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Developmental Parameters of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) Immature Stages Under Controlled and Standardized Conditions

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Abstract

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith, 1797), is the most important noctuid pest in the Americas and has recently become an invasive pest in Africa and in India. Having a detailed and standardized record of the biology and the larval development of *S. frugiperda* will be critical to further studies on integrated pest management, toxicology, and applied ecology. This study reports the temporal and morphological parameters of the immature stages of *S. frugiperda* for larvae fed on artificial diet under controlled conditions (25±1 °C, 70±10% RH and 14 hour photophase). The survival of the egg, larval, prepupal and pupal stages was 97.40, 98.33, 99.32 and 97.95%, respectively. The average duration of the egg, larval, prepupal and pupal stages were 2.69, 13.73, 1.43, and 9.24 days, respectively. All larvae passed through six instars, with significantly slower larval development for females. However, females had faster pupal development and heavier pupae, thus total time from egg to adult was not significantly different between sexes. With the growing importance of this highly polyphagous species, centralizing the fragmented information in the literature and standardizing its rearing methods will improve and facilitate future studies on this pest.

Keywords: fall armyworm, artificial diet, development, crop pests, polyphagous pest

1. Introduction

Spodoptera spp. belong to the Noctuidae family, which is the largest family of the order Lepidoptera (Zahiri et al., 2010). The genus includes approximately thirty species distributed across six continents. Among *Spodoptera* species, at least fifteen are considered key pests of cultivated plants (Tood & Poole, 1980; Pogue, 2002; Angulo, Olivares, & Weigert, 2008). The fall armyworm, *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae), is recognized as one of the most important noctuid moth pests of North and South America (e.g., Chittenden, 1901; Luginbill, 1928; Vickery, 1929; Ashley, Wiseman, Davis, & Andrews, 1989; Pogue, 2002; Casmuz et al., 2010; Murúa et al., 2015). Recently, *S. frugiperda* has also been detected causing damage in the

African continent (Goergen, Kumar, Sankung, Togola, & Tamò, 2016), in India (Sharanabasappa et al., 2018), and there have been interception reports in Europe, with specimens detected in Germany and The Netherlands (CABI, 2017). In a recent host plant review of *S. frugiperda*, it was identified that larvae have the potential to consume 353 different plant species belonging to 76 botanical families (Montezano et al., 2018), including crops, weeds, ornamental plants and seedlings in nurseries (e.g., Luginbill 1928; Silva et al., 1968; Labrador, 1967; Coto, Saunders, Vargas, & King, 1995; Pogue, 2002; Pastrana, 2004; Casmuz et al., 2010; Montezano et al., 2018). In addition, resistant phenotypes have been reported to Bt corn (Storer et al., 2010) and insecticides (Yu, 1991). *Spodoptera frugiperda* is a pest of the majority of cultivated plant species (Montezano et al., 2018), but greatest damage occurs in grasses such as maize and sorghum, and in other monoculture crops such as cotton and soybean (Pitre & Hogg, 1983; Bueno, Bueno, Moscardi, Parra, & Hoffmann-Campo, 2011; Hardke, Lorenz, & Leonard, 2015). Although *S. frugiperda* is such a widespread pest of many crop species, detailed biological and developmental information is deficient; the majority of the literature varies in rearing methodology and sometimes does not count for differences between sexes. Detailed information on this pest's biology and standardization of its rearing methods is necessary for the development of robust *S. frugiperda* integrated pest management (IPM) and insect resistance management (IRM). Considering the importance of *S. frugiperda* and other *Spodoptera* spp. for several crops of economic interest, this study compares the biology of the main representatives of *Spodoptera* occurring in the Americas, reared under the same conditions. This study complements previous contributions on the biology of immatures and adults of *S. albula* (Walker, 1857) (Montezano et al., 2013a, 2014a), *S. eridania* (Stoll, 1782) (Montezano, Specht, Sosa-Gómez, Roque-Specht, & Barros, 2013b, 2014b), *S. dolichos* (Fabricius, 1794) (Montezano et al., 2015a, 2015b) and *S. cosmioides* (Walker, 1858) (Specht & Roque-Specht, 2016) reared under the same conditions. Montezano et al. (2013a) employed and validated a methodology that incorporated detailed rearing procedures not made by others studies, e.g., a larger number of neonates evaluated individually to adult emergence, including a more complete detailing of biological parameters, with minimal interference in its development.

2. Materials and Methods

2.1 Insects and Laboratory Conditions

Experiments were conducted under laboratory conditions at the Entomology Laboratory of Embrapa Cerrados, Planaltina, Federal District, Brazil. The *Spodoptera frugiperda* colony was initiated by collecting 54 caterpillars from conventional maize ears at Embrapa Cerrados experimental station (15°36'34.9" S, 47°44'36.7" W, 1170 m a.s.l.). Collected *S. frugiperda* larvae were reared on artificial larval diet that has also been used for rearing *S. eridania*, *S. albula*, *S. dolichos* and *S. cosmioides* (Montezano et al., 2013a; 2014b; 2015a; Specht & Roque-Specht, 2016). The artificial diet was adapted from Greene, Leppla, and Dickerson (1976) with full recipe and preparation instructions published in Montezano et al. (2013a). One female and one male moth that emerged on the same day were placed inside an oviposition cage consisting of cylindrical plastic containers (20 cm diameter, 15 cm height). The top of each cage was closed with clear plastic film with filter paper strips attached for oviposition. The bottom of each cage was lined with filter paper and sealed with a plastic cover (20.5 cm diameter). Containers were examined daily to record adult survival and to remove and count the number of eggs in each egg mass. Dead females were dissected to determine the number of spermatophores they had received from males during copulation. Egg, larval and pupal development were evaluated as described in those sections below. All experiments were performed in a rearing room (25±1 °C, 70±10% RH and a 14 hour photophase) with evaluations performed daily at 2:00 PM.

2.2 Molecular Confirmation of Species and Strain Identity

Due to intraspecific divergence, *S. frugiperda* populations can be characterized as two strains: maize and rice. These strains differ in genetics (Pashley, 1986; Levy, García, & Maruniak, 2002; Nagoshi & Meagher, 2003, 2004; Prowell, McMichael, & Silvain, 2004; Cañas-Hoyos, Lobo-Echeverri, & Saldamando-Benjumea, 2017), morphometry (Cañas-Hoyos, Márquez, & Saldamando-Benjumea, 2014), reproductive behavior (Pashley & Martin, 1987; Pashley, Hammond, & Hardy, 1992; Groot, Marr, Heckel, & Schöf, 2010) and pheromone composition (Cañas-Hoyos et al., 2017); therefore we consider it relevant to verify the identity of our insect colony in order to make our results comparable with previous and future studies.

DNA from 16 first generation larvae was obtained using a CTAB-based protocol (Rogers & Bendich, 1998) and the mitochondrial COI gene was amplified in a 25 µL PCR reaction mix containing 2.5 µL of 10× reaction buffer, 2.0 µL of 2.5 mM dNTP, 1.0 µL of 5 µM forward primer, 1.0 µL of 5 µM reverse primer, 1.25 µL of 50 mM MgCl₂, 5.0 µL of 5 ηg µL⁻¹ DNA template, and 0.2 µL of 5 U µL⁻¹ Taq DNA polymerase (Invitrogen, Carlsbad, CA, USA). The thermocycling program was 94 °C (1 min), followed by 35 cycles of 92 °C (45 s), 50

°C (45 s), 72 °C (1 min), and a final segment of 72 °C for 5 min. Primers were synthesized by Invitrogen (Carlsbad, CA, USA). Partial amplification of the COI region used the primer pair COI-893F (5'-CACGAGCATATTTTACATCWGCA-3') and COI-1303R (5'-CAGGATAGTCAGAATATCGACG-3') to produce a 410-bp fragment (Nagoshi, Meagher, & Hay-Roe, 2012). *Spodoptera frugiperda* samples were identified by digestion of the PCR product with 0.25 µl of the restriction enzyme EcoRV (2,000 U 10 µL⁻¹) (Invitrogen, Carlsbad, CA, USA) and incubated at 37 °C for 5 h. Gel loading buffer (50% sucrose, 0.15% bromophenol blue in water) was added (2 µL per sample), and the entire reaction was loaded on a 1.3% agarose horizontal gel in SB buffer (10 mM NaOH, pH 8.5, adjustment with boric acid). Fragments were visualized on a UV light box (LTB-21 × 26 HE model, Loccus, Cotia, SP, Brazil).

2.3 Egg Stage

The viability and embryonic period were evaluated for 8,508 eggs (from 27 egg masses). The egg masses were obtained from eight oviposition cages with one moth pair each. The egg masses selected were representative of the oviposition period (including the first and last oviposition). Copulation was confirmed by counting the number of spermatophores in the bursa copulatrix of females, indicating that they had been inseminated during the experiment. The egg masses used were from females with one (n = 5) or two (n = 3) spermatophores. Each one-day-old egg mass was individually placed in a Petri dish (10 cm diameter, 1.5 cm height) lined with filter paper moistened with distilled water and observed daily until eclosion.

2.4 Larval Stage

The larval development study was conducted using 300 neonates 24 h after hatching. Larvae were reared on artificial larval diet adapted from Greene et al. (1976) according to Montezano et al. (2013a) that has also been used for rearing *S. eridania*, *S. albula*, *S. dolichos* and *S. cosmioides* (Montezano et al., 2013a, 2014b, 2015a; Specht & Roque-Specht, 2016).

Neonates were selected from the same egg mass and were individually placed in plastic containers (300 mL volume, 10 cm diameter, 15 cm height). A small wad of cotton (~1 cm in diameter) moistened with distilled water to maintain humidity and a ~1 cm³ piece of artificial diet were deposited in the plastic container. Daily observations were made to verify the survival and development of the larvae by collection of the molted head capsules. The head capsules were individually stored and labeled by larva in microcentrifuge tubes and measured with a micrometer under a microscope. In cases where the head capsule was not recovered (presumed to have been consumed by the larva), instar changes were noted by comparing its size with other larvae. The diet and moist cotton were replaced daily. The growth ratio was determined by head capsule size, measuring the distance between genae (mm) of each instar of 40 randomly sampled larvae (20 females and 20 males). The mean growth ratio was calculated by dividing the mean head capsule width of each instar by the mean head capsule width of the previous instar.

2.5 Prepupal Stage

When larvae reached the prepupal period, characterized by a decrease in size and the interruption of feeding, the insect was transferred into a transparent plastic container (10 cm diameter, 5 cm height) containing expanded vermiculite moistened with distilled water. Prepupae built the pupal chamber attached to the wall, which made it possible to observe metamorphosis and determine the end of the prepupal period.

2.6 Pupal Stage

Pupae were kept in the same container and conditions as in the prepupal stage. The daily activities consisted of maintaining the moisture, with a few drops of distilled water, and recording the emergence of adults. Sex determination was performed following Angulo and Jana (1982) on the second day after pupation, when the cuticle is further hardened. Considering that precise sex determination is only possible during the pupal stage, the identity of each larva was preserved throughout the study. Therefore, it was possible to track the development of each *S. frugiperda*, including the sex. Weight was measured using a high precision semi-analytical balance.

2.7 Data Analysis

Biological parameters, such as stage duration, size and weight were analyzed using descriptive statistics with the calculation of means and standard deviations. The sex ratio considers the number of females divided by number of females plus number of males. When necessary, means of sexes were compared using a t-test assuming unequal variances, at a significance level of 5% ($\alpha = 0.05$) using SPSS® (Statistical Package for Social Sciences) version 19 for Windows.

3. Results

3.1 Molecular Confirmation of Species Identity

The amplification product after digestion with EcoRV was uncut, producing a single 410-bp fragment. The presence of one fragment after digestion with EcoRV means that the *S. frugiperda* population belongs to the maize-strain, whereas the digested rice-strain product produces two bands of 289 and 121 bp (Nagoshi, Silvie, & Meagher et al., 2007).

3.2 Biology of Egg, Larval, Prepupal, and Pupal Stages

The overall survival of immature stages of *S. frugiperda* was approximately 93% (Table 1). The embryonic period ranged from 2 to 3 days and the mean period for all eggs to complete development was 2.69 days (Table 1). Developmental time for female larvae during the fifth and sixth instar, as well as total developmental time (including prepupal period), was significantly longer than for male larvae (Table 2). The prepupal developmental time did not differ between sexes (Table 2). However, in pupal stage the duration of females was significantly shorter than males. Thus, differences in developmental duration between sexes (females with longer duration in the larval stage and shorter in the pupal stage), resulted in no difference for the total immature development period. A significant difference in size between sexes was detected at the end of larval development, in the fifth and sixth instar, when female larvae were bigger than males and the growth rate of female larvae was greater (Table 3). The sex ratio determined from 146 female and 141 male pupae was 0.509, which does not differ significantly from a 1:1 ratio ($\chi^2 = 0.087$; $p = 0.289$). Pupal weight was highly variable (150-342 mg), although mean pupal weight was significantly higher in females (Table 4).

Table 1. Survival (%) and duration, in days, presented as mean±standard deviation (\bar{X} ±SD) and range (minimum and maximum) of *Spodoptera frugiperda* immature stages reared on artificial diet under controlled conditions (25±1 °C, 70±10% RH and 14 hours of photophase)

Stage	Number of insects (initial–final)	Survival (%)	Duration days (\bar{X} ±SD)	Range (days)
Egg	8508-8267	97.40	2.69±0.46	2-3
Larval	300-295	98.33	13.73±1.91	11-20
Prepupal	295-293	99.32	1.43±0.57	1-3
Pupal	293-287	97.95	9.24±1.76	7-14
Overall	-	93.18	27.09	-

Table 2. Duration of *Spodoptera frugiperda* immature stages presented as mean±standard deviation (\bar{X} ±SD) for females and males reared on artificial diet under controlled conditions (25±1 °C, 70±10% RH and 14 hour photophase)

Stage	Duration days		Sig. ¹
	Females (n = 146)	Males (n = 141)	
Larval Instars	----- \bar{X} ±SD -----		
I	2.57±0.54	2.57±0.54	ns
II	2.07±0.56	2.07±0.54	ns
III	2.13±0.49	2.11±0.46	ns
IV	2.48±0.65	2.38±0.57	ns
V	2.57±0.56	2.44±0.51	*
VI	2.13±0.39	1.92±0.52	**
Prepupae	1.48±0.61	1.38±0.51	ns
Larvae + Prepupae	15.44±3.80	14.87±1.76	**
Pupae	8.93±1.80	9.57±1.65	**
Overall ²	24.37±2.68	24.44±2.44	ns

Note. ¹ Comparisons between growth stage duration means of females and males, using a Student t-test, considering different variances, at a significance level of 95% (ns = $p > 0.05$; * = $p < 0.01$; ** = $p < 0.001$)

² Larval + prepupal + pupal developmental time.

Table 3. Head capsule widths (mm) presented as mean±standard deviation ($\bar{X}\pm SD$) of *Spodoptera frugiperda* larvae at each instar and respective growth ratios, reared on artificial diet under controlled conditions (25±1 °C, 70±10% RH and 14 hour photophase)

Instar	Both sexes (n = 40)		Females (n = 20)		Males (n = 20)		Sig. ²
	$\bar{X}\pm SD$	GR ¹	$\bar{X}\pm SD$	GR	$\bar{X}\pm SD$	GR	
I	0.35±0.02	-	0.35±0.02	-	0.35±0.02	-	ns
II	0.56±0.03	1.63	0.57±0.03	1.63	0.56±0.03	1.62	ns
III	0.87±0.04	1.54	0.87±0.04	1.53	0.87±0.05	1.56	ns
IV	1.27±0.06	1.46	1.29±0.06	1.49	1.25±0.07	1.44	ns
V	1.85±0.12	1.46	1.89±0.12	1.47	1.81±0.09	1.44	*
VI	2.72±0.20	1.47	2.80±0.23	1.48	2.64±0.13	1.46	*
Mean	-	1.51	-	1.52	-	1.43	

Note. ¹ GR = Growth ratio (value that represents the division of each instar by the previous one).

² Sig. = Comparisons between head capsule width means of females and males using a Student t-test, considering different variances, at a significance level of 95% (ns = p > 0.05; * = p < 0.01)

Table 4. Pupal weight (mg) of *Spodoptera frugiperda* presented as mean±standard deviation ($\bar{X}\pm SD$) and range (minimum and maximum) reared on artificial diet under controlled conditions (25±1 °C, 70±10% RH and 14 hour photophase)

Sex	Number of insects	Pupal weight (mg) ($\bar{X}\pm SD$)	Range (mg)
Female	146	230.53±43.47	150-342
Male	141	189.67±22.16	143-243
Significance ¹		*	-

Note. ¹ Comparison of means using a Student t-test, considering different variances, at a significance level of 95% (* = p < 0.001)

4. Discussion

The overall survival of immature of *S. frugiperda* reared on artificial diet under controlled conditions and minimal interference was approximately 93% (Table 1). The high survival observed for *S. frugiperda* in this study, as well as for other species reared under the same conditions: *S. albula*, *S. eridania*, *S. dolichos* and *S. cosmioides* (Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016), indicates the adequacy of the rearing method and the diet for comparative studies. These results can also be considered satisfactory based on a report from Singh (1983), which states that artificial diets should provide survival rates higher than 75%.

The relatively high egg viability (Table 1) is consistent with studies reported in the literature for *S. frugiperda* (e.g., Luginbill, 1928; Leiderman & Sauer, 1953; Busato et al., 2008; Milano, Berti Filho, Parra, & C onsoli, 2008) and other species from the same genus (e.g., Sadek & Anderson, 2007; Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016). The egg incubation period of *S. frugiperda* ranged from two to three days (Table 1) and was similar to other reports for *S. frugiperda* reared under similar temperatures and conditions (e.g., Hynes, 1942; Veloso, Parra, & Nakano, 1983; Nieto-Hern andez & Llanderal-C azares, 1982; Machado, Giannotti, & Oliveira, 1985; Clavijo, Fern andez, Ram irez, Delgado, & Lathullerie, 1991; Rizzo & La Rossa, 1992; Valverde, Toledo, & Popich, 1995; Santos, Redaelli, Diefenbach, & Efrom, 2004; Busato et al., 2005). This study also shows that the egg incubation period for *S. frugiperda* is shorter than the one observed for *S. albula*, *S. cosmioides*, *S. dolichos* and *S. eridania* reared under the same conditions (Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016).

The larval survival (Table 1) was high when compared to other reports for *S. frugiperda* fed on artificial diet (Pencoe & Martin, 1982; Lynch, Nwanze, Wiseman, & Perkins, 1989; Clavijo et al., 1991; Giolo, Grutzmacher, Garcia, & Busato, 2002) and some of its main hosts (Pencoe & Martin, 1982; Ali, Luttrell, & Pitre, 1990). In addition, larval survival was higher than that reported in the majority of studies with this species, both on artificial and natural diet when larvae are exposed to less favorable temperatures and unsuitable host plants (e.g., Piedra, 1974; Kasten, Precetti, & Parra, 1978; Garner & Lynch, 1981; Pitre & Hogg, 1983; Parra & Carvalho, 1984; Crocomo & Parra, 1985; Ali et al., 1990; Silveira, Vendramim, & Rossetto, 1997; Botton, Carbonari,

Garcí, & Martins, 1998; Murúa, Defagó, & Virla 2003; Busato et al., 2005; Boregas, Mendes, Waquil, & Fernandes, 2013; Dias et al., 2016; Silva et al., 2017).

It is important to note that all *S. frugiperda* larvae in this study developed through six instars (Table 2). *Spodoptera frugiperda* is known to have highly variable larval development, ranging from five to ten instars, with a higher number of instars on less suitable host plants and at lower temperatures throughout its geographic range. The number of instars reported in the literature include: five (Leiderman & Sauer, 1953; Campos, 1970; Escalante, 1974; Ali et al., 1990; Santos, Redaelli, Diefenbach, & Efron, 2003), six (Luginbill, 1928; Marques, 1932; Hynes, 1942; Leiderman & Sauer, 1953; Doporto & Enkerlin, 1964; Labrador, 1967; Campos, 1970; Vázquez, Carrillo, Granados, & García, 1975; Pencoe & Martin, 1981, 1982; Nieto-Hernández & Llanderal-Cázares, 1982; Alvarez & Sánchez, 1983; Veloso et al., 1983; Parra & Carvalho, 1984; Crocomo & Parra, 1985; Machado et al., 1985; Castro & Pitre, 1988; Ali et al., 1990; Rizzo & La Rossa, 1992), seven (Luginbill, 1928; Campos, 1970; Vázquez-G. et al., 1975; Pencoe & Martin, 1981, 1982; Alvarez & Sánchez, 1983; Veloso et al., 1983; Parra & Carvalho, 1984; Ali et al., 1990; Valverde et al., 1995; Murúa et al., 2003; Lopes, Lemos, Machado, Maciel, & Ottati, 2008), eight (Pencoe & Martin, 1981; Alvarez & Sánchez, 1983; Ali et al., 1990; Murúa et al., 2003), nine (Bourquin, 1939; Pencoe & Martin, 1981; Ali et al., 1990; Murúa et al., 2003) and ten (Murúa et al., 2003). This variation in larval development is related to the biological plasticity of this species, which increases its chances of development and survival in adverse conditions (Esperk, Tammaru, & Nylin, 2007). Other studies of *Spodoptera* spp. using the same rearing conditions as this study showed an additional (seventh) instar. A seventh instar was more common in females of *S. albula*, *S. cosmioides*, *S. dolichos* and *S. eridania*, (Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016). Considering the fact that additional instars are related to physiological or nutritional deficiencies, this result, along with the very high survival rates (98% from larvae to prepupae and 93% from egg to adult), suggest that *S. frugiperda* is either better adapted than other *Spodoptera* spp. to the specific rearing conditions and diet provided in this study, or *S. frugiperda* has a higher adaptive ability in general when compared to other species. The highly polyphagous host range of *S. frugiperda* (Montezano et al., 2018) and developmental plasticity in instar number reported above would support that *S. frugiperda* is an overall highly adaptive species.

The total larval developmental time (including prepupal period) for *S. frugiperda* of ~15.1 days (Table 2) is similar to that reported for the same species reared under similar temperatures with suitable artificial diets or suitable host plants (e.g., Pencoe & Marti, 1981; Nieto-Hernández & Llanderal-Cázares, 1982; Pitre & Hogg, 1983; Machado et al., 1985; Castro & Pitre, 1988; Rizzo & La Rossa, 1992; Valverde et al., 1995; Silveira et al., 1997; Giolo et al., 2002; Busato et al., 2005, 2008; Campos, Boiça Jr, Jesus, & Godoy 2011; Boregas et al., 2013; Martínez-Martínez, Padilla-Cortes, Jarquín-Lopes, Sánchez-García, & Cisneros-Palacios, 2015). However, even when exposed to similar temperature conditions, there are reports of significantly longer larval development periods when *S. frugiperda* are fed less adequate artificial diet (Clavijo et al., 1991; Murúa et al., 2003), less suitable host plants (e.g., Marques, 1932; Leiderman & Sauer, 1953; Pencoe & Marti, 1981, 1982; Nieto-Hernández & Llanderal-Cázares, 1982; Pitre & Hogg, 1983; Silveira et al., 1997; Botton et al., 1998; Lopes et al., 2008; Campos et al., 2011), or obtained from different collection locations (Giolo et al., 2002, Busato et al., 2005, 2008; Boregas et al., 2013). Under similar conditions of suitable food and temperature, such variations are related to genetic variation from different geographic locations or biotypes related to the host plant (e.g., Giolo et al., 2002; Busato et al., 2005; Vélez-Arango, Arango, Villanueva, Aguilera, & Saldamando, 2008; Murúa et al., 2008, Murúa, Juárez, Prieto, & Willink, 2009, Murúa et al., 2015; Salinas-Hernandez & Saldamando-Benjumea, 2011; Nagoshi et al., 2017).

The mean width of the larval head capsules (Table 3) range from 0.346 mm in the first instar to 2.723 mm in the final (sixth) instar, similar to the sizes described in the literature independent of instar numbers (Bourquin, 1939; Nieto-Hernández & Llanderal-Cázares, 1982; Alvarez & Sánchez, 1983; Veloso et al., 1983; Crocomo & Parra, 1985; Machado et al., 1985; Valverde et al., 1995; Capinera, 2008; Maroneze & Gallegos, 2009). The head capsule size in the first and last instar, regardless of the number of instars, is related to a compensation scenario, where additional instars are inserted in poor conditions when larvae fail to reach a species-specific threshold-size with the “normal” instar number (Esperk et al., 2007).

The growth ratio decreased progressively until the last instar (Table 3), a characteristic also reported in other studies of *S. frugiperda* (Nieto-Hernández & Llanderal-Cázares, 1982; Machado et al., 1985; Valverde et al., 1995; Santos et al., 2003; Capinera, 2008; Lopes et al., 2008; Maroneze & Gallegos, 2009) and other *Spodoptera* species, such as *S. eridania* (Parra, Precetti, & Karsten, 1977, Valverde & Sarmiento, 1987; Montezano et al., 2014b), *S. albula* (Montezano et al., 2013a), *S. dolichos* (Montezano et al., 2015a) and *S. cosmioides* (Specht & Roque-Specht, 2016).

The prepupal period, which is usually critical for holometabolous insects due to the metamorphosis process (e.g., Parra, 1991; Schneider, 2009), had the highest survival rate of any growth stage in this study (Table 1). The prepupal duration observed (mean 1.4 days) was similar to reports for the majority of *S. frugiperda* studies under similar conditions (e.g., Leiderman & Sauer, 1953; Campos F. 1970; Nieto-Hernández & Llanderal-Cázares, 1982; Machado et al., 1985; Giolo et al., 2002; Busato et al., 2005, 2008).

Pupal survival was high (97.95%, Table 1), with only one female and three males dying during this period. This is similar to other studies using artificial diet and different maize cultivars (Silveira et al., 1997; Murúa et al., 2003). However, the survival rate was significantly higher when compared to other studies using natural and artificial diets (Kasten Jr. et al., 1978; Garcia, 1981; Veloso et al., 1983; Parra & Carvalho, 1984; Crocomo & Parra, 1985; Clavijo et al., 1991; Silveira et al., 1997; Botton et al., 1998; Giolo et al., 2002; Busato et al., 2005; Reinert & Read, 2008; Barros, Torres, Ruberson, & Oliveira, 2010). The high pupal survival reported here may be related to the availability of sterilized vermiculite, which avoids contamination, and facilitates the burrowing and chamber construction process, facilitating gaseous exchange and maintenance of humidity. Pupal duration was approximately nine days (Table 1), similar to other studies with favorable temperature conditions and suitable artificial diets or host plants (e.g., Campos F. 1970; Piedra, 1974; Kasten Jr. et al., 1978; Combs & Valerio, 1980; Penceo & Martin, 1982; Pitre & Hogg, 1983; Parra & Carvalho, 1984; Crocomo & Parra, 1985; Pantoja, Smith, & Robinson, 1987; Castro & Pitre, 1988; Clavijo et al., 1991; Rizzo & La Rossa, 1992; Giolo et al., 2002; Murúa et al., 2003, 2008; Santos et al., 2003; Busato et al., 2005, 2008). Pupal weight was extremely variable (143 to 342 mg) (Table 4) but this variation was similar to that reported for specimens collected and reared in similar conditions in Brazil (140-340 mg) (Giolo et al., 2002) and in the United States (150-350 mg) (Leuck & Perkins 1972). However, the literature indicates that some populations, in similar conditions, may have higher weights (336-519 mg) (Bowling, 1967). The mean pupal weight in this study (210.456±40.113 mg) is similar to other studies when larvae were fed natural or artificial diet (e.g., Campos, 1970; Kasten et al., 1978; Parra & Carvalho, 1984; Castro & Pitre, 1988; Silveira et al., 1997; Giolo et al., 2002; Lopes et al., 2008; Murúa et al., 2008; Reinert & Read, 2008; Boregas et al., 2013).

Significant differences between male and female *S. frugiperda* were found for several life stages. Total larval developmental time (larval + prepupal duration) was longer for females compared to males of *S. frugiperda* (Table 2). When broken down by stadium, small however significant differences were found for the final two larval stages (fifth and six instar) only (Table 2). This difference in the duration of the larval instars after the fourth instar agrees with observations reported for *S. albula*, *S. cosmioides*, *S. dolichos* and *S. eridania* reared under the same conditions (Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016). Studies addressing the differences between sexes during *S. frugiperda* larval development report those findings can depend on diet, temperature and biotype (host plant and locality), with reports of no differences (Combs & Valerio, 1980; Clavijo et al., 1991; Giolo et al., 2002) or females developing faster than males (Giolo et al., 2002; Nagoshi, 2011). For duration of pupal development, however, this study reported that development was longer for males than females (Table 2); this difference between sexes is well documented for *S. frugiperda* (e.g., Combs & Valerio, 1980; Penceo & Martin, 1982; Parra & Carvalho, 1984; Crocomo & Parra, 1985; Lynch et al., 1989; Pantoja et al., 1987; Clavijo et al., 1991, Santos et al., 2003). The developmental delay of females during the larval stage was compensated by a faster pupal development, resulting in synchronization between male and female adult emergence, which was also reported for other species of *Spodoptera* reared under the same conditions (Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016). This result demonstrates how important it is to account for larval, prepupal, and pupal developmental time between males and females. As reported here (Table 4), other studies also found female pupae to be significantly heavier than males at the majority of temperatures and diets tested (Kasten et al., 1978; Combs & Valerio, 1980; Parra & Carvalho, 1984; Machado et al., 1985; Pantoja et al., 1987; Giolo et al., 2002). A higher female pupal weight was also reported for other *Spodoptera* species (Habib, Paleari, & Amaral, 1983; Xue, Pang, Wang, Li, & Liu, 2010; Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016). The greater pupal weight of females, which is established due to feeding during the larval stage, is likely due to the role of the female in egg production (Allen, Zwaan, & Brakefield, 2011; Specht et al., 2016).

The present study increases the biological knowledge of *S. frugiperda*, the most important *Spodoptera* species in the Americas and recently reported on the African, European and Asian continents (Goergen et al., 2016; CABI, 2017). Having baseline data on developmental parameters for this species under controlled conditions and with a highly suitable diet can be essential for comparison with studies of development under stresses such as adverse field conditions, host plants of variable suitability, or toxicology studies using Bt or other types of insecticides. For example, Lopes et al. (2008) reported head capsule widths of 0.2 mm (first instar) to 1.4 mm (seventh instar)

for *S. frugiperda* reared on cassava; a comparison to the range of 0.3 mm (first instar) to 2.7 mm (sixth instar) in the current study would suggest that cassava is a less suitable host. Alternatively, Santos et al. (2003) reported only five instars (compared to six instars reported here for artificial diet) for *S. frugiperda* reared on certain cultivars of maize, indicating maize to be a highly suitable host plant. Other ecological stresses may be indicated if developmental parameters vary significantly from the established pattern; for example, parasitized *S. frugiperda* larvae may be smaller at the time of the final instar (e.g., Ashley, 1983; Ashley et al., 1989; Viana & Prates, 2003; Maroneze & Gallegos, 2009).

Despite the lack of exhaustive studies to which to compare, the parameters evaluated in this study show that *S. frugiperda* stands out in some biological aspects related to its status as a major pest of important crops such as maize, sorghum and other grasses, and also as a secondary pest of several crops including soybean, sugarcane, cotton, vegetables and flax. It is important to point out that immature stages of *S. frugiperda* are able to survive and develop faster than other pest species from the same genus under similar laboratory conditions (Montezano et al., 2013a, 2014b, 2015b; Specht & Roque-Specht, 2016), potentially due to the developmental plasticity of this species. In order to develop more effective insect pest management strategies, a better understanding of survival, developmental time, polyphagia and most suitable diet are crucial.

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