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Effects of Different Wheat Tissues on the Population Parameters of the Fall Armyworm (*Spodoptera frugiperda*)

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Abstract: The fall armyworm (FAW), *Spodoptera frugiperda*, is an invasive migratory pest that prefers to feed on crops of the Gramineae family such as maize and wheat. It has been recorded in different locations in China since its invasion in 2019. To assess its effect on different wheat tissues and to provide a risk evaluation for wheat fields, FAW larvae were reared on the wheat seedling (WS), spike (SPK), peduncle (PDC), flag leaf blade (F-b), and blade of the first leaf under flag (F-1b). The population parameters were recorded, and the data were analyzed using the age-stage, two-sex life table method. The results showed that the FAW achieved successful development on all the substrates, although those fed on F-1b grew the slowest, had the smallest pupal weight, and deposited the fewest eggs. The larval survival rates of those fed on WS, SPK, and PDC were more than 80%, while for F-b and F-1b they were 56.58% and 32.03%, respectively. Feeding on leaf blades also resulted in lower fertility, reproductive capacity, life expectancy, net reproductive rate, intrinsic rate of increase, and finite rate of increase. These results indicated that feeding on WS, SPK, and PDC were more beneficial for development compared to F-b and F-1b alone. However, leaf blades alone can still support the full FAW lifecycle and thus could play an important role in nutrition, especially when quantities of the preferred host tissues are not sufficient. These results provide guidance for assessing the FAW risk in China.

Keywords: *Spodoptera frugiperda*; fall army worm; wheat; life table

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1. Introduction

The fall armyworm (FAW) *Spodoptera frugiperda* (J.E. Smith), native to tropical and subtropical regions of the Americas, is a lepidopteran agricultural pest notorious for its strong flight capacity and destructive effect on corn, sorghum, forage and turf grasses [1–3]. FAWs have a very wide host range that includes more than 353 different plant species belonging to 76 families [4]. Based on genetic heterogeneity and related preferential host plants, FAW could be designated as corn-strain or rice-strain [5]. The corn-strain FAW prefers plants such as maize, sorghum, barley, sorghum, sugar beet, Sudan grass, soybean, sugarcane, timothy, tobacco, and wheat [4,6].

In recent years, the corn-strain of FAW achieved a global distribution. In 2016, it was reported for the first time in Africa, where it caused significant damage to maize crops. In 2018, it was reported in India, Myanmar, Thailand, and other Southeast Asian countries [7,8]. In December 2018, the FAW moth was captured in the western part of Yunnan Province in China, and within three months, FAW larvae were confirmed during a maize field survey [9,10]. Subsequently, by October 2019, the FAW rapidly migrated

to 1524 counties in 26 provinces (autonomous regions and municipalities) and infested more than 15 crops including maize, sugarcane and sorghum. In 2020, it was recorded in 1426 counties in 27 provinces (autonomous regions and municipalities) [10,11]. Since this invasion, the Chinese Government has paid great attention to integrated management of this pest. The FAW is a regular annual migrant in the Americas and disperses throughout the U.S. in spring and summer from its overwintering areas [12,13]. Based on this feature, all potential FAW-infested areas in China were zoned into: (1) year-round breeding areas in Southwest and South China, (2) transitional migration areas in Jiangnan and Jianghuai, and (3) key preventive areas in the Huang–Huai–Hai region and North China [10].

Wheat is a host plant for the FAW and severe damage has been recorded in some U.S. states [1,4]. A study carried in Brazil showed that the FAW females prefer to oviposit more eggs on the upper canopy of wheat than that of other plants [14]. In China, wheat is a main staple and comprises the second largest cultivated area of any crop. Since the FAW invasion, damage to wheat at the seedling or tillering stage has been recorded in Yunnan, Sichuan, Anhui, and other central or south provinces [15]. Furthermore, a study conducted under cage conditions confirmed that the FAW causes damage from the booting to the milk developmental stage in wheat fields. A high density of FAW larvae may cause the early ripening of wheat in year-round areas or in transitional areas to where FAW migrate during the following season [16].

Diet quality and quantity may affect the growth, survival, and fecundity of herbivorous insects [17]. For example, the larvae of *Samea multiplicalis* reared on low-nitrogenous *Salvinia molesta* plants increased their consumption but grew more slowly than larvae fed on high-nitrogenous plants. Additionally, developmental time, biomass, growth rates and nitrogen assimilation rates were all adversely affected, and the larvae were 40% smaller [18]. Due to the wide distribution of wheat in China, different FAW generations can feed on wheat at different stages. Pest status is usually associated with the specific developmental stages of their host plant, so greater damage would be caused if FAW feed directly on reproductive structures rather than on leaves or other tissues [19]. It is therefore important to know the effect of different wheat tissues on FAW development to gain a better understanding of the damage risk.

In this study, we reared FAWs on wheat seedling (WS), spike (SPK), peduncle (PDC), flag leaf blade (F-b), and blade of the first leaf under flag (F-1b) and then analyzed the recorded population parameters using the age-stage, two-sex life table method. The results provided suggestions for the FAW monitoring and forecasting in China's wheat fields.

2. Materials and Methods

2.1. Host Plants

Wheat seedlings and tillers with spikes were obtained from wheat seeds (Aikang 58) provided by the Xinxiang Experiment Station of the Chinese Academy of Agricultural Sciences in Henan Province (35°18′13.71″ N, 113°55′15.05″ E). The wheat cultivar 'Aikang 58′ has strong ability on cold tolerance and on disease (Wheat Stripe Rust, Wheat Stem Rust, Wheat Powery Mildew) resistance, and is widely cropped in the Huang–Huai–Hai region. In October 2019, 15 kg of undressed wheat seeds were planted in a 667 m^2 plot at the Station. No pesticides, herbicides, or fungicides were used in this field during the growing season. In early May 2020, about 2000 tillers at the milk developmental stage were sampled and preserved in a refrigerator at 4 °C to maintain their consistency until they were used to feed FAW larvae in case there was an insufficient supply of field tillers. Wheat seedlings were also obtained from seeds of the same cultivar that were planted every three days in pots (12 cm in height × 15.5 and 8 cm (upper and lower diameters, respectively) × 0.5 cm in wall thickness). This took place about 10 days before tiller sampling at the milk developmental stage, so that preferable wheat seedlings could reach the 3–4 leaf stage for the larva to feed on [20]. To provide different wheat tissues, a whole wheat plant at the milk-developmental stage was sectioned into spike, peduncle, flag leaf blade, and blade of the first leaf under flag.

2.2. Insects

The FAW population was provided by the Cotton Insect Pests Group, Institute of Plant Protection, Chinese Academy of Agricultural Sciences. This population was collected in early 2019 in the Dehong Prefecture in Yunnan Province and reared on corn seedlings for more than 10 consecutive generations in the laboratory. All FAW individuals were kept at 25 ± 1 °C, under 75 ± 5% relative humidity (RH), and with a 16:8 h light/dark cycle [21].

2.3. Life Table Trials

Life table trials were carried out from early May to late June 2020 based on the stage of wheat tiller at the Xinxiang Experiment Station. Each egg mass was collected and reserved in a fresh-keeper bag and labeled with date and estimated number. To avoid damage while separating them, the eggs were observed daily as a mass until hatching. Neonatal larvae were then transferred to the prepared feed, of which there were five treatments: wheat seedling (WS), spike (SPK), peduncle (PDC), flag leaf blade (F-b) and blade of the first leaf under flag (F-1b). All tissues were cut into 1–2 cm sections and separately placed into Petri dishes (9 cm in diameter). Due to the need for a lifetable study and to avoid cannibalism of older FAW larvae, each dish hosted just one larva. The total numbers of neonatal larvae used were 143, 162, 146, 149, and 149 on WS, SPK, PDC, F-b, and F-1b, respectively. All the FAW individuals were kept at 25 ± 1 °C, under 75 ± 5% relative humidity (RH), and with a 16:8 h light/dark cycle [21]. Larval development and survival were checked daily until death. During the early larval stage, fresh wheat tissues or seedlings were provided every two days. As the larvae developed, the frequency of supplying fresh diet was adjusted to one day or several hours depending on consumption. Larval instars were determined from molting times, visual features, and head capsule widths without measurement because the head capsule widths and larval features could give our experienced workers a distinguishing impression [22]. Pupation, or eclosion, was also recorded every day. On the second day after pupation, the pupae were weighed on an electronic balance (Sartorius BSA224S-CW; Sartorius Scientific Instrument (Beijing) Co., Ltd., China, No. 33 Building, Tianzhu Airport Industrial B Zone, Shunyi District, Beijing, China, 101312). After eclosion, single pairs of adults were kept in a plastic cylinder made of overhead projector film (7 × 12 cm). The mouths of the cylinders were covered with cotton gauze fastened by elastic bands. All moths were kept under the same environmental conditions as the larvae and fed daily with 5% honey water [21]. Every day, the survival state for each pair was checked and recorded, and the cylinders and cotton gauze were checked to determine if the female had laid eggs. If egg masses were oviposited on the cylinder, they were gently removed and cotton gauze pieces with eggs were taken out and replaced with new pieces. Thereafter, the daily egg deposition was counted and recorded, and sampling lasted until the female moth died. The male did not always outlive the female of same pair. Those that died in the pre-oviposition period (3–4 days) [7] were removed from the dataset along with the fecundity data of the female. If the male died while the female was laying eggs, those data were included in the analysis.

2.4. Life Table Analysis

A setup version of TWOSEX-MSChart software, run under a License Agreement from Professor Chi, was used to calculate and analyze life parameters of FAWs fed on different tissues using our raw data based on the theory of an age-stage, two-sex life table [23,24]. The program can be downloaded for free from the website (http://140.120.197.173/Ecology/prod02.htm, accessed on 8 October 2021) [23]. The population parameters that were calculated included the age-stage specific survival rate (s_{xj}, where x = age in days and j = developmental stage), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), and the age-specific fecundity (m_x). The population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase; R_0, the net reproductive rate; T, the mean generation time; e_{xj}, the life expectancy) were calculated using the equations in Appendix A Table A1 [24–27].

2.5. Statistical Analysis

The bootstrap technique was conducted with TWOSEX-MSChart for 100,000 resamplings to estimate the standard errors of the population parameters following Wei et al. [28] and Yu et al. [29]. The difference between two treatments was compared by a paired bootstrap test with the results of the above 100,000 bootstrap resamplings. All graphs were created using SigmaPlot v.14.0.

3. Results

3.1. Basic Life History Statistics of the FAW

The FAW has 10 life stages: egg, six larval instars, pre-pupa, pupa, and adult. In our study, they successfully completed development by feeding on different wheat tissues. However, those had varying influences from the first to the six instar stage, which also resulted in significant differences at the larvae stage and total pre-oviposition period (TPOP) of the female (Table 1). The longest larval-stage duration was for F-1b at 21.44 ± 0.59 d, and the shortest was for WS at 13.48 ± 0.07 d. There were no significant differences among the different treatments for the pupal stage, female longevity, male longevity, or. However, there was a significant difference for the pre-pupa stage, oviposition days, the adult pre-oviposition period (APOP) of adult females (Table 1).

Table 1. Developmental duration of the FAW fed on different wheat tissues in the laboratory.

Stages	Developmental Duration (Mean ± SE) (Day)				
	WS	SPK	PDC	F-b	F-1b
1st instar	2.79 ± 0.03 b	2.96 ± 0.01 a	3.00 ± 0.02 a	2.29 ± 0.04 c	2.72 ± 0.04 b
2nd instar	1.81 ± 0.03 d	2.05 ± 0.02 c	1.89 ± 0.05 d	2.79 ± 0.05 a	2.60 ± 0.09 b
3rd instar	1.52 ± 0.05 c	1.32 ± 0.04 d	2.03 ± 0.08 b	1.65 ± 0.08 c	2.53 ± 0.13 a
4th instar	1.45 ± 0.05 d	1.90 ± 0.03 c	2.41 ± 0.08 b	2.17 ± 0.07 b	2.68 ± 0.10 a
5th instar	1.91 ± 0.03 c	2.16 ± 0.04 c	2.90 ± 0.08 b	2.62 ± 0.09 b	3.99 ± 0.19 a
6th instar	2.79 ± 0.04 d	3.28 ± 0.06 c	5.03 ± 0.11 b	5.46 ± 0.28 b	7.19 ± 0.37 a
Pre-pupa	1.30 ± 0.04 b	1.35 ± 0.04 b	1.48 ± 0.05 b	1.52 ± 0.09 a	1.48 ± 0.14 b
Larva	13.48 ± 0.07 e	14.85 ± 0.10 d	18.81 ± 0.26 b	17.16 ± 0.34 c	21.44 ± 0.59 a
Pupa	12.73 ± 0.11 a	12.75 ± 0.11 a	12.75 ± 0.09 a	12.37 ± 0.13 a	12.43 ± 0.27 a
Pre-adult	29.19 ± 0.14 e	30.59 ± 0.17 d	34.50 ± 0.28 b	32.26 ± 0.32 c	37.04 ± 0.74 a
Adult	15.58 ± 0.47 a	14.72 ± 0.45 a	15.99 ± 0.45 a	14.32 ± 0.66 a	16.52 ± 1.30 a
APOP	6.08 ± 0.33 b	7.14 ± 0.41 a	7.76 ± 0.57 a	7.34 ± 0.62 a	8.18 ± 1.28 a
TPOP	34.19 ± 0.26 d	36.32 ± 0.34 c	41.39 ± 0.61 a	38.55 ± 0.71 b	43.55 ± 1.63 a
Oviposition days	6.63 ± 0.35 a	5.75 ± 0.28 b	5.55 ± 0.34 b	5.21 ± 0.54 b	5.55 ± 0.99 b
Female longevity	15.45 ± 0.63 a	15.00 ± 0.52 a	15.77 ± 0.60 a	14.47 ± 0.99 a	17.27 ± 1.78 a
Male longevity	15.71 ± 0.69 a	14.49 ± 0.70 a	16.23 ± 0.66 a	14.17 ± 0.84 a	15.83 ± 1.89 a

Notes: WS: wheat seedling; SPK: spike; PDC: peduncle; F-b: flag leaf blade; and F-1b: blade of the first leaf under flag; APOP: Adult pre-oviposition period of female adult; TPOP: Total pre-oviposition period of female counted from birth. Data are represented as mean ± SE. SEs were estimated with the bootstrap technique (100,000) in a TWOSEX-MS Chart program and data followed by different letters in the same row are results of the paired bootstrap test ($\alpha = 0.05$).

The treatments also had significant effects on pupal weight and fecundity. The biggest pupal weight was recorded from FAW females that fed on WS. The pupal weight of FAW females that fed on SPK or PDC were much smaller than those fed on WS but was higher than those fed on F-b and F-1b (Table 2). A similar trend was recorded for the effect of treatments on the number of oviposited eggs. FAW females that fed on WS oviposited the highest number (1488.06 ± 92.41) and those that fed on F-1b oviposited the least number (561.36 ± 110.80) (Table 2).

Table 2. Pupal weight and fecundity of the FAW fed on different wheat tissues in the laboratory.

Index	Treatments				
	WS	SPK	PDC	F-b	F-1b
Pupae weight (mg)	230.38 ± 2.06 a	186.33 ± 2.70 b	154.52 ± 2.66 c	122.31 ± 3.90 d	127.84 ± 6.06 d
Fecundity (eggs/female)	1488 ± 92 a	1108 ± 64 b	698 ± 58 c	590 ± 79 c	561 ± 110 c

Notes: WS: wheat seedling; SPK: spike; PDC: peduncle; F-b: flag leaf blade; and F-1b: blade of the first leaf under flag; Data are represented as mean ± SE. SEs were estimated with the bootstrap technique (100,000) in a TWOSEX-MS Chart program, and data followed by different letters in the same row are results of the paired bootstrap test (α = 0.05).

The number of adult males exceed females under all the treatments except for the WS. There were significant differences among the proportion of females (N_f/N) and males (N_m/N) emerging from eggs at the beginning of the life table study under different treatments (Table 3). The largest and smallest N_f/N values were 0.43 ± 0.04 and 0.07 ± 0.02 under WS and F-1b treatments, respectively. The largest and smallest N_m/N values were 0.44 ± 0.04 and 0.08 ± 0.02 under PDC and F-1b treatments, respectively. However, there were no significant differences between N_f/N and N_m/N in each treatment.

Table 3. The proportion of female and male adults emerging from eggs used at the beginning of the life table study according to wheat tissues.

Index	Treatments				
	WS	SPK	PDC	F-b	F-1b
N_f:N_m	62:56	56:70	62:65	29:33	11:12
N_f/N	0.43 ± 0.04 a	0.35 ± 0.04 a	0.42 ± 0.04 a	0.19 ± 0.03 b	0.07 ± 0.02 c
N_m/N	0.39 ± 0.04 a	0.43 ± 0.04 a	0.44 ± 0.04 a	0.23 ± 0.03 b	0.08 ± 0.02 c

Notes: WS: wheat seedling; SPK: spike; PDC: peduncle; F-b: flag leaf blade; and F-1b: blade of the first leaf under flag; Data are represented as mean ± SE. SEs were estimated with the bootstrap technique (100,000) in a TWOSEX-MS Chart program and data followed by different letters in the same row are results of the paired bootstrap test (α = 0.05).

3.2. Life Table Analysis

The egg-to-adult survival rates were 83.77%, 81.07%, 84.71%, 44.08%, and 17.65% when they fed on WS, SPK, PDC, F-b, and F-1b respectively. The age-stage specific survival rates (s_{xj}) showed the probability that a newborn would survive to age x and develop to stage j (Figure 1). For a specific treatment, there were overlaps in the stage survival curves owing to the variable developmental rates among individuals. The survival rate curves varied significantly between treatments. FAWs fed on PDC had the longest survival (67 d) compared with the other treatments (Figure 1). Larvae fed on PDC, F-b and F-1b had longer developmental times. For instars, feeding on F-b and F-1b caused steeper declines in survival compared with feeding on WS, SPK, and PDC (Figure 1). For pupa and adult stages, the survival rate curves were much lower for the population fed on PDC, F-b, and F-1b (Figure 1).

The plots of the l_x, m_x, f_{xj}, and l_xm_x curves are given for the different wheat tissues (Figure 2). Total female fecundity was statistically different among treatments (Table 3) and showed varying oviposition patterns (Figure 2). The l_x curve gave the probability that an egg would survive to age x by feeding on different wheat tissues (Figure 2). The l_x curves of FAWs that fed on SPK, PDC, F-b, and F-1b were different and extended until day 61, 67, 64, and 67, respectively. They were longer than for WS (58). The l_x curve of FAW fed on F-b and F-1b declined abruptly, and survival rates decreased to 50% on day 40, 40, 46, 26, and 19, respectively for WS, SPK, PDC, F-b, and F-1b, respectively. The l_x curves tended to be gentle in the later stages, indicating that the larval stage had the highest mortality. The curve of age-specific fecundity (m_x) showed that reproduction began at different ages depending on the tissue: 27, 29, 31, 30, and 32 days, respectively, for WS, SPK, PDC, F-b, and F-1b. The corresponding oviposition periods were 19, 23, 29, 21, and 21 days, respectively. The m_x, f_{xj}, and l_xm_x curves for the seedling stage were the highest

compared with other treatments. The peak oviposition day of m_x and $l_x m_x$ for WS, SPK, PDC, F-b, and F-1b was on day 31, 35, 38, 36, and 40 respectively. The maximum value for the age-stage specific fecundity for females (f_{x10}) that fed on WS, SPK, PDC, F-b, and F-1b was 247.76, 189.44, 104.81, 87.07, and 52.56, respectively. In addition, the m_x, f_{xj}, and $l_x m_x$ curves showed more fluctuations, indicating that emergence and oviposition were not concentrated but intermittent.

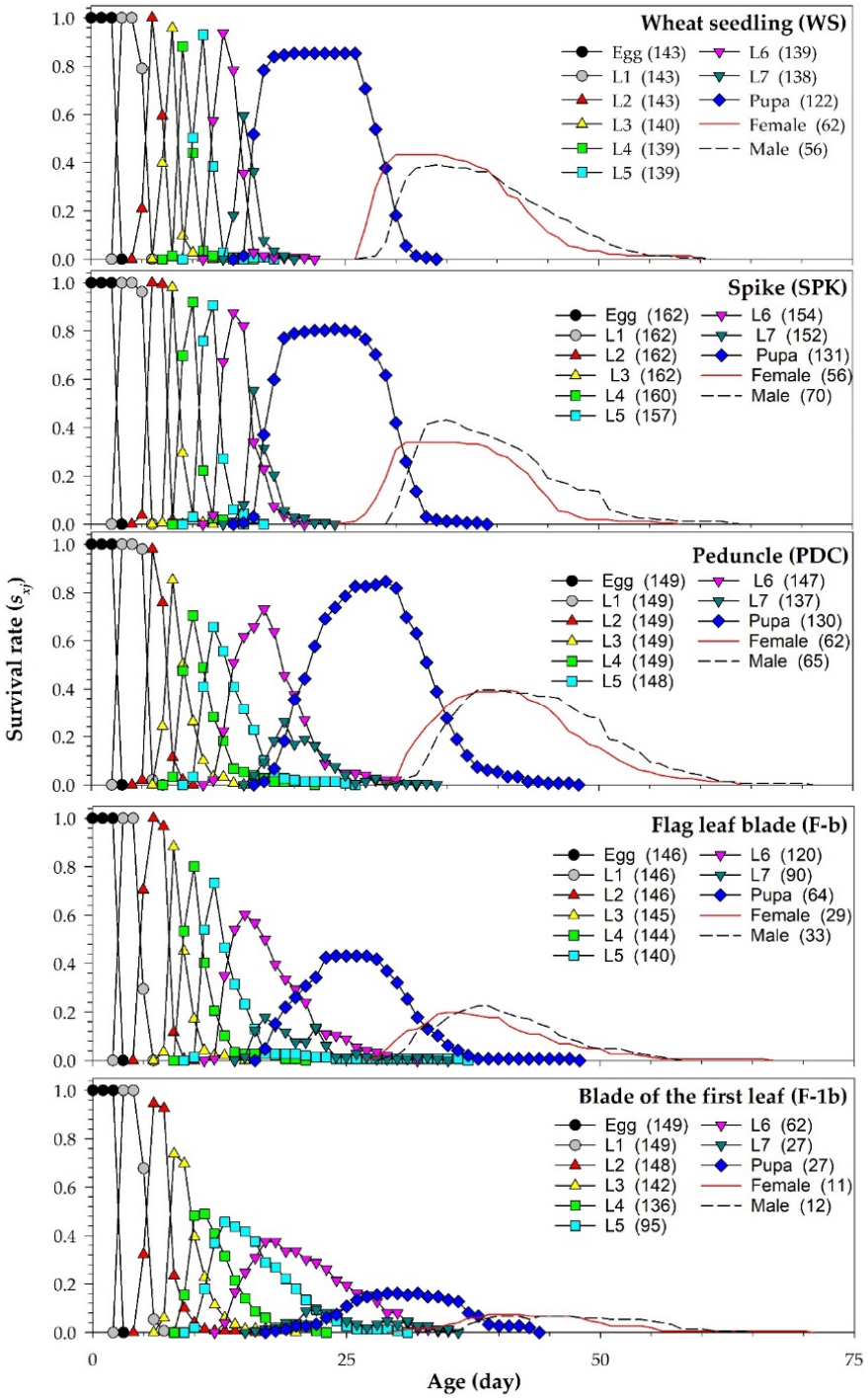

Figure 1. Age-stage specific survival rate (s_{xj}) of the FAW fed on different wheat tissues in the laboratory. Numbers in the bracket after each stage represent the number of individuals developed to that stage.

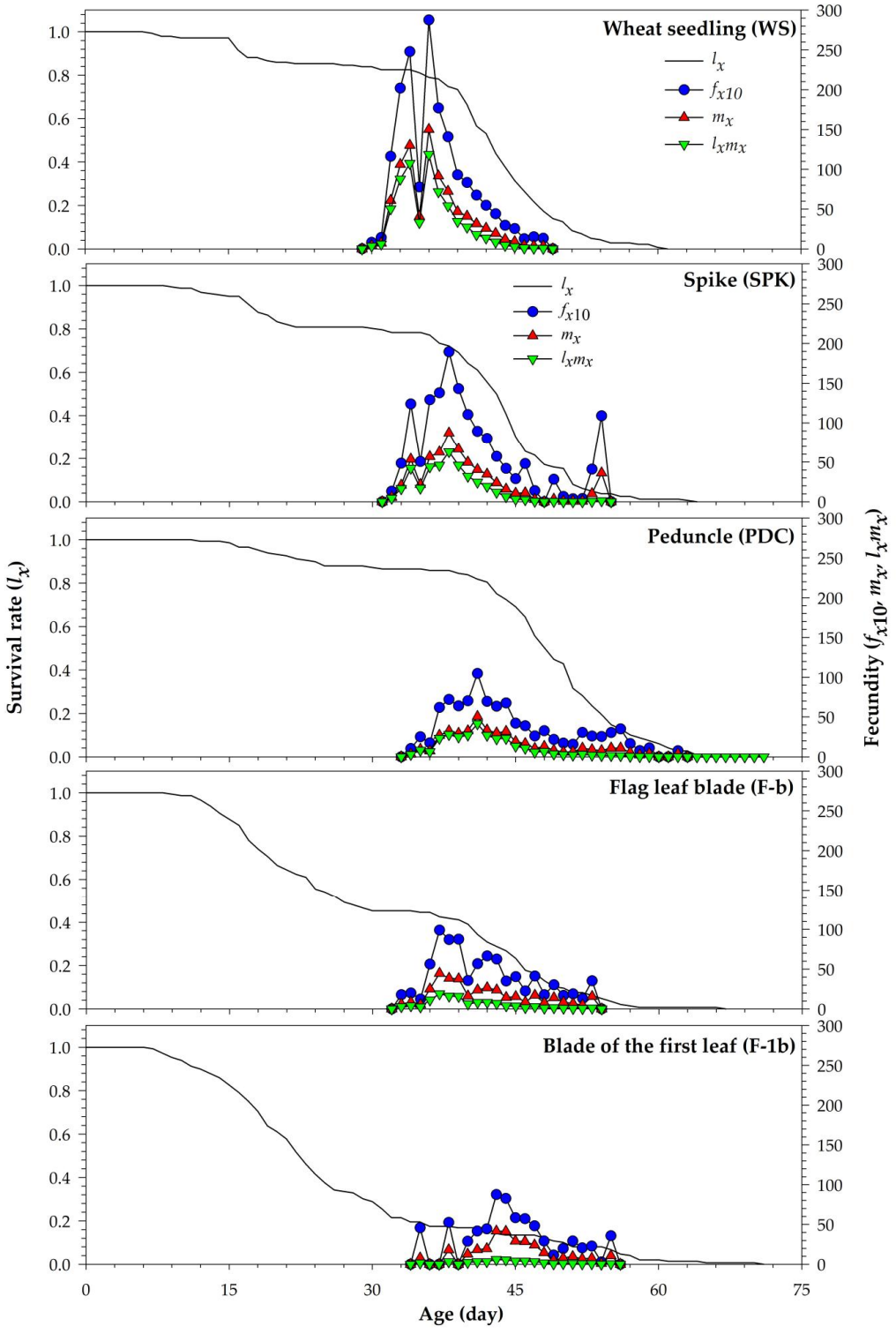

Figure 2. Age-specific survival rate (l_x), female age-specific fecundity (f_{x10}), age-specific fecundity of total cohort (m_x), and age-specific maternity ($l_x m_x$) of the FAW fed on different wheat tissues.

The life expectancy recorded under most of the treatments decreased with age, except for F-b or F-1b. For a new first instar fed on WS, SPK, PDC, F-b, and F-1b, it was 39.57, 38.47, 44.45, 29.76, and 23.28 d, respectively. However, the maximum life expectancy of the FAWs fed on F-b and F-1b was recorded at the pre-pupa (29.45) or pupa stage (33.22). This indicated that the larval stage had an important effect on life expectancy (Figure 3).

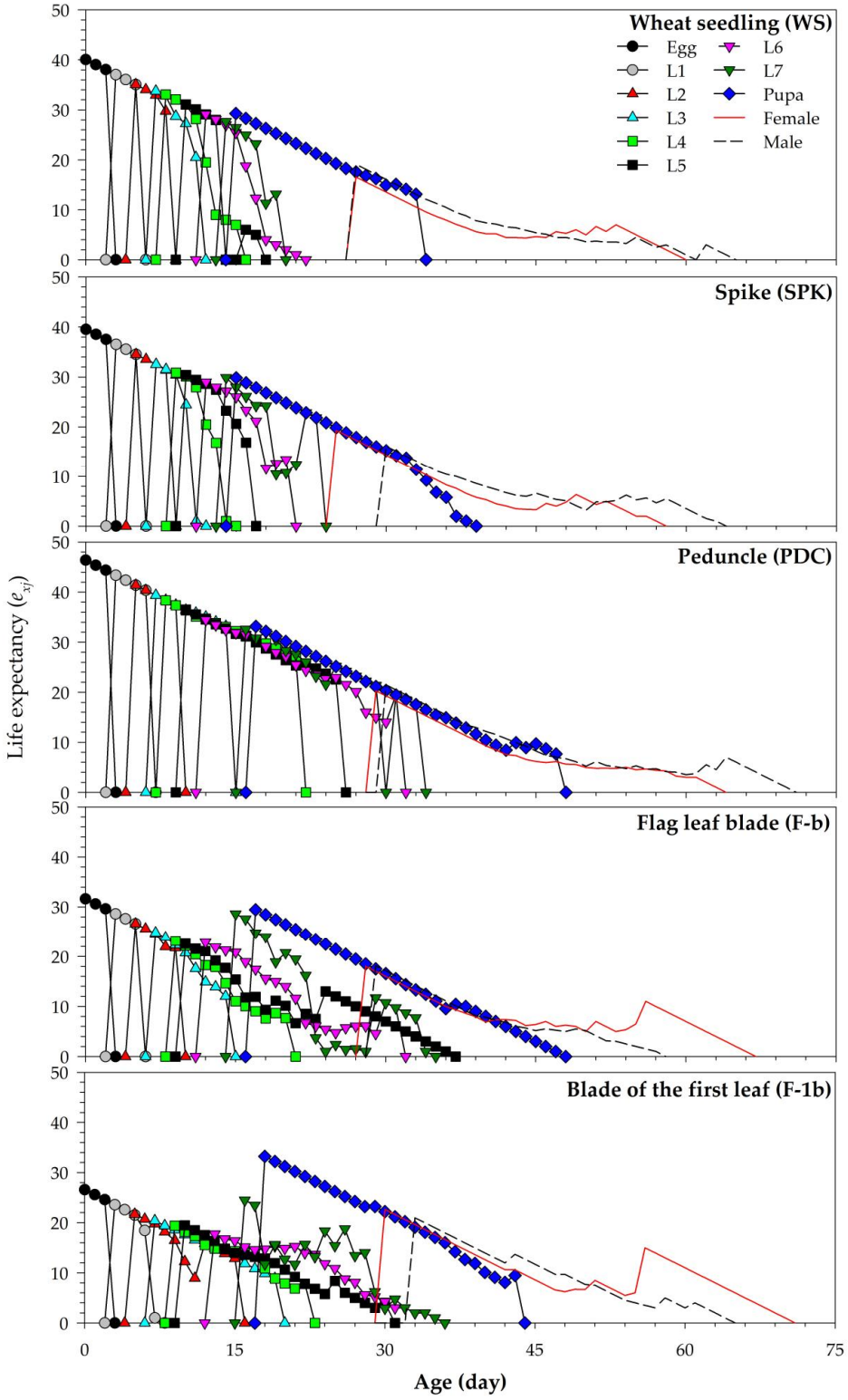

Figure 3. Age-stage-specific life expectancy (e_{xj}) of the FAW fed on different wheat tissues in the laboratory.

3.3. Effects on FAW Population Parameters

Paired bootstrap tests showed significant differences in life history parameters: mean generation time (T), net reproductive rate (R_0), intrinsic rate of increase (r), and finite rate of increase (λ) estimated at different treatments (Table 4). Specifically, FAWs reared

on WS had the shortest mean generation time (36.2480 ± 0.2719 d) but the largest net reproductive rate (645.1748 ± 73.116), intrinsic rate of increase (0.1785 ± 0.0038), and finite rate of increase (1.1954 ± 0.0045). Conversely, FAWs reared on the F-1b had the longest mean generation time (44.2694 ± 1.1160 d) but the smallest net reproductive rate (41.4430 ± 14.3762), intrinsic rate of increase (0.0841 ± 0.0091), and finite rate of increase (1.0878 ± 0.0099) (Table 4).

Table 4. Population parameters of the FAW fed on different wheat tissues in the laboratory.

Index	Treatments				
	WS	SPK	PDC	F-b	F-1b
R_0	645.1748 ± 73.1169 a	383.1481 ± 47.0621 b	290.7987 ± 37.1213 b	117.2877 ± 24.9445 c	41.4430 ± 14.3762 d
λ	1.1954 ± 0.0045 a	1.1681 ± 0.0043 b	1.1459 ± 0.0042 c	1.1270 ± 0.0065 d	1.0878 ± 0.0099 e
r	0.1785 ± 0.0038 a	0.1554 ± 0.0037 b	0.1362 ± 0.0036 c	0.1196 ± 0.0058 d	0.0841 ± 0.0091 e
T	36.2480 ± 0.2719 e	38.2740 ± 0.3487 c	41.6423 ± 0.4825 b	39.8491 ± 0.6113 d	44.2694 ± 1.1160 a

Notes: WS: wheat seedling; SPK: spike; PDC: peduncle; F-b: flag leaf blade; and F-1b: blade of the first leaf under flag; Data are represented as mean ± SE. SEs were estimated with the bootstrap technique (100,000) in a TWOSEX-MS Chart program and data followed by different letters in the same row are results of the paired bootstrap test ($\alpha = 0.05$).

4. Discussion

The FAW is a serious noctuid corn pest originating from North and South America. Its polyphagous nature, lack of a diapause mechanism, and periodic outbreak have been widely reported [1,2,4]. It invaded China via Yunnan province in 2019 and became established as another important pest due to factors, such as geography, climate, and crop distribution [9,10].

The FAW feeds on wheat by frequently eating out the heart or bud in fields during the seedling or ripening stage of wheat leaves and spikes, as do *Mythimna separata* and *Helicoverpa armigera*, to complete its development and cause damage [1,16,19,20]. Wheat is a better host for FAW and the FAW fed on wheat seedlings showed the greatest consumption and the shortest larva-adult period [14]. However, little was known about the effect of different wheat tissues on FAW development. Different wheat tissues have varying palatability and nutritional content that can have an impact on the growth of the FAW. Here, we used the life table method to illustrate how different wheat tissues affect its development. The FAW completed its development by feeding on WS, SPK, PDC, F-b, and F-1b, and there were no significant differences between N_f/N and N_m/N in any treatment. However different tissues resulted in significant differences in the developmental duration of the larval stage, the generation time, N_f/N and N_m/N. Those that fed on F-1b grew more slowly and experienced higher mortality than those that fed on other tissues. The developmental duration of larvae on the different tissues followed the sequence: WS (13.48 ± 0.07 d) < SPK (14.85 ± 0.10 d) < F-b (17.16 ± 0.34 d) < PDC (18.81 ± 0.26 d) < F-1b (21.44 ± 0.59 d). The developmental duration under WS and SPK treatments were nearly equal to those of stock populations (Appendix A Table A2). The sequence of the generation time was also similar (Tables 2 and 4), but if the larval duration were subtracted from the corresponding generation time, the residuals would be almost equal. This indicated that effects of the different wheat tissues contributed little to the development of the FAW during all but the larval stage. This point was confirmed in the outputs of the life table analysis, such as the age-specific survival rate (l_x) and age-specific life expectancy (e_{xj}) (Figures 2 and 3). The quality of host plant parts directly affected potential and actual herbivore fecundity [17]. This effect was confirmed by the results obtained from the FAW feeding on different wheat tissues (Tables 2 and 4). When sex was considered, N_f/N and N_m/N were significantly different among the treatments (Table 3).

The population parameters r and λ for the FAWs fed on different wheat tissues were greater than 0 and 1, respectively (Table 4). This indicated that all tissues were suitable. The values of most parameters from the WS and SPK were similar with those of stock populations (Appendix A Table A2), but changes in these values were likely to be reflected by the quality of the diet for the larvae [21]. In the field, the values of r and λ may be very

different from that recorded in the laboratory, because the FAW would encounter more complicated situations. Different patterns of host plant use by herbivorous insects are associated with the physiology, morphology, chemical and physical defenses of the host plant [30]. The SPK and PDC of these mature wheat plants may not be suitable for FAW larvae because their feeding on them was rarely recorded [1,15]. In this study, the FAW feeding on tender SPK and PDC achieved preferable fitness, but if its development were not completed on more suitable tissues, F-1bs and the lower leaves may be an important replacement food source to complete development. Wheat is China's second largest crop by planting area and widely distributed in the east. Wheat in China can be classified to spring wheat and winter wheat. Major spring wheat is distributed in the north of great wall and major winter wheat grows in the Huang–Huai–Hai region, the Yangtze River Region, and Southwest China. In the south of China, winter wheat is often planted adjacent to staggered maize fields where the FAW could achieve a continuous habitat that may result in an increased FAW population with the establishment of FAW populations south of 27° N in winter [10]. In China, migration FAW population is much smaller when compared to *M. separata* or *H. armigera* because at all levels the government paid greatest attention to it. Therefore, FAW did not break out in fields.

In the field, FAWs can damage corn plants in nearly all stages of development, but they concentrate on later plantings that have not yet silked. This indicates that late-planted wheat fields and later-maturing wheat are more likely to become infested [1,2,11]. For wheat production in the source area of FAW, staggered planting should be avoided to prevent the provision of a continuous habitat that may result in an increased FAW population. Staggered planting also exposes fields to higher infestations because FAWs feed on seedlings are likely to be fitter (Table 4). Therefore, dressing or coating, seeds with pesticide should be considered when planting wheat and FAW population monitoring needs to be increased during the seedling stage. From this research, we also confirmed that mature plants could suffer attack on reproductive structures because FAW can complete its development by feeding on SPK (Figures 1 and 2). The damage caused by feeding on reproductive structures is greater than on other parts [16,19]. The key time for wheat planting is from March to early June as this is important for yield formation. A large area of wheat planting that spans from the south of China (the source region) to the Yangtze river or Huang–Huai–Hai region (the transitional migration area) could serve as a large source of food for larvae. This study showed that the FAW could complete its development by feeding on different wheat tissues. If more FAWs are migrating to North China with a similar migration pattern to that of *M. separata*, which could migrate to the north and northeast of China in later April or early May, wheat may be a vital food resource for the migrating FAW population to feed on and may result in a greater risk due to the absence of maize during that period in the above-mentioned area. Thus, attention should be given to recording FAW occurrence and following provisions for their monitoring and forecasting, as well as their integrated management.

FAW larvae prefer to feed within the whorls of corn [1,2,7], but since the wheat plant has no whorl, larvae directly infest the leaves and stems, as was observed in cage trials [16]. This affects the efficacy of pesticides because they can be sprayed on directly. Feeding on wheat also exposes the larvae to more natural enemies, which leads to much lower r and λ values compared to those under laboratory conditions. The FAW wheat invasion could also change pesticide practices, which could result in a population dynamic in which resident insect communities are replaced, as happened in corn fields [31]. Therefore, attention should be paid to the risk and effects to other wheat insect pests.

5. Conclusions

The objective of this research was to study the effect of different wheat tissues on the developmental attributes and population parameters of the FAW. Here, we demonstrated that it could complete its development on all the wheat tissues tested. The wheat seedling was the best food for FAW growth, development, and reproduction, while SPK and PDC

were better for fitness. However, the F-b and F-1b resulted in significantly lower developmental success and fitness. Records of FAW field occurrence in 2019 and trials in cages also confirmed that the damage was most serious in the seedling stage. Because the FAW is expected to migrate in spring from overwintering areas to the Huang–Huai–Hai region, China's main wheat planting area, monitoring and protection of wheat plants at the middle to late stages during the growing season should be carried out because the SPK can serve as suitable food for the FAW.

Author Contributions: Z.Z. and Y.Z. designed the studies. B. and Y.J. reared the FAW and collected the data. Z.Z., B. and Y.Z. analyzed the data with the TWOSEX-MS Chart software. Z.Z. and B. wrote the original draft manuscript. X.L., Z.Z., A.Z., X.Z. and Y.Z. reviewed and revised the manuscript before submission. All authors have read and agreed to the published version of the manuscript.

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Appendix A

Table A1. Parameters, equations, and definitions used in this life table analysis.

Parameters and Equation	Explanation
$s_{xj} = \frac{n_{xj}}{n_{01}}$	Age-stage survival rate: n_{01} is the number of eggs used for life table study and n_{xj} is the number of surviving individuals at age x and stage j [28].
$N_f/N, N_m/N$	N_f/N: the proportion of female adults emerged from the N eggs used at the beginning of life table study. N_m/N: the proportion of male adults.
$l_x = \sum_{j=1}^{k} s_{xj}$	Age-specific survival rate: where k is the number of stages.
$f_{xj}, f_{x10} = \frac{E_{x10}}{n_{x10}}$	Age-stage-specific fecundity of individuals of n_{xj}. Because only female adults (the 10th stage) lay eggs, there is only f_{x10} in this study [32,33]; therefore, fx_{10} is the female age-stage-specific fecundity.
$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}}$	Age-specific fecundity of cohort: where k is the number of stages [32]. It is the mean fecundity of surviving individuals.
$l_x m_x = \sum_{j=1}^{k} s_{xj} f_{xj}$	Age-specific net maternity: the mean fecundity of the cohort at age x when the survival rate is considered [34].
$R_0 = \sum_{x=0}^{\infty} l_x m_x$	Net reproductive rate: the total offspring produced by an average individual during its lifetime. It is the sum of $l_x m_x$ over all age groups.
$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$	The Euler-Lotka equation was used to calculate the intrinsic rate of increase (r) with the age indexed from 0 [32].
$T = \frac{\ln R_0}{r}$	Mean generation time.
$\lambda = e^r$	Finite rate of increase
$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{k} S'_{iy}$	Age-stage life expectancy: S'_{iy} is the probability that an individual of age x and stage j will survive to age i and stage y by assuming s_{xj} = 1 [26].

Table A2. Population parameters of stock FAW population fed on corn seedlings in the laboratory.

Index	Mean ± SE	Index	Mean ± SE
Larval stage duration	16.31 ± 0.15	Pupae weight (mg)	180.30 ± 16.11
Pupae stage duration	10.95 ± 0.56	Fecundity (eggs/female)	825 ± 32
Adult longevity	13.06 ± 0.27	R_0	363.21 ± 31.56
N_f:N_m	92:88	λ	1.1978 ± 0.0037
N_f/N	0.4402 ± 0.0342	r	0.1805 ± 0.0031
N_m/N	0.4210 ± 0.0341	T	33.50 ± 0.24

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