

Article

Wheat-Bran-Based Artificial Diet for Mass Culturing of the Fall Armyworm, *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae)

Shishuai Ge ^{1,2}, Bo Chu ^{2,3}, Wei He ^{1,2}, Shan Jiang ^{2,4} , Chunyang Lv ², Lingyun Gao ^{2,3}, Xiaoting Sun ^{2,5}, Xianming Yang ² and Kongming Wu ^{2,*} 

- ¹ State Key Laboratory of Ecological Pest Control for Fujian and Taiwan Crops, Fujian Agriculture and Forestry University, Fuzhou 350002, China
- ² State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China
- ³ College of Plant Protection, Henan Agricultural University, Zhengzhou 450002, China
- ⁴ Key Laboratory of Economic and Applied Entomology of Liaoning Province, College of Plant Protection, Shenyang Agricultural University, Shenyang 110866, China
- ⁵ College of Tropical Crops, Hainan University, Haikou 570228, China
- * Correspondence: wukongming@caas.cn

Simple Summary: The fall armyworm (FAW), *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae), has become a global agricultural pest. Reducing the rearing cost of FAWs will be helpful for developing new environmentally friendly management strategies for this pest. As such, we researched an artificial wheat-bran-based diet for FAWs. The biological indicators (developmental duration, pupal weight, reproductive parameters, and flight ability) of the FAWs fed this diet were consistent with those of FAWs fed a traditional artificial diet in a laboratory setting. The rearing cost of using this new diet was lower by nearly 24%. These findings indicate that this artificial diet, based on wheat bran, is suitable for rearing FAW larvae, which will effectively reduce the rearing cost of FAWs.



Citation: Ge, S.; Chu, B.; He, W.; Jiang, S.; Lv, C.; Gao, L.; Sun, X.; Yang, X.; Wu, K. Wheat-Bran-Based Artificial Diet for Mass Culturing of the Fall Armyworm, *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae). *Insects* **2022**, *13*, 1177. <https://doi.org/10.3390/insects13121177>

Academic Editor: Brian T. Forschler

Received: 21 November 2022

Accepted: 17 December 2022

Published: 19 December 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Abstract: *Spodoptera frugiperda* Smith (fall armyworm (FAW)) has invaded many countries in Africa and Asia in recent years, considerably restricting global agricultural production. In this study, we assessed the rearing performance of four artificial diets (D₁: an artificial FAW diet based on wheat bran and soybean, maize, and yeast powders; D₂: an artificial diet developed for *Helicoverpa armigera* (Hübner), based on wheat bran and soybean and yeast powders; D₃: an artificial diet based on soybean powder; D₄: an artificial diet based on wheat bran) for FAWs. We designed D₄ based on a traditional diet (D₂) but substituted the wheat bran for soybean and yeast powders. At 25 ± 1 °C, 75% ± 5% RH, and a 16:8 h L:D photoperiod, the larval stage of FAWs fed on D₄ lasted 15.88 d, the pupal stage lasted 9.48 d, the pupal mass was 270.45 mg, the number of eggs deposited was 1364.78, and the mating rate was 89.53%. Most biological indicators of the larvae that were fed D₄ were basically consistent with those of the larvae fed on the traditional diet (D₂), but the intrinsic rate of increase (*r*), finite rate of increase (*λ*), and net reproduction rate (*R*₀) of the D₄ FAWs were lower than those of the D₂ FAWs. The flight capacity (flight distance, duration, and velocity were 19.73 km, 6.91 h, and 2.90 km/h, respectively) of the D₄ FAWs was comparable to that of the FAWs fed a traditional diet and maize leaves. Compared with the three other formulas, the cost of using D₄ was lower by 26.42% on average. These results show that using cheap wheat bran instead of soybean flour and yeast powder as the basic material for an artificial diet for FAWs is feasible, which will substantially reduce rearing costs and promote the development of new controlling measures for FAWs. In addition, this study also has a reference value for reducing the cost of artificial diets for other insects.

Keywords: fall armyworm; artificial diet; mass rearing; developmental period; flight ability

1. Introduction

Spodoptera frugiperda (J.E. Smith) (fall armyworm (FAW)) originates from the tropical and subtropical regions of the Americas [1] and has recently developed into an important global agricultural pest [2–5]. FAWs are polyphagous herbivores [1,6]; the larvae can feed on a variety of important food and cash crops, such as maize, wheat, rice, cotton, sugarcane, and soybean. The invasive populations of FAWs are mainly maize-strain specific [7]: the preferred host is maize, and the seedlings and tender parts of maize plants are the preferred parts. Pest attacks can reduce maize production levels by 12% [8] and by over 40% in severely affected areas [9].

Chemical control strategies are still the main measures used against FAWs in many areas, especially in newly invaded areas (such as Africa and south and southeast Asia). The long-term use of chemical pesticides leads to a series of problems, such as environmental pollution, the killing of natural enemies, and enhanced pest resistance [10]. Studies have shown that FAW populations have developed high resistance to dozens of insecticides, e.g., carbamate, organophosphates, and pyrethroids [7,11,12]. Moreover, due to the long-term, large-scale planting of transgenic insect-resistant maize in the Americas, FAWs have also developed a certain resistance to most transgenic maize varieties [13–15]. For example, Cry1F maize was first commercially planted in Brazil in 2009, and FAWs became resistant to it within three years [16].

The long-term use of chemical pesticides or planting a single resistant crop variety does not conform to the ideal of integrated pest management (IPM). Sterile insect technology (SIT) is an environmentally friendly strategy with considerable potential [17]. Since the 1950s, SIT has been widely used to control a variety of agricultural pests and threats to human health [18–20]. SIT has been used to control the lepidopteran pests *Pectinophora gossypiella* (Saunders) and *Cydia pomonella* (L.) in the United States and Canada, respectively, achieving effective results [21,22]. We recently evaluated the effects of X-ray irradiation on FAWs and determined the appropriate doses for sterilization [23]. After irradiation with a dose of 250 Gy, the sterility rate was more than 85%, dramatically limiting the number of offspring. We thus theoretically confirmed the feasibility of using SIT via X-ray radiation for the control of FAWs in the field. Although the FAW is a typical migratory insect [24,25], due to the absence of diapause [1], this insect may mainly concentrate in maize fields as a year-round breeding ground, particularly in winter. Southwest China is a suitable wintering area for FAW, and sweet maize is one of the preferred hosts of FAW [26]. Sweet maize, as a fresh food, provides considerable economic benefits to the local area; thus, chemical pesticides and resistant plant varieties cannot be used to control local pests. Thus, we think the application of SIT in winter may be an effective method of controlling FAWs in their year-round breeding grounds. SIT requires a sufficient supply of FAWs for field release. In addition, the use of natural enemy insects and viral pesticides for pest control is rapidly developing [27–29] and producing these products will also require large quantities of FAWs.

In response to various research and economic needs, artificial diets for rearing insects in the laboratory have rapidly developed [30–32]. Given the economic importance of the FAW, especially with its worldwide spread, studies of artificial diets for FAWs have rapidly increased in recent years [33–39]. The basic materials used in FAW diets are soybean flour, wheat germ, and yeast powder [33–39]. The generally high price of these materials made rearing FAWs extremely expensive, which limited the development of various studies on FAWs. As such, in this study, we aimed to produce a cost-effective FAW artificial diet to reduce the rearing costs. We used two artificial and two traditional diets as follows: D₁: an artificial diet based on soybean, maize, and yeast powders and wheat bran; D₂: an artificial *Helicoverpa armigera* (Hübner) diet based on soybean and yeast powders and wheat bran; and two new diets designed based on D₂, i.e., D₃ (based on soybean powder) and D₄ (based on wheat bran). We assessed the effects of these diets, using a diet of maize leaves as the control, on the development, survival, reproduction, and flight ability of FAWs using two

sex life tables and a flight mill and evaluated the basic material costs and economic benefits of these diets.

2. Materials and Methods

2.1. Insects

In January 2019, we collected FAW larvae from maize fields in Dehong Prefecture (Yunnan, China). We transported the larvae to the laboratory and fed them maize leaves until pupation. After eclosion, we left the moths to lay eggs. We kept the offspring larvae in transparent plastic containers (22 × 15 × 8 cm; 30–40 individuals per container) and fed them an artificial diet (D₂) [40], thus establishing a laboratory FAW colony. We reared both the larvae and adults under controlled conditions at 25 ± 1 °C, 70% ± 10% RH, and a 16:8 h L:D photoperiod. At the time of this study, the FAWs of the laboratory population had been reared over 20 generations with no abnormalities, which indicated that D₂ fully met the long-term rearing needs of FAWs.

2.2. Diet Formula and Preparation Method

Both D₃ and D₄ were based on D₂. We designed D₃ by replacing all the wheat bran and yeast powder in D₂ with soybean flour, and we designed D₄ by replacing all the soybean flour and yeast powder in D₂ with wheat bran. The specific formulas of the four diets are shown in Table 1.

Table 1. Formulas of four artificial diets fed to fall armyworms (*Spodoptera frugiperda*).

Material	D ₁	D ₂	D ₃	D ₄
Wheat bran (g)	50	150	-	260
Soybean powder (g)	40	80	260	-
Maize powder (g)	100	-	-	-
Yeast powder (g)	30	30	-	-
Agar (g)	24	20	20	20
Casein (g)	40	40	40	40
Sorbic acid (g)	3	3	3	3
Ascorbic acid (g)	3.5	3	3	3
Vitamins (g)	0.15	0.1	0.1	0.1
Formaldehyde (mL)	4	2	2	2
Glacial acetic acid (mL)	4	4	4	4
Distilled water (mL)	1200	1500	1500	1500

The composition of vitamins was as follows: aneurine hydrochloride (7.6%), riboflavin (15.2%), nicotinic acid (30.4%), D-pantothenic acid hemicalcium salt (30.4%), pyridoxine hydrochloride (7.6%), cyanocobalamin (0.6%), folic acid (7.6%) and nicotinamide (0.6%).

We sterilized the wheat bran, soybean powder, and maize powder in a pressure cooker (120 °C, 30 min) before use. We weighed each substance according to the diet formulas provided in Table 1. According to the type of diet, we placed the wheat bran and soybean, yeast, and maize powders into a container and mixed them well. We heated 800 mL of distilled water (D₁: 500 mL) to boiling point and added sorbic acid, waited for the sorbic acid to dissolve, then poured it into the container and stirred well. We heated 600 mL of distilled water, added agar and casein, continuously stirred until it boiled, and then poured the mixture into the container and stirred well. We dissolved ascorbic acid and vitamins into 100 mL of distilled water, which we added to the container when the temperature had decreased to approximately 40 °C. We then added formaldehyde and glacial acetic acid, stirred well, and poured the mixture into a sterilized box, which was cooled to room temperature and placed in a sealed refrigerator at 4 °C.

In addition to the four diets, we also used maize leaves to rear FAWs as the experimental control. We used the maize variety, Zhengdan 958 (Henan Qiule Seeds Technology, Co., Ltd., Zhengzhou, China). We cultivated the maize indoors under conditions of 26 ± 1 °C, 80% ± 5% RH, and a 16:8 h L:D photoperiod. We fed maize seedlings to the larvae at the 2–3-leaf stage.

2.3. Experimental Assays

2.3.1. Effects of Different Diets on Development, Survival, and Reproduction of FAWs (*Spodoptera frugiperda*)

For the experiments, we reared FAWs in climate chambers (MGC- 450HP; Yiheng Technology Instrument Co., Ltd., Shanghai, China) with 5000 Lx illumination at 25 °C, 75% RH, and a 16:8 h L:D photoperiod. Each diet treatment consisted of 80 FAW individuals, with three replicates giving a total of 240 individuals. We collected egg masses deposited by adults from the laboratory colony at the same time and observed them daily until hatching. We placed the newly hatched larvae in plastic cups (25 mL, 38 × 30 × 30 mm) with an appropriate amount of diet or maize leaves. To prevent mechanical damage to or the death of larvae caused by human operation, we added 2–3 larvae to each cup, and we left one randomly selected healthy larva in the cup on the following day. We transferred the other larvae to a new cup (1 larva/cup), which we fed in the same way until the emergence and testing of their flight ability. We renewed the diets every 2–3 days (the maize leaves were changed daily) to avoid the influence of food freshness on the experimental results. We recorded the development and survival of the larvae daily until pupation. We determined the larval instar by the number of molts. The pupae were fragile at the early stage, so we weighed them on an electronic balance (0.0001 g, Mettler Toledo ME204; Beijing Haitian Youcheng Technology Co., Ltd., Beijing, China) on the third day after pupation. We checked the pupae for survival daily until death or eclosion. Following adult eclosion, we recorded the adult sex and checked the adults for deformity. We recorded the longevity of any deformed adult as 1 day. We paired healthy adults in disposable plastic cups (500 mL) (1 mating pair/cup). We covered each plastic cup with sterile gauze for collecting the egg masses and placed a cotton ball immersed in 10% v/v honey/water solution at the bottom of the cup to provide water and nutrients to the FAWs. On a daily basis, we refreshed the cotton ball and the gauze with egg masses. We replaced the cup if the egg masses were deposited on the cup wall or bottom. We documented the pre-oviposition period, daily fecundity, oviposition period, egg hatchability, and adult longevity. We determined the mating status via the presence of spermatophores in the female after death.

2.3.2. Effects of Diet on Flight Ability of FAWs (*Spodoptera frugiperda*)

We transferred the adults in each diet treatment to different cages after eclosion and fed them a 10% v/v honey/water solution. We individually attached 2-day-old adults to a flight mill (FXMD-24-USB flight mill; Jiaduo Science, Industry and Trade Co., Ltd., Hebi, China) in artificial climate chambers using the method described by Ge et al. [41]. We gently collected active, undamaged adults from the rearing cage. We expanded their wings, brushed the scales from the junction of the abdomen and thorax, and performed tethering using a small droplet of cyanoacrylate glue (Deli Group Co., Ltd., Zhejiang, China). After the moths recovered, we attached only undamaged and active individuals to the flight mill, which was kept under 25 °C and 75% RH. The chamber was completely darkened, and the moths were allowed to engage freely in tethered flight. We conducted these tests from 8 p.m. until 8 a.m. the following day (Chinese standard time).

2.3.3. Comparison of Cost of Different Diets

The purchase price of each material used in the diets and each vitamin are shown in Tables S1 and S2, respectively. According to Tables 1, S1 and S2, we calculated the weight and material cost of each diet. Then, we accordingly assessed the costs of culturing 1 million FAWs.

2.4. Data Analyses

To assess the effects of different diets (and maize leaves) on the development, reproductive parameters, and flight ability of FAWs, we used a one-way analysis of variance (ANOVA) followed by Tukey's HSD post hoc test. Before ANOVA, we first tested the data for normality using the Shapiro–Wilk test and for homogeneity of variances using

Levene's test. If the data did not meet the conditions, we performed arcsine transformation; proportional data were arcsine square-root-transformed. We analyzed the interaction of diet and sex (with diet and sex as the fixed effects) on the development and pupal weight of FAWs using a general linear mixed model. We used log-rank (survival analysis) testing for differences and linear trends in the survival curves of FAWs fed different diets. We used SPSS Statistics for Windows, version 20.0 (IBM, Armonk, NY, USA) for the above analyses, with a significance level of $p < 0.05$. We used TWOSEX-MSChart to investigate the life tables (l_x , f_x , m_x , and $l_x m_x$) and demographic parameters (R_0 , T , r , and λ) [42–45]. We used a paired bootstrap test with 100,000 replications in TWOSEX-MSChart for the precise estimation of the mean and standard error among the demographic parameters of FAWs fed different diets [43,46].

3. Results

3.1. Developmental Period and Reproductive Parameters

The diets considerably affected the developmental period of the FAWs at each life stage, except for the egg stage (Table 2). Specifically, the developmental duration of each instar phase significantly differed (first-instar larvae: $F_{4, 1195} = 22.043$, $p < 0.001$; second-instar larvae: $F_{4, 1195} = 200.981$, $p < 0.001$; third-instar larvae: $F_{4, 1190} = 72.966$, $p < 0.001$; fourth-instar larvae: $F_{4, 1188} = 88.444$, $p < 0.001$; fifth-instar larvae: $F_{4, 1183} = 177.289$, $p < 0.001$; sixth-/seventh-instar larvae: $F_{4, 1050} = 160.393$, $p < 0.001$), the larval stage ($F_{4, 1050} = 504.817$, $p < 0.001$), pupal stage ($F_{4, 901} = 19.146$, $p < 0.001$), egg-pupa stage ($F_{4, 901} = 287.092$, $p < 0.001$), adult stage ($F_{4, 901} = 17.257$, $p < 0.001$), and total generations ($F_{4, 901} = 17.020$, $p < 0.001$) among the different diet treatments. FAWs that were fed maize leaves (14.22 d) had the shortest larval stages, followed by FAWs fed with D₂ (15.54 d) and D₄ (15.88 d). The larval stages in the D₁ (18.90 d) and D₃ (20.94 d) groups were significantly longer than those of FAWs fed on other diets, and some larvae developed into the seventh instar. The pupal stage of D₄-fed FAWs was significantly shorter than that of FAWs fed the other three diets, but we found no significant difference between D₄ and maize leaves. The adult stage of D₂-fed FAWs was the longest (14.63 d), followed by that of those fed D₄ (13.70 d), with no significant difference between them. The adult stage of D₃-fed FAWs was the shortest, only 9.96 days. FAWs fed maize leaves had the shortest total generation (39.86 d); FAWs fed D₁ had the longest total generation (44.70 d). We found significant differences among the different diet treatments in pupal mass ($F_{4, 901} = 120.395$, $p < 0.001$), with the highest in D₄ (270.45 mg) and the smallest in the maize leaf group (209.17 mg).

The diets notably affected the reproduction of FAWs (Table 2). The pre-oviposition period ($F_{4, 353} = 3.219$, $p = 0.013$), oviposition period ($F_{4, 353} = 10.608$, $p < 0.001$), eggs deposited per female ($F_{4, 353} = 17.466$, $p < 0.001$), and mating rate ($F_{4, 10} = 4.961$, $p = 0.018$) significantly differed among the different diet treatments. FAWs fed on maize leaves (3.96 d) had the shortest pre-oviposition period, with no significant difference among the four artificial diets. The oviposition period and eggs deposited per female did not differ among the FAW groups fed D₂, D₄, and maize leaves and were significantly higher than those in D₁ and D₄. The mating rate of the D₃-fed FAWs was significantly lower than that of those fed maize leaves, with no significant difference among the other diet treatments.

The larval stage ($F_1 = 5.087$, $p = 0.024$), pupal stage ($F_1 = 273.503$, $p < 0.001$), total generation ($F_1 = 27.84$, $p < 0.001$), and pupal mass ($F_1 = 26.376$, $p < 0.001$) differed between the sexes among the different diet treatments, with no significant differences between the sexes in the adult stage ($F_1 = 2.906$, $p = 0.089$). We noted significant diet \times sex interactions in the pupal stage ($F_4 = 11.997$, $p < 0.001$), adult stage ($F_4 = 3.477$, $p = 0.008$), total generation ($F_4 = 4.305$, $p = 0.002$), and pupal mass ($F_4 = 3.096$, $p = 0.015$). The larval stage, pupal stage, adult stage (except D₃ and D₄), total generation, and pupal weight of females were smaller than those of males (Figure 1).

Table 2. Mean duration and reproductive performance (\pm SE) of developmental stages of FAWs (*Spodoptera frugiperda*) fed different diets.

Parameter	D ₁	D ₂	D ₃	D ₄	Maize Leaves
Egg (day)	3.00 \pm 0.00	3.00 \pm 0.00	3.00 \pm 0.00	3.00 \pm 0.00	3.00 \pm 0.00
1st-instar larva (day)	3.15 \pm 0.02 b	3.12 \pm 0.02 bc	3.08 \pm 0.02 cd	3.26 \pm 0.03 a	3.00 \pm 0.00 d
2nd-instar larva (day)	2.25 \pm 0.03 b	1.97 \pm 0.02 c	2.37 \pm 0.03 a	1.90 \pm 0.03 c	1.36 \pm 0.03 d
3rd-instar larva (day)	2.24 \pm 0.03 b	2.04 \pm 0.03 c	2.56 \pm 0.07 a	2.15 \pm 0.03 bc	1.55 \pm 0.03 d
4th-instar larva (day)	2.27 \pm 0.03 b	1.57 \pm 0.03 d	2.75 \pm 0.10 a	1.83 \pm 0.03 c	1.74 \pm 0.03 cd
5th-instar larva (day)	3.08 \pm 0.05 b	2.10 \pm 0.02 c	3.50 \pm 0.09 c	2.18 \pm 0.03 c	2.04 \pm 0.02 a
6th-/7th-instar larva (day)	5.91 \pm 0.08 b	4.73 \pm 0.04 c	6.47 \pm 0.11 a	4.62 \pm 0.04 c	4.50 \pm 0.06 c
Larval stage (day)	18.90 \pm 0.08 b	15.54 \pm 0.06 c	20.94 \pm 0.27 a	15.88 \pm 0.06 c	14.22 \pm 0.08 d
Pupa (day)	10.22 \pm 0.07 a	10.08 \pm 0.06 ab	9.82 \pm 0.08 bc	9.48 \pm 0.06 d	9.74 \pm 0.07 cd
Egg-pupa (day)	32.10 \pm 0.12 b	28.59 \pm 0.10 c	33.80 \pm 0.33 a	28.40 \pm 0.10 c	27.01 \pm 0.13 d
Adult longevity (day)	12.60 \pm 0.36 b	14.63 \pm 0.31 a	9.96 \pm 0.50 c	13.70 \pm 0.47 ab	12.85 \pm 0.42 b
Total generation (day)	44.70 \pm 0.39 a	43.28 \pm 0.33 ab	42.29 \pm 0.55 b	42.10 \pm 0.49 b	39.86 \pm 0.42 c
Pupal mass (mg)	241.00 \pm 1.98 c	261.65 \pm 1.90 b	231.48 \pm 3.35 d	270.45 \pm 1.64 a	209.17 \pm 2.22 e
Pre-oviposition period (day)	4.85 \pm 0.21 a	4.58 \pm 0.21 ab	4.21 \pm 0.24 ab	4.71 \pm 0.18 ab	3.96 \pm 0.16 b
Oviposition period (day)	5.22 \pm 0.23 b	6.84 \pm 0.21 a	4.90 \pm 0.29 b	6.26 \pm 0.27 a	6.32 \pm 0.23 a
Eggs deposited per female (<i>n</i>)	859.69 \pm 43.40 b	1439.16 \pm 53.71 a	1005.38 \pm 77.77 b	1364.78 \pm 70.51 a	1261.41 \pm 62.72 a
Mating rate (%)	86.57 \pm 2.11 ab	93.93 \pm 1.92 ab	83.89 \pm 2.98 b	89.53 \pm 2.13 ab	94.86 \pm 1.43 a

Values in the same row followed by different lowercase letters indicate significant differences between different diets (one-way ANOVA, Tukey’s HSD; $p < 0.05$).

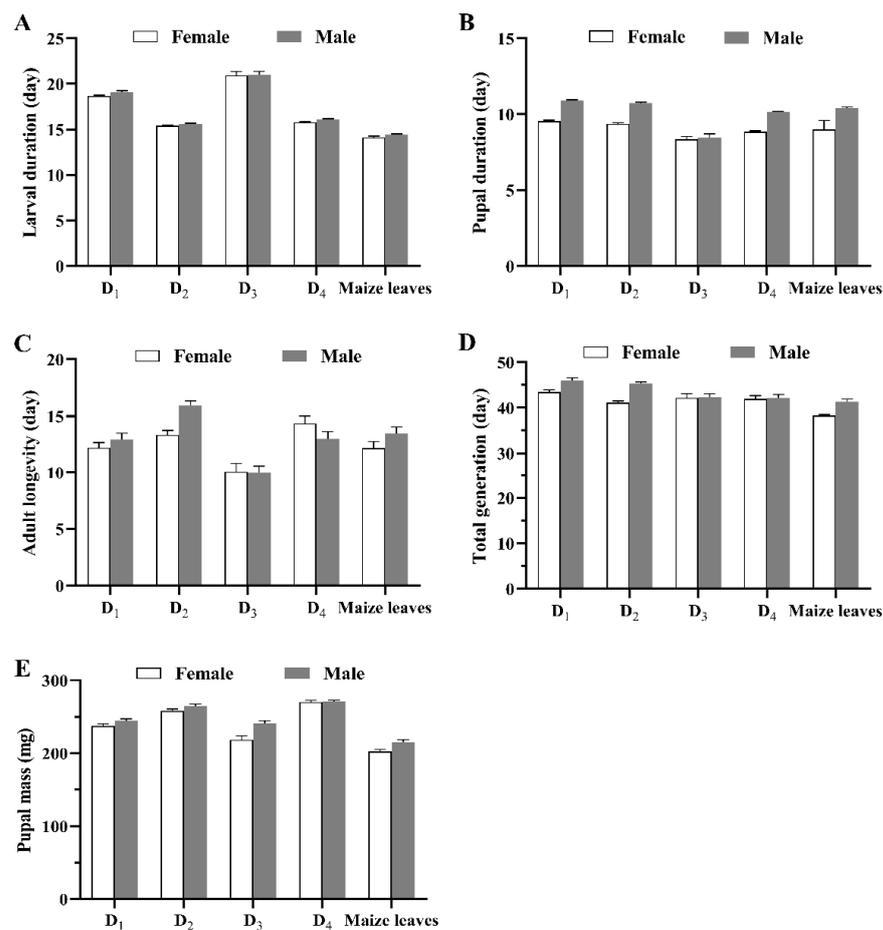


Figure 1. Mean duration (\pm SE) of developmental stages ((A): larval duration; (B): pupal duration; (C): adult longevity; (D): total longevity) and pupal mass (E) of female and male *Spodoptera frugiperda* individuals fed different diets.

3.2. Survival Rate, Fecundity and Life Expectancy

Diet strongly affected the age-stage survival rate (s_{xj}) of the studied *Spodoptera frugiperda* individuals (Figure 2). We identified significant differences in the larval survival rate among FAWs fed different diets ($F_{4,10} = 6.392, p = 0.008$); the larval survival rate of D₃-fed FAWs (71.25%) was significantly lower than that of the D₂-fed FAWs (98.33%), with no significant difference among the other diet treatments. The pupal survival rate did not significantly differ among the diet treatments ($F_{4,10} = 1.669, p = 0.233$). We found significant differences in the adult deformity rate of FAWs fed different diets ($F_{4,10} = 8.836, p = 0.003$), with the highest adult deformity rate occurring in the group fed D₃ (14.36%), followed by those fed with D₄ (6.05%) and maize leaves (5.67%) (Table 3).

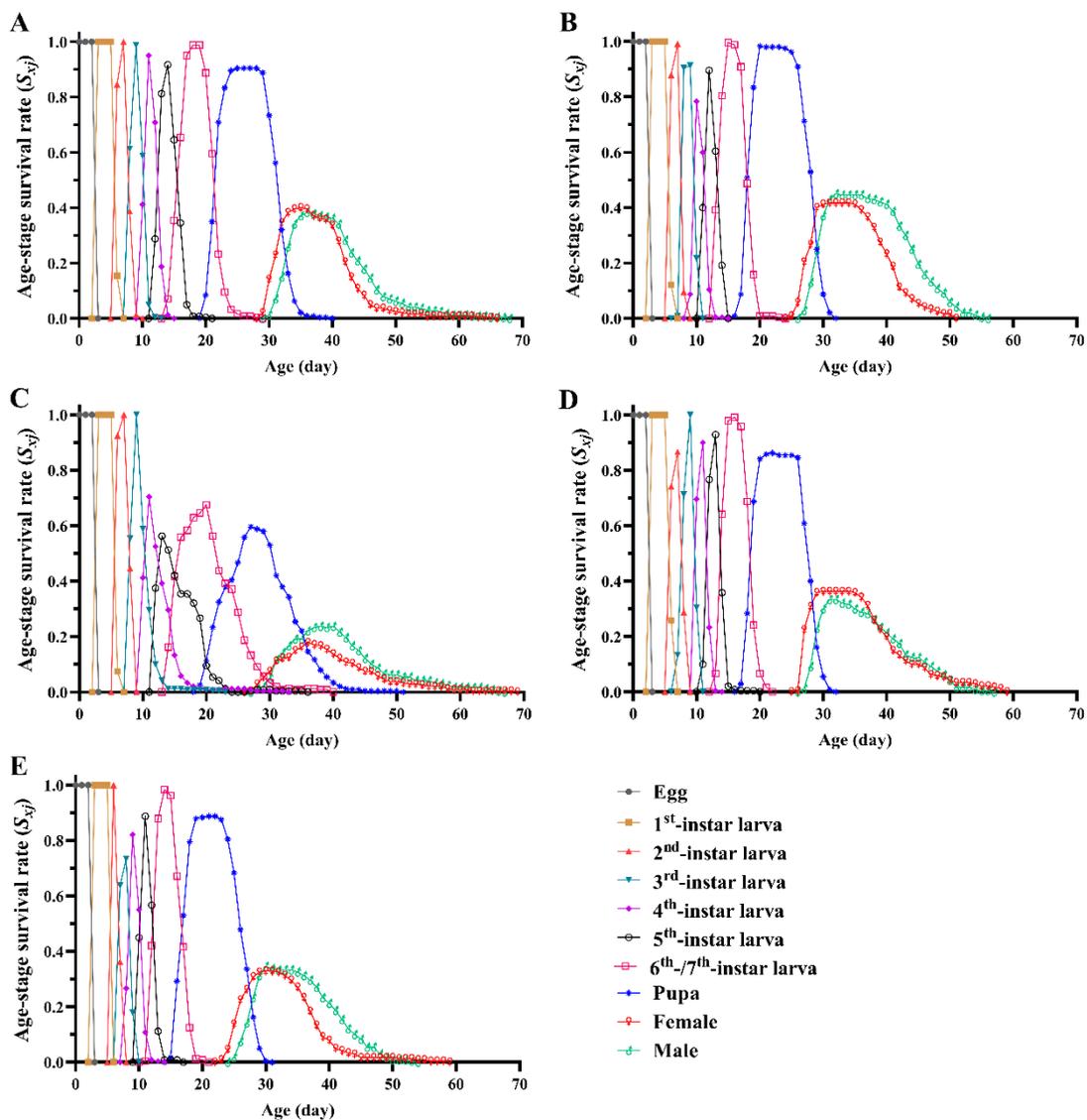


Figure 2. Age-stage survival rate (s_{xj}) of *Spodoptera frugiperda* individuals fed different diets. (A): D₁; (B): D₂; (C): D₃; (D): D₄; (E): maize leaves.

The results of the survival analysis indicated significant differences in the age-specific survival rate (l_x) of the FAW groups fed different diets ($\chi^2 = 63.168, df = 4, p < 0.001$), with a significant linear trend ($\chi^2 = 52.905, df = 1, p < 0.001$) (Figure 3). The maximum value of age-specific fecundity of female adults (f_x) fed D₁, D₂, D₃, D₄, and maize leaves was 132.16, 241.36, 130.90, 228.68, and 227.29, respectively. The age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) curves indicated that the order of peak oviposition day was

maize leaves > D₄ = D₂ > D₁ > D₃. The maximum values of m_x of the FAW groups fed D₁, D₂, D₃, D₄, and maize leaves occurred on days 37, 33, 35, 33 and 30, respectively; and on days 37, 33, 42, 33, and 30 for $l_x m_x$, respectively. The age-stage specific life expectancy (e_{xj}) curve showed that the life expectancy was longer for the FAWs fed D₁ and D₃, with the shortest e_{xj} occurring for those fed D₂ (Figure 4).

Table 3. Larval and pupal survival rate and adult deformity rate of FAWs (*Spodoptera frugiperda*) fed different diets.

Parameters	D ₁	D ₂	D ₃	D ₄	Maize Leaves
Larval survival rate %	92.08 ± 2.08 ab	98.33 ± 1.10 a	71.25 ± 8.20 b	87.08 ± 4.81 ab	90.83 ± 2.08 ab
Pupal survival rate %	86.44 ± 2.83 a	91.55 ± 2.89 a	89.29 ± 3.63 a	85.15 ± 5.40 a	78.87 ± 2.15 a
adult deformity rate %	0.57 ± 0.56 c	2.37 ± 0.49 bc	14.36 ± 3.48 a	6.05 ± 2.32 ab	5.67 ± 1.91 abc

Values in the same row followed by different lowercase letters indicate a significant difference between different diets (one-way ANOVA, Tukey’s HSD; $p < 0.05$).

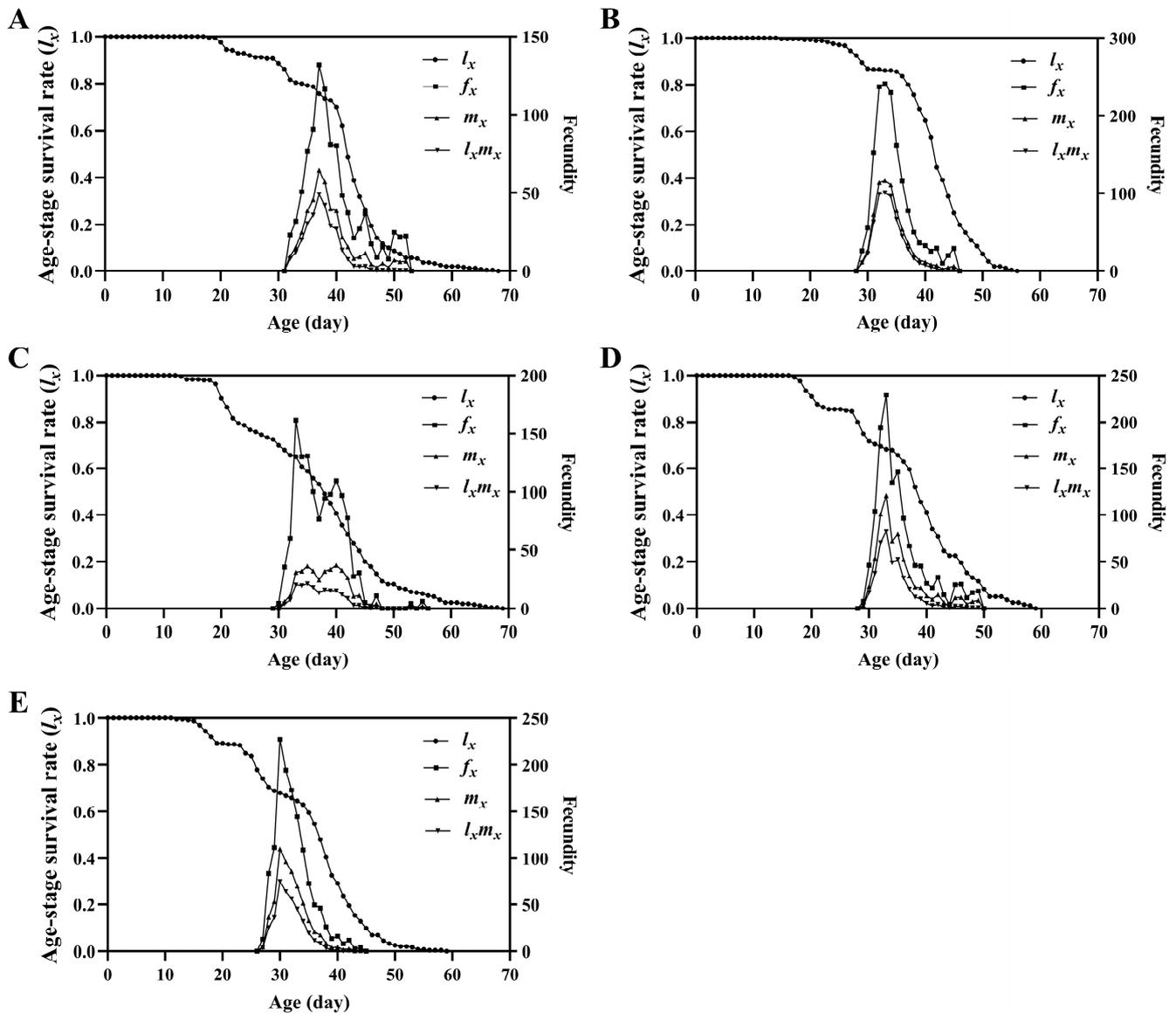


Figure 3. Age-specific survival rate (l_x), age-specific fecundity of female adults (f_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *Spodoptera frugiperda* individuals fed different diets. (A): D₁; (B): D₂; (C): D₃; (D): D₄; (E): maize leaves.

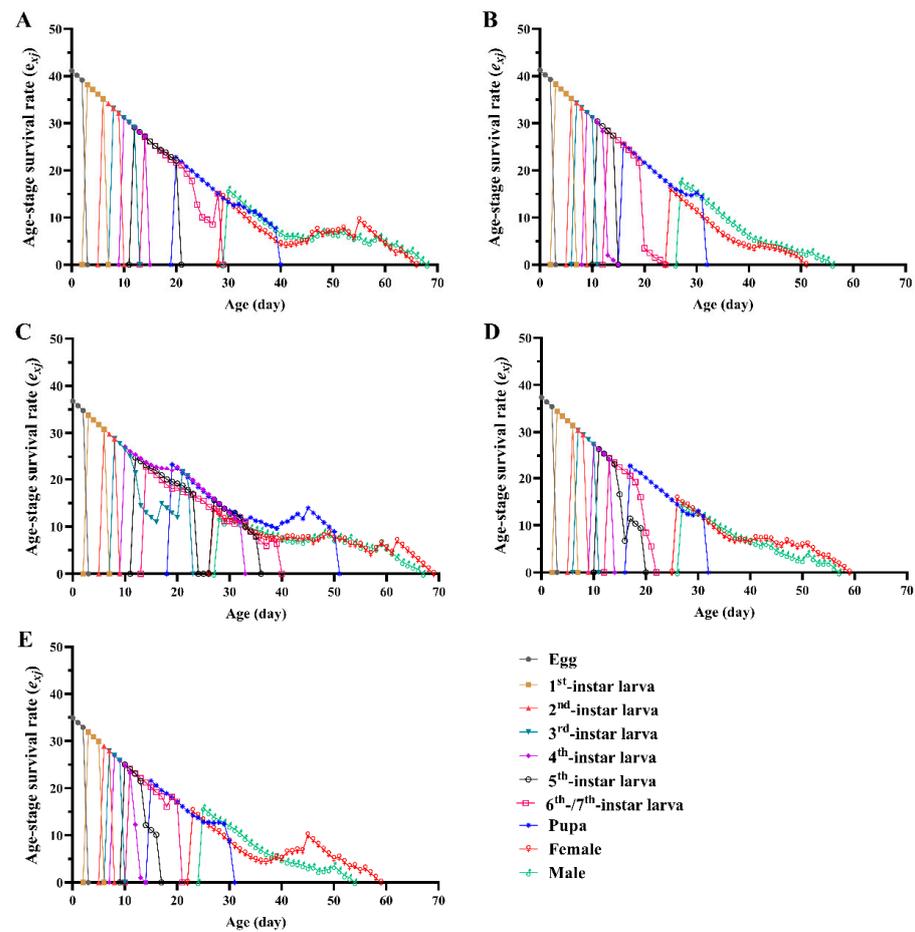


Figure 4. Age-stage specific life expectancy (e_{xj}) of *Spodoptera frugiperda* individuals fed different diets. (A): D₁; (B): D₂; (C): D₃; (D): D₄; (E): maize leaves.

3.3. Life Table Parameters

Diet substantially affected the life table parameters of FAW (Table 4). The net reproductive rate (R_0) of D₂-fed FAWs was the highest (580.37 offspring/individual); therefore, this diet was the best for population growth, followed by D₄ (410.23 offspring/individual) and maize leaves (384.64 offspring/individual), with the lowest R_0 for D₃-fed FAWs (176.53 offspring/individual). The FAW populations fed on D₁ and D₃ had longer mean generation times (T) and lower finite rates of increase (λ), which indicates that D₁ and D₃ are not suitable for rapid FAW population growth.

Table 4. Life table parameters (mean \pm SE) of *Spodoptera frugiperda* individuals fed different diets.

Parameter	D ₁	D ₂	D ₃	D ₄	Maize Leaves
Net reproductive rate R_0 (offspring/individual)	288.59 \pm 29.55 c	580.37 \pm 50.13 a	176.53 \pm 28.10 d	410.23 \pm 44.28 b	384.64 \pm 41.97 bc
Mean generation time T (d)	37.89 \pm 0.27 a	34.25 \pm 0.17 b	37.11 \pm 0.49 a	34.52 \pm 0.22 b	32.16 \pm 0.20 c
Intrinsic rate of natural increase r (d ⁻¹)	0.1495 \pm 0.0031 c	0.1858 \pm 0.0028 a	0.1394 \pm 0.0050 c	0.1743 \pm 0.0036 b	0.1851 \pm 0.0037a
Finite rate of increase λ (d ⁻¹)	1.161 \pm 0.0035 c	1.204 \pm 0.0033 a	1.150 \pm 0.0057 c	1.1904 \pm 0.0043 b	1.203 \pm 0.0044 a

Data in same row followed by different letters significantly differed (paired bootstrap test, $p < 0.05$).

3.4. Flight Ability

Over a 12-h assessment period, the flight ability of the FAW was significantly affected by diets (Table 5). The flight distance ($F_{4, 276} = 2.891$, $p = 0.023$) and velocity ($F_{4, 276} = 2.902$, $p = 0.022$) differed among different diet treatments, with no difference recorded for flight duration ($F_{4, 276} = 2.055$, $p = 0.087$). The flight ability of FAW in D₃ was weak, and its flight distance and velocity were significantly lower than those in D₁ and D₂. The flight ability did not differ among other diet treatments.

Table 5. Flight performance (mean ± SE) of *Spodoptera frugiperda* individuals fed different diets, recorded in a laboratory using tethered flight mills. Flight performance is expressed using multiple parameters (i.e., distance, duration, and mean velocity).

Parameter	D ₁	D ₂	D ₃	D ₄	Maize Leaves
Flight distance (km)	24.14 ± 1.80 a	22.97 ± 2.19 a	18.88 ± 2.95 b	19.73 ± 1.58 ab	18.71 ± 1.27 ab
Flight duration (h)	7.11 ± 0.39 a	7.12 ± 0.54 a	6.20 ± 0.71 a	6.91 ± 0.46 a	5.65 ± 0.35 a
Flight velocity (km/h)	3.34 ± 0.14 a	3.30 ± 0.18 a	2.67 ± 0.21 b	2.90 ± 0.13 ab	3.44 ± 0.16 a

Different letters in same column indicate significantly different flight parameters (one-way ANOVA, $p < 0.05$, Tukey's HSD).

3.5. Evaluation of Cost of Four Artificial Diets

We calculated the cost per ton of production for each diet (D₁, D₂, D₃, and D₄) as RMB 6890.00, 5670.00, 5900.00, and 3970.00, respectively. The total cost of materials per ton of wheat bran, soybean powder, and yeast powder for D₂ was RMB 2041.37; the total cost per ton of wheat bran for D₄ was only RMB 340.59. According to the rearing number of FAWs for each diet, the diet amounts of culturing 1 million FAWs for each diet (D₁, D₂, D₃, and D₄) were 6.62 t, 6.00 t, 5.03 t, and 6.54 t, respectively. Therefore, compared with D₂, using D₄ as the artificial diet for rearing 1 million FAWs will save RMB 8056.2 (about USD 1111.76) and reduce the cost by nearly 24% (Table 6).

Table 6. Cost per ton of diet material, diet amounts of culturing 1 million FAWs and the cost saving of D₂ compared with other diets.

Diet	Cost Per Ton (RMB)	Diet Amount of Culturing 1 Million FAWs (ton)	Saving Cost by Culturing 1 Million FAWs (%)
D ₁	6890.00	6.62	43.08
D ₂	5670.00	6.00	23.68
D ₃	5900.00	5.03	12.51
D ₄	3970.00	6.54	-

Exchange rate at the time of writing: RMB 1 = USD 0.1380.

4. Discussion

As a notorious global agricultural pest, the rearing cost for FAWs must be reduced, and controlling the cost of the artificial diet required is a key step towards this goal. In this study, we developed an inexpensive and high-performance wheat-bran-based artificial diet (D₄) for FAWs. The biological indicators (e.g., development duration, pupal mass, reproductive parameters, and flight ability) of the FAWs fed this diet were consistent with those of the FAWs fed a traditional artificial diet (D₂), and the rearing cost of the new diet was nearly 24% lower. These findings indicate that using cheap wheat bran instead of soybean and yeast powders as the base material of an artificial FAW diet is feasible, which will improve the cost-effectiveness of the mass rearing of FAWs.

Natural diets are limited by many factors (e.g., season, growth cycle, and conditions) and can easily rot and deteriorate, making the mass rearing of insects difficult. Artificial diets are advantageous over natural diets owing to their low cost and ease of obtaining, preserving, and use. The nutritional quality of artificial diets is generally evaluated by examining the biological indicators, e.g., the development, uniformity, survival rate, and

fecundity of reared insects [47–49]. In this study, the development of FAWs fed the D₄ diet was similar to that observed by Pinto et al., who reported a larval stage of 15.6 days, a larval survival rate of 92.0%, and a pupal mass of 253.3 mg [34]. According to Wang et al. [35] and Su et al. [36], the highest fecundity was 452 and 836 eggs/female, respectively; these values are significantly lower than that of the D₄-fed FAWs (1364.78 eggs/female) in this study. The differences in these findings may be related to the nutritional quality of the diet, rearing conditions, and the study of insects. Laboratory populations of insects can become degraded after rearing multiple generations owing to rearing conditions or genetic factors [50,51]. Therefore, we will evaluate the rearing performance of D₄-fed FAWs after multiple generations in long-term experiments.

An appropriate artificial diet should contain all the nutrients needed for insect development in appropriate proportions; otherwise, it will substantially affect the life activities of the insects [52–54]. For example, Wu et al. found that the protein content in an artificial diet enhanced the reproductive capacity of *H. armigera* within a certain range but inhibited it when this range was exceeded [55]. Soybean powder, yeast powder, and wheat germ are rich in protein and various nutrients, and they are usually used as the base materials of artificial diets. In this study, the soybean-powder-based diet (D₃) exhibited poor effects in rearing FAWs, which may be related to an improper proportion of nutrients or the presence of protease inhibitors in this diet [56]. We also tried to replace all the wheat bran, soybean powder, and yeast powder in D₂ with maize powder, but the reared larvae all died several days later. The FAW larvae that were fed D₁ grew slowly, and some larvae developed into the seventh instar, which may have been related to the high proportion of maize powder in the diet. High maize powder content may inhibit the development of FAWs, in contrast to our previous assumptions. According to Chen et al., high contents of lysine, methionine, and tryptophan in maize may affect the development of some insects [57]. Thus, reducing the proportion of maize powder may improve the rearing effect of D₁.

The use and nutritional value of wheat bran are often underestimated. Wheat bran is not only rich in nutrients but also has other features, such as good water retention, easy availability, and low cost [57]. Our study showed that an artificial diet for FAWs, using only wheat bran as the base material, was able to meet the nutritional requirements of this insect fully. According to Pascacio-Villafan et al., the high content and multiple sources of protein (yeast and wheat germ) in artificial diets did not improve the rearing quality of *Anastrepha ludens* (Loew) because these proteins could not be fully used by the larvae [58]. Reducing the yeast content in an artificial diet did not affect the rearing effect and substantially reduced the cost [59]. Combined with the results of this study, we speculate that some materials in many artificial diets may be unnecessary; therefore, cost reductions for other diets may also be possible. In addition to the high price of yeast powder, agar, and casein are also relatively expensive, accounting for more than half of the total material costs of D₂ and D₄. Reducing the amounts of agar and casein used or using cheaper alternatives will further reduce the cost. Researchers have previously reported several partial or complete alternatives to agar [60–62]. In addition, the cost of the mass rearing of FAWs can also be reduced by optimizing rearing equipment and methods.

In this study, we designed an economical and effective artificial diet for FAWs, which could substantially reduce the cost of the mass rearing of FAWs. FAW irradiation with X-rays after mass rearing for field release can be combined with other control methods, such as light trapping, pheromone trapping, and planting resistant crop varieties in year-round breeding regions, which will help to control the number of resident pests and migrants effectively, and achieve large-scale, sustainable, and long-term management of FAWs. The wintering area of FAWs involves multiple countries and regions, and the insect has cross-border migratory abilities [63]. Therefore, the implementation of SIT programs requires the joint efforts and collaboration of multiple affected countries or regions. In addition, the mass rearing of FAWs can be used for the propagation of natural enemy insects and the production of viral pesticides to promote the rapid development of biological control technology effectively. Much remains to be achieved to mass rear FAWs successfully.

Overall, our findings can be applied to effectively reduce the rearing cost of FAWs, promote various studies of FAWs, and provide a reference for reducing the costs of artificial diets for other insects.

5. Conclusion

Spodoptera frugiperda (FAW) is a newly important invasive pest in many countries in the old world and developing new environmentally friendly management strategies needs a low-cost mass-rearing method for the insect. Here, we designed an economical and effective artificial diet for FAWs based on wheat bran. The rearing performance of this diet was consistent with the traditional artificial diets, but the rearing cost dropped by 26.42% compared to other formulas. This work can promote the mass rearing of FAWs for the application of sterile insect techniques or the production of viral pesticides to control the pest.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/insects13121177/s1>, Table S1: Purchase price of each material in diet, Table S2: Purchase price of each vitamin in diet.

Author Contributions: Conceptualization, all; methodology, S.G. and K.W.; formal analysis, S.G. and S.J.; investigation, S.G., B.C., W.H., S.J., C.L., L.G. and X.S.; resources, S.G., X.Y. and K.W.; data curation, S.G. and K.W.; writing—original draft preparation, S.G.; writing—review and editing, all; visualization, S.G.; supervision, X.Y. and K.W.; project administration, K.W.; funding acquisition, K.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Research Fund of the Ministry of Industry and Information Technology of the People’s Republic of China: “Crop Varietal Improvement and Insect Pests Control by Nuclear Radiation”.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to privacy restrictions.

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

References

1. Sparks, A.N. A review of the biology of the fall Armyworm. *Fla. Entomol.* **1979**, *62*, 82–87. [[CrossRef](#)]
2. Goergen, G.; Kumar, P.L.; Sankung, S.B.; Togola, A.; Tamò, M. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J E Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. *PLoS ONE* **2016**, *11*, e165632. [[CrossRef](#)] [[PubMed](#)]
3. Sharanabasappa, D.; Kalleshwaraswamy, C.M.; Asokan, R.; Swamy, M.; Maruthi, M.S.; Pavithra, H.B.; Hegde, K.; Navi, S.; Prabhu, S.T.; Goergen, G. First report of the fall armyworm, *Spodoptera frugiperda* (J E Smith) (Lepidoptera: Noctuidae), an alien invasive pest on maize in India. *Pest Manag. Hortic. Ecosyst.* **2018**, *24*, 23–29.
4. IPPC (International Plant Protection Convention). *First Detection Report of the Fall Armyworm Spodoptera frugiperda* (Lepidoptera: Noctuidae) on Maize in Myanmar; Food and Agriculture Organization of the United Nations: Rome, Italy, 2019.
5. Sun, X.X.; Hu, C.X.; Jia, H.R.; Wu, Q.L.; Shen, X.J.; Zhao, S.Y.; Jiang, Y.Y.; Wu, K.M. Case study on the first immigration of fall armyworm *Spodoptera frugiperda* invading into China. *J. Integr. Agric.* **2021**, *20*, 664–672. [[CrossRef](#)]
6. Montezano, D. Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *Afr. Entomol.* **2018**, *26*, 286–300. [[CrossRef](#)]
7. Zhang, L.; Liu, B.; Zheng, W.G.; Liu, C.H.; Zhang, D.D.; Zhao, S.Y.; Li, Z.Y.; Xu, P.J.; Wilson, K.; Withers, A.; et al. Genetic structure and insecticide resistance characteristics of fall armyworm populations invading China. *Mol. Ecol. Resour.* **2020**, *20*, 1682–1696. [[CrossRef](#)]
8. Baudron, F.; Zaman-Allah, M.A.; Chaipa, I.; Chari, N.; Chinwada, P. Understanding the factors influencing fall armyworm (*Spodoptera frugiperda* JE Smith) damage in African smallholder maize fields and quantifying its impact on yield. A case study in Eastern Zimbabwe. *Crop Prot.* **2019**, *120*, 141–150. [[CrossRef](#)]
9. Wyckhuys, K.A.; O’Neil, R.J. Population dynamics of *Spodoptera frugiperda* smith (Lepidoptera: Noctuidae) and associated arthropod natural enemies in Honduran subsistence maize. *Crop Prot.* **2006**, *25*, 1180–1190. [[CrossRef](#)]
10. Mahmood, I.; Imadi, S.R.; Shazadi, K.; Gul, A.; Hakeem, K.R. Effects of pesticides on environment. In *Plant, Soil and Microbes*; Springer: Cham, Switzerland, 2016; pp. 253–269.

11. Pitre, H.N. Chemical control of the fall armyworm (Lepidoptera: Noctuidae): An update. *Fla. Entomol.* **1986**, *69*, 570–578. [[CrossRef](#)]
12. Yu, S.J. Insecticide resistance in the fall armyworm, *Spodoptera frugiperda* (Smith, J.E.). *Pestic. Biochem. Phys.* **1991**, *39*, 84–91. [[CrossRef](#)]
13. Storer, N.P.; Babcock, J.M.; Schlenz, M.; Meade, T.; Thompson, G.D.; Bing, J.W.; Huckaba, R.M. Discovery and characterization of field resistance to Bt maize: *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Puerto Rico. *J. Econ. Entomol.* **2010**, *103*, 1031–1038. [[CrossRef](#)] [[PubMed](#)]
14. Huang, F.; Qureshi, J.A.; Head, G.P.; Price, P.A.; Levy, R.; Yang, F.; Niu, Y. Frequency of *Bacillus thuringiensis* Cry1A. 105 resistance alleles in field populations of the fall armyworm, *Spodoptera frugiperda*, in Louisiana and Florida. *Crop Prot.* **2016**, *83*, 83–89. [[CrossRef](#)]
15. Chandrasena, D.I.; Signorini, A.M.; Abratti, G.; Storer, N.P.; Olaciregui, M.L.; Alves, A.P.; Pilcher, C.D. Characterization of field-evolved resistance to *Bacillus thuringiensis*-derived Cry1F δ -endotoxin in *Spodoptera frugiperda* populations from Argentina. *Pest Manag. Sci.* **2018**, *74*, 746–754. [[CrossRef](#)] [[PubMed](#)]
16. Farias, J.R.; Andow, D.A.; Horikoshi, R.J.; Sorgatto, R.J.; Fresia, P.; dos Santos, A.C.; Omoto, C. Field-evolved resistance to Cry1F maize by *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Brazil. *Crop Prot.* **2014**, *64*, 150–158. [[CrossRef](#)]
17. Knippling, E.F. Possibilities of insect control or eradication through the use of sexually sterile males. *J. Econ. Entomol.* **1955**, *48*, 459–462. [[CrossRef](#)]
18. Klassen, W. Area-wide integrated pest management and the sterile insect technique. In *Sterile Insect Technique*; Springer: Dordrecht, The Netherlands, 2005; pp. 39–68.
19. Baumhover, A.H.; Graham, A.J.; Bitter, B.A.; Hopkins, D.E.; New, W.D.; Dudley, F.H.; Bushland, R.C. Screw-Worm Control Through Release of Sterilized Flies. *J. Econ. Entomol.* **1955**, *48*, 462–466. [[CrossRef](#)]
20. Wyss, J.H. Screwworm eradication in the Americas. *Ann. N. Y. Acad. Sci.* **2000**, *916*, 186–193. [[CrossRef](#)]
21. Walters, M.L.; Staten, R.T.; Roberson, R.C. Pink bollworm integrated management using sterile insects under field trial conditions, Imperial Valley, California. In *Area-Wide Control of Fruit Flies and Other Insect Pests*; Penerbit Universiti Sains Malaysia: Penang, Malaysia, 2000; pp. 201–206.
22. Bloem, K.A.; Bloem, S. SIT for codling moth eradication in British Columbia, Canada. In *Area-Wide Control of Fruit Flies and Other Insect Pests*; Penerbit Universiti Sains Malaysia: Penang, Malaysia, 2000; pp. 207–214.
23. Jiang, S.; He, L.M.; He, W.; Zhao, H.Y.; Yang, X.M.; Yang, X.Q.; Wu, K.M. Effects of X-ray irradiation on the fitness of the established invasive pest fall armyworm *Spodoptera frugiperda*. *Pest Manag. Sci.* **2022**, *78*, 2806–2815. [[CrossRef](#)]
24. Rose, A.H.; Silveriders, R.H.; Lindquist, O.H. Migration flight by an aphid, *Rhopalosiphum maidis* (Hemiptera: Aphididae), and a noctuid, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Can. Entomol.* **1975**, *107*, 567–576. [[CrossRef](#)]
25. Mitchell, E.R.; McNeil, J.N.; Westbrook, J.K.; Silvain, J.F.; Lalanne-Cassou, B.; Chalfant, R.B.; Pair, S.D.; Waddill, V.H.; Sotomayor-Rios, A.; Proshold, F.I. Seasonal periodicity of fall armyworm (Lepidoptera: Noctuidae) in the Caribbean basin and northward to Canada. *J. Entomol. Sci.* **1991**, *26*, 39–50. [[CrossRef](#)]
26. Song, Y.F.; Wu, K.M. Investigation on controlling status of fall armyworm in sweet/waxy corn fields in western Yunnan province. *Plant Prot.* **2020**, *46*, 217–222.
27. Gonzalez-Maldonado, M.B.; Hernandez-Zetina, D.A.; Ruiz-Cancino, E. Parasitoids (Diptera: Tachinidae) of the fall armyworm *Spodoptera frugiperda* (J. E. Smith) in maize in Durango, Mexico. *Southwest Entomol.* **2018**, *43*, 183–187. [[CrossRef](#)]
28. López, M.A.; Martínez-Castillo, A.M.; García-Gutiérrez, C.; Cortez-Mondaca, E.; Escobedo-Bonilla, C.M. Parasitoids and entomopathogens associated with fall armyworm, *Spodoptera frugiperda*, in Northern Sinaloa. *Southwest Entomol.* **2018**, *43*, 867–881. [[CrossRef](#)]
29. Hussain, A.G.; Wennmann, J.T.; Goergen, G.; Bryon, A.; Ros, V.I. Viruses of the fall armyworm *Spodoptera frugiperda*: A review with prospects for biological control. *Viruses* **2021**, *13*, 2220. [[CrossRef](#)] [[PubMed](#)]
30. Cohen, A.C. Standards for Effective Insect Rearing Science and Technology Papers. *Adv. Entomol.* **2018**, *6*, 256–284. [[CrossRef](#)]
31. Cohen, A.C. Ecology of Insect Rearing Systems: A Mini-Review of Insect Rearing Papers from 1906–2017. *Adv. Entomol.* **2018**, *6*, 86–115. [[CrossRef](#)]
32. Zeng, F.R. Research of insect artificial diet. *Chin. J. Biol. Control* **2018**, *34*, 184–197.
33. Bowling, C.C. Rearing of two Lepidopterous pests of rice on a common artificial diet. *Ann. Entomol. Soc. Am.* **1967**, *60*, 1215–1216. [[CrossRef](#)]
34. Pinto, J.R.L.; Torres, A.F.; Truzzi, C.C.; Vieira, N.F.; Vacari, A.M.; De Bortoli, S.A. Artificial corn-based diet for rearing *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *J. Insect Sci.* **2019**, *19*, 2. [[CrossRef](#)]
35. Wang, R.F.; Zhang, M.F.; Xu, H.H.; Zhang, Z.X. Artificial diets and rearing technique of *Spodoptera frugiperda* (J. E. Smith) in laboratory. *J. Environ. Entomol.* **2019**, *41*, 742–747.
36. Su, X.N.; Li, C.Y.; Huang, S.H.; Liu, W.L.; Zhang, Y.P.; Pan, Z.P. Optimization of artificial diet and rearing condition of fall armyworm, *Spodoptera frugiperda* (J. E. Smith). *J. Environ. Entomol.* **2019**, *41*, 992–998.
37. Li, C.Y.; Zhang, Y.P.; Huang, S.H.; Liu, W.L.; Su, X.N.; Pan, Z.P. A study on artificial rearing technique of *Spodoptera frugiperda* (J. E. Smith) in the laboratory. *J. Environ. Entomol.* **2019**, *41*, 986–991.
38. Li, Z.Y.; Dai, Q.X.; Kuang, Z.L.; Liang, M.R.; Wang, L.; Lu, Y.Y.; Chen, K.W. Effects of three artificial diets on development and reproduction of the fall armyworm *Spodoptera frugiperda* (J. E. Smith). *J. Environ. Entomol.* **2019**, *41*, 1147–1154.

39. Lekha, M.K.; Swami, H.; Vyas, A.K.; Ahir, K.C. Biology of fall armyworm, *Spodoptera frugiperda* (JE Smith) on different artificial diets. *J. Entomol. Zool. Stud.* **2020**, *8*, 584–586.
40. Liang, G.M.; Tan, W.J.; Guo, Y.Y. Improvement of artificial rearing technique of *Helicoverpa armigera*. *Plant Prot.* **1999**, *25*, 15–17.
41. Ge, S.S.; He, L.M.; He, W.; Yan, R.; Wyckhuys, K.A.G.; Wu, K.M. Laboratory-based flight performance of the fall armyworm *Spodoptera frugiperda*. *J. Integr. Agric.* **2021**, *20*, 707–714. [[CrossRef](#)]
42. Chi, H. Life-table analysis incorporating both sexes and variable development rate among individuals. *Environ. Entomol.* **1988**, *17*, 26–34. [[CrossRef](#)]
43. Chi, H. TWOSEX-MSChart: A Computer Program for Age-Stage, Two-Sex Life Table Analysis. 2020. Available online: <http://140.120.197.173/Ecology/> (accessed on 27 March 2020).
44. Chi, H.; Su, H.Y. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environ. Entomol.* **2006**, *35*, 10–21. [[CrossRef](#)]
45. He, L.M.; Zhao, S.Y.; Ali, A.; Ge, S.S.; Wu, K.M. Ambient Humidity Affects Development, Survival, and Reproduction of the Invasive Fall Armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), in China. *J. Econ. Entomol.* **2021**, *114*, 1145–1158. [[CrossRef](#)]
46. Akca, I.; Ayvaz, T.; Yazici, E.; Smith, C.L.; Chi, H. Demography and population projection of *Aphis fabae* (Hemiptera: Aphididae): With additional comments on life table research criteria. *J. Econ. Entomol.* **2015**, *108*, 1466–1478. [[CrossRef](#)]
47. Murúa, M.G.; Vera, M.T.; Abraham, S.; Juárez, M.L.; Prieto, S.; Head, G.P.; Willink, E. Fitness and mating compatibility of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) populations from different host plant species and regions in Argentina. *Ann. Entomol. Soc. Am.* **2008**, *101*, 639–649. [[CrossRef](#)]
48. He, L.M.; Wu, Q.L.; Gao, X.W.; Wu, K.M. Population life tables for the invasive fall armyworm, *Spodoptera frugiperda* fed on major oil crops planted in China. *J. Integr. Agric.* **2021**, *20*, 745–754. [[CrossRef](#)]
49. Chen, Y.C.; Chen, D.F.; Yang, M.F.; Liu, J.F. The Effect of Temperatures and Hosts on the Life Cycle of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Insects* **2022**, *13*, 211. [[CrossRef](#)]
50. Meunier, J.; Kölliker, M. Inbreeding depression in an insect with maternal care: Influences of family interactions, life stage and offspring sex. *J. Evol. Biol.* **2013**, *26*, 2209–2220. [[CrossRef](#)] [[PubMed](#)]
51. Matthey, S.N.; Strutt, L.; Smiseth, P.T. Intergenerational effects of inbreeding in *Nicrophorus vespilloides*: Offspring suffer fitness costs when either they or their parents are inbred. *J. Evol. Biol.* **2013**, *26*, 843–853. [[CrossRef](#)] [[PubMed](#)]
52. Scriber, J.M.; Slansky Jr, F. The nutritional ecology of immature insects. *Annu. Rev. Entomol.* **1981**, *26*, 183–211. [[CrossRef](#)]
53. Brodbeck, B.V.; Peter, C.A.; Russell, F.M. Effects of total dietary nitrogen and nitrogen form on the development of xylophagous leafhoppers. *Arch. Insect Biochem.* **1999**, *42*, 37–50. [[CrossRef](#)]
54. Opit, G.P.; Throne, J.E. Effects of diet on population growth of the psocids *Lepinotus reticulatus* and *Liposcelis entomophila*. *J. Econ. Entomol.* **2014**, *101*, 616–622. [[CrossRef](#)]
55. Wu, K.J.; Li, M.H. Nutritional ecology of the cotton bollworm, *Heliothis armigera* (Hübner): Life tables of the population on the artificial diets with different protein levels. *Acta Entomol. Sin.* **1993**, *36*, 21–28.
56. Cohen, A.C.; Zeng, F.; Crittenden, P. Adverse effects of raw soybean extract on survival and growth of *Lygus hesperus*. *J. Entomol. Sci.* **2005**, *40*, 390–400. [[CrossRef](#)]
57. Chen, Y.C.; Chen, L.; Shang, H.W.; Zhu, C.Y. Research advances and nutrition analysis of the artificial diets for Tephritid fruit flies. *Plant Quarant.* **2013**, *27*, 13–19.
58. Pascacio-Villafán, C.; Williams, T.; Sivinski, J.; Birke, A.; Aluja, M. Costly nutritious diets do not necessarily translate into better performance of artificially reared fruit flies (Diptera: Tephritidae). *J. Econ. Entomol.* **2015**, *108*, 53–59. [[CrossRef](#)] [[PubMed](#)]
59. Pascacio-Villafán, C.; Birke, A.; Williams, T.; Aluja, M. Modeling the cost-effectiveness of insect rearing on artificial diets: A test with a tephritid fly used in the sterile insect technique. *PLoS ONE* **2017**, *12*, e0173205. [[CrossRef](#)] [[PubMed](#)]
60. Taylor, D.B. Comparison of two gelling agents for screwworm (Diptera: Calliphoridae) larval diets. *J. Econ. Entomol.* **1988**, *81*, 1414–1419. [[CrossRef](#)] [[PubMed](#)]
61. Taylor, D.B.; Bruce, J.C.; Garcia, R. Gelled diet for screwworm (Diptera: Calliphoridae) mass production. *J. Econ. Entomol.* **1991**, *84*, 927–935. [[CrossRef](#)]
62. Chaudhury, M.F.; Alvarez, L.A. A new starch-grafted gelling agent for screwworm (Diptera: Calliphoridae) larval diet. *J. Econ. Entomol.* **1999**, *92*, 1138–1141. [[CrossRef](#)]
63. Ge, S.S.; Zhang, H.W.; Liu, D.Z.; Lv, C.Y.; Cang, X.Z.; Sun, X.X.; Song, Y.F.; He, W.; Chu, B.; Zhao, S.Y.; et al. Seasonal migratory activity of *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) across China and Myanmar. *Pest Manag. Sci.* **2022**, *78*, 4975–4982. [[CrossRef](#)] [[PubMed](#)]