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Fitness and Survival of the Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on Maize in West Java, Indonesia

(Kecergasan dan Kemandirian Ulat Ratus, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) pada Jagung di Jawa Barat, Indonesia)

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ABSTRACT

An important pest of maize is a new invasive species called *Spodoptera frugiperda*, also known as the fall armyworm (FAW), causing a considerable economic impact in Indonesia since 2019. This insect has a large host range, a quick generation time at the right temperature, a high rate of reproduction, and a high dispersal capacity. In population ecology and pest management, fitness and survival are crucial. This research was aimed to determine some biological aspects and demographic statistics of three FAW populations (lowland, midland, and highland) in a laboratory setting with 25 ± 2 °C, 75 ± 5% relative humidity, and a 12:12 (L:D) hour photoperiod. Findings indicated no variation in the length of the FAW life stage or its reproductive capacity. Nonetheless, notable variations were noted in the average fecundity of females, with FAW of the highland population laying the most eggs (1242.1 eggs). FAW had the shortest mean generation time (T), the highest intrinsic rate of increase (r_m), the finite rate of increase (λ), and the highest net reproductive rate (R_0) of the highland population. Overall FAW collected from highland, midland, and lowland can adapt well when brought to a laboratory with a constant temperature at 25 ± 2 °C without detriment to the parameters of the life table. The knowledge gained from this study is crucial for managing FAW because it improves comprehension of its life cycle and adaptability to various altitudes, enabling us to take appropriate action to stop its spread.

Keywords: Adaptability; highland; lowland; midland; *Spodoptera frugiperda*

ABSTRAK

Salah satu serangga perosak utama pada jagung adalah spesies invasif baru dikenali sebagai *Spodoptera frugiperda* atau dikenali dengan nama ulat ratus, yang memberikan impak ekonomi yang cukup besar di Indonesia sejak tahun 2019. Serangga ini mempunyai julat perumah yang besar, masa penjanaan yang cepat pada suhu yang betul, kadar pembiakan yang tinggi dan kapasiti penyebaran yang tinggi. Dalam ekologi populasi dan pengurusan perosak, kecergasan dan kemandirian adalah penting. Penyelidikan ini bertujuan untuk menentukan beberapa aspek biologi dan statistik demografi tiga populasi FAW (tanah rendah, tanah tengah dan tanah tinggi) dalam persekitaran makmal dengan 25 ± 2 °C, 75 ± 5% kelembapan relatif dan 12:12 (L: D) tempoh fotokala. Penemuan menunjukkan tiada variasi dalam panjang peringkat hayat FAW atau kapasiti pembiakannya. Walau bagaimanapun, variasi ketara telah dicatatkan dalam kesuburan purata betina, dengan FAW daripada populasi tanah tinggi bertelur paling banyak (1242.1 telur). FAW mempunyai masa penjanaan min (T) terpendek, kadar kenaikan intrinsik tertinggi (rm), kadar peningkatan terhingga (λ) dan kadar pembiakan bersih tertinggi (R_0) penduduk tanah tinggi. FAW keseluruhan yang dikumpul dari tanah tinggi, tanah tengah dan tanah pamah boleh menyesuaikan diri dengan baik apabila dibawa ke makmal dengan suhu malar pada 25 ± 2 °C tanpa menjejaskan parameter jadual hayat. Pengetahuan yang diperoleh daripada kajian ini adalah penting untuk mengurus FAW kerana ia meningkatkan pemahaman kitaran hayatnya dan kebolehsuaian kepada pelbagai ketinggian, membolehkan kami mengambil tindakan yang sewajarnya untuk menghentikan penyebarannya.

Kata kunci: Kebolehsuaian; *Spodoptera frugiperda*; tanah rendah; tanah tengah; tanah tinggi

INTRODUCTION

One of the most significant economic pests at the moment is the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), which feeds on 353 different plant species (Montezano, Specht & Sosa-Gomez 2018). There are 76 plant families known to serve as hosts, but maize is the most prevalent (Da Silva et al. 2017). Losses in agricultural production due to the FAW affect the economies of both farmers and nations. Yield losses in maize range from 21 to 53% in Africa, 72% in Argentina, and up to 40% in Honduras (Rwomushana et al. 2017), 33% in South Africa (Van Den Berg, Brewer & Reisig 2021) and between 26.5 and 56.8% in India (Balla et al. 2019). In Indonesia, Nonci et al. (2019) reviewed that yield loss caused by FAW was estimated as high as 73% of the maize production.

Globally, there is now a serious matter over the invasion of FAW. The insect originated in the tropical and subtropical Americas (Montezano, Specht & Sosa-Gomez 2018), later spreading to other parts of the world, such as Africa (Georgen et al. 2016); India (Sharanabasappa et al. 2018a), Indonesia (Nonci et al. 2019), China (Jiang et al. 2019); Korea (Lee et al. 2020); Bangladesh, Thailand, Myanmar, Sri Lanka (Wang et al. 2020), Nigeria (Bista, Thapa & Khana 2020), Taiwan (Tsai et al. 2020), Vietnam (Hang et al. 2020), Malaysia (Jamil et al. 2021), Syria (Heinoun et al. 2021), and Japan (Wu et al. 2022). Across six continents; Asia, Africa, Australia, and North and South America, fall armyworms have emerged as one of the most significant pests (Rwomushana 2019).

Within a short period, the FAW had a great potential to cover a wider geographical location and cause damage to crop production (Early et al. 2018; Rwomushana et al. 2017; Yang et al. 2021). The primary causes of FAW's quick spread are its high dispersion capacity, high fecundity, and adaptability, comparatively short generation time (roughly 30 days) at optimal temperature, high biotic potential, significant crop-damaging potential, ecological flexibility, and lack of diapause (Chen et al. 2022). The primary factor is most likely the adult FAWs' capacity for long-distance moves. The adult's migratory and dispersal habits allow them to cover roughly 500 km before oviposition (Prasanna et al. 2018) and keep them at several hundred meters above the ground, where upper winds can carry them in a specific direction. Previous research reported that as a typical migratory pest, FAW uses its migration behavior as an adaptive mechanism to locate more hospitable environments to cause widespread outbreaks (Li et al. 2019).

Phenotypic plasticity traits, crucial for pest fitness and survival, have been identified as one of the factors contributing to the attainment of FAW invasion and establishment in new environments. Temperature is the main environmental factor affecting an insect's survival, spread, development, and reproduction ability. Temperature and elevation are strongly correlated. According to a study on how temperature affects plant development, plants growing in warm climates sustain less damage than those growing in cold climates (Hatfield & John 2015). This is because warm temperatures speed up crop development and protect it from FAW, which can seriously harm immature maize plants (Goergen et al. 2016). Based on previous reports, this species can survive under various climate conditions. The insect's rapid spread is influenced by climatic variability. For instance, relative humidity (RH) of 80% is optimal for its development, survival, and reproduction, while soil moisture between 6.8% and 47.6% is suitable for pupation and eclosion (Van Den Berg, Brewer & Reisig 2022).

With Indonesia's tropical climate allowing for the year-round growth of a variety of host crops, it is predicted that FAW will become a significant migratory insect pest with the potential to have a major impact on staple foods and future food security (Sun et al. 2021). Consequently, there is an urgent need to develop pest control techniques. Ecologists, environmentalists, and the Food and Agriculture Organization of the United Nations (FAO) recommended strategies for managing FAW outbreaks by implementing sustainable Integrated Pest Management (IPM) methods. Because of the varied climate in Indonesia, the pest has evolved to suit various climates and has spread rapidly throughout most of the country. Therefore, to develop an eco-friendly management strategy for the pest, information about its potential distribution and environmental constraints is urgently needed. This study's primary goal was to examine, in laboratory conditions, the effects of three distinct altitudes on the biological traits, life table parameters, and reproductive characteristics of FAW. The outcomes should provide a baseline for updating the FAW pest status, potential suitable areas for FAW under current and future climatic conditions, and creating IPM plans for the entire area in Indonesia, especially in areas where maize is planted simultaneously.

MATERIALS AND METHODS

INSECT REARING

The initial FAW population was gathered from maize under various bioclimatic conditions (Table 1). Before the commencement of the life table examination, the population was kept in the Department of Entomology laboratory at the Faculty of Agriculture, Universitas Padjadjaran, Indonesia. Insects were kept at 25.0 ± 2.0 °C, 75.0 ± 5.0% RH, and a photoperiod of 12 h: 12 h (L:D). The research was conducted in October-December 2021.

BIOLOGY OF FALL ARMYWORM

The observations were made from the time of the egg phase until the adult's death. A daily check was made for the hatching of eggs that spawned simultaneously, and the hatch rates of the eggs were calculated until hatching. The larvae's development and survival were documented every day until they perished, pupated, or emerged as pupae. To prevent biting each other, the 3rd stage larvae were put in separate containers and allowed to produce pupae. After pupae emerged, adults (♀:♂=1:1) were housed in 500 mL plastic cups and given 10% (v/v) honey water as a daily meal (Maharani et al. 2021). The eggs in the plastic cup were counted daily and removed using a fine brush. Egg-hatching rate, adult survival, oviposition, post-oviposition, and pre-oviposition time were recorded for every FAW individual (Aprianti, Hidayat & Dono 2021). A total of 100 individuals per location were observed using a stereo microscope Olympus SZ61.

Three brood stock eggs totaling one hundred identical eggs were raised on baby corn. Each egg was put into a plastic container that measured 5 cm in diameter by 8 cm in height, and tissue paper was used to line the container to guarantee a constant dry surface. Up until the adult stage, the number of live larvae and molting was totaled every day. The sex ratio is observed based on offspring who grow up to be successful adults. The percentage of the population was computed utilizing the formula that follows:

Sex ratio = Number of female adults/Number of male adults

Only the female population was used to calculate the net reproductive rate (R_0), and it was believed that there were enough males in the area. The information needed for the computation consisted of the age of FAW (x), age-specific survival rate (l_x), and age-specific fecundity (m_x). The average number of FAW eggs laid by the adult each day at age (x) is known as age-specific fecundity. During the cohort generation, the percentage of eggs laid by all individuals (females) was ($\sum l_x m_x$).

LIFE TABLE AND POPULATION PARAMETER OF FALL ARMYWORM

The intrinsic rate of increase (r_m), finite rate of increase (λ), gross reproductive rate (GRR), net reproductive rate (R0), mean generation time (t), and double time (T) were the population parameters and Chi was estimated. The two-sex life table theory was used to analyze the life table data (Chi et al. 2020): The gross reproductive rate (GRR) = $\sum m_x$; The net reproductive rate (R_0) = $\sum l_x m$; The intrinsic rate of increase (r_m) = $\sum l_x m_x e^{-rmx} = 1$ With initial r= $\sum$ (ln)/T; The mean generation time (t) = $\sum x l_x m_x / \sum l_x m_x$; The double time (DT) = ln (2) /r; The finite rate of increase (λ)=er.

In this case, x represents the time interval in days (d); m denotes the number of stages; S_{xj} represents the survival rate of FAW from egg development to x days old and developmental stage j; l_x stands for population age-specific survival rate; and f_x10 denotes age-specific fecundity at age x. Additionally, m_x stands for population age-specific fecundity, which is the average population fecundity from egg to x days old, and lxmx, or population age-specific maternity, is the product of l_x and m_x. The Jackknife method (Abdi & Williams 2010; Frield & Stampfer 2002), was used to determine the demographic statistics' median value and diversity.

STATISTICAL ANALYSIS

For each of the three treatments, a one-way analysis of variance (ANOVA) was employed to investigate the variations in life history parameters. A post hoc test called Tukey's honestly significant difference (HSD) was employed. The difference and linear trend of the FAW survival curves from various locations were tested using log rank. To fit the survival rate of the FAW population at a given age, a logistic model was employed. TWOSEX-MS Chart, a computer program, was utilized for the life table analysis to ease the raw data analysis.

RESULTS AND DISCUSSION

LIFE HISTORY CHARACTERISTICS

A common research tool in insect population ecology and pest management is the life table. The four stages of the FAW life cycle are comprised of complete metamorphosis, or holometabolous development i.e., egg, larva (six instars caterpillar stage), pupae, and adult. Table 2 displays the length of each life stage. The results showed that larvae of FAW reared on baby corn in laboratory conditions could complete their development to the adult stage. The three sample locations' developmental times did not differ significantly (Table 1). It was observed that the FAW lay eggs in groups and the duration was around 2.9 to 3.0 days. More than 90% of eggs were hatched (Table 2). The incubation period of FAW was observed with an average of 2.63 ± 0.03 days on maize crop (Balla et al. 2019). Similar incubation periods were noted in maize crops ranging from 2.0 to 3.0 with an average of 2.50 ± 0.50 days in ideal circumstances (Sharanabasappa et al. 2018b).

TABLE 1. Description of location of FAW population collection

Place of origin	Altitude (m above sea level)	Average of temperature (°C)	Average of RH (%)	Coordinates
Majalengka	103	28.7	70	19°24′50.9″ South 108°12-108°25’ East
Sumedang	858	25.5	74	06^0 34' 46,18” South 107^0 01' 45,63” Sast
Lembang	1250	20.4	90	6°45’30” South 107°35’00” East

Larvae of FAW completing 6 instars were most common throughout this study. First instar (development period: 2.9-3 days); second instar (2-2.14 days); third instar (2.03-2.30 days); fourth instar (2.07-2.27 days); fifth instar (2.00-2.19 days); and sixth instar (3.00-3.30 days). The larval period ranged from 14.18 to 15.02 days, and 94.89% to 100% of the larvae survived. A similar larval period of about 14-19 days has been reported when insects were reared in baby corn and 14-30 days which may fluctuate by weather conditions, the pupal period ranged from 7.99 to 8.09 days. In Florida, the pupal stage lasts between 8.0 and 9.0 days in the summer and 20 to 30 days in the winter (Sharanabasappa et al. 2018b).

The mean duration of the lifecycle of FAW under different conditions was 24.07-24.55 days. This study found that the life cycle duration of FAW was shorter than that of Chen et al. (2022) and Sharanabasappa et al. (2018b). Various authors have reported varying life spans for distinct FAW stages based on different climatic conditions. Du Plessis, Schlemmer and Van den Berg (2020) reported that the population of FAW from different elevations, such as lowland, midland, and highland performed the same biological parameters. Additionally, it was noted that the temperature affects how long FAW larvae develop, with the maximum survival of these stages around 25 °C and 35 °C appearing to be the upper limit at which the pest can survive its life cycle (Hardke et al. 2015). Fall armyworms will become an endemic and multigenerational pest due to the right host plants and agroecological circumstances (Goergen et al. 2016; Prasanna et al. 2018).

The results of this study (Table 2 & 3) showed that there was no difference among the FAW populations of low land (Majalengka), medium land (Sumedang), and high land (Lembang) both in life stages and survival rate of each life stages when adjusted to a new condition, the laboratory conditions with constant temperature at 25 ± 2 °C. This result supports the finding of Wang et al. (2020) who stated that FAW is an insect that can rapidly adapt to temperature conditions. The implication of this finding to FAW management is that wherever the population originated, when migrating to the new ecosystem, FAW will establish well and control measures must be performed.

OVIPOSITION AND FECUNDITY

Table 4 displays the pre-ovipositional period, the fecundity of females, and the lifespan of adults. The FAW population collected from three different elevations showed different longevity and fecundity. Adult lifespan differences were substantial between populations (F 4.51; df 2,11; P <0.001). The adult longevity of both male and female insects of the highland population was noticeably higher compared to that of lowland and medium land. Female longevity was 11.83 ± 0.89 days in the lowland, 12.96± 0.54 days in medium land, and 13.18 ± 0.65 days in highland. Whereas for males it ranges from 11.03 days (lowland), 13.02 days (medium land), and 15.84 days (highland). The fact that males were more vulnerable to rising temperatures than females (Huang et al. 2021; Yan et al. 2022) was further supported by our observations. The longer development times at high altitudes are due to the lower temperatures (Huang et al. 2021).

The life cycle of males is 7.03 ± 0.25 days and 7.50 ± 0.36 days for females (Wu et al. 2022). The female adult survived for 10.80 days, with a range of 9.0-12.0 days, while the males survived for 7.0 - 9.0 days (Sharanabasappa et al. 2018b). The average estimated lifespan for adults is 10.0 days, with a range of 7.0-21.0 days (Prasanna et al. 2018). In this experiment, it was indicated that males lived longer than females in the maize population, especially in medium land and high land (Table 4). The population can be impacted by the imago's life cycle. FAW imago's long lifespan contributes to its quick population expansion.

Adult sex ratios were not significantly different. The ratio of male: female was 1.0: 0.66 for lowland (X2= 0.91; df=1.86; P=0.35), 1.0: 0.67 for medium land (X2= 0.68; df=1.40; P=0.47), and 1.0:0.65 for highland (X2= 0.75; df=1.68; P=0.19). A low male-to-female ratio raises the fitness of the progeny. Females had the shortest Adult Pre-Oviposition Period (APOP) i.e., days before a female begins to lay eggs, and counted from adult emergence collection sites in lowland and medium land (2.20-2.42 days). On the other hand, 5.19 days after emerging, highland females began to lay their eggs. On maize crops, the pre-oviposition phase of FAW is 3.0 to 4.0 days (Prasanna et al. 2018). In line with this, the mean Total Pre-Oviposition Period (TPOP) i.e., in comparison to females from highland, some days that comprise the pre-adult stage + APOP were substantially shorter 10-12 days than in lowland and medium land.

The oviposition period varied significantly among populations, with the highland population having the longest oviposition period (i.e., the total number of days during which the females gave birth to their progeny), compared to lowland and medium land the oviposition period averaged 5.80-5.84 days. Likewise, the total fecundity was higher (F=8.02, df= 52; P<0.001) in insects from highland 1242.1 eggs, which was significantly higher than those from medium land (1016.5 eggs) and lowland (943.3 eggs). There was no discernible variation in the number of egg masses laid by each female across populations. Published reports of *S. frugiperda* fecundity indicate a wide range of values, e.g., 835-1169 eggs (Sharanabasappa et al. 2018b), 514-943 eggs (Wu et al. 2022), and 1000 eggs (Tsai et al. 2020).

This variation and differences in adult survival may be influenced by temperature, larval host availability, geographic location, and genetic strain (Balla et al. 2019). Young females mated on day 1 have greater reproductive potential than females mated on day 3. Females older than 10 days have lower reproductive potential (average

607 eggs/female). The fecundity of adults increased when exposed to increased photoperiod. These outcomes support the notion that FAW fecundity declines as temperature rises. Elevated temperatures have been shown to inhibit sperm transfer and mating behavior, which likely contributed to a decrease in egg laying (Li et al. 2020).

Research on the biology of FAW has been carried out in several nations. In addition, several studies focused on the species distribution modeling of FAW concerning climate change and the results have shown that altitude and temperature affect this pest's fecundity and rate of development (Garcia et al. 2018; Listyawati et al. 2022). A temperature rise shortens the pest's developmental period. Additionally, fecundity declines as temperature rises (Early et al. 2018). As altitude escalates, insects may exhibit decreasing fecundity. At different temperatures, the fecundity rate of FAW varied. The highest observed fecundity was at 22.0 °C, decreasing at high temperatures. This could be connected to a reduction in body mass, a decrease in food quality, or a reduction in oviposition time. Elevated temperatures have the potential to induce either transient or permanent infertility or to cause ovarian stagnation, which would diminish fertility (Li et al. 2020).

TABLE 2. Duration of different life stages of FAW on maize*

Stage	Origin of insect					
	Majalengka (Low land)		Sumedang (Medium land)		Lembang (High land)	
Egg	2.69 ± 0.05	a	3.00 ± 0.00	a	3.00 ± 0.00	a
Larva						
1st instar	2.90 ± 0.03	a	3.00 ± 0.00	a	3.00 ± 0.00	a
2nd instar	2.06 ± 0.02	a	2.00 ± 0.35	a	2.14 ± 0.02	a
3rd instar	2.08 ± 0.03	a	2.03 ± 0.36	a	2.30 ± 0.03	a
4th instar	2.13 ± 0.03	a	2.07 ± 0.48	a	2.27 ± 0.03	a
5th instar	2.16 ± 0.04	a	2.00 ± 0.45	a	2.90 ± 0.02	a
6th instar	3.18 ± 0.05	a	3.00 ± 1.23	a	3.30 ± 0.09	a
Pupa	7.99 ± 0.16	a	8.09 ± 0.12	a	8.05 ± 0.07	a
Total cycle	24.07 ± 0.28	a	24.36 ± 0.23	a	24.55 ± 0.11	a

*A value in columns 2, 3, and 4 was a mean ± its standard error (n=100);
There were no significant differences between the means in each row of a stage

TABLE 3. Survival rate at each stage of fall armyworm (FAW) before its emergence on maize*

Stage	Origin of insect					
	Majalengka (Low land)		Sumedang (Medium land)		Lembang (High land)	
Egg	96,89 ± 0,62	a	97,34 ± 0,48	a	95,44 ± 0,42	a
Larva:						
1st instar	100,00 ± 0,00	a	96,00 ± 1,87	a	98,00 ± 1,22	a
2nd instar	98,00 ± 2,00	a	99,00 ± 1,00	a	99,00 ± 1,00	a
3rd instar	98,00 ± 1,22	a	100,00 ± 0,00	a	100,00 ± 0,00	a
4th instar	100,00 ± 0,00	a	100,00 ± 0,00	a	97,89 ± 2,11	a
5th instar	100,00 ± 0,00	a	100,00 ± 0,00	a	100,00 ± 0,00	a
6th instar	94,89 ± 3,21	a	96,84 ± 2,11	a	95,89 ± 2,52	a
Pupa	93,43 ± 2,45	a	88,08 ± 3,03	a	87,63 ± 2,29	a

*A value in columns 2, 3, and 4 was a mean ± its standard error;
There were no statistical differences between the means in a row of each stage

Female FAW's egg production capacity is more than 1000 eggs annually, so FAW can spread to new areas and seriously harm crops (Tsai et al. 2020). A solitary adult female can deposit over 1000 eggs, but these migratory pests cause little damage when the invasion first starts because of their small population. Furthermore, Karuppannasamy et al. (2023) reported that the highest reproductive value occurs at 34 °C (600 individuals per day) but it decreases at higher temperatures (35 °C: 206 individuals per day, 36 °C: 120 individuals per day).

Fall armyworm eggs develop in about 2 to 3 days, and the larval stage lasts between 14.18 and 15.02 days. As a result, FAW damage to crops can increase rapidly within 1 to 2 weeks after the adult molting. In 2020, FAW was only found in areas with altitudes below 500 meters above sea level (masl). Currently, the distribution of FAW in Indonesia has increased and found with altitude >1000 masl (Listyawati et al. 2022). Mutyambai et al. (2020), reported that the incidence of FAW attacks is significantly higher in lowland areas compared to mi or highland regions. Global warming changes the distribution patterns of pests which aids in the establishment of new habitats or ecological niches (Gong et al. 2020). Environmental variables can be used to predict current and future potential suitable areas for the FAW.

SURVIVAL RATES

Three different sample locations' age-specific survival rates (lx) for the FAW origin showed a similar pattern, beginning early in adulthood, peaking, and then diminishing with age. From Figure 1, It was evident that the female perished at 9 days, whereas the maximum age was 38 days. This discrepancy could be attributed to mated and unmated individuals, with unmated males and females generally living longer than pairs of individuals. The values of the population parameters can vary under different field and laboratory conditions. Elevation and environmental factors play a crucial role in shaping *S. frugiperda*'s life history traits. Altitude and temperature are closely related. As altitude increases, the temperature tends to decrease. Temperature decreases with altitude can compromise insect thermoregulation, such as affecting insect activity, growth, reproduction, and overall fitness (Lahondère 2023). Temperature is emerging as the most important abiotic factor because it can influence insect formation and population growth. Many parameters of insect life, such as development, mortality, and reproduction depend on temperature (Ma et al. 2017). Temperature changes affect various aspects of insects, such as body size, stamina, feeding ability, metabolism, and insect mating (Cui et al. 2017). *S. frugiperda* showed very characteristic patterns of longevity and preoviposition period as temperature increased. Higher temperatures accelerate development, impact longevity, and influence fecundity. Thus, the fitness of *S. frugiperda* appears to be high in the low- to mid-temperature range rather than at high temperatures (Heo, Kim & Kim 2012).

Given that the old individuals were disproportionately affected by the mortality of FAW females, the female survivorship curve displayed a Type I which describes lower insect mortality in early stages and higher mortality in later stages. In terms of multiplication, the Type I curve may be helpful because of the high endurance rate of female FAW, which will increase the population's rate. A comparable survivorship curve was also noted with this pest, showing that FAW frequently demonstrates Type I survivorship (Maharani et al. 2021). Higher organisms, particularly vertebrates, frequently exhibit type I curves. The survival table of insects is affected by various factors, namely species, host, climatic conditions in the study area, and insect reproduction methods.

The m_x curve demonstrates that in *S. frugiperda* origin from low land, medium land, and high land reproduction commenced at ages 30, 28, and 29 days, respectively. The maximal daily oviposition rate of FAW origin from high land was at age 32 days with an average fecundity of 84.77 eggs, higher than *S. frugiperda* origin from low land (34 days, 53.13 eggs) and medium land (32 days, 53.13 eggs). As adult females aged and died, there was a corresponding decrease in egg production (m_x).

It has been demonstrated that the Jackknife method is insufficient for life table analysis to estimate the population parameters' means and variances. The intrinsic rate of increase (r_m), among other population parameters, is a crucial demographic factor for determining insect environmental resistance levels. Statistical analyses showed that the intrinsic rate of natural increase (r_m) for FAW from low land was 0.10 per day, with no significant difference from FAW from medium land (0.12 per day) and high land (0.17 per day) (Table 4). The present findings agreed with the results which reported that the intrinsic rate of natural increase (r_m) of the population ranges from 0.153 to 0.195 females/day (Ashok et al. 2020). In comparison to other locations, high land was the most suitable for FAW population growth, as evidenced by the higher rm values of FAW. These factors could also be attributed to the significantly higher net reproductive rate, survival rate, and shorter developmental time from this location. Major factors affecting the population's rate of increase (r_m) in any place are the size of the initial moth population, the rate of reproduction, survival, and the strong migratory capability of FAW moths (Niassy et al. 2021).

Based on Table 5, the study determined that the FAW from high land had a finite rate of increase (λ) of 1.36 per day and a net reproductive rate (R_0) of 52.4 offspring per female, respectively. These values were significantly higher than those of FAW from low land ($\lambda =$ 1.30 per day, R_0 = 25.22 offspring per female) and medium land (λ = 1.32 per day, R_0 = 36.3 offspring per female) (all

P values <0.01). The life table theory states that a population can only grow when $R_0 > 1$ and $r > 0$. According to the results of the current study, the FAW population grew in three of the sample locations, with $R_0 > 1$ and $r > 0$. High land's fall armyworm population will increase more quickly than other sites because they were raised at a higher room temperature in the laboratory. This could have led to an abnormality in survival and reproduction as well as a shortened developmental period. FAW are typically poikilothermic animals, and environmental change has a significant impact on them. Environmental change affects insect distribution patterns, growth, and development, phenological synchronization with host plants, egg-laying rates, and genetic composition (Karuppannasamy et al. 2023; Menzel & Feldmeyer 2021). The highland population's adaptation to lowland conditions may involve specific genetic or physiological traits that enhance its reproductive. However, further research is needed to fully understand these mechanisms.

FAW from highlands exhibited shorter highest values of mean generation time (T) and doubling time (D_t) in comparison to medium land and low land. The highest gross reproductive rate (GRR) was observed from low land and showed significant differences with medium land and high land. Temperature, duration of exposure, and precipitation during the warm/wet season are among the climate factors that seem to be most frequently cited as responsible for FAW (Early et al. 2018). Numerous experimental findings indicate that changes in the climate also affect development, dispersion, mortality, and reproduction (Dar & Jamal 2021). It is commonly known that, even when the materials under examination were gathered from the same area, many insects find that lower rearing temperatures result in longer developmental times and greater longevity.

TABLE 4. Adult longevity and reproduction on fall armyworm (FAW)*

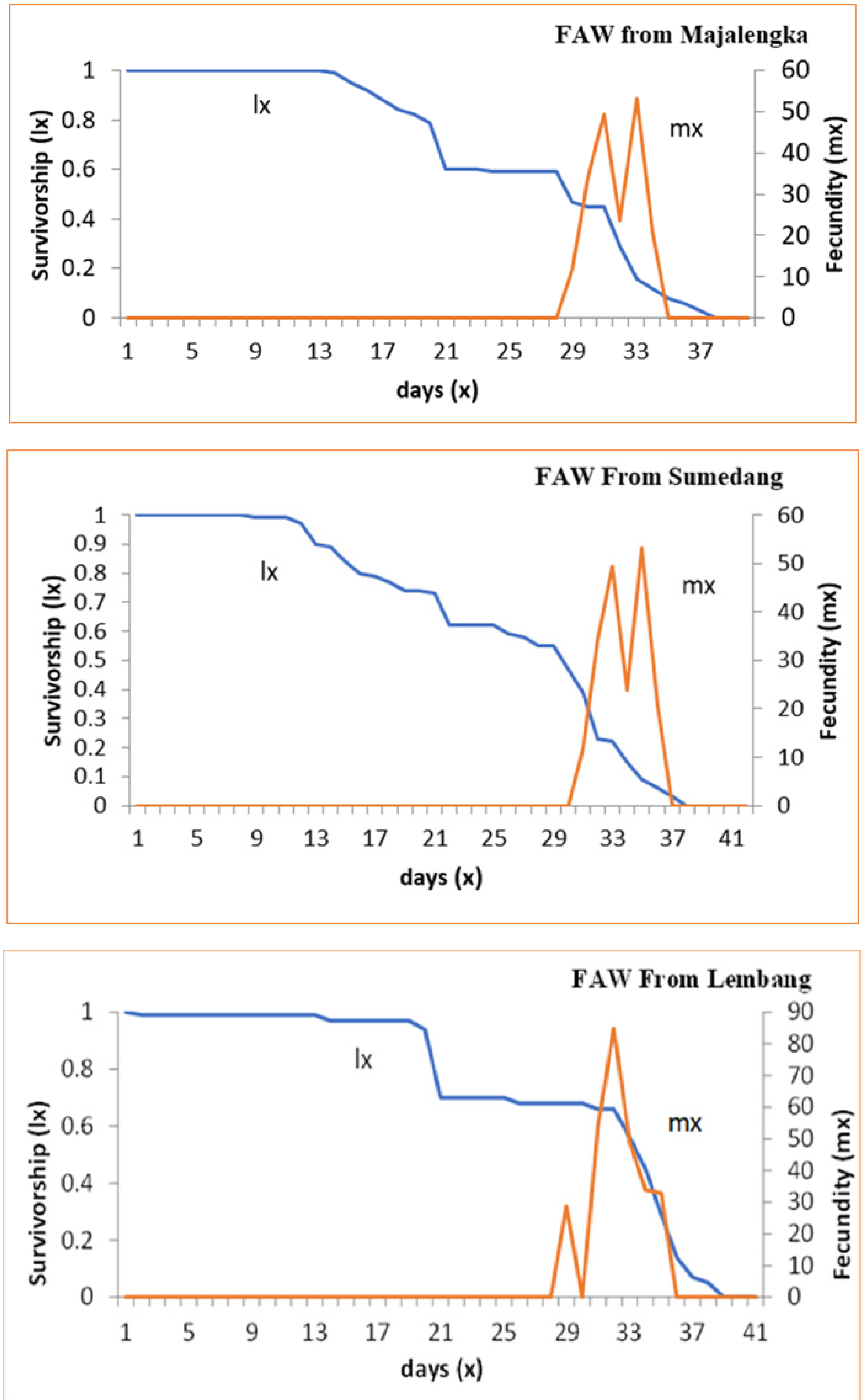
Parameters	Origin of Insect					
	Majalengka (Low land)		Sumedang (Medium land)		Lembang (High land)	
Male longevity (d)	11.03 ± 0.89	b	13.02 ± 0.54	b	15.84 ± 0.65	b
Female longevity (d)	11.83 ± 0.89	a	12.96 ± 0.54	a	13.18 ± 0.65	a
Pre-oviposition period (d)	2.42 ± 0.15	b	2.20 ± 0.08	b	5.19 ± 0.11	a
Total pre-oviposition period (d)	30.86 ± 0.36	b	32.64 ± 0.41	b	40.86 ± 0.81	a
Oviposition period (d)	5.82 ± 0,15	a	5.80 ± 0,09	a	5.84 ± 0,08	a
Fecundity (eggs/female)	943.3 ± 76.7	b	1016.5 ± 112.6	a	1242.1 ± 204.3	a
Sex ratio (male: female)	1.0: 0.66	a	1.0: 0.67	a	1.0: 0.65	a

*The means in each row of a parameter followed by different letters are significantly difference ($P < 0.05$) according to the honestly significant difference (HSD) test

TABLE 5. Population growth parameters of FAW for three different climatic locations*

Parameters	Origin of Insect					
	Majalengka (Low land)		Sumedang (Medium land)		Lembang (High land)	
Gross reproduction rate (GRR)	144.06 ± 2.2	a	115.83 ± 39.1	b	90.85 ± 18.1	c
The net reproductive rate (R_0)	25.22 ± 6.8	b	36.63 ± 13.8	b	52.4 ±17.8	a
The intrinsic rate of increase (r_m)	0.10 ± 0.0043	a	0.12 ± 0.0035	a	0.17 ± 0.0035	a
Finite rate of population increase (λ)	1.30 ± 0.001	a	1.32 ± 0.003	a	1.36 ± 0.004	a
The mean generation time (T)	33.54 ± 0.3	a	31.8 ± 0.3	a	30.45 ± 0.4	a
Doubling time (Dt)	7.00 ± 0.11	a	5.98 ± 0.14	a	5.59 ± 0.18	a

*The means in each row of a parameter followed by different letters are significantly difference ($P < 0.05$) according to the honestly significant difference (HSD) test



Blue= survivorship (l_x); light brown = fecundity (m_x); FAW= fall armyworm

FIGURE 1. Daily age-specific survival (l_x) and fecundity (m_x) of female FAW on maize

The intrinsic rate of increase (Rm) is influenced by a variety of factors, including fecundity, survival rate, and generation time in particular. This parameter effectively captures an insect's physiological characteristics regarding its ability to increase, making it a highly suitable indicator for assessing its performance on an alternative host. Demographic processes occur through death, birth, and immigration, affecting populations' size and composition. Based on the obtained results, high land and medium land are favorable habitats for the development of FAW. This information is also beneficial in selecting elevation for planting FAW host plants, especially maize. By understanding how FAW development is slowed by cooler temperatures at higher elevations, control strategies can be developed such as adjusted planting calendars or targeted insecticide uses based on pest pressure in each zone. This could even lead to research on heat-tolerant maize varieties for areas where FAW is still a threat at higher elevations.

CONCLUSIONS

This finding showed that highland and medium land provide the ideal conditions for the growth, survival, and rate of reproduction of the fall armyworm (FAW), *Spodoptera frugiperda*, a pest that is important for seasonal abundance and population growth. The findings demonstrated that FAW has been able to adapt to colder, higher-elevation zones without negatively affecting the parameters of the life table. These outcomes are essential for creating pest management plans, particularly in light of climate change. The knowledge gained from this research is crucial for managing FAW because it improves comprehension of its life cycle and adaptability to various altitudes, enabling people to take appropriate action to stop the pest spread. Furthermore, the results could be used to develop management strategies adapted to different elevation zones. Some potential applications based on development time, temperature, and elevation are planting calendars for each zone, insecticide use based on pest pressure, and the development of heat-tolerant maize varieties.

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