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ECOLOGY, BEHAVIOR AND BIONOMICS

Immature Development of *Spodoptera dolichos* (Fabricius) (Lepidoptera: Noctuidae)

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Abstract
We provide detailed temporal and morphological parameters of the immature stages of *Spodoptera dolichos* (Fabricius) larvae fed on artificial diet under controlled conditions (25±1°C, 70±10% RH, and 14 h photophase). The viability of the egg, larval, pupal, and prepupal stages was 97.5%, 97.0%, 93.1%, and 98.9%, respectively. The average duration of the egg, larval, prepupal, and pupal stages was 5.0, 23.4, 3.2, and 21.5 days, respectively. Females took longer at the larval stage than males, with 10.5% of them having seven instars. The growth rate of female larvae that developed through six and seven instars was 1.72 and 1.54, respectively. Female pupae were significantly larger, exhibiting slower development than males.

Introduction

The genus *Spodoptera* Guenée (Lepidoptera: Noctuidae) comprises one of the most important pest groups worldwide (Pogue 2002). The species *Spodoptera dolichos* (Fabricius) is reported from North to South America (e.g., Silva *et al* 1968, Ferguson *et al* 1991, Pogue 2002, Pastrana 2004), with adults being captured in light traps throughout the year (e.g., Specht & Corseuil 2002, Zagatti *et al* 2006, Zenker *et al* 2010). Chile is the only South American country that has not reported the presence of *S. dolichos* (Angulo *et al* 2008).

The economic importance of *S. dolichos* is widely reported in the literature (Crumb 1929, Silva *et al* 1968, Pastrana 2004). Several crops are reported as hosts of *S. dolichos*, such as asparagus, bean, brinjal, cabbage, cassava, coffee, corn, cotton, ground pea, onion, potato, strawberry, sweet potato, tobacco, tomato, and watermelon (e.g., Silva *et al* 1968, Pogue 2002, Pastrana 2004). Moreira (1929) described *S. dolichos* as a pest causing significant economic damage in vegetables. The injury caused by *S. dolichos* larvae in many hosts is defoliation (Teixeira & Yokomizo 1987, Dias *et al* 2009), but feeding on fruits of watermelon (Adlerz 1975), stigmas of corn (Matrangolo *et al* 1997), and cutting young plants at the soil surface (Crumb 1929, Moreira 1929) are also reported.

The biology of *S. dolichos* is poorly characterized. One of the possible reasons is the similarity with other species from the *Spodoptera* genus, such as *Spodoptera albula* (Walker) and *Spodoptera eridania* (Stoll), which has caused frequent misidentification (Pogue 2002). In the present study, the immatures of *S. dolichos* are described using neonates evaluated individually until adult emergence. The investigation of the biological parameters of male and female immatures was performed by preserving the identity of each larva throughout the study with minimal interference in development. The rearing conditions and artificial diet were the same used in studies with *S. albula*

and *S. eridania* in order to allow interspecific biology comparison among the three species.

Material and Methods

Insects and laboratory conditions

Four females and five males were collected from light traps in the municipality of Pinto Bandeira, state of Rio Grande do Sul, Brazil (29°02′50″S, 51°28′12″W; 613 m a.s.l). Identification was conducted by comparing adults including genitalia with descriptions in Pogue (2002). Adults of *S. dolichos* were placed in oviposition cages and 1-day-old egg masses were collected. Egg, larval, and pupal development were then evaluated. All the experiments were performed in a rearing room (25±1°C, 70±10% RH, and a 14 h photophase), and the evaluations were performed daily at 2:00 p.m.

Egg stage

The viability and embryonic period were evaluated for 6485 eggs (from 53 egg masses). The egg masses were obtained from 12 oviposition cages with one couple 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, indicating that they had been inseminated during the experiment. The egg masses used were from females with one (n=9) and two (n=3) spermatophores. Every 1-day egg mass was individually placed into a Petri dish (10 cm diameter and 1.5 cm height) lined with filter paper moistened with distilled water until eclosion.

Larval stage

The larval development study was conducted using three hundred 1-day-old neonates. The artificial diet used to rear the larvae was adapted from Greene *et al* (1976) according to Montezano *et al* (2013a). The neonates were selected from the same female and were individually placed in plastic containers (300 mL). A small wad of cotton (~1 cm in diameter) moistened with distilled water to maintain humidity and a ~1 cm^3 piece of artificial diet were deposited in the plastic container. Daily observations were made to verify the survival and development of the larva by collection of shed head capsules. The head capsules were individually stored in tubes and measured under microscopy. In cases where the head capsule was not recovered due to larval consumption, changes of instar were noted by comparing its size with other larvae. The diet and the moist cotton were also replaced daily.

Head capsule measurement was based on the distance between the frontal setae of the head capsule because it is more precise than the traditional method that measures the distance between genas (Pérez *et al* 2005). The distance between the frontal setae was used to compare development of larvae that went through six and seven instars. The distance between genas was only measured in the first and in the last instar to allow data comparison with other species of *Spodoptera*.

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

Growth ratio was determined by measuring the frontal setae of each instar of 30 randomly sampled larvae (15 females and 15 males) that reached sixth instar. All larvae that reached seventh instar (n=13) had their frontal setae measured for each instar (Table 3). The mean growth ratio was calculated by subtracting the mean of each instar by the predecessor.

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 on the second day after pupation when the cuticle was further hardened following Angulo & Jana (1982). Mass was measured using a high-precision semi-analytical balance. Considering that precise sex determination is only possible during the pupal stage, the identity of each larva was preserved from throughout the study. Therefore, it was possible to track the development of each *S. dolichos*, including the gender.

The biological parameters such as 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 the number of females and males. When necessary, means of sexes and larvae that underwent six or seven instars were compared using a t test assuming unequal variances at a significance level of 5% and 1% using SPSS® (Statistical Package for the Social Sciences) version 11.0 for Windows.

Results

The overall survival of immature stages of *S. dolichos* was approximately 87% (Table 1), and embryonic development took 5 days (Table 1). Survival at the larval stage was

Table 1 Survival and duration of the *Spodoptera dolichos* immature stages, on artificial diet, under controlled conditions (25±1°C, 70±10% RH, and 14 h photophase).

Stage	*N* initial–final	Survival (%)	Duration (days)	Range (days)
Egg	6485–6321	97.5±0.31	5.0±0.00	5
Larval	300–291	97.0±0.27	21.3±1.63	19–33
Prepupal	291–271	93.1±0.92	3.1±0.78	1–5
Pupal	271–268	98.9±0.12	20.8±2.25	17–34
Total	–	87.1	50.2	–

90.3%, and it was the lowest survival of all other stages. Most of the larvae (95.2%) developed through six instars, and only 13 females (4.9%) went through seven instars (Table 2). The total development time of the female larvae that went through six instars (24.9 days) was significantly longer than that of male larvae (23.7 days) (Table 2). The larval development time was the same in both sexes through the third instar. The development time of female larvae that went through seven instars (26.6 days) was significantly longer than that of female larvae that completed six instars (24.9) (Table 2). However, the larval development time was the same through the fourth instar, and females with an additional instar (seven instars) experienced a significantly faster larval development during both the fifth and sixth instars (Table 2). The prepupal development time did not differ between sexes or between larvae that went through six and seven instars (Table 2).

Table 2 Development time (days) (mean ± SE) of *Spodoptera dolichos*, during each instar, including the larvae of each sex which developed for six and seven instars, fed with an artificial diet, under controlled conditions (25±1°C, 70±10% RH, and 14 h photophase).

Larval instars	6 instars		A	7 instars	B
	Females (124)	Males (131)		Females (13)	
I	4.1±0.38	4.1±0.46	ns	4.0±0.00	ns
II	3.0±0.33	3.0±0.37	ns	3.0±0.00	ns
III	3.2±0.44	3.1±0.53	ns	3.0±0.00	ns
IV	3.5±0.53	3.3±0.96	*	3.2±0.39	ns
V	4.4±0.58	4.0±0.83	**	3.8±0.56	*
VI	3.5±0.92	3.2±0.65	**	2.8±0.56	*
VII	–	–		3.5±0.66	
Prepupae	3.2±0.82	3.0±0.76	ns	3.2±0.60	ns
Total[a]	24.9±1.52	23.7±1.73	**	26.6±1.50	**
Pupae	20.3±1.66	21.1±2.50	*	21.5±3.55	ns
Larvae+pupae	45.2±2.14	44.8±3.00	ns	48.2±3.58	*

A comparisons between means of females and males that underwent six instars using a Student *t* test, considering different variances, at a significance level of 95%; *B* comparisons between means of females that underwent six instars and females that underwent seven instars, using a Student *t* test, considering different variances, at a significance level of 95%; *ns* $p>0.05$.

*$p<0.01$; **$p<0.001$.

[a] Larval developmental time, including prepupae period.

Concerning the size of the larvae, differences between sexes were only detected at the end of larval development in the sixth instar. Female larvae were larger than males at this stage (Table 3). In addition, females that went through six instars were significantly larger at the fifth and sixth instar stages than those that underwent seven instars (Table 3). However, the 13 larvae that had the additional seventh instar were larger in size (Table 3). The growth rate of larvae was faster for females undergoing through six instars than males with the same number of instars. Females that underwent seven instars had a slower growth rate (Table 3).

The sex ratio determined from 137 female and 131 male pupae was 0.51, which does not differ significantly from a 1:1 ratio ($\chi^2=0.07$; $p=0.796$). Pupal weight was variable within sex, and some pupae weighted approximately half that of others (Table 4). Considering larvae which went through six instars, female pupae were heavier than male. Female pupae from larvae that went through an additional seventh instar were the heaviest (Table 4).

Based on reports in the literature, larvae of *S. dolichos* can feed on 78 plant species. Our additional surveys identified 19 new host plants, which resulted in a list with 97 plant species belonging to 33 plant families (Table 4). The botanic families with the greatest number of plants consumed by *S. dolichos* larvae include Solanaceae (12), Asteraceae and Fabaceae (11), and Poaceae (6). The current list of plants includes cultivated and natural species, with an increase in the number of species commonly considered weeds, such as *Vernonia tweedieana*, *Lolium multiflorum*, *Portulaca oleracea*, and *Datura stramonium* (Online Supplementary Material – Table S1).

Discussion

Singh (1983) stated that a suitable artificial diet provides for at least 75% of insect survival. In the present study, immatures of *S. dolichos* were reared on an artificial diet under controlled conditions, with minimal interference, which resulted in a higher overall survival (87.1%) (Table 1).

The relatively high egg viability and fecundity observed for *S. dolichos* (Table 1) are common attributes of representatives of *Spodoptera*. In addition, previous studies on *Spodoptera* reported that multiple mating is known to enhance the reproductive capacity, including fertility (Sadek 2001, Sadek & Anderson 2007, Busato *et al* 2008, Montezano *et al* 2013b, 2014a). The incubation period of *S. dolichos* was constant and is longer than the one reported elsewhere at the same temperatures for other species of

Table 3 Distance between frontal setae (mm) (mean ± SE) of *Spodoptera dolichos* larvae at each instar and respective growth ratios, including larvae which developed for six (15 females and 15 males) and seven instars (9 females), fed with an artificial diet, under controlled conditions (25±1°C, 70± 10% RH, and 14 h photophase).

Instar	6 instars				A	7 instars		B
	Females (15)	Growth ratio	Males (15)	Growth ratio		Females (13)	Growth ratio	
I	0.1±0.01	–	0.1±0.01	–	ns	0.1±0.01	–	ns
II	0.2±0.03	1.79	0.2±0.05	1.87	ns	0.2±0.04	1.74	ns
III	0.4±0.09	1.87	0.5±0.07	1.87	ns	0.4±0.08	1.76	ns
IV	0.7±0.09	1.66	0.7±0.11	1.55	ns	0.7±0.14	1.64	ns
V	1.2±0.10	1.57	1.1±0.08	1.58	ns	1.0±0.10	1.47	*
VI	1.9±0.17	1.69	1.7±0.13	1.53	**	1.5±0.13	1.55	**
VII	–	–	–	–		2.1±0.33	1.41	–
Mean	–	1.72	–	1.68		–	1.59	–

A comparisons between means of females and males that underwent six instars using a Student *t* test, considering different variances, at a significance level of 95%; *B* comparisons between means of females that underwent six instars and females that underwent seven instars, using a Student *t* test, considering different variances, at a significance level of 95%; *ns* $p>0.05$.

*$p<0.01$; **$p<0.001$.

Spodoptera (Bavaresco *et al* 2002, Montezano *et al* 2013a, 2014b).

Overall larval survival was also high (Table 1) and similar to those observed under the same conditions for *S. albula* (Montezano *et al* 2013a) and *S. eridania* (Montezano *et al* 2014b). The observation that most of the larvae (95.2%) developed through six instars and only few *S. dolichos* females developed through seven instars (Table 2) indicates that diet and rearing conditions were satisfactory for their larval development in the laboratory. This is supported by earlier reports relating additional larval molts with unsuitable food plants or artificial diets (Parra *et al* 1977, Mattana & Foerster 1988, Bavaresco *et al* 2004, Santos *et al* 2005).

However, besides food quantity and quality, several other factors could influence the number of larval instars (Esperk *et al* 2007). In our study, only female *S. dolichos* developed an additional instar (Tables 2 and 3). This additional instar is probably due to the large body size of females (Table 4), and these results are consistent with observations in *S. albula* and *S. eridania* (Montezano *et al* 2013a, 2014b).

Table 4 Pupal weight (mg) (mean ± SE) of *Spodoptera dolichos* reared on artificial diet, including pupae whose larvae developed for six and seven instars (only females), under controlled conditions (25±1°C, 70± 10% RH, and 14 h photophase).

Larval instars	Gender	*N*	Pupal weight (mg)	Range
6	Female	124	740.8±55.96	568–1026
	Male	131	700.8±63.21	492–848
	Significance[a]		*	–
7	Female	13	893.8±121.63	714–1109
	Significance[b]		*	–

Comparison of means using a Student *t* test, considering different variances, at a significance level of 95%.

*$p<0.001$.

[a] Comparisons between females/males with six larval instars.

[b] Comparisons between females/females with six and seven larval instars.

The longest developmental time for female larvae which went through seven instars (Table 2) was similar to that observed for *S. albula* (Montezano *et al* 2013a) and *S. eridania* (Montezano *et al* 2014b). It is also consistent with other studies of *Spodoptera*, where an increased larval period is associated with additional instars (e.g., Santos *et al* 2005, Cabezas *et al* 2013).

There was a significant difference in the overall developmental time between female and male *S. dolichos* larvae that underwent six instars (Table 2). The sex difference in the duration of the stages was significant from the fourth instar on. These results agree with the observations reported for *S. albula* and *S. eridania* (Montezano *et al* 2013a, 2014b). However, in the end, there was synchronization between male and female adult emergence of *S. dolichos*, since the development delay of females during the larval stage was compensated by a faster pupal development.

The mean width of the larval head capsule demonstrated that *S. dolichos* larvae are larger than those of *S. albula* (Montezano *et al* 2013a), *Spodoptera cosmioides* (Walker) (Zenker *et al* 2007), and *S. eridania* (Montezano *et al* 2014b) reared on a similar artificial diet and temperature. Even the comparison with the head capsule width of *S. latifascia* (Walker) reported by Levy & Habeck (1976) demonstrated that *S. dolichos* have one of the largest larvae of the genus.

The growth rate decreased progressively until the last instar (Table 3). This pattern was similar for both sexes of

larvae, and it is especially noticeable in female larvae that underwent seven instars. Similar decrease in growth rate was also observed for *S. eridania* (Mayer & Babers 1944, Parra *et al* 1977, Valverde & Sarmiento 1987, Mattana & Foerster 1988, Montezano *et al* 2014b) and *S. albula* (Montezano *et al* 2013a).

Lower survival was observed during the prepupal period, along with a shorter period of development (Table 1). This period corresponds to the time when the larvae stop feeding and are preparing for the pupal stage, which is usually critical for holometabolous insects due to metamorphosis processes (Schneider 2009).

Pupal survivorship for both sexes of *S. dolichos* (Table 1) differed from those observed for *S. albula* (Montezano *et al* 2013a) and *S. eridania* (Santos *et al* 2005, Montezano *et al* 2014b).

The difference of weight between sexes during the pupal stage is relatively well documented in *Spodoptera* (e.g., Mattana & Foerster 1988, Bavaresco *et al* 2004, Santos *et al* 2005, Montezano *et al* 2013a) and other Lepidoptera. The larger size of females undergoing seven instars (Table 4) is attributed to the additional instar (e.g., Esperk *et al* 2007, Nagoshi 2011, Montezano *et al* 2013a, Montezano *et al* 2014b).

The records of 94 plants from 33 families consumed by *S. dolichos* larvae (Online Supplementary Material - Table S1) show the high degree of polyphagy of this species as earlier indicated (e.g., Crumb 1929, Silva *et al* 1968, Pogue 2002, Pastrana 2004). The large number of plants consumed by *S. dolichos* is comparable to *S. albula* (Montezano *et al* 2013a), *S. eridania* (Montezano *et al* 2014b), and *Spodoptera frugiperda* (JE Smith) (Casmuz *et al* 2010). However, each *Spodoptera* species was reported to consume more representatives of a certain botanic family: Fabaceae for *S. albula* (Montezano *et al* 2013a), Asteraceae for *S. eridania* (Montezano *et al* 2014b), Poaceae for *S. frugiperda* (Casmuz *et al* 2010), and Solanaceae for *S. dolichos* (Online Supplementary Material - Table S1).

In summary, the present study increases the biological knowledge of *S. dolichos*, an important *Spodoptera* species in the Americas. The larvae of this species are one of the largest in the *Spodoptera* genus, and it is expected to have a longer development time than other species. However, the investigation detailing the biological parameters of male and female immatures allowed documentation of differences between sexes during larval and the pupal stages.

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