the weather in the Americas allow the FAW, to migrate to other countries, continually which has no diapause (Geogern et al., 2016). In late 2016, the first case of FAW was reported in West Africa and since spread rapidly across Sub-Saharan Africa, with its presence now confirmed in 44 African countries (Sisay et al., 2019). In 2018 it was reported in Asia damage was primarily in India (Karnataka) (Sharanabasappa et al., 2018). In Sri Lanka, a recent outbreak of FAW caused significant yield losses of maize, especially in the Uva, Eastern, and North Central provinces. The damage was first recorded in October 2018, and the majority of small-scale farming families have been severely (Perera et al., 2019). It was later recorded in the districts of Anuradhapura, Monaragala, Kurunegala, Kandy, Badulla and Rathnapura which belongs to Dry and dry intermediate agro ecological zones in the country (Wijerathna et al., 2020). As such the temperature might have a direct impact on the life cycle of FAW.

Theoretically, the thermal optimum is defined as the temperature at which a species thrives well in terms of growth, reproduction, and survival (Begon et al., 2006). When the maximum and minimum temperatures are within the species' optimum it promotes insects' growth and development (Hagstrum & Hagstrum, 1970; Howe, 1967). Further the length and number of each instar that larvae go through before reaching adulthood is influenced by temperature (Aguilon et al., 2015). Moreover, the relationship between temperature and development rate has a huge impact on pest biology, distribution, and abundance (Tobin et al., 2003). Increased ambient temperature near the thermal optimum of insects causes an increase in metabolic activities (Jaworski et al., 2013).

In ecological perspective, life tables are useful resources for evaluating, predicting and comprehending insect population development rates (Ashok et al., 2020). However, recent publications have focus on revealing the impact of FAW in selected specific temperatures, though the impact of various temperature has not been revealed. Owing to such limitations, our present study was carried out with the aim of evaluating the life tables of FAW on selected three different temperatures regimes under laboratory conditions.

Materials And Methods

Insect stock colony

The FAW larvae (F_0 generation) were collected from naturally infected maize fields from the University experimental station at the Agrotech park Malwatte, the South Eastern University of Sri Lanka in Ampara district belongs to the low country dry zone (DL 2b; N 07° 19' 17.30" E 81° 43' 56.19). The collected larvae were reared under constant laboratory conditions (Temperature 26 ± 1 °C, 70% RH and 12L:12D photoperiod) by providing a natural diet (Plessis et al., 2020) and maintained until the pupal stage in the Biosystems Technology laboratory facilities at the Faculty of Technology. The pupae were separated under the optical stereo microscope (LAB 20, Optika, Italy) according to the method previously described by Plessis et al., (2020). Separated pupae were placed in oviposition cages (30 cm H. × 10cm D.) for adult emergence.

Life table study

The uniform three batches of 100 to 150 eggs (F_1 generation) were obtained from the stock (F_0) colony and kept in three insect incubators (DI 120 Drag Lab Germany) and were maintained constant different temperature conditions viz. 25 ± 1 °C (T25), 30 ± 1 °C (T30) and 35 ± 1 °C (T35) until completion of progeny. The eggs were inspected under the Optical stereo microscope on daily basics to record the egg hatchability and days taken for hatching. As soon as 1st instar larvae emerged, they were transferred to the individual transparent plastic bottles (10 cm D. × 5 cm H.) and reared on the natural diet according to the Plessis et al., (2020). Then the individual larvae were observed under the optical stereo microscope to determine the duration of 1st, 2nd, 3rd, 4th, 5th and 6th larval instars and were recorded until pupation by

observing at their head capsules and exuviae (Plessis et al., 2020). Moreover, the duration of prepupal, pupal and adult stages were recorded.

Determination of oviposition, fecundity and longevity of FAW

Ten couples from the emerging population of the above progeny were placed in oviposition cages and maintained in respective three different temperatures to obtain the age-specific fecundity data. The procedure continued until end of the adult emergence. A moistened muslin cloth was provided as oviposition substrate with 10 % sucrose solution was provided to feed the adults. In each cage, the pre oviposition, oviposition, and post oviposition periods, number of eggs per day were recorded at daily intervals until the death of the female while oviposition substrate was replaced on a daily. Then the number of female birth (mx) was estimated by assuming the 1:1 sex ratio as the number of eggs/day divided by two (Ashok et al., 2020).

Determination of the age-specific fecundity tables

The age-specific fecundity tables for different temperatures were prepared using daily observations of confined FAW couples (Equation 1, 2, 3 and 4) here x = Pivotal age in days; lx = Survival of female at age 'X'; mx = Age schedule for female births at age 'X' and e = 2.71828. The Net productive rate (Ro) in generation as measured in females deliver per generation, Mean duration of generation (Tc) or mean age of the mothers in a cohort at the birth of female offspring, Innate capacity for increase (rm) or at each age interval, the total number of individuals who survived and the mean number of female offspring births were recorded (Atwal & Bains, 1974; Howe, 1953). Subsequently, estimated the precise generation time (T), the finite rate of natural increase (λ) or a number of females per female per day, the population's weekly multiplication and hypothetical F₂ females were calculated.

$$\text{Net Reproductive rate (Ro)} = \sum l_x m_x \quad (1)$$

$$\text{Mean duration of generation (Tc)} = \frac{\sum l_x m_x}{R_0} \quad (2)$$

$$\text{Innate capacity for increase (rm)} = \frac{\log_e R_0}{T_c} \quad (3)$$

$$\text{Finite rate of natural increase } (\lambda) = \text{antilog } e^{rm} \quad (4)$$

Cohort life tables

Age-specific life table or cohort life table for fall armyworm was developed by Kyi et al., (1991) and Krebs (1978a and 2001b) Equation 5, 6, 7, 8 and 9 were used. The Krebs formulas were applied to calculate the results, *i. e.* x = age interval (days) of each stage, egg, 1st, 2nd, 3rd, 4th, 5th, 6th larval instar, pupa and adult,

n_x = number of survivors at start of the age of interval x , dx = number of dying during the age interval x to $x+1$, q_x is the rate of mortality during the age interval x to $x+1$, l_x is the proportion of organisms surviving to start at age interval x , L_x is the number of individuals alive on the average during the age interval x to $x+1$, Cumulative number of alive in age interval x to $x+1$, e_x mean expectation of life for organism alive at the start of age x .

$$\text{Rate of mortality during the age interval } x \text{ to } x+1, q_x = \frac{dx}{n_x} \quad (5)$$

$$\text{Proportion of organisms surviving to start at age interval } x, l_x = \frac{n_x}{n_0} \quad (6)$$

Number of individuals alive on the average during the age interval x to $x+1$,

$$L_x = \frac{n_x + n_{x+1}}{2} \quad (7)$$

$$\text{Cumulative number of alive in age interval } x \text{ to } x+1, T_x = \sum_x^{\infty} L_x \quad (8)$$

$$\text{Mean expectation of life for organism alive at the start of age } x, e_x = \frac{T_x}{n_x} \quad (9)$$

Data analysis

The mean duration of each stage of the FAW life cycle in different temperatures was compared using a one-way analysis of variance (ANOVA) followed by Tukey's post hoc test at a 5% significant level.

Results And Discussion

Biology of FAW

The present results indicated that the mean longevity for each stage of development at three different temperatures was significantly ($p < 0.05$, $df = 2$) vary except for the egg hatching period. Where 1st to 3rd instar larvae recorded the longest longevity at T25 and 4th to 6th instar larval longevity was longer at T35 (Table 1). However, the total larval longevity was higher at T25 (20.17 days) and T35 (17.89 days) compare to the T30 (14.92 days). Conversely, pupal duration at T35 (5.75 days) was the shortest compared to the other tested temperatures. The longevity of female moths at T35 was significantly lower (5.66 days) than T30 and T25 (Table 1).

Table 1. Longevity (days) of each stage of the FAW life cycle in different temperatures.

Particulars	Longevity (Days) (Mean $\pm$ SD)		
	35°C	30°C	25°C
Egg	2.78 $\pm$ 0.46 ^a	2.17 $\pm$ 0.38 ^a	2.14 $\pm$ 0.35 ^a
1st instar	2.78 $\pm$ 0.42 ^b	2.33 $\pm$ 0.50 ^c	3.14 $\pm$ 0.79 ^a
2nd instar	2.38 $\pm$ 0.76 ^b	1.92 $\pm$ 0.60 ^c	3.02 $\pm$ 0.85 ^a
3rd instar	2.71 $\pm$ 0.75 ^a	2.13 $\pm$ 0.60 ^b	2.72 $\pm$ 0.88 ^a
4th instar	3.20 $\pm$ 1.48 ^a	2.01 $\pm$ 0.72 ^b	2.54 $\pm$ 0.95 ^a
5th instar	4.00 $\pm$ 0.70 ^a	2.81 $\pm$ 0.82 ^b	2.81 $\pm$ 0.72 ^b
6th instar	5.20 $\pm$ 0.83 ^a	3.72 $\pm$ 1.07 ^b	3.66 $\pm$ 0.63 ^b
Pre pupae	1.20 $\pm$ 0.44 ^b	1.64 $\pm$ 0.75 ^a	1.84 $\pm$ 1.02 ^a
Pupae	5.75 $\pm$ 0.50 ^b	8.61 $\pm$ 0.75 ^a	9.21 $\pm$ 1.02 ^a
Total pre adult period	29.50 $\pm$ 4.43 ^{ab}	27.56 $\pm$ 1.89 ^b	30.93 $\pm$ 2.38 ^a
Male	-	9.29 $\pm$ 0.46	10.00 $\pm$ 0.75
Pre oviposition	-	2.85 $\pm$ 1.11	2.82 $\pm$ 0.52
Oviposition	-	4.73 $\pm$ 1.77	5.25 $\pm$ 1.73
Post oviposition	-	1.23 $\pm$ 0.59	1.62 $\pm$ 1.06
Total female duration	5.00 $\pm$ 1.73 ^b	9.38 $\pm$ 2.06 ^a	9.00 $\pm$ 1.60 ^a
Total duration of the life cycle	34.5 $\pm$ 1.08 ^b	36.07 $\pm$ 0.69 ^{ab}	38.62 $\pm$ 0.70 ^a

Values indicates mean $\pm$ standard deviation (SD) (days) and different letters show significant differences at 5% significant level

Table 2. Cohort life table of Fall Armyworm at 35°C

Stage	n_x	l_x	d_x	q_x	e_x	L_x	T_x
Egg	100	1.00	42	0.42	1.84	79	184.5
1st instar	58	0.58	36	0.62	1.81	40	105.5
2nd instar	22	0.37	7	0.31	2.97	18.5	65.5
3rd instar	15	0.68	2	0.13	3.13	14	47
4th instar	13	0.86	3	0.23	2.53	11.5	33
5th instar	10	0.76	2	0.2	2.15	9	21.5
6th instar	8	0.8	2	0.25	1.56	7	12.5
Pupae	6	0.75	1	0.16	0.91	5.5	5.5
Adult	5	0.83	5	1.00	0	0	0
Accumulated Survival	5%						
Accumulated mortality	=95%						

The table indicates the; n_x = number of survivors at start of the age of interval x , l_x = Survival of female at age x , d_x = number of dying during the age interval x to $x+1$, q_x = rate of mortality during the age interval x to $x+1$, L_x is the number of individuals alive on the average during the age interval x to $x+1$, Cumulative number of alive in age interval x to $x+1$, e_x = mean expectation of life for organism alive at the start of age x ($n = 100$).

The cohort life table result of each temperature revealed that the lowest survivorship at T35 resulted from 95% accumulated mortality (d_x) from 100 eggs followed by five adults with a sex ratio (3:1). Besides high mortality was observed in the egg (42) and 1st instar larval (36) stages with q_x values 0.42 and 0.62 respectively (Table 2). The results further reveal that egg hatchability and survivorship of subsequent larval stage were highly dependent on temperature whereas constant T35 exhibited increase mortality of eggs, early instars and males are more prone to heat stresses and vulnerability.

Table 3. Cohort life table of Fall Armyworm temperature at 30°C

Stages	n_x	l_x	d_x	q_x	e_x	L_x	T_x
Egg	150	1.00	13	0.08	4.64	143.5	696.5
1st instar	137	0.91	32	0.23	4.03	121	553
2nd instar	105	0.76	15	0.14	4.11	97.5	432
3rd instar	90	0.85	24	0.26	3.71	78	334.5
4th instar	66	0.73	0	0	3.88	66	256.5
5th instar	66	1	1	0.01	2.88	65.5	190.5
6th instar	65	0.98	2	0.03	1.92	64	125
Pupae	63	0.96	4	0.06	0.96	61	61
Adult	59	0.93	59	1.00	0	0	0
Accumulated survival	39%						
Accumulated mortality	61%						

The table indicates the; n_x = number of survivors at start of the age of interval x , l_x = Survival of female at age x , d_x = number of dying during the age interval x to $x+1$, q_x = rate of mortality during the age interval x to $x+1$, L_x is the number of individuals alive on the average during the age interval x to $x+1$, Cumulative number of alive in age interval x to $x+1$, e_x = mean expectation of life for organism alive at the start of age x ($n = 150$).

On the other hand, the highest survivorship was observed at T30 (39%) (Table 3) with less accumulated mortality rate (61%) were resulting in 59 adults from 150 eggs. In addition, egg mortality was less compared to the T35 and the highest d_x was in the 1st instar larval stage (32). Similarly, the q_x values are very low in egg (0.08), 5th (0.01), 6th (0.03) and pupal (0.06) stages. Though, this temperature range lies between optimum thermal condition recorded the considerably higher mortality percentage due to constant temperature conditions and daily handling the larvae for observation influencing the natural behavior of the FAW.

Table 4. Cohort life table of Fall Armyworm temperature at 25°C

Stages	n_x	l_x	d_x	q_x	e_x	L_x	T_x
Egg	150	1.00	22	0.14	4.18	139	628
1st instar	128	0.85	39	0.3	3.82	108.5	489
2nd instar	89	0.69	22	0.24	4.27	78	380.5
3rd instar	67	0.75	5	0.07	4.51	64.5	302.5
4th instar	62	0.92	0	0	3.83	62	238
5th instar	62	0	3	0.04	2.83	60.5	176
6th instar	59	0.95	0	0	1.95	59	115.5
Pupae	59	0	5	0.08	0.95	56.5	56.5
Adult	54	0.91	54	1.00	0	0	0
Accumulated survival	36%						
Accumulated mortality	64%						

The table indicates the; n_x = number of survivors at start of the age of interval x , l_x = Survival of female at age x , d_x = number of dying during the age interval x to $x+1$, q_x = rate of mortality during the age interval x to $x+1$, L_x is the number of individuals alive on the average during the age interval x to $x+1$, Cumulative number of alive in age interval x to $x+1$, e_x = mean expectation of life for organism alive at the start of age x ($n = 150$).

Similar to T30, higher survivorship (36%) was observed with less mortality at T25 than T35. It resulted 54 adults with the sex ratio of 2:1. However, as similar to the other two temperature conditions high q_x was found in the 1st instar stage (0.3) meantime the zero q_x values were found in the 4th and 6th instar larval stages.

Table 5: Life fecundity table of fall armyworm under different temperatures

Population growth statistics	Temperature		
	30°C	25°C	35° C
Net reproductive rate (R_0)	132.17	118.74	0.00
Mean length of generation (T_c)	32.3138	35.90	0.00
Innate capacity for an increase in numbers (r_m) (Females/ Female/day)	0.1511	0.1330	0.00
Arbitrary ' r_m ' (r_c)	0.15 - 0.16	0.15 - 0.16	0.00
Corrected ' r_m ' (Female/ Females/day)	0.1577	0.1330	0.00
Corrected generation time (T) (days)	30.97	35.91	0.00
Finite rate of increase in numbers (λ) (Female/Females/ day)	1.1702	1.1417	0.00
Weekly multiplication of population (λ^7)	3.004	2.5285	0.00
Hypothetical F_2 females	17468.20	14099.18	0.00

The present study revealed that, female pre-oviposition period remained at 28 to 30 days and pivotal age was 31 to 33 days at T30. The first batch of eggs was laid by females after 31 days with m_x of 160.27 and lasted until the 38 days ($m_x = 11$), where l_x values of 0.28 and 0.03 respectively for 31 and 38 days (Figure 1). At 32 days of pivotal age, the first female mortality was recorded on the 4 days after the emergence and the female mortality increased, as evidenced by a steady decrease in the l_x values. It had a l_x value of 0.24 on the 32 days of pivotal age. The maximum mean progeny production/day ($m_x = 168.57$) was reported on the 32 days.

As same in T25 pre oviposition and oviposition periods took comparatively longer durations while the first batch of eggs was laid by females on the 34 days. They had m_x of 258.86 and lasted until the 42 day ($m_x = 09$), with l_x values of 0.17 and 0.03 respectively (Table 5). After the 34 days of pivotal age, the first female mortality was observed on the 3 days after the emergence. Moreover, the net reproductive rate (R_0) was 132.17 and 118.74 respectively in T30 and T25, which represents the ratio of total female birth in a generation. Similarly, the average period of generation time (T_c) was lower in T30 (32.31 days) compared to T25 (35.90 days). However daily finite rate of increase in number (λ) in T30 1.1702 females/female/day with a population doubling time of 3.004 days whereas in T25 (λ) 1.1417 females/female/day and a population doubling time of 2.5285 days. The intrinsic rate of natural increase in number (r_m) was 0.1511 females/ female/ day (T30) and 0.1330 females/ female/ day (T25). Finally, the hypothetical female population in the F_2 generation was found to be higher in T30 (17468.20) than T25 (14, 099.18) was reported (Table 5). Similar observations were reported earlier by

Ashok et al., (2020) by evaluating adult longevity, oviposition period, fecundity and fertility using 30 pairs of FAW at 27 °C. They reported adult longevity of 12.6 days and 11.1 days for females and males, respectively.

Based on our findings, the net reproductive rate (R_o) was 480.33 ($n = 36$) with a generation time (T_c) of 31.24 days. The determined intrinsic rate of natural increase (r_m) and the finite rate of increase (λ) was 0.20 and 1.22 females/ female/ day, respectively. The population doubling time was found to be 3.51 days. The FAW life cycle follows complete metamorphosis (holometabolous) consisting of 4 stages *viz*, egg, larva, pupae and adult stages (Assefa & Ayalew., 2019). The longevity of each stage was varying different day intervals *viz*, 2 days for egg hatching, larval longevity (12 days), pupal (7 days) and adult longevity (14 days) (Tendeng et al., 2019). However, several authors reported various longevity for different stages of FAW according to the various climatic conditions (Ashok et al., 2020; Plessis et al., 2020). As per the biological parameters of FAW at 25°C Kalyan et al., (2020) reported that the larval, pupal, pre oviposition, oviposition and post-oviposition period were 16.97, 8.96, 3.30, 16.97, 8.96, 3.47, 2.96 and 6.13 days respectively but those durations were in disagreement with present findings.

However, present findings were in agreement with results reported by Pitre & Hogg (1983) when the larvae were reared at 25°C. The total life cycle was completed within 30 days at the daily temperature at 28°C during warm climate conditions but may extend up to 60-90 days in cooler temperatures including 20-30 days of pupal period. Overall, the present results indicated that total life cycle durations were 34.5 ± 1.08 , 36.07 ± 0.69 and 38.62 ± 0.70 days for T35, T30 and T25 respectively and were in line with the previous studies.

The FAW female moth normally deposits the majority of her eggs during the first 4 to 5 days of life followed by 3-4 days pre oviposition period, but oviposition can continue up to 3 weeks. Adult life expectancy is estimated to be about 10 days on average, with a range of 7-21 days (Prasanna et al., 2018). According to our study pre-oviposition periods lay between 2.5 to 3 days and total female longevity extends to a maximum of 9 days for both T25 and T30 conditions while 5 days of total life durations are reported at T35.

In higher temperature conditions like T35 results, only 5 adults survive from 100 eggs while the remainder fails to rescue compared to the other two temperature conditions. This may be due to continuous exposure of high temperature to eggs at early development instars tend to increase water losses through the unsclerotized cuticle while on the other hand increasing metabolic rates may lead to rapid depleting the foods reserves. In contrast, other tested two temperatures may lie within the optimum thermal range required for their growth and development. Our observation further confirms that males were more susceptible to rising temperatures than females. Due to the low male to female ratio at T35, the progeny fitness became lower and mating was not taken place thereby both males and females were died within 6-7 days without laying eggs. Therefore, it was not possible to construct the life fecundity table, mean length of a generation, innate capacity for an increase in numbers and finite rate of increase in numbers of FAW at T35. Further, our results indicated that the egg hatchability and survivorship of the first instar larvae were more susceptible to temperature changes. Therefore, the changing temperature can be used

in the field conditions at the stage of eggs and first instar larvae for the manipulation of FAW populations. Our findings could be useful implicating in pest forecasting and integrated pest management programs in the field and control environmental conditions.

Declarations

Author Contribution

ADNTK and GKMMKR conceived and designed the study. AMKGM and MBA conducted experimental work, data collected. ADNTK and GKMMKR analyzed the data, and drafted the manuscript. ANM and ADNT supervised the AMKGM and MBA corrected the draft manuscript and improved. SRS supply the planting materials and improved the manuscript. All authors critically revised the draft and approved the final manuscript for publication.

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Disclosure

The authors declare that they have no any conflicts of interest.

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Figures

Figure 1

Age-specific fecundity (mx), age-specific mortality (lxx) of fall armyworm at 25°C and 30 °C temperatures under control conditions ($n > 100$).