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# Sublethal Effects of Emamectin Benzoate on Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

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**Abstract:** Fall armyworm (FAW), *Spodoptera frugiperda* (Lepidoptera: Noctuidae), is a highly invasive polyphagous pest that causes great economic losses to agricultural production. Emamectin benzoate (EMB) is one of the most popular biopesticides with high antipest, anti-parasitic and anti-nematode activities and low toxicity. The present study was conducted to determine the lethality of EMB to FAW for 24 h. Sublethal effects of EMB on FAW parental and offspring generations were also assessed. $LC_{10}$, $LC_{20}$ and $LC_{50}$ EMB for 24 h on FAW third instar larvae were 0.0127 mg/L, 0.0589 mg/L, and 0.1062 mg/L, respectively. A low dose of sublethal concentrations of EMB could significantly influence the life cycle of FAW parental and offspring generations. Sublethal concentration ($LC_{20}$) of EMB significantly prolonged the pupal period of male and increased the pupal weight of male but not of female, and significantly delayed the oviposition period and longevity of adult FAW. In the FAW offspring generation, sublethal concentrations significantly increased the mortality of offspring pupae and pre-adults, and reduced the development time of offspring larvae and pre-adult male and female. Sublethal concentrations ($LC_{10}$ and $LC_{20}$) of EMB significantly decreased the FAW oviposition period. However, only $LC_{10}$ significantly reduced FAW $F_1$ female fecundity. No significant difference was found in the intrinsic rates of natural increase ($r_m$), finite rate of population increase ($\lambda$), and net reproductive rate ($R_0$) of FAW offspring exposed to sublethal concentrations. This is the first study to determine the sublethal concentrations of EMB on the life table parameters of two FAW generations. These findings can provide important implications for the rational utilization of FAW insecticides.

**Keywords:** lethality determination; life table; generation; longevity; fecundity



**Citation:** Liu, Z.-K.; Li, X.-L.; Tan, X.-F.; Yang, M.-F.; Idrees, A.; Liu, J.-F.; Song, S.-J.; Shen, J. Sublethal Effects of Emamectin Benzoate on Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Agriculture* **2022**, *12*, 959. https://doi.org/10.3390/agriculture12070959

Academic Editor: Renata Bažok

Received: 4 June 2022
Accepted: 30 June 2022
Published: 3 July 2022



## 1. Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a polyphagous pest native to tropical and subtropical Americas. FAW has a wide host range of more than 353 plants and poses a severe threat to agricultural production [1]. In recent years, FAW has invaded Africa, Asia, and Oceania, and was detected in Yunnan, China, for the first time in December 2018 [1,2]. The invasiveness of FAW might be associated with its superior biological characteristics, such as shorter generation time, high fecundity, polyphagy, long-distance migration ability, and high resistance to a range of pesticides [1].

FAW has severely damaged many crops, especially corn [3]. For example, FAW caused economic losses to a third of the annual corn production in Kenya in 2018 season [4]. Chemical pesticides have become one of the most effective tools to control FAW on an emergency basis due to their acute efficiency and economic convenience [5]. In 2020, for the effective control against FAW, the Ministry of Agriculture and Rural Affairs (MARA) of China recommended the pesticides emamectin benzoate (EMB), indoxacarb, tetrachlorantraniliprole, chlorantraniliprole, lufenuron, chlorfenapyr, spinetoram, and flubendiamide [6]. FAW developed different degrees of resistance to at least 29 insecticides in the Americas in 2017, owing to the extensive use of chemical pesticides [1]. In China, some of the FAW populations have developed resistance to organophosphate and pyrethroid pesticides [7].

Emamectin benzoate (4″-epi-methylamino-4″-deoxyavermectin B1) is a member of the avermectin family, which is a class of natural fermentation product of the soil microorganism, *Streptomyces avermitilis* [8,9]. EMB is a highly efficient, broad-spectrum, semi-synthetic and macrocyclic lactone insecticide against agricultural and forestry pests and an effective anti-parasiticide for both marine and freshwater fish species with less toxic effects in most beneficial arthropods (e.g., predators, honeybees and parasitoids) [9,10]. As a chloride channel activator, EMB stimulates high-affinity γ-aminobutyric acid receptor (GABA-R) and glutamate-gated chloride channels (GluCls), and produces a consequent increasing in membrane chloride ion permeability and disrupts nerve signals within nematodes, arthropods and platyhelminths [11], and eventually leading to death [12,13]. Based on Lepidopteran cell lines, EMB could also induce apoptosis and DNA damage in the FAW Sf-9 cell line [11]. Spray application of EMB can reduce FAW larval populations, lower plant damage, and achieve a higher fodder yield [14,15]. The toxicity of pesticides can be impacted and may not directly kill target and non-target insects because of volatilization, degradation, or other effects [16]. However, this toxicity of pesticides may also cause negative sublethal effects on insects [17]. The sublethal effects can be defined as physiological, biological, behavioral and/or demographic effects on individuals that survive an exposure to a pesticide at low lethal or sublethal concentration or dose [18–20]. Sublethal dose ($LC_{30}$) of EMB has significant effects on development time, feeding potential or reproduction parameters of *Paederus fuscipes* Curtis [16], and the life-table and physiological parameters of *Panonychus citri* (McGregor) [21]. The sublethal concentration ($LC_5$ and $LC_{15}$) of EMB prolong the development time and longevity of *Spodoptera littoralis* (Boisd.), and reduce their population parameters [22]. $LC_{30}$ of EMB decrease the pupal weight, longevity and fecundity of *Tuta absoluta* (Meyrick) [23], and inhibit the body weight of *Lymantria dispar* (L.) [24]. EMB is mainly stomach toxicity, which has a specific contact-killing effect. These sublethal effects of EMB on pests might be by influencing gamma-amino butyric acid (GABA) content, midgut injury, digestive dysfunction and nutrient metabolism disorder [24,25]. However, there is no information on the sublethal effect of EMB on the performance of FAW. Therefore, it is very necessary to assess the sublethal effect of EMB through a life study on the life history of parental and offspring generations.

Chemical control has become the main method for the prevention and control of FAW around the world, especially in China, and EMB is one of the main insecticides used to control FAW [7]. Therefore, evaluating the resistance of EMB to FAW and understanding the sublethal effects of EMB are key to assess the potential risks of this pesticide. However, to our knowledge, no information is available on the lethal and sublethal effects of EMB on the FAW life cycle. Thus, the present study was conducted to determine the lethality of EMB to FAW and to evaluate the sublethal ($LC_{10}$ and $LC_{20}$) effects of EMB on the life table parameters of FAW parental and offspring generations. Data of the lethal and sublethal effects could provide a scientific basis for further development application of EMB in the management of FAW and other lepidopteran pests around the world.

## 2. Materials and Methods

### *2.1. Insects and Test Pesticides*

FAW larval populations were collected from the corn fields of Luoertang Village (27°46′44″ N, 107°40′41″ E), Yanchang Town, Fenggang County, Zunyi City, Guizhou Province, China. Larvae were fed with fresh corn leaves and reared in a climatic chamber with temperature set at 25 ± 2 °C, relative humidity of 70 ± 5%, and photoperiod of 14 light:10 dark as described by Chen et al. [26]. Emamectin benzoate technical material (TC), with a purity of 70%, was purchased from Guangxi Tianyuan Biochemical Co., Ltd. (Nanning, China). Acetone (analytical grade) was purchased from Shantou Xilong Chemical Co., Ltd. (Shantou, China).

### *2.2. Toxicity of EMB to FAW Larvae*

The leaf dip method was used to determine the toxicity of EMB to FAW larvae. EMB was diluted in 1 g/L stock solution with acetone. On the basis of the preliminary experiment, the alcohol was diluted in distilled water to seven serial concentrations: 0.5000, 0.2500, 0.1250, 0.0625, 0.0313, 0.0156, and 0.0070 mg/L. Fresh corn leaves were cut into small segments (approximately 3 cm length and 1.25 cm width) and immersed in the seven concentrations of EMB for 10 s, and then the leaves were dried naturally at room temperature and transferred to a transparent plastic pudding box (diameter of 6 cm, height of 3 cm), which modified from the method described by Zhao et al. (2018) [27] and Mokbel and Huesien (2020) [22]. The lid of the pudding box was punched with a needle to ensure air circulation. Each pudding box contained one FAW third instar larvae kept under starvation for 4 h before EMB treatment. Each treatment was repeated 3 times and each replicate contained 24 larvae. The control was fresh corn leaves soaked in acetone and distilled water. The test larvae were reared in a climate chamber at 25 ± 2 °C, a relative humidity of 70 ± 5%, and a photoperiod of 14 light:10 dark. Larval mortality was assessed 24 h post-treatment, and larvae that turned black or did not respond to brush strokes were considered dead. Larval mortality values were corrected using Abbott's formula, and the virulence regression equation, median lethal concentration ($LC_{50}$), and 95% confidence interval were calculated according to the corrected larval mortality values.

### *2.3. Sublethal Effects of EMB on the FAW Parental Generation*

Based on the concentration–mortality assays of EMB to FAW third instar larvae, the larvae were treated with $LC_{10}$ and $LC_{20}$ EMB by the leaf dip method. FAW third instar larvae were transferred to a pudding box and provided with fresh corn leaves treated with $LC_{10}$ and $LC_{20}$ EMB described in the previous experiment. The control was fresh corn leaves treated with acetone and distilled water. A total of 100 FAW third instar larvae were used for each treatment, and larvae were transferred to a clean pudding box provided with insecticide-free leaves at 24 h post-treatment. FAW mortality and development time were recorded daily. Male and female pupae were weighed after the larvae pupated. The sex of pupae was determined by the morphological characteristics of the ventral gonopores on the eighth and ninth abdominal segments [28]. A pupa was considered dead if it did not show any movement on touch, had turned black, or could not emerge within 15 days after pupation. After adult eclosion, a pair of male and female was placed in a 300-mL plastic cup. A cotton ball soaked with 10% honey water was placed at the bottom of the plastic cup for nutritional supplementation, and 160-mesh gauze was used to seal the cup with a rubber band. We recorded the pre-oviposition period, oviposition period, fecundity, and longevity of adult male and female every day until all adult male and female died. After female laid eggs, the egg masses were randomly collected under a microscope. A total of 100 FAW eggs were collected for each treatment, which was repeated 10 times. The egg masses were immersed in 0.5% sodium hypochlorite solution for 10 s for disinfection. The egg hatching rate was recorded by calculating the number of neonate larvae emerging from the egg.

### *2.4. Sublethal Effects of EMB on FAW Offspring*

To evaluate the carry-over activity of EMB on the FAW offspring, we collected 100 first instar larvae from the above treatment and individually transferred them to a pudding box provided with fresh corn leaves. Fresh corn leaves in each pudding box were replaced daily. The development time and mortality rate of FAW larvae and pupae were recorded daily. Newly emerged FAW male and female were paired in a 300-mL plastic cup. The number of eggs laid by FAW female was recorded daily. Pre-oviposition, oviposition, post-oviposition, and fecundity of FAW offspring were assessed daily. Longevity of adult male and female was recorded daily until the death of the last adult.

### *2.5. Statistical Analysis*

SPSS (version 24.0) was used to determine the toxicity of EMB to FAW larvae, analyze the data, fit the virulence regression equation, and calculate the correlation coefficient, chi-square value, $LC_{10}$, $LC_{20}$, and $LC_{50}$, and 95% confidence interval. The data obtained from the FAW parental generation was analyzed by Analysis of Variance (ANOVA), followed by Tukey's' Honestly Significant Difference (HSD) test ($p \leq 0.05$). Percentage values of the FAW parental generation were subjected to angular transformation before ANOVA. Raw data of mortality, development time, and reproduction parameters of the FAW offspring generation were analyzed by using an age-stage, two-sex life table [29–31]. The mean values and standard errors of mortality rates, development time, longevity, fecundity, reproduction, and population parameters of the FAW offspring generation were estimated using 100,000 bootstraps. A paired bootstrap test was performed using TWOSEX-MSChart to compare the differences between the sublethal concentration ($LC_{10}$ and $LC_{20}$) groups and the control group on the life table parameters of the FAW offspring generation. The curves of survival rates, fecundity, life expectancy, and reproductive value were constructed using SigmaPlot 13.0 software.

## 3. Results

### *3.1. Lethal Effects of EMB on FAW Larvae*

The concentration-dependent mortality responses for the lethal effects of EMB on FAW third instar larvae were estimated with $LC_{50}$ EMB for 24 h; $LC_{50}$ EMB was 0.1062 (0.0932–0.1214) mg/L(Tables 1 and 2). Lethal concentration to 10% and 20% of a population ($LC_{10}$) and ($LC_{20}$) values were 0.0127 mg/L and 0.0589 (0.0455–0.0714) mg/L, respectively, which were used for subsequent experimental treatments.

**Table 1.** Lethal effects of different concentrations of EMB on FAW third instar larvae 24 h post-treatment.

| Concentration | Number of Test Insects | (%) Mortality ± SE | Corrected Mortality (%) |
|---|---|---|---|
| 0.5000 | 72 | 100 ± 0 a | 91.74 ± 2.38 a |
| 0.2500 | 72 | 93.06 ± 1.39 b | 84.46 ± 3.91 b |
| 0.1250 | 72 | 59.72 ± 3.68 c | 51.43 ± 5.55 c |
| 0.0625 | 72 | 37.5 ± 2.41 d | 29.19 ± 4.81 d |
| 0.0313 | 72 | 18.05 ± 2.78 e | 9.73 ± 3.67 e |
| 0.0156 | 72 | 15.28 ± 1.39 e | 6.95 ± 2.78 e |
| 0.0070 | 72 | 11.11 ± 1.39 e | 2.78 ± 3.68 e |
| Control | 72 | 8.33 ± 2.40 e | / |

Means within a column followed by the different lower-case differ significantly between different concentrations and the control (Tukey's HSD multiple range test, $p > 0.05$). SE: standard error; mg/L: milligram per liter.

**Table 2.** Acute toxicity of EMB against FAW third instar larvae 24 h post-treatment.

| Model | $LC_{10}$ (mg/L) (95% CL) | $LC_{20}$ (mg/L) (95% CL) | $LC_{50}$ (mg/L) (95% CL) | r | $\chi^2$ | *p* |
|---|---|---|---|---|---|---|
| Y = 0.1266 + 1.8963x | 0.0127 (−0.0061–0.0276) | 0.0589 (0.0455–0.0714) | 0.1062 (0.0932–0.1214) | 0.9129 | 2.1852 | 0.995 |

LC, CL, r, and $\chi^2$ indicate lethal concentration, confidence limit, correlation coefficient, and chi-square, respectively.

### *3.2. Sublethal Effects of EMB on FAW Parental Generation*

Sublethal concentrations ($LC_{20}$) of EMB significantly prolonged the pupal period of male and increased the pupal weight of male but not of female (Table 3). The pupation rate of FAW larvae was not significantly influenced by sublethal concentrations, but there was a significant difference in the eclosion rate of FAW with $LC_{20}$. $LC_{20}$ significantly delayed the oviposition period and adult longevity. Although sublethal concentrations ($LC_{10}$ and $LC_{20}$) of EMB did not influence FAW fecundity, the FAW hatching rate was significantly reduced.

**Table 3.** Sublethal effects of EMB on the development time and reproduction parameters of the FAW parental generation.

| Parameters | Control | $LC_{10}$ | $LC_{20}$ |
|---|---|---|---|
| Pupation rate (%) | 74.67 ± 3.89 a | 77.33 ± 3.40 a | 64.00 ± 4.52 a |
| Pupal period (female) | 12.81 ± 0.13 a | 12.54 ± 0.19 a | 12.76 ± 0.16 a |
| Pupal period (male) | 13.75 ± 0.29 b | 14.37 ± 0.19 ab | 14.77 ± 0.19 a |
| Pupal weight (mg, female) | 2015.70 ± 52.10 a | 2003.47 ± 59.83 a | 2043.03 ± 50.48 a |
| Pupal weight (mg, male) | 2017.13 ± 71.83 b | 2169.11 ± 53.92 a | 2210.57 ± 40.49 a |
| Eclosion rate (%) | 78.67 ± 3.89 a | 69.33 ± 3.40 ab | 62.67 ± 3.40 b |
| Pre-oviposition period (day) | 3.45 ± 0.27 a | 4.00 ± 0.28 a | 3.60 ± 0.20 a |
| Oviposition period (day) | 5.55 ± 0.37 b | 6.00 ± 0.55 b | 8.50 ± 0.47 a |
| Fecundity (day) | 1161.90 ± 41.11 a | 1049.35 ± 71.26 a | 1079.70 ± 60.42 a |
| Longevity (d, female) | 9.90 ± 0.34 b | 10.00 ± 0.62 b | 13.00 ± 0.58 a |
| Longevity (d, male) | 8.75 ± 0.26 b | 9.50 ± 0.57 b | 11.55 ± 0.49 a |
| Hatching rate (%) | 95.70 ± 0.98 a | 82.00 ± 1.45 b | 79.60 ± 2.44 b |

Means within a row followed by the different lower-case differ significantly between the sublethal concentration (LC10 and LC20) groups and the control group (Tukey's HSD multiple range test, $p > 0.05$).

### *3.3. Sublethal Effects of EMB on the Mortality and Development Rate of the FAW Offspring Generation*

Sublethal concentrations ($LC_{10}$ and $LC_{20}$) did not influence FAW larval mortality but significantly increased the mortality of pupae and pre-adults (Table 4). In addition, the sublethal concentrations not only reduced the development time of the FAW larval stage and pre-adult male and female but also significantly prolonged the pupal periods (Table 5). Both $LC_{10}$ and $LC_{20}$ mainly reduced the sixth instar larvae of FAW male and female, but less significantly influenced the first to fifth instar larvae. $LC_{20}$ significantly reduced the larval and pre-adult stages of male, but no significant differences were observed for these stages in female. When the parental generation was exposed to $LC_{10}$, the FAW larval and pre-adult stages were significantly shortened. As for adult longevity, $LC_{20}$ only reduced male longevity, but not female longevity.

**Table 4.** Sublethal effects of EMB on FAW offspring mortality.

| Immature Stages | Control | $LC_{10}$ | $LC_{20}$ |
|---|---|---|---|
| L1 (%) | 0 a | 0 a | 2.20 ± 1.53 a |
| L2 (%) | 2.08 ± 1.45 b | 4.21 ± 2.06 ab | 9.89 ± 3.10 a |
| L3 (%) | 4.17 ± 2.04 a | 5.26 ± 2.29 a | 2.20 ± 1.53 a |
| L4 (%) | 4.17 ± 2.04 a | 4.21 ± 2.06 a | 0 b |
| L5 (%) | 2.08 ± 1.46 a | 2.11 ± 1.48 a | 4.40 ± 2.16 a |
| L6 (%) | 2.08 ± 1.46 b | 2.11 ± 1.48 b | 15.38 ± 3.79 a |
| Pupa (%) | 2.08 ±1.46 b | 23.16 ± 4.31 a | 27.47 ± 4.67 a |
| Pre-adult (%) | 16.67 ± 3.80 c | 41.05 ± 5.03 b | 61.54 ± 5.08 a |

L1–L6 indicate first to sixth instar FAW larvae. A paired bootstrap test was performed to detect significant differences in FAW mortality with different sublethal concentrations ($LC_{10}$ and $LC_{20}$). Standard errors were estimated using 100,000 bootstrap resampling. The different lowercase letters indicate significant differences in FAW mortality with different sublethal concentrations ($LC_{10}$ and $LC_{20}$).

**Table 5.** Sublethal effects of EMB on the development time of FAW offspring.

| | Control | | | | n | $LC_{10}$ | | | n | $LC_{20}$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | Female | | Male | n | Female | | Male | n | Female | n | Male |
| L1 (day) | 43 | 2.12 ± 0.05 a A | 37 | 2.14 ± 0.06 a A | 37 | 2.05 ± 0.04 a A | 19 | 2.05 ± 0.05 a A | 17 | 2.06 ± 0.06 a A | 18 | 2.11 ± 0.08 a A |
| L2 (day) | 43 | 2.86 ± 0.05 b A | 37 | 2.97 ± 0.03 a A | 37 | 2.95 ± 0.04 ab A | 19 | 2.95 ± 0.05 a A | 17 | 3.00 ± 0.00 a A | 18 | 3.00 ± 0.00 a A |
| L3 (day) | 43 | 2.95 ± 0.03 ab A | 37 | 2.97 ± 0.03 a A | 37 | 2.86 ± 0.06 b B | 19 | 3.05 ± 0.05 a A | 17 | 3.12 ± 0.08 a A | 18 | 3.00 ± 0.00 a A |
| L4 (day) | 43 | 2.95 ± 0.03 a B | 37 | 3.14 ± 0.06 a A | 37 | 2.92 ± 0.05 a A | 19 | 3.05 ± 0.05 ab A | 17 | 3.06 ± 0.06 a A | 18 | 3.00 ± 0.00 b A |
| L5 (day) | 43 | 3.14 ± 0.05 a A | 37 | 3.22 ± 0.07 a A | 37 | 3.00 ± 0.00 a B | 19 | 3.21 ± 0.10 a A | 17 | 3.24 ± 0.14 a A | 18 | 3.17 ± 0.12 a A |
| L6 (day) | 43 | 6.47 ± 0.10 a B | 37 | 6.78 ± 0.07 a A | 37 | 4.54 ± 0.16 c B | 19 | 5.11 ± 0.19 b A | 17 | 5.41 ± 0.24 b A | 18 | 4.89 ± 0.21 b A |
| Larva (day) | 43 | 20.49 ± 0.16 a B | 37 | 21.22 ± 0.13 a A | 37 | 18.32 ± 0.21 b B | 19 | 19.42 ± 0.28 b A | 17 | 19.88 ± 0.42 a A | 18 | 19.17 ± 0.35 b A |
| Pupa (day) | 43 | 11.51 ± 0.11 b B | 37 | 13.43 ± 0.17 c A | 37 | 12.11 ± 0.13 a B | 19 | 13.89 ± 0.15 b A | 17 | 12.12 ± 0.24 a B | 18 | 14.50 ± 0.22 a A |
| Pre-adult (day) | 43 | 32.00 ± 0.16 a B | 37 | 34.65 ± 0.25 a A | 37 | 30.43 ± 0.23 b B | 19 | 33.32 ± 0.35 b A | 17 | 32.00 ± 0.44 a B | 18 | 33.67 ± 0.28 b A |
| Adult longevity (day) | 43 | 12.47 ± 0.40 a A | 37 | 11.70 ± 0.32 a A | 37 | 12.05 ± 0.40 a A | 19 | 11.37 ± 0.31 ab A | 17 | 11.29 ± 0.55 a A | 18 | 10.11 ± 0.57 b A |

L1–L6 indicate first to sixth instar FAW larvae. A paired bootstrap test was performed to detect significant differences in the development time of FAW with different sublethal concentrations ($LC_{10}$ and $LC_{20}$). Standard errors were estimated using 100,000 bootstrap resampling. The different lowercase letters indicate significant differences in the development time of FAW with different sublethal concentrations ($LC_{10}$ and $LC_{20}$). Different capital letters indicate significant differences in the development time of FAW between male and female for each treatment.

Age-developmental stage survival ($S_{xj}$) curves in Figure 1 overlapped because of differences in developmental rates between treatments. The results showed that the survival rate of offspring treated with $LC_{10}$ and $LC_{20}$ at all ages decreased to varying degrees compared with the control, indicating that $LC_{10}$ and $LC_{20}$ would have a prolonged impact on treated FAW offspring. Combined with the mortality of progeny at each stage (Table 4), the survival rates of the $LC_{10}$ and $LC_{20}$ treatment groups at the pupal and adult stages were significantly lower than those of the control group. The age-specific survival rate ($l_x$), age-specific fecundity ($m_x$), and age-specific maternity ($l_x m_x$) curves are shown in Figure 2. Compared with the control group, the age-specific survival rate curves of the $LC_{10}$ and $LC_{20}$ treatment groups significantly decreased 15 days after treatment, which corresponded to the period from the sixth instar larval stage to the pupal stage. Combined with offspring mortality at each stage (Table 4), the sublethal concentrations of EMB might affect FAW pupae. Age-specific fecundity and maternity of FAW offspring showed a trend of first increasing and then decreasing, reaching the peak of reproduction at 35–36 days, but the peaks of $LC_{10}$ ($m_x$, $l_x m_x$) and $LC_{20}$ (43) treatment groups were lower than those of the control group (167).

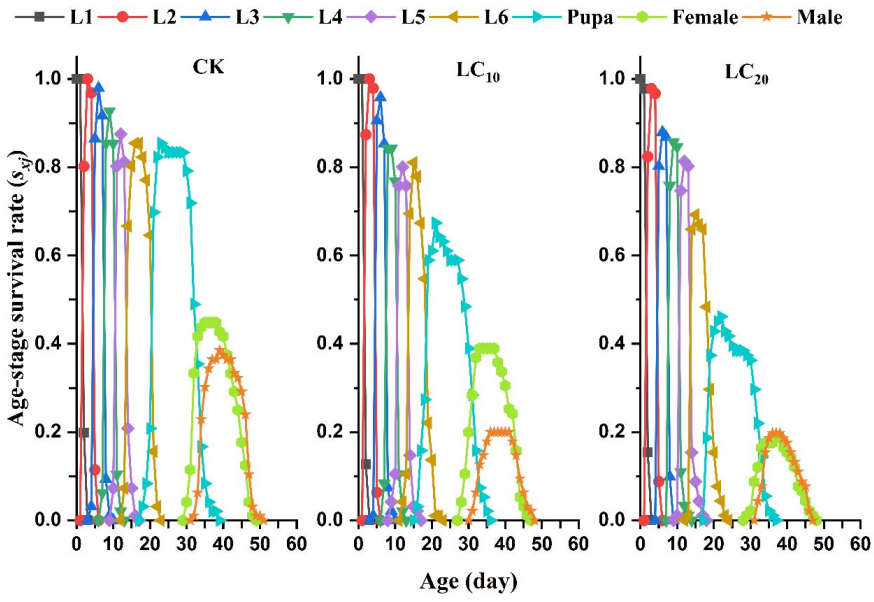


**Figure 1.** Age-stage specific survival rate ($S_{xj}$) of FAW exposed to sublethal concentrations ($LC_{10}$ and $LC_{20}$).

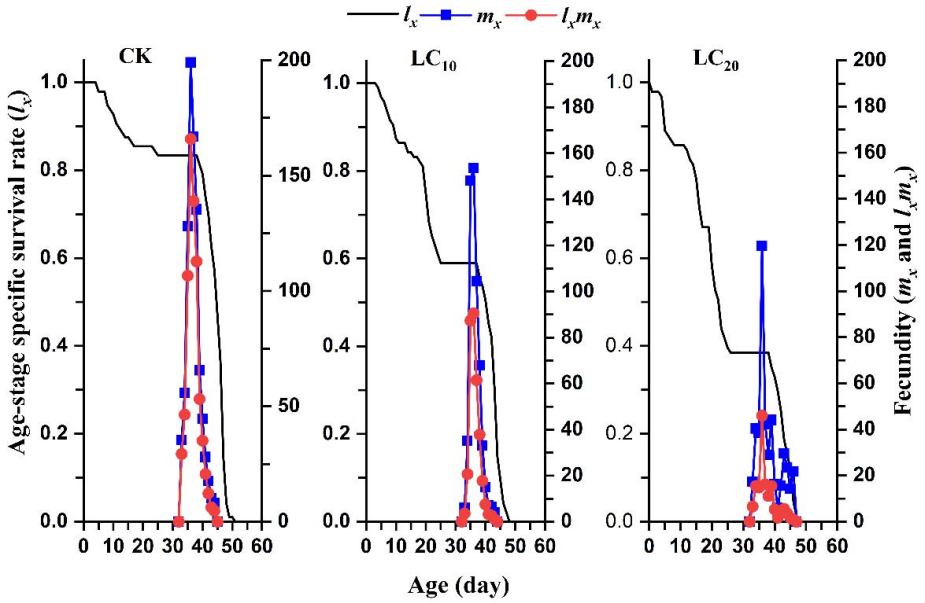


**Figure 2.** Age-specific survival rate ($l_x$), age-specific fecundity ($m_x$), and age-specific maternity ($l_xm_x$) curves of the FAW offspring generation from the FAW parental generation exposed to sublethal concentrations ($LC_{10}$ and $LC_{20}$).

### *3.4. Sublethal Effects of EMB on the Reproduction Parameters of the FAW Offspring Generation*

Sublethal concentrations ($LC_{10}$ and $LC_{20}$) that did not influence the total pre-oviposition of FAW $F_1$ are listed in Table 6. The life expectancy ($e_{xj}$) was higher in the control group than in the $LC_{10}$ and $LC_{20}$ treatment groups for each stage (Figure 3). Life expectancy of the first instar larvae in each treatment was the highest in the entire life cycle, and life expectancy decreased with the development of larvae.

**Table 6.** Sublethal effects of EMB on the reproduction and population parameters of the FAW offspring generation.

| | n | Control | n | $LC_{10}$ | n | $LC_{20}$ |
|---|---|---|---|---|---|---|
| Total pre-oviposition (TPOP)/d | 35 | 35.37 ± 0.22 a | 27 | 35.19 ± 0.22 a | 8 | 35.75 ± 0.98 a |
| Pre-oviposition (APOP)/d | 35 | 3.63 ± 0.16 b | 27 | 4.67 ± 0.24 a | 8 | 3.75 ± 0.37 b |
| Oviposition period/d | 35 | 6.14 ± 0.24 a | 27 | 3.96 ± 0.25 c | 8 | 5.25 ± 0.37 b |
| Fecundity (egg/female) | 35 | 2008.74 ± 78.77 a | 27 | 1174.26 ± 75.11 b | 8 | 1689.25 ± 157.74 a |
| $r_m$ ($day^{-1}$) | 35 | 0.1758 ± 0.0040 a | 27 | 0.1563 ± 0.0049 a | 8 | 0.1328 ± 0.0106 a |
| λ ($day^{-1}$) | 35 | 1.1923 ± 0.0048 a | 27 | 1.1692 ± 0.0058 a | 8 | 1.1420 ± 0.0121 a |
| $R_0$ (Offspring/ individual) | 35 | 732.35 ± 102.70 a | 27 | 333.74 ± 58.28 a | 8 | 148.51 ± 51.57 a |
| T (day) | 35 | 37.51 ± 0.22 a | 27 | 37.17 ± 0.20 a | 8 | 37.66 ± 0.75 a |
| GRR (Offspring) | 35 | 893.72 ± 118.89 a | 27 | 580.16 ± 89.06 b | 8 | 457.15 ± 154.51 b |

$r_m$—intrinsic rates of natural increase, λ—finite rate of population increase, T—mean generation time, $R_0$—net reproductive rate, GRR—gross reproduction rate. A paired bootstrap test was performed to detect significant differences in the reproduction and population parameters of FAW with different sublethal concentrations ($LC_{10}$ and $LC_{20}$). Standard errors were estimated using 100,000 bootstrap resampling. The different lowercase letters indicate significant differences in the reproduction and population parameters of FAW with different sublethal concentrations ($LC_{10}$ and $LC_{20}$).

The FAW oviposition period $F_1$ was significantly decreased by the sublethal concentrations ($LC_{10}$ and $LC_{20}$). However, only $LC_{10}$ significantly reduced FAW $F_1$ female fecundity. The age-stage specific reproductive value ($V_{xj}$) curve began to rapidly rise when the female laid eggs, reached the reproductive peak, and then gradually decreased with time (Figure 4). However, the reproductive peak of the FAW offspring in the $LC_{10}$ and $LC_{20}$ treatment groups reached 638.92 eggs on the 35th day and 539.24 eggs on the 34th day post-treatment, which were lower than those in the control group, which reached a reproductive peak of 952.07 eggs on the 36th day post-treatment.

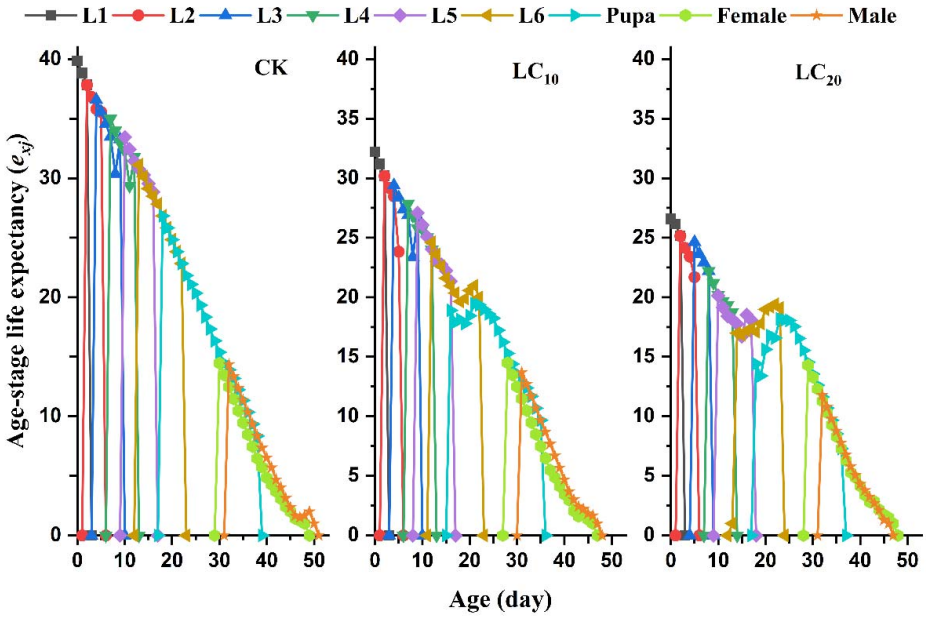


**Figure 3.** Age-specific life expectancy ($e_{xy}$) of the immature and adult FAW offspring generation from the FAW parental generation exposed to sublethal concentrations ($LC_{10}$ and $LC_{20}$).

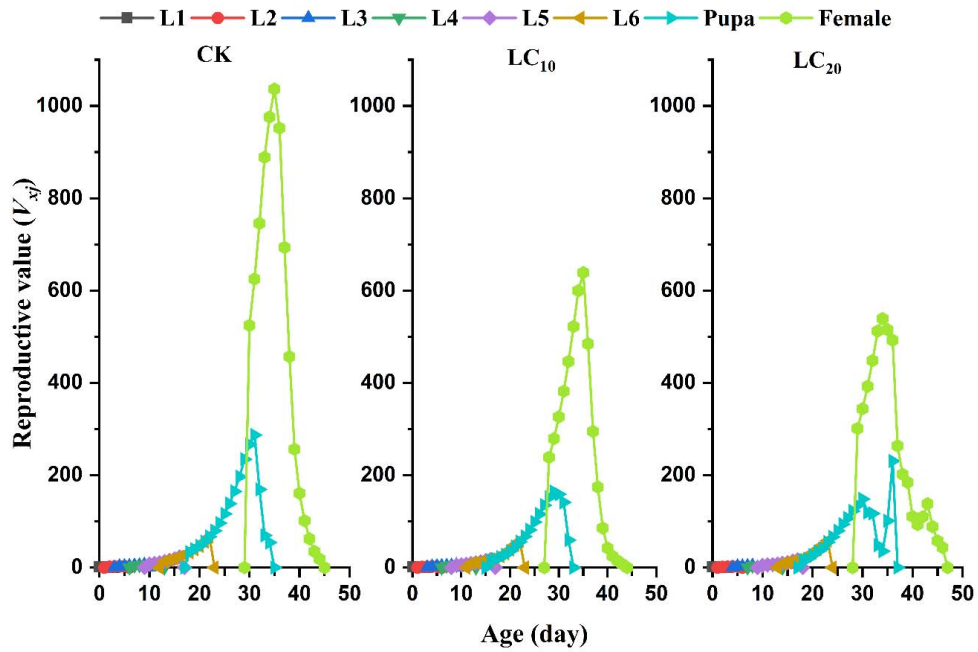


**Figure 4.** Age-stage specific reproductive value ($V_{xj}$) of the immature and adult FAW offspring generation from the FAW parental generation exposed to sublethal concentrations ($LC_{10}$ and $LC_{20}$).

### *3.5. Sublethal Effects of EMB on the Population Parameters of the FAW Offspring Generation*

The intrinsic rates of natural increase ($r_m$), finite rate of population increase (λ), and net reproductive rate ($R_0$) decreased with the increase in the sublethal concentration groups compared with the control group, but no significant differences were found in life table parameters (Table 6). Sublethal concentrations ($LC_{10}$ and $LC_{20}$) significantly reduced the gross reproduction rate (GRR) of the FAW offspring generation.

## 4. Discussion

Avermectins (Ave) are composed of a 16-membered macrocyclic lactone, which have a similar mode of action in the GABA-R and GluCls of insect chloride channels [9]. EMB derived from abamectin using a five-step chemical synthesis is one of the most popular biopesticides with higher antipest, anti-parasitic and anti-nematode activities and lower toxicity compared with avermectin and other conventional insecticides [32,33]. Due to its burst release and rapid degradation of EMB under natural sun light, EMB shows a short half-lives (0.37–0.64 days) in the crops [32,34]. However, the residues of EMB might lead to sublethal effects over space and time, including influencing the developmental time, weight, fecundity, longevity and physiological parameters without directly causing death [16,22–25,35]. FAW is a highly destructive polyphagous invasive pest that causes substantial losses to agricultural production. In order to conduct the emergency prevention system against FAW, the application of EMB recommended by MARA may not only cause direct FAW larval mortality but also indirectly negatively lead to sublethal effects [18]. However, information on the sublethal effects of EMB on FAW is little [36]. The results of the present study showed that even a low dose of EMB could influence the performance of FAW parental and offspring generations. To the best of our knowledge, this is the first study to determine the sublethal concentrations of EMB on the life table parameters of two FAW generations. The findings of this study can provide important implications for delaying the development of resistance to FAW.

### *4.1. Effect of EMB on the Performance of FAW Parental Generation*

Sublethal concentration of EMB could significantly influence the growth and development of pest [16,22,24,37]. Sublethal concentration exposure ($LC_{30}$) of EMB could delay the immature stages (larva, protonymph, and deutonymph) of *P. citri* [35]. The developmental time of *Helicoverpa armigera* (Hübner) larva and female pupa could be inhibited by the sublethal dose ($LC_{25}$) of EMB [37]. EMB sublethal concentrations ($LC_5$ and $LC_{15}$) increased the larval period and decreased the pre-pupal and pupal weight of *S. littoralis* [22]. Sublehal concentration ($LC_{30}$) of EMB exposure decreased the larval weight of *L. dispar* at 48 and 72 h [24]. Lethal dose ($LD_{10}$) of EMB also reduced the larval weight of *S. littoralis* at 24 h [25]. There was a similar pattern for the developmental time and weight of FAW in the present study that $LC_{20}$ significantly prolonged the pupal period of FAW male and increased the pupal weight of male but not of female. However, $LC_{10}$ and $LC_{25}$ abamectin had no significant effect on the nymphal stage duration of *Nilaparvata lugens* Stål [38].

Effects on fecundity after exposure to sublethal concentrations of pesticides were induced more negatively and less positively [18]. In *N. lugens*, $LC_{10}$ and $LC_{25}$ abamectin significantly inhibited the fecundity of brachypterous [38]. $LC_{10}$, $LC_{20}$ and $LC_{30}$ abamectin severely affected the fecundity of predatory mite, *Phytoseius plumifer* (Canestrini and Fanzago) and *Scolothrips longicornis* Priesner [39,40]. Similar, the fecundity of *T. absoluta* treated with $LC_{10}$ and $LC_{30}$ abamectin was significantly lower than the control [41]. Although sublethal concentrations ($LC_{10}$ and $LC_{20}$) of EMB did not influence FAW fecundity in our study, both concentrations could cause a significant reduction in viable eggs laid by female. Thus, EMB does not stimulate the fecundity of FAW, suggesting that it might be an ideal insecticide for lepidopteran pests.

Sublethal concentrations of pesticides could significantly influence arthropod longevity [18,42]. $LC_{30}$ values of EMB significantly reduced the longevity of *H. armigera* female and male [43]. Low-lethal concentrations ($LC_{10}$, $LC_{20}$ and $LC_{30}$) of abamectin significantly reduced the longevity of predatory thrips *S. longicornis* [40]. The longevity of *T. absoluta* female and male exposed to the $LC_{10}$ and $LC_{30}$ treatment of abamectin was significant lower than the control [41]. Similarly, $LC_{50}$ value of abamectin caused significant reduction in female longevity of *Cryptolaemus montrouzieri* Mulsant [44]. In contrast, $LC_{10}$ and $LC_{25}$ of abamectin significantly prolonged the longevity of *N. lugens* brachypterous [38]. In this study, $LC_{20}$ EMB could significantly prolong FAW longevity, but this trend was not observed on exposure to $LC_{10}$ EMB. The extended longevity of FAW induced by $LC_{20}$ EMB

might be associated with the reduction in hatching rate of FAW egg. Exposure to $LC_{30}$ dose of EMB showed a significant negative influence on egg-laying and ovarian development of *Conopomorpha sinensis* Bradley, and caused a significantly diminished transcriptional level of CsVg and CsVgR [45]. Extended in the longevity might be interpreted as a result of diminished consumed energy of reproduction-related proteins in FAW.

EMB, a 4′-deoxy-4′-epi-methylamino derivative of avermectin, is a disruptor of neurotransmitter activity and induces developmental neurotoxicity and cardiotoxicity in the target organism [46,47]. These negative sublethal effects of EMB on FAW might be associated with the induction of GABA content. Kandil et al. (2020) find that $LD_{10}$, $LD_{25}$, and $LD_{50}$ doses of EMB cause a significant decrease in GABA content of *S. littoralis* [25]. The growth inhibition induced by EMB may be related to midgut damage, digestive dysfunction, and nutritional metabolism disorders [24]. The midgut damage of *L. dispar* induced by EMB shows the typical characteristics of apoptosis. In addition, exposure to EMB could induce the apoptosis in FAW Sf-9 cells [11]. However, further experiments would need to be performed to investigate the detailed mechanism of EMB in the performance of FAW.

### *4.2. Sublethal Effects of EMB on the Performance of the FAW Offspring Generation*

On exposure to pesticides, transgenerational insecticide-mediated effects on demographic parameters of pests may occur [48]. In this study, sublethal concentrations of EMB significantly increased the mortality rates of pupae and pre-adults; reduced the larval and pre-adult stage development times, longevity of male, oviposition period, and fecundity of FAW; and prolonged pupal periods. Similarly, these transgenerational sublethal effects of Abamectin and EMB were found in *Tetranychus urticae* Koch, *P. plumifer*, *Phytonemus pallidus* (Banks), *T. absoluta*, and *S. longicornis*, when the parental generation exposed to low lethal concentrations [39–42,49]. Some hypotheses sought to explain this phenomenon in the offspring generation. In FAW, EMB might influence the activity of detoxifying enzymes that are responsible for the reduced toxicity of insecticides [50]. Furthermore, EMB could induce histological changes in important organs of *S. littoralis*, such as body wall, fat bodies, muscles, midgut, and Malpighian tubules [51]. Negative sublethal effects of EMB might disrupt the histological effects of the FAW parental generation, and then influence the reproductive parameters of the offspring generation [22]. Moreover, EMB could induce apoptosis and DNA damage, which might also destroy the cell physiological function in FAW parental generation [11].

## 5. Conclusions

$LC_{20}$ EMB could prolong the development time of pupa, oviposition period, and longevity, and reduce the pupal weight, eclosion, and hatching rate of the FAW parental generation, whereas no significant difference was observed in fecundity. As for the transgenerational effect of EMB on the life cycle of the FAW offspring generation, sublethal concentrations significantly influenced the development time, mortality rate, oviposition period, longevity, and life table parameters ($r_m$, λ, and $R_0$) of FAW. According to the results, EMB could significantly influence the life cycle of FAW parental and offspring generations under laboratory conditions. Field studies are required to evaluate and validate the laboratory results of the present study. Our results provide important implications for the rational application of FAW insecticides in China and around the world.

**Author Contributions:** Conceptualization, X.-L.L., X.-F.T., J.-F.L. and S.-J.S.; methodology, Z.-K.L. and J.-F.L.; software, J.-F.L.; validation, J.-F.L., S.-J.S. and J.S.; formal analysis, Z.-K.L.; investigation, Z.-K.L.; resources, X.-L.L., X.-F.T. and J.-F.L.; data curation, Z.-K.L. and J.-F.L.; writing—original draft preparation, Z.-K.L., A.I. and J.-F.L.; writing—review and editing, Z.-K.L., M.-F.Y., A.I., J.-F.L., S.-J.S. and J.S.; visualization, J.-F.L.; supervision, J.-F.L., S.-J.S. and J.S.; project administration, J.-F.L.; funding acquisition, M.-F.Y. and J.-F.L. All authors have read and agreed to the published version of the manuscript.

**Funding:** This study was supported by the National Natural Science Foundation of China (32060637), the Growth Project of Youth Talent in Ordinary Universities in Guizhou Province ([2021]079), the Natural Science Special Project of Guizhou University (Special post, [2020]-02), and High-level Talent Innovation and Entrepreneurship Funding Project in Guizhou Province ([2021]01).

**Institutional Review Board Statement:** Not applicable for studies not involving humans or animals.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Dataset is available from the first author on reasonable request.

**Acknowledgments:** The authors are grateful to Tai-An Tian (Guizhou University) for help in the experiment.

**Conflicts of Interest:** The authors declare no conflict of interest.

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