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Research Article

Life Table Studies of Invasive *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on Maize under Laboratory Conditions

Arfan Ahmed Gilal[1*], Lubna Bashir Rajput[1], Muhammad Ibrahim Kubar[1], Ghulam Murtaza Kaleri[2], Tanzeela-ul-Zahra[1,3], Muhammad Ishaque Mastoi[4] and Zeeshan Rasheed[1]

[1]Department of Entomology, Faculty of Crop Protection, Sindh Agriculture University, Tandojam, Pakistan; [2]Institute of Plant Sciences, University of Sindh, Jamshoro, Pakistan; [3]Centre of Agriculture and Bioscience Institute, Pakistan; [4]Pakistan Agriculture Research Council, Islamabad, Pakistan.

Abstract | Fall armyworm (FAW) *Spodoptera frugiperda* has shown invasive characteristics, especially against maize production in African and Asian countries including Pakistan. Therefore, understandings of its biological features in introduced locations could improve understanding of its invasive features, which is necessary for better management. Accordingly, life table and fertility schedule studies of FAW were conducted under laboratory conditions on maize leaves and stems. Three cohorts comprised of 131, 112 and 105 eggs of similar age were used for both leaves and stems. The results indicated that maximum mortality of FAW in both maize stems and leaves were recorded in pupa and 1st larval instar, respectively whereas, maximum survival was recorded in 4th and 5th larval instars. Almost, similar male to female sex ratio was recorded in leaves and stems with higher female longevity in leaves than stems. No significant difference was recorded in approximate and corrected generation time of FAW between leaves and stems. Innate capacity of increase (r_c) and intrinsic rate of natural increase (r_m) recorded on stems (0.1237±0.0032 and 0.1248±0.0033, respectively) were higher than leaves (0.1027±0.0025 and 0.1034±0.0026, respectively). Finite rate of increase (λ), doubling time (DT) and net reproductive rate (R_o) observed on maize stems (0.3363±0.0086, 5.61±0.14 days and 143.29±12.27 offspring/individual, respectively) were higher than those observed on leaves (0.2791±0.0069, 6.76±0.16 days and 69.63±6.22 offspring/individual, respectively). As FAW showed better population and reproductive parameters on maize stems than leaves, it should be managed as early as possible to restrict losses to maize before establishment of perfect stems.

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***Correspondence** | Arfan Ahmed Gilal, Department of Entomology, Faculty of Crop Protection, Sindh Agriculture University, Tandojam, Pakistan; **Email:** aagilal@sau.edu.pk
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Introduction

Maize holds a key position as cereal along with wheat and rice to fight the war against hunger in the world (Pingali, 2001). However, in recent years, fall armyworm (FAW) *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) has pose a great threat to production of maize throughout the world

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(Westbrook *et al*., 2016; Montezano *et al*., 2018). It originated from tropical and sub-tropical America but has invaded almost all maize growing areas of Africa, Asia, and Australia within a period of three years (Wan *et al*., 2021). Thus, Centre for Agriculture and Biosciences International in its State of the World's Plants report of 2017 has regarded FAW as one of the 10 most dangerous arthropod pest from the list of 1187 pests (Wild, 2016) because of its invasive features of high reproductive potential, strong migratory potential along with a wide host range (Lu *et al*., 2019). It has been reported that FAW can feed on 350 plant species form 76 families with Gramineae, Compositae, and Leguminosae being its favorite hosts (Montezano *et al*., 2018). Generally, larvae are the most devastating stage that feed in almost all maize parts i.e., stems, leaves and reproductive parts; thus, causing huge economic losses (Midega *et al*., 2018; Montezano *et al*., 2018; Jiang *et al*., 2019).

Considering the huge losses of FAW, an effective management strategy for its management in its new invasive habitats could only be possible after understanding its basic biological and ecological behavior (Wang *et al*., 2020). Accordingly, life table studies are considering as a basic and powerful tool for understanding and analyzing the growth, survival and reproductive potential of pests, especially invasive species like FAW. Many methods of lifetables i.e., (Deevey, 1947; Birch, 1948; Southwood, 1978; Carey, 1993) have been developed and widely used in ecological studies.

Many studies have focused on various reproductive and growth parameters of FAW under variable experimental conditions including both field and laboratory (Ashok *et al*., 2020; Guo *et al*., 2021; He *et al*., 2021a, b). However, all such studies showed a great variation in the obtained results that may be due to experimental conditions, environmental factors, larval diet, and the strains of FAW used in the studies (Simmons and Lynch, 1990; Rogers and Marti, 1994; Wang *et al*., 2020). As FAW is rapidly expanding its invasiveness in the maize growing areas of Pakistan (Naeem-Ullah *et al*., 2019; Gilal *et al*., 2020), therefore, it become inevitable to understand its basic growth and reproductive features feeding on maize to devise appropriate management strategies to restrict its further spread and damage. Accordingly, life table studies of FAW were conducted under laboratory conditions offering maize leaves and stems as food.

Materials and Methods

The study was carried out at Stored Grain Research Laboratory, Department of Entomology, Sindh Agriculture University Tando Jam, Pakistan under controlled conditions of 30±2°C and 65±5% relative humidity. The basic culture of FAW was obtained from the surrounding maize fields of the university and reared in the lab on maize. The adults were reared on 10% honey solution in 50 cm^3 rearing cages, where they were allowed to mate and oviposit. The life table studies were carried out on maize leaves and stems separately to assess which plant part affect the growth and reproduction of the FAW significantly. Three cohorts comprised of 131, 112 and 105 eggs, having the same age were used for the individual food. After emergence, each larva was placed separately in 45-mL plastic cups to avoid cannibalism and provided with fresh maize leaves and stems on daily basis. Observations were taken daily to record survival and growth of larvae till they pupate, and adults emerged. After adult emergence, coupled adults were transferred to rearing cages to record the fecundity and a standard diet (10% honey solution) was provided to them as food. The observations and data were taken daily on fecundity and mortality till the death of last individual. The procedures described by Birch (1948) and Southwood (1978) were followed for the constructions of various life table and fecundity parameters as given below:

Life table parameters

x = The pivotal age (days) or developmental stage

l_x = The number of surviving individuals at the start of age class x.

L_x = The number of individuals alive between age class x and x+1.

T_x = Total number of individuals beyond age class x.

d_x = The number of individuals dying during age interval x.

e_x = The expectation of life remaining for individuals of age class x.

S_x = The probability of surviving into the next age group.

Fecundity schedule

m_x = The number of female eggs laid by age class x.

$l_x m_x$ = Total number of female eggs laid by age class x.

R_o = Net reproductive rate $[\Sigma\, l_x m_x]$

T_c = Approximate generation time (days) = $\Sigma x\, l_x m_x / \Sigma\, l_x m_x$

T = Corrected generation time (days)= ln R_o / r_m
rc = Innate capacity for increase = ln R_o/T_c.
rm = The intrinsic rate of increase, calculated by iteration of Euler's equation, $\Sigma e^{-rmx} l_x m_x = 1$
λ = Finite rate of increase, number of female offspring per female per day, calculated using, $\lambda = e^r$
DT = Doubling time, the number of days required by a population to double [DT = ln 2/r]

Various life and fecundity parameters of FAW on leaves and stems were constructed separately. Moreover, student t-test was used to determine whether leaves or stems as food exhibited any significant impact on various life and fecundity parameters of FAW. All analysis was done using STATISTIX 8.1 computer software.

Results and Discussion

Age-specific survival life table

Figure 1 show the survivorship pattern of the FAW when reared on either maize stems or leaves. Almost similar pattern in the survivorship of FAW was recorded in both maize stems and leaves as majority of the mortality was observed during the egg and early nymphal instars (1-3) along with pupal stage. Relatively lower mortality was recorded during the 4th to 6th larval instars of FAW when fed with either maize stems or leaves. Thus, FAW reared on either maize stems or leaves exhibited type-III survivorship curve pattern. The results obtained by Ashok *et al.* (2020) partially support the findings of this study as they also obtained maximum mortality of FAW in the first instar larva and egg stage, whereas mortality reduce in later larval instar with minimum mortality recorded in 6th larval instar. Like many other insect species, FAW also exhibited type-III type of survivorship pattern as classified and supported by previous studies of Pearl (1928), Speight *et al.* (1999) and Schowalter (2006).

Pooled life table of FAW based on all three cohorts reared on stems and leaves of maize is given in Table 1. According to the results, comparatively higher mortality percentage of FAW at various life stages was recorded when it was reared on maize leaves than stems. The maximum stage-specific mortality of FAW i.e., 25.89 and 36.95% was recorded in pupal stage when fed with stems and leaves, respectively, followed by egg stage with mortality recorded in leaves and stems as 23.27 and 20.97%, respectively. Accordingly, the highest stage-specific survivorship of FAW recorded in stem was in 4th larval instar 89.28%, followed by 88.88, 87.33 and 86.69% survivorship recorded in 3rd, 5th, and 2nd larval instars, respectively. However, the highest FAW survivorship in leaves was recorded in 5th larval instar (86.40), followed by 3rd (85.63), 2nd (84.46) and 4th (83.89) larval instar. The lowest survivorship in stem (74.10) and leaves (63.95) treatments was recorded in pupal stage. The results also indicated that the maximum life expectancy (e_x) of FAW in stem and leaves was recorded in 1st larval instars with 4.33 and 3.88, respectively that gradually reduced to 1.24 and 1.13, respectively in the pupal stage. Moreover, k-value results indicated that pupal and egg stage were more susceptible to the mortality in both stems and leaves i.e., stems (k = 0.130 and 0.102, respectively) and leaves (k = 0.194 and 0.115, respectively). The lowest k-values recorded in stem and leaves were 0.049 and 0.063 observed during 4th and 5th larval instars, respectively. Moreover, almost similar results were observed regarding the sex ratio (Male: Female) of FAW when reared on maize stems (1:1.37) and leaves (1:1.39).

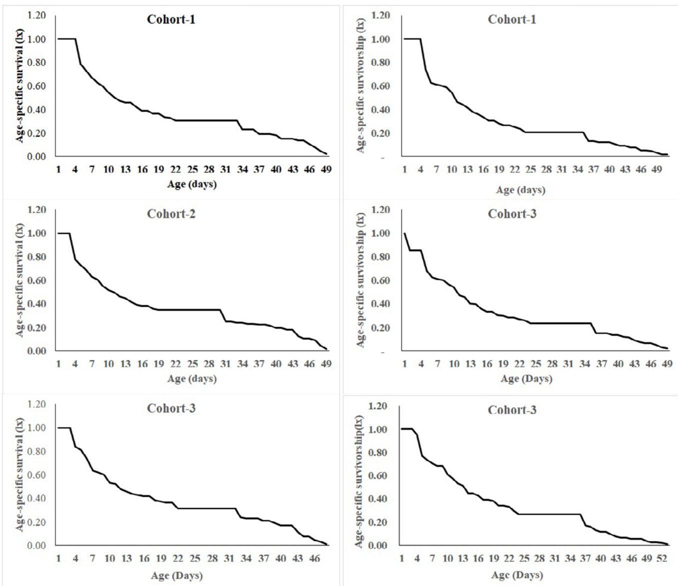

Figure 1: *Survivorship curve (l_x) of FAW feeding on maize stems (A) and leaves (B).*

Findings of life table studies of FAW conducted by Priyanka *et al.* (2021) under laboratory conditions reveals that the maximum apparent mortality of 33.82% in the 1st larval instar, whereas minimum mortality was recorded in pupae, 4th, 3rd, and 6th larval instars. However, maximum survival fraction (S_x) was recorded in 6th larval instar, followed by pupa and 4th larval instar. Thus, these results partially supported the outcomes of this study as the maximum mortality in maize stems and leaves was observed in pupa and

1st instar larva, respectively. Moreover, the maximum survivorship S_x of FAW was recorded in 4th and 5th larval instars, respectively. Ashok *et al.* (2020) also recorded maximum (20%) and minimum (1.79%) apparent mortality in 1st and 6th instar, respectively, with maximum and minimum survival fraction in 4th and 1st instars, respectively. In comparison to these findings, Priyanka *et al.* (2021) observed highest k-values of FAW in the 1st larval instar when fed with maize leaves, however, they observed lowest values in 3rd, 4th and 6th larval instars and the same support our studies. The maximum and minimum k-value of 0.10 and 0.01 was recorded in 1st and 6th instar, respectively by Ashok *et al.* (2020). The variation in findings of this study in comparison to others may be due to the type of food (maize stems/ leaves), maize variety and source of the FAW culture used in the studies. He *et al.* (2021a) also report significant effect of diet on the survival of FAW as they recorded higher survival rate of adult FAW on rapeseed, followed by sunflower and soyabean. Another study also conformed the significant impact of host on the development of various life stages of FAW (Sotelo-Cardona *et al.*, 2021). According to the study, shorter developmental period for 3rd to 7th FAW larval instars was recorded on maize ears and leaves, whereas cabbage and soyabean supported shorter developmental period of 1st and 2nd FAW instars. Moreover, female-based sex ratio of adults was recorded in this study did not agrees with the findings of Xie *et al.* (2021) who recorded 50% females in their studies.

Age-specific fertility schedule

Figure 2 elicited that first adult female emerged on day 31 when reared on maize stems, whereas it took 36 days while feeding on maize leaves. The death of last female fed with stem and leaves occurred on day 49 and 51, respectively, whereas first oviposition in stem and leaves treatments was recorded after 3 and 1 day of female emergence, respectively. Accordingly, the maximum life span of females fed on maize stems and leaves was 19 and 17, respectively. Xie *et al.* (2021) while evaluating the biological parameters of FAW recorded longer developmental duration of FAW adults (16.15 days for females and 16.25 days for males) on maize in comparison to kidney beans, and the same are not in accordance with our findings as relatively shorted adult longevity for both sexes was recorded in our study. The possible reasons for such variations may include the difference in the experimental conditions, especially the maize cultivar used as food in both the studies was not same.

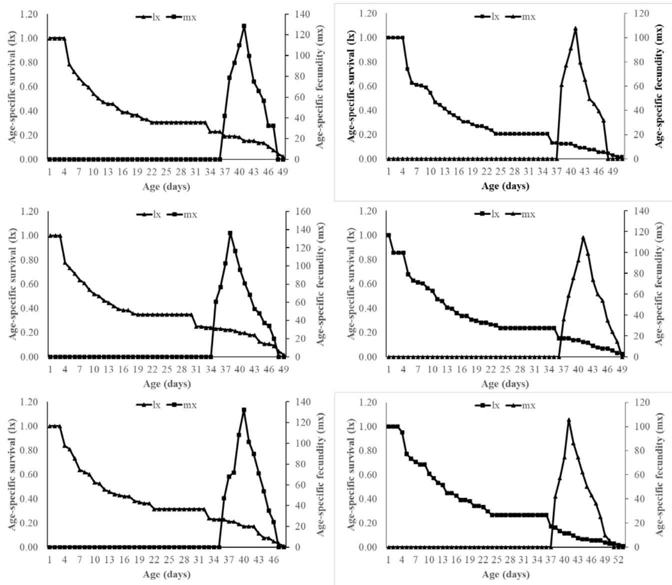

Figure 2: *Life and age-specific fecundity of FAW feeding on maize stems and leaves.*

Table 1: *Pooled life table of FAW feeding on maize stems and leaves under laboratory conditions.*

Stage	l_x		L_x		d_x		$100q_x$		S_x		T_x		e_x		K-value	
	Stem	Leaves	Stem	Leaves	Stem	Leaves	Stem	Leaves	Stem	Leaves	Stem	Leaves	Stem	Leaves	Stem	Leaves
Eggs	348	348	311.50	307.5	73	81	20.97	23.27	79.02	76.72	1500	1344	4.31	3.86	0.102	0.115
Larva																
Instar-1	275	267	246.50	236.5	57	61	20.72	22.84	79.27	77.15	1188.5	1036.5	4.331	3.88	0.101	0.113
Instar-2	218	206	203.50	190	29	32	13.30	15.53	86.69	84.46	942	800	4.32	3.88	0.062	0.073
Instar-3	189	174	178.50	161.5	21	25	11.11	14.36	88.88	85.63	738.5	610	3.90	3.50	0.051	0.067
Instar-4	168	149	159.00	137	18	24	10.71	16.10	89.28	83.89	560	448.5	3.33	3.01	0.049	0.076
Instar-5	150	125	140.50	116.5	19	17	12.66	13.6	87.33	86.4	401	311.5	2.67	2.49	0.059	0.063
Instar-6	131	108	121.50	97	19	22	14.50	20.37	85.29	79.62	260.5	195	1.98	1.80	0.068	0.099
Pupa	112	86	97.50	70.5	29	31	25.89	36.95	74.10	63.95	139	63.93	1.24	1.13	0.130	0.194
Adult	83	55	41.50	27.5												
Sex ratio	1: 1.37	1: 1.39														

Table 2: *Population and reproductive parameters of FAW feeding on maize stems and leaves (Mean ± SE) based on three cohorts.*

Parameter	Formula	Values	
		Maize stems	Maize leaves
Approximate generation time (Tc), (days)	$\Sigma\, xl_x m_x / \Sigma l_x m_x$	40.10±0.10a	41.26±0.21a
Corrected generation time (T), (days)	$\ln R_o / r_m$	40.74±0.74a	40.96±0.20a
Innate capacity for increase (rc)	$\ln R_o / T_c$	0.1237±0.0032a	0.1027±0.0025b
Intrinsic rate of natural increase (rm)	$\Sigma e^{-rmx} l_x m_x = 1$	0.1248±0.0033a	0.1034±0.0026b
Finite rate of increase (λ)	e^r	0.3363±0.0086a	0.2791±0.0069b
Doubling time (DT), (days)	ln 2/r	5.61±0.14b	6.76±0.16a
Net reproduction rate (Ro)	$\Sigma\, l_x m_x$	143.29±12.27a	69.63±6.22b

The maximum oviposition per female of 245 and 191 eggs for maize stem and maize leaves respectively were recorded on 5th day of the oviposition. Comparative studies of FAW on maize, potato and tobacco confirmed that females lay significantly higher eggs (444) on maize than potato (136) and tobacco (90) (Guo *et al*., 2021).

Table 2 describe various population and reproductive parameters of FAW when reared on maize stems and leaves. According to results, no significant difference was recorded in approximate (t= 2.37; p = 0.0770) and corrected (t= 2.53; p = 0.0649) generation time of FAW when reared on maize stems (40.10±0.10 and 40.74±0.74, respectively) and leaves (41.26±0.21 and 40.96±0.20, respectively). However, significant difference between stem and leaves was recorded on the remaining reproductive and population parameters of FAW. The innate capacity of increase (r_c) and intrinsic rate of natural increase (r_m) of FAW recorded on stems was 0.1237±0.0032 and 0.1248±0.0033, respectively that were significantly higher (t = 5.19; p = 0.0066 and t = 5.16; p = 0.0067, respectively) than those reared on leaves i.e., 0.1027±0.0025 and 0.1034±0.0026, respectively. The finite rate of increase (λ) of FAW was also higher (t = 5.19; P = 0.0066) on maize stems (0.3363±0.0086) than leaves (0.2791±0.0069). The doubling time (DT) and net reproductive rate (Ro) of FAW recorded on stems were 5.61±0.14 days and 143.29±12.27 offspring/individual, respectively that were significantly higher (t = 5.30; p = 0.0061 and t = 5.35; p = 0.0059, respectively) than maize leaves i.e., 6.76±0.16 days and 69.63±6.22 offspring/individual, respectively.

The studies by Xie *et al.* (2021) found the mean generation time of 40.92±0.59 and 42.05±0.60 days for FAW when its larvae were provided with maize leaves and kidney beans, respectively. The mean generation time of 35.47±0.51 days and 36.63±3.546 days for FAW was also recorded by He *et al.* (2021b) and Ashok *et al.* (2020) Hence, the corrected generation time (T) of FAW observed on maize stems (40.96±0.20 days) and leaves (40.74±0.74 days) was in accordance with studies of Xie *et al.* (2021) and Ashok *et al.* (2020). However, the mean generation time of 28.02±1.27 and 32.10±0.35 days on maize ears and leaves observed by Sotelo-Cardona *et al.* (2021) and 29.21±0.32 days by Wang *et al.* (2020) was relatively shorter than our studies.

The net reproductive rate (R_0) (206.03±40.74), intrinsic rate of increase (rm) (0.13±0.01) and finite rate of increase (λ) (1.14±0.01) observed by Xie *et al.* (2021) supported our results for rm (0.1248±0.0033 and 0.1034±0.0026), whereas value for λ and net reproductive rates in the study undertaken were comparatively lower. However, Sotelo-Cardona *et al.* (2021) studies recorded R_0 of 50.20±26.19 to 88.07±21.14 offspring/individual and rm of 0.1397±0.0362 to 0.1395±0.008 on maize ear and leaves that corresponds to values obtained in our studies, however, comparatively higher net reproductive values of 480.33 and 406.37±74.43 was recorded by Ashok *et al.* (2020) and Wang *et al.* (2020), respectively. Wang *et al.* (2020) also observed rm (0.2056±0.0072) and λ (1.2283±0.0088) of FAW while fed with maize.

The doubling time of 4.487±0.001 days recorded by Russianzi *et al.* (2021) for FAW on maize which was comparatively shorter than that of our study i.e., 5.61±0.14 and 6.76±0.16 days for maize stems and leaves, respectively. However, net reproduction with shorter developmental period indicated that pest has potential to grow rapidly to double its population in shorter period (Hidayat *et al*., 2019)

Conclusions and Recommendations

Spodoptera frugiperda (FAW) showed strong preference for both stems and leaves of maize, with comparatively better performance of various population and biological parameters on stems. Therefore, it is suggested that management of FAW should be started as early as possible i.e., immediately after germinations of maize stems to restrict its damage and population growth.

Novelty Statement

Life table study results obtained will provide a better understandings of growth pattern of invasive *Spodoptera frugiperda* on maize, its main host. Thus, using this information growers can take appropriate measures to restrict *S. frugiperda* populations before they cause economic losses.

Author's Contribution

Arfan Ahmed Gilal: Developed the idea, designed study and finalized manuscript.
Lubna Bashir Rajput: Helped in idea and designed of the study. Rough draft of manuscript.
Muhammad Ibrahim Kubar: Conducted the study.
Ghulam Murtaza Kaleri: Analyzed the data.
Tanzeela-ul-Zahra: Conducted the study
Muhammad Ishaque Mastoi: Helped in the data analysis and presentation
Zeeshan Rasheed: Helped to conduct study.

Conflict of interest
The authors have declared no conflict of interest.

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