Immature Stages of *Spodoptera eridania* (Lepidoptera: Noctuidae): Developmental Parameters and Host Plants

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**ABSTRACT.** This study aimed to detail the temporal and morphological parameters of the immature stages of southern armyworm *Spodoptera eridania* (Stoll, 1782) with larvae feed on artificial diet, under controlled conditions (25 ± 1°C, 70 ± 10% relative humidity and 14-h photophase) and gather information about their larval host plants. The viability of the egg, larval, pupal, and prepupal stages was 97.82, 93.62, 96.42, and 97.03%, respectively. The average duration of the egg, larval, pupal, and pre-pupal stages was 4.00, 16.18, 1.58, and 9.17 d, respectively. During the larval stage, 43.44% of females passed through seven instars, observing that the female’s development was significantly slower than males. The female larvae that developed through six and seven instars exhibited a mean growth rate of 1.52 and 1.44, respectively. Female pupae were significantly larger, exhibiting faster development than males. The rearing method proved to be adequate, providing more detailed observations of the biological cycle, especially at the larval stage, and resulting in an overall survival of almost 85%. Two hundred two plant species belonging to 58 families are listed as natural hosts for *S. eridania*, mainly including Asteraceae, Fabaceae, Solanaceae, Poaceae, Amaranthaceae, and Malvaceae.

**Key Words:** caterpillar, developmental parameter, egg, pupae, southern armyworm

The genus *Spodoptera* Guenée, 1852 (Lepidoptera: Noctuidae: Noctuinae) (Lafontaine and Schmidth 2010) is cosmopolitan and includes many of the most important agricultural caterpillars (Pogue 2002). *Spodoptera eridania* (Stoll 1782) occurs from South America through North America (e.g., Pogue 2002, Pastrana 2004, Bentancourt and Scatoni 2006, Angulo et al. 2008).

Since the beginning of the last century, *S. eridania* has a high reported degree of polyphagy (e.g., Chittenden and Russel 1909, Crumb 1956, Silva et al. 1968, Pastrana 2004, Angulo et al. 2008). The polyphagy of this species led to important studies on the selection and use of various host plants by polyphagous insects (e.g., Soo Hoo and Fraenkel 1966a,b; Scriber 1979, 1981; Manuwoto and Scriber 1982, 1985).

In the “World *Spodoptera* Database (Lepidoptera: Noctuidae)” (Pogue 2012), the largest *Spodoptera* database, 106 host plants are presently indicated for *S. eridania*, mostly with records from North and Central America. A large number of records are from crop pest survey studies (e.g., Crumb 1929) together with 56 host plants of 31 families from a population outbreak after Hurricane Hugo in 1989 (Torres 1992), mostly native to Puerto Rico. Furthermore, studies by Soo Hoo and Fraenkel (1966a,b) reveal that this species tolerates, and grows well on, several species on which their larvae were not collected in nature.

The large number of references of this species indicates the importance of this insect to different crops such as alfalfa, bean, beet, cabbage, cassava, collard, cotton, onion, peanuts, quinoa, soybean, tobacco, tomato, sweet potato, sunflower, and truck crops, in various locations throughout American continent (e.g., Silva et al. 1968, Pastrana 2004, Angulo et al. 2008, Pogue 2012). Additionally, this species has been reported from outbreaks under different conditions, such as after the passage of a hurricane (Torres 1992), in reforestation projects of native species (Mattana and Foerster 1988), in truck crops (Michereff-Filho et al. 2008), reaching economic injury levels in commercial crops, especially alfalfa (Hichings and Rabinovich 1974) cotton and soybeans (Parra et al. 1977; Santos et al. 2005, 2010; Sujii et al. 2006; Quintela et al. 2007; Valverde 2007).

Beyond its great voracity and reproductive capacity (e.g., Valverde and Sarmiento 1987 [1986], Mattana and Foerster 1988, Santos et al. 2005), *S. eridania* develops on weeds, which generally constitute a primary source of cultivated plant infestations (Tingle et al. 1978, Savio 1988, Sánchez and Vergara 1996 [1995], Santos et al. 2005), and presents different degrees of tolerance to several chemical insecticides (e.g., González 1966; Campos 1972, 1982; Aziz 1973; Aguilera and Vasquez 1974), botanical insecticides, and soap (Valler and Capinera 1988, 1993, Rosseti et al. 2008), and to the *Bacillus thuringiensis* Cry1Ac gene (Zemmer-de-Polania et al. 2008, Amaya et al. 2009).

Considering the importance of *S. eridania* for several crops of economic interest and a possibility of outbreaks, this study is part of a project that aims to compare the biology of the main representatives of *Spodoptera* occurring in the Americas, particularly in South America, under same conditions. In these studies, we compare in sequence the biological aspects of *Spodoptera albula* (Montezano et al., 2013), *S. eridania*, *Spodoptera dolichos*, *Spodoptera cosmioides*, and *Spodoptera frugiperda*. We employ and validate a methodology that incorporated detail setting not made by others studies, e.e., a larger number of neonates evaluated individually to adult emergence, including a more complete detailing of biological parameters, with minimal interference in its development. Additionally, this study aimed to gather and organize information relating to host plants, emphasizing South American records.

**Materials and Methods**

**Insects and Rearing.** These experiments only used first generation specimens whose ancestor moths were reared from 32 larvae collected...
on soybean, within the Jataizinho and Ibiporã municipalities, Paraná State, Brazil (23° 11'11.9" S, 51° 01'58.3" W, Datum WGS84, 424 m.a.s.l.). Identification was accomplished by comparing larvae and adults with descriptions in Pogue (2002). All the experiments were performed, with one daily observation indicated at 2:00 p.m., in a climate-controlled room (25 ± 1°C, 70 ± 10% relative humidity [RH], and a 14-h photophase).

**Egg Stage.** The egg masses were individually placed into a Petri dish (Pyrex® St. Louis, MO) lined with filter paper moistened with distilled water, where it remained until the eclosion of the larvae. We evaluated the feasibility (fertility) and the embryonic period, in days, of 28 egg masses (2,383 eggs) taken randomly from five couples, including the first and last ovipositions. The egg masses used were from females that presented one \( n = 2 \) and two \( n = 3 \) spermatotheca in the bursa copulatrix, indicating that they had been fertilized during the experiment. For this purpose, adults were kept in pairs \( n = 15 \) within cylindrical plastic containers, 10 cm in diameter and 15 cm in height, with tops closed using plastic film, to which container with long filter paper strips were attached, to stimulate oviposition. The bottom part of the container was closed with a Petri dish (10.5 cm in diameter) lined with filter paper.

**Larval Stage.** Soon after hatching, 298 larvae from the second-laid egg mass of a single female were individually placed in properly identified 150-ml plastic cups, covered with a transparent plastic cap. A small wad of cotton wool (~1 cm in diameter), moistened with distilled water to maintain humidity, along with a small piece of ~1 cm³ of artificial diet were deposited with a sterilized tweezer each cup, as described below. Daily observations were made to verify the survival and development of the larva (with the removal of the head capsule). During these observations, the diet and the cotton were replaced, to maintain humidity, always being careful to not interfere and to touch the larva as little as possible. The head capsules were individually stored, by larvae, in microcentrifuge tubes, for posterior measurement. In some cases, the change of instar was noticed through the development of the larva, but the capsule was not found, most likely because it had been eaten by the larva, which is relatively common among insects. In these cases, the date of ecdysis was recorded, and the size was then compared with the other larvae to confirm ecdysis, and the corresponding duration of each stage.

When the larvae reached the prepupal period, characterized by a decrease in size and the interruption of feeding, the diet and the cotton swab were removed. Thereafter, expanded vermiculite, moistened with distilled water, was added to each cup to a height of 0.5 cm to encourage the development of the pupal chamber and to allow the observation of metamorphosis, recording the prepupal period.

We maintained the identification number from the larval to the pupal stage to record the number of instars, the survival, and the individual duration of each stadia and prepupal period, taking into account the sex of each larva. It also allowed us to evaluate growth as a function of the number of larval instars.

To record the average size of each larval instar of *S. eridania*, the width of the cephalic capsule was measured, with a micrometer under a microscope. Most of the larvae developed through six instars, of which randomly selected 15 specimens that originate females and males to measure the head capsules. Only nine females went through seven instars, which were all measured. The mean growth rate was calculated by taking the average of the subsequent instar subtracted by the previous.

**Composition and Preparation of Larval Diet.** The artificial diet (adapted from Greene et al. 1976) composed of 2,150 ml of distilled water; 35 g of agar; 125 g of type 1 carioca bean; 100 g of wheat germ; 25 g of powdered whole milk; 62.5 g of yeast extract; 6 g of ascorbic acid; 10 ml of Vanderzant vitamin mixture; 250 mg of tetracycline; 6 ml of 40% formaldehyde; 5 g of methyl parahydroxybenzoate (Nipagin); 3 g of sorbic acid; and 50 g of soy protein, modified according to Montezano et al. (2013).

Initially, the beans, placed in an Erlenmeyer flask (500 ml) with distilled water (150 ml) and capped with a wad of hydrophobic cotton wrapped in gauze, were cooked in an autoclave, at one atmosphere, for 40 min. After which the flask with the baked beans was removed from the autoclave, capped with aluminum foil, and kept on the laboratory table until the temperature reached 25°C.

The prebaked beans were then ground together with the remaining ingredients (wheat germ, powdered milk, yeast extract, soy protein, and agar), which were added slowly along with the distilled water (1,500 ml) into a domestic blender at full power for at least 10 min, forming a homogeneous mass. This homogenized mass was transferred to a stainless steel pot and cooked for 5 min, after the boiling point. After cooking, the mass was removed from the heat and was cooled to 40°C, by mixing it manually.

At the same time, the ascorbic acid, sorbic acid, Nipagin, tetracycline chlorhydrate, vitamin mixture, and formaldehyde solution were manually mixed in a 1-liter beaker containing distilled water (500 ml), until the complete homogenization of the ingredients. This solution was added to the cooked mass, and both were manually mixed together until completely homogenized.

The finished diet was placed in polyethylene boxes (11 by 11 by 3.5 cm) to the maximum height of 2.5 cm of diet. The boxes were immediately transferred to a laminar flow chamber with ultraviolet light, until the temperature of 25°C was reached. After that, the polyethylene boxes were closed and kept under refrigeration (5°C) until the diet was used.

The diet was cut with a stainless steel spatula, previously cleaned with 70% alcohol, and individually offered to each caterpillar, in cubes of ~1 cm³, during the daily maintenance activities.

Considering the polyphagous habit and lack of organization of information relating to larval host plants, a survey of the plants cited in literature and in the internet sites hosted by educational or research institutions was performed, gathering information on the botanical family, specific and common names, and bibliographic references. The nomenclature of the plants has been updated mainly using Backes and Nardino (2001). Furthermore, this work gathered additional information including records from Rio Grande do Sul State, Brazil, especially in the mountainous region during two population outbreaks occurring in the spring of 1997 and 2004.

**Pupal Stage.** The pupae were kept without food, under the same conditions, and in the same containers of the prepupa. On the second day after pupation, when the cuticle was further hardened, the sex was determined according to the drawings in Angulo and Jana (1982). In addition to duration, the mass was measured using a semi-analytical balance, accurate to 100th of a gram. As the sex can only be precisely identified during the pupal stage, the identification number of each larva was maintained until pupation to know whether it was male or female, allowing comparisons between genders, even during the larval stage. The daily maintenance activities consisted of maintaining the moisture, with a few drops of distilled water, and detecting the emergence of the adult.

The biological parameters such as duration, size, and weight were analyzed using descriptive statistics with the calculation of means and standard deviations. When necessary, means were compared using a t-test assuming unequal variances, at a significance level of 5%.

**Results**

The eggs from females, which had copulated once or twice, have viability of 97.82%, and the embryonic period has no variation (Table 1). In the larval stage, including the prepupal period (Table 1), we observed the lowest survival (90.27%), driven especially by the larvae that died between the first and second instars. Most larvae (96.56%) developed through six instars, and only a few females (3.44%) went through seven instars (Table 2).

The duration of the female larvae, which developed six instars, was significantly higher than that of the male larvae. However, it was
significantly lower than those of larvae female, which developed through seven instars. The differences in the duration of the six and seven instar female larvae were detected during the fifth instar, when it was observed that both in the fifth and sixth instars, the larvae with an additional instar experienced a significantly faster larval development (Table 2).

The length of the prepupal period was quite variable and did not differ between gender and among females who developed for six and seven instars.

With respect to the size of the head capsule of individuals who passed through six instars, the females were significantly larger than males from the fifth instar on. Similarly, six instar females were significantly larger than those of seven instars, from fourth instar on. However, the additional instar resulted in a significantly larger final size ($P = 0.038$) of the female larvae that developed through seven instars (Table 3).

The literature search and author’s field observations records of the plants consumed by *S. eridania* provided a list of 202 taxa belonging to 58 plant families. In Rio Grande do Sul, 69 host plants were recorded, of which 38 had not been previously reported (Table 4).

The botanical families with the greatest number of species consumed include Asteraceae (20), Fabaceae (19), Solanaceae (14), Poaceae (10); Amaranthaceae (9); Malvaceae (8); Brassicaceae; Cucurbitaceae; Polygonaceae; Rubiaceae (7); Lamiales, Phytolaccaceae, and Rosaceae (6); and both Convolvulaceae and Euphorbiaceae (5) (Table 4). Besides the large number of cultivated species, the large number of weeds and native plants stand out.

The sex ratio obtained from 135 female and 134 male pupae was 0.502, which does not differ significantly from a 1:1 ratio ($\chi^2 = 0.951$; $P < 0.05$). Female pupae were significantly heavier than male, among individuals who had six larval instars. Furthermore, the females that experienced an additional instar were significantly heavier than those who went through six instars (Table 5).

**Discussion**

**Egg Stage.** Our results (Table 1) indicate that the duration of the incubation period of *S. eridania* is invariable, similar to that observed by under the same temperatures using different host plants (Chittenden and Russel 1909, Valverde and Sarmiento 1987 [1986], Mattana and Foerster 1988).

The egg viability (Table 1) obtained from fertilized females corresponds to those described by Valverde and Sarmiento 1987 [1986], for the first generation of the same species on four host plants. The differences with respect to other publications that are reported smaller percentages of viability (e.g., Parra et al. 1977, Mattana and Foerster 1988, Bortoli et al. 2012) may be due to eggs from couples that did not copulate. In these cases, high fecundity values are always attributed to repre- sentatives of *Spodoptera* in studies where multiple mating is known to enhance the reproductive capacity, including fertility (Kehat and Gordon 1975, Sadek 2001, Sadek and Anderson 2007, Busato et al. 2008, Milano et al. 2008, Montezano et al. 2013).

**Larval Stage.** The larval survival (Table 1) indicates that the diet and the rearing conditions were satisfactory for the development of *S. eridania* in the laboratory.

The fact that most of the larvae (96.56%) developed through six instars indicates that the diet met the specific needs similarly to that observed with host plants considered as adequate. In this direction, under the same conditions of this study, Mattana and Foerster (1988) found that *S. eridania* presented six instars when created in sweet potatoes (a suitable plant) and seven instars in bracatinga an unsuitable plant. It should be emphasized that the same species had only five instars when reared on slim amaranth [*Amaranthus hybridus* (L.)] considered as the most appropriate, among the four tested (Valverde and Sarmiento 1987 [1986]). The observation that only a few *S. eridania* females developed through seven instars (Table 2) is consistent with observations that in *S. albula* many more females than males develop through an additional instar, probably due to their larger size (see Pupal Stage) (Montezano et al. 2013). In previous studies of *S. eri- dania*, all subjects which fed on bracatinga passed through an additional instar (Mattana and Foerster 1988). Though in Parra et al. (1977) and Santos et al. (2005), ~20% of the individuals had additional instars on less adequate diets, although their rearing methods did not allow us to infer the gender of the individuals who developed through seven instars.

Duration of the larval stage, including the prepupal period (Tables 1 and 2) is similar to descriptions for the same species reared under similar temperatures, on more adequate food plants (Parra et al. 1977, Valverde and Sarmiento 1987 [1986], Mattana and Foerster 1988). The several temporal differences detected between the number of larval instars, including the longer duration of the first instar, than the subsequent three (Table 2), is also described for the same species (Parra et al. 1977, Valverde and Sarmiento 1987 [1986], Mattana and Foerster 1988, Santos et al. 2005) and for several *Spodoptera* representatives (e.g., Santos et al. 2003, Azidah and Sofian-Azirum 2006, Montezano et al. 2013). The temporal differences between sexes are also described for *S. albula* and probably are related to the sex dimorphism (Montezano et al. 2013).

The longer duration of *S. eridania* female larvae, which developed through seven instars (Table 2), is similar to that observed for *S. albula* (Montezano et al. 2013) and is consistent with experiments with other *Spodoptera* species in which the authors associated a longer larval period with an increased number of instars (e.g., Santos et al. 2005, Azidah and Sofian-Azirum 2006).

The significant difference in the overall developmental time of female and male *S. eridania* larvae that underwent six instars (Table 2) and the corresponding differences between the duration of the stages, which are more pronounced (significant) from the fifth instar on, agree with the observations reported for *S. albula* under the same conditions (Montezano et al. 2013).

The mean width of the head capsule (Table 3) is very similar to that described by Parra et al. (1977) and Mattana and Foerster (1988) and is slightly larger than that described by Mayer and Babers (1944), and Valverde and Sarmiento 1987 [1986] for the first instar, but not for the last instar.

Both the larvae that had six instars and those which went through seven instars (Table 3) showed higher growth rates during the first instars, decreasing progressively until the last, especially noticeable in larvae that underwent seven instars. Similar behavior was also observed for the same species (Mayer and Babers 1944, Parra et al. 1977, Valverde and Sarmiento 1987 [1986], Mattana and Foerster 1988) and for *S. albula* (Montezano et al. 2013). However, the largest mean growth rate recorded for larvae that develop through a fewer number of instars (Table 3) is consistent with that described for the same species feeding on slim amaranth [*Amaranthus hibridus* (L.)], considered the best food plant under which the larvae completed their development for only five instars. In the fifth instar, the larvae fed on slim amaranth reached the size resembling sixth instar larvae fed on tomato, sweet potato, and purslane (Valverde and Sarmiento 1987 [1986]).

The measurement of the largest width of the head capsule of the last instar of *S. eridania* (Table 3) is very similar to the values described in several studies of the same species (Mayer and Babers 1944, Parra et al. 1977, Valverde and Sarmiento 1987 [1986], Mattana and Foerster 1988).

### Table 1. Survival and duration of the *S. eridania* life cycle during different developmental stages, on artificial diet under controlled conditions (25 ± 1°C; 70 ± 10% RH, and 14-h photophase)

| Stage  | N initial–final | Survival (%) | Duration (d) | Range (d) |
|--------|-----------------|--------------|--------------|-----------|
| Egg    | 2,383–2,331     | 97.818       | 4.00 ± 0.000 | 4         |
| Larval | 298–279         | 93.624       | 16.183 ± 1.59 | 14–21     |
| Prepu- pal | 279–269 | 96.416       | 1.575 ± 0.588 | 1–3       |
| Pupal  | 269–261         | 97.026       | 9.169 ± 1.328 | 7–14      |
| Total  |                 | 85.673       | 30.927       |           |
Table 2. Mean larval and pupal duration (d) of *S. eridania*, 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)

| Developmental period | Six instars (mean ± SD) | Seven instars (mean ± SD) |
|----------------------|--------------------------|---------------------------|
|                      | Females (120) | Significance | Males (132) | Significance | Females (9) |
| I                    | 3.008 ± 0.330 | NS | 3.023 ± 0.380 | NS | 3.222 ± 0.441 |
| II                   | 2.408 ± 0.587 | NS | 2.318 ± 0.529 | NS | 2.222 ± 0.441 |
| III                  | 2.333 ± 0.599 | NS | 2.242 ± 0.526 | NS | 2.444 ± 0.726 |
| IV                   | 2.500 ± 0.710 | NS | 2.402 ± 0.652 | NS | 2.444 ± 0.726 |
| V                    | 2.867 ± 0.733 | NS | 2.674 ± 0.682 | * | 2.444 ± 0.527 |
| VI                   | 4.875 ± 1.142 | NS | 4.606 ± 0.979 | ** | 3.111 ± 0.928 |
| VII                  | — | NS | — | NS* | 5.222 ± 0.66 |
| Prepupal             | 1.525 ± 0.549 | NS | 1.629 ± 0.623 | NS | 4.844 ± 1.333 |
| Totala               | 17.992 ± 1.452 | ** | 17.265 ± 1.353 | ** | 21.111 ± 1.167 |
| Pupal                | 8.933 ± 1.352 | ** | 9.500 ± 1.485 | NS | 8.444 ± 1.333 |
| Larval + pupal       | 26.925 ± 2.087 | NS | 26.765 ± 1.773 | ** | 29.556 ± 2.007 |

Comparisons of means using a Student’s *t*-test, considering different variances, at a significance level of 95% (NS, *P* > 0.05; **P** < 0.05; ***P*** < 0.01).

* Nine females.

*a* Larval including prepupal period.

Table 3. Width (mm) of head capsules of *S. eridania* larvae reared on artificial diet, at each instar and respective growth rates, including larvae which developed for six (15 females and 15 males) and seven instars (9 females), under controlled conditions (25 ± 1°C, 70 ± 10% RH, and 14-h photophase)

| Instar     | Females (15) | Six instars | Males (15) | Seven instars |
|------------|--------------|-------------|-------------|---------------|
|            | Mean ± SD    | Growth rate | Significance | Mean ± SD    | Growth rate | Significance | Females (9) | Mean ± SD | Growth rate |
| I          | 0.323 ± 0.021 | — | NS | 0.318 ± 0.030 | — | NS | 0.313 ± 0.026 |
| II         | 0.485 ± 0.026 | 1.501 | NS | 0.483 ± 0.046 | 1.520 | NS | 0.484 ± 0.041 |
| III        | 0.783 ± 0.038 | 1.614 | NS | 0.785 ± 0.047 | 1.625 | NS | 0.747 ± 0.046 |
| IV         | 1.183 ± 0.060 | 1.510 | NS | 1.189 ± 0.035 | 1.514 | * | 1.114 ± 0.066 |
| V          | 1.773 ± 0.104 | 1.499 | * | 1.664 ± 0.087 | 1.400 | ** | 1.540 ± 0.101 |
| VI         | 2.636 ± 0.105 | 1.486 | * | 2.505 ± 0.117 | 1.505 | ** | 2.096 ± 0.119 |
| VII        | — | — | — | 2.720 ± 0.077 | 1.298 | — | 1.437 |
| Mean       | — | 1.522 | — | 1.513 | — | — | — |

Comparison of means using a Student’s *t*-test, considering different variances, at a significance level of 95% (NS, *P* > 0.05; **P** < 0.05; ***P*** < 0.01).

This is certainly related to the theory that the absolute size of caterpillars at the end of development triggers the process of metamorphosis (Nijhout 1975). This also explains the low growth rate between the penultimate and last larval instar of specimens that have undergone additional instars (Table 3), also described by Parra et al. (1977) and Mattana and Foerster (1988).

During the prepupal period (Tables 1 and 2), which corresponds to the time when the larvae do not feed and prepare for the pupal stage, a relatively high survival was observed, along with a relatively short duration, without any significant differences between sexes and individuals which underwent six or seven larval instars. The only data in the literature referring to prepupal survival for this species (Santos et al. 2005) indicates 100.0, 90.0, and 37.5% survival during this period, with larvae feeding on cotton, morning glory, and soybean leaves, respectively. In any case, *S. eridania* was very well adapted to its rearing conditions, even during this period, usually considered critical for holometabolous insects due to metamorphosis (Parra 1991).

The records of at least 202 natural host plants of *S. eridania* (Table 4) is certainly related to the high degree of polyphagy described by several authors in North America (e.g., Chittenden and Russel 1909, Cumb 1929, Soo Hoo and Fraenkel 1966a,b), Central America (e.g., Maes and Tellez 1988, Torres 1992, Coto et al. 1995), and South America (e.g., Silva et al. 1968, Biezanko et al. 1974, Pastrana 2004).

The large number of natural host plants of *S. eridania* (Table 4) is only comparable to *S. frugiperda* (Smith 1797) for which there are 186 host plants (Casmuz et al. 2010). However, for *S. frugiperda*, there is a clear preference for Poaceae (66 species), which is not observed in *S. eridania*, with only 10 Poaceae; the number of Fabaceae (21) recorded for *S. frugiperda* is almost equal to that obtained for *S. eridania* (20); yet the numbers of Asteraceae and Solanaceae (8) reported for *S. frugiperda* are much lower than those recorded for *S. eridania* (20 and 19, respectively). Besides these differences, it should be noted that *S. eridania* seems to have a preference for certain groups of plants not commonly used by other species such as *S. albula* (Montezano et al. 2013) and *S. frugiperda* (Casmuz et al. 2010), with few or no records of Amaranthaceae and Phytolaccaceae (Table 4). The fact that this species was initially recorded very early in North (Smith 1797), Central (Puerto Rico) (Chittenden and Russel 1909) and South America (e.g., Lima 1928 [1927], Marques 1932) as feeding on Phytolaccaceae (Table 4) in all these localities supports the hypothesis presented by Scriber (1986) that pokeweeds are their natural hosts.

We highlight the occurrence of this species in crops of regional importance or which have been explored with greater intensity at different locations during the same periods or at different times (Table 4). This data relate to the versatility and ability of this species to rapidly adapt in various regions of the continent feeding on cultivated plants such as alfalfa, bean, beet, cabbage, cassava, corn, cotton, potato, sweet potato, and tomato (e.g., Chittenden and Russel 1909; Lima 1928 [1927]; Cumb 1929; Marques 1932; Wolcott 1936, 1948 [1951]; Hambleton 1939; Tucker 1939; Waterston 1939, 1947; Corseuil 1955; Olalquiaga 1955; Costa 1958; Nickell 1958; Harris 1959; Kimbal 1965; González 1966; McGuire and Crandal 1967; Silva et al. 1968; Cantu and Wolfenbarger 1970; Creighton et al. 1971; Tietz 1972; Valencia and Valdivia 1973; Biezanko et al. 1974; Hickings and Rabinovich 1974;
**Table 4. Natural host plants of *S. eridania* larvae recorded in several bibliographic sources and new records from Rio Grande do Sul State, Brazil, especially within the mountainous region from two population outbreaks, during the spring of 1997 and 2004**

| Botanic family   | Scientific name                                                                 | Common name                                           | References |
|------------------|----------------------------------------------------------------------------------|-------------------------------------------------------|------------|
| 1. Acanthaceae   | *Odontonema strictum* (Nees) Kuntze                                                |                                                       | 55, 71     |
| 2. Acanthaceae   | *Sanchezia speciosa* Leonard                                                      |                                                       | 55, 71     |
| 3. Acanthaceae   | *Telostachya alopecuroidea* (Vahl) Ness                                           |                                                       | 55, 71     |
| 4. Acanthaceae   | *Achyranthes aspera* L.                                                           | Devil’s horsewhip                                    | 67         |
| 5. Acanthaceae   | *Amaranthus deflexus* L.                                                          | Red-root amaranth                                     | 31, 63, a  |
| 6. Acanthaceae   | *Amaranthus hibiridus* L.                                                         | Slim amaranth                                         | 37, 54, 31, 71 |
| 7. Acanthaceae   | *Amaranthus quitensis* Kunth                                                       | Ataco                                                | 63         |
| 8. Acanthaceae   | *Amaranthus retroflexus.* L.                                                       | Rough pigweed                                        | 54         |
| 9. Acanthaceae   | *Amaranthus spinosus* L.                                                          | Spiny amaranth                                        | 1, 2, 6, 29, 51, 67, 71, a |
| 10. Acanthaceae  | *Amaranthus viridis* L.                                                            | Callaloe                                              | 59         |
| 11. Acanthaceae  | *Celosia cristata* L.                                                             | Cockscob                                             | a          |
| 12. Acanthaceae  | *Spinacia oleracea* L.                                                             | Spinach                                              | 54         |
| 13. Anacardiaceae| *Schinus terebentifolium* Raddi                                                    | Brazilian peppertree                                 | a          |
| 14. Apiaceae     | *Apium graveolens* L.                                                             | Celery                                                | 3, 22, 29, 54, 56, a |
| 15. Apiaceae     | *Daucus carota* L.                                                                | Carrot                                               | 2, 29, 71  |
| 16. Asteraceae   | *Hydrocotyle ranunculoides* L.                                                     | Water pennwort                                       | 70         |
| 17. Apocynaceae  | *Nerium oleander* L.                                                              | Oleander                                             | 2, 29, 71  |
| 18. Araceae      | *Xanthosoma sp.*                                                                    |                                                       | 55, 71     |
| 19. Araliaceae   | *Didymopanax morototoni* (Aubl.) Decne & Pl.                                       |                                                       | 55, 71     |
| 20. Asteraceae   | *Artemisia absinthium* L.                                                         | Absinthium                                            | a          |
| 21. Asteraceae   | *Baccharis trimera* (Lessing) de Candolle                                         | Carqueja                                             | a          |
| 22. Asteraceae   | *Bidens pilosa* L.                                                                | Hairy beggarticks                                    | a          |
| 23. Cactaceae    | *Chrysanthemum morifolium* Ramat                                                  | Chrysanthemum                                        | 38, 39, 71 |
| 24. Cactaceae    | *Clibadium erasum* (Swartz) de Candolle                                           | Weed                                                 | 55, 71     |
| 25. Cactaceae    | *Coryza bonariensis* (L.) Cron.                                                   | Weed                                                 | 55, 71     |
| 26. Cactaceae    | *Coryza canadensis* (L.) Cron.                                                     | Weed                                                 | 55, 71     |
| 27. Caryophyllaceae| *Eclipta prostrata* (L.) L.                                                       | Eclipta                                              | 55, 71     |
| 28. Caryophyllaceae| *Erechtites valerianaeoflia* (Wolf) DC.                                            | Brazilian fireweed                                   | 55, 71     |
| 29. Caryophyllaceae| *Gerbera jamesonii Bolus*                                                         | Gerbera daisy                                        | a          |
| 30. Caryophyllaceae| *Helianthus annuus* L.                                                             | Sunflower                                            | 2, 43, 71  |
| 31. Caryophyllaceae| *Lactuca sativa* L.                                                                | Lettuce                                              | 23, 48, 56, 71, a |
| 32. Caryophyllaceae| *Mikania cordifolia* (L.) Wildenow                                                 | Guaco                                                | 55, 71     |
| 33. Caryophyllaceae| *Neurobocha lobata* (L.) Cassini                                                   |                                                      | 55, 71     |
| 34. Caryophyllaceae| *Pseudoelephantopus spicatus* (Jussieu ex Aublet)                                 | Weed                                                 | 55, 71     |
| 35. Caryophyllaceae| *Sonnchus sp.*                                                                      | Sonchus                                              | 2, 71      |
| 36. Caryophyllaceae| *Sonnchus oleraceus* L.                                                            | Common sowthistle                                    | 29, a      |
| 37. Caryophyllaceae| *Taraxacum officinale* Webber                                                     | Blowball                                             | a          |
| 38. Caryophyllaceae| *Vernonia tweedleiana* Baker                                                       | Ironweeds                                            | a          |
| 39. Caryophyllaceae| *Impatiens sultana* Hook                                                           | Balsamine                                            | 55, 71     |
| 40. Caryophyllaceae| *Impatiens wallera* Hook                                                           |                                                       | 55, 71     |
| 41. Begoniaceae  | *Begonia rex Putz*                                                                 | Begonia                                              | a          |
| 42. Begoniaceae  | *Begonia rex Putz*                                                                 | Lesser swinecress                                    | a          |
| 43. Brassicaceae | *Coronopus didymus* (L.) Smith                                                     |                                                       |            |
| 44. Brassicaceae | *Brassica napus* L. var. *oleifera* (de Candolle) Metzger                          |                                                       |            |
| 45. Brassicaceae | *Brassica nigra* (L.) W.D.J. Koch                                                  |                                                       |            |
| 46. Brassicaceae | *Brassica oleracea var. capitata* L.                                               | Cabbage                                              | 2, 29, 34, 48, 56, 71, a |
| 47. Brassicaceae | *Brassica oleracea* L. var. *viridis* L.                                           | Collard                                              | 1, 2, 29, 71, a |
| 48. Brassicaceae | *Eruca sativa* Gars.                                                               | Garden rocket                                        | a          |
| 49. Brassicaceae | *Nasturium officinale* R. Brown                                                    | Watercress                                           | a          |
| 50. Campanulaceae| *Lobelia portorcisgris* (Vatke) Urban                                              |                                                       | 55, 71     |
| 51. Caprifoliaceae| *Lonicer a japonica* Thumberg                                                      | Japanese honeysuckle                                 | a          |
| 52. Caricaceae   | *Carica papaya* L.                                                                 | Papaya                                               | 68         |
| 53. Caryophyllaceae| *Dianthus caryophyllus* L.                                                        | Carnation                                            | 4, 10, 17, 19, 24 |
| 54. Cecropiaceae | *Cecropia peltata* L.                                                              | Trumpet tree                                         | 55, 71     |
| 55. Chenopodiaceae| *Beta vulgaris* L.                                                                  | Beet                                                 | 2, 24, 29, 48, 54, 56, 62, 63, 65, 71, a |
| 56. Chenopodiaceae| *Beta vulgaris* L.                                                                  | Sugar beet                                           | 31         |
| 57. Chenopodiaceae| *Beta vulgaris* L. var. *ciclo* L.                                                 | Swiss chard                                          | 16, 62, 65, 71, a |
| 58. Chenopodiaceae| *Chenopodium quinoa* Wildenow                                                      | Quinoa                                               | 12, 60, 71 |
| 59. Commelinaceae| *Commelina diffusa* Burman                                                         |                                                       | 55, 71     |
| 60. Commelinaceae| *Tripogandra serrula* (Wahl) Handles                                               |                                                       | 55, 71     |
| 61. Convolvulaceae| *Calonyctium speciosum* Choisy                                                    | Good night                                           | a          |
| 62. Convolvulaceae| *Ipomea batatas* (L.) Lamarck                                                      | Sweet potato                                         | 1, 2, 4, 5, 13, 15, 17, 19, 20, 22, 24, 29, 31, 33, 48, 56, 62, 63, 71, a |
| 63. Convolvulaceae| *Ipomeoa grandiflora* L.                                                           | Moonflower                                           | 64         |
| 64. Convolvulaceae| *Ipomea purpurea* Roth                                                             | Handbell                                             | a          |
| 65. Convolvulaceae| *Ipomea lutea* (Wildenow) Choisy                                                 |                                                       | 55, 71     |
| 66. Cucurbitaceae| *Cucumis melo* L.                                                                  |                                                       | 48, a      |
| 67. Cucurbitaceae| *Cucumis sativus* L.                                                               | Cucumber                                             | 24, 48, 56, a |
| 68. Cucurbitaceae| *Cucurbita maxima* Duch                                                            | Squash                                              | 29         |
| 69. Cucurbitaceae| *Citrullus lanatus var. *lanatus* (Thumberg) Matsumura & Naka                     | Watermelon                                           | 2, 29, 48, 56, 71 |

(continued)
| Botanic family | Scientific name | Common name | References |
|----------------|-----------------|-------------|------------|
| 72. | Sechium edule (Jacquin.) Swartz | Chayote | a |
| 73. | Dioscoreaceae | Dioscorea polygoonides Humboldt Bonpland | 55, 71 |
| 74. | Ericaceae | Vaccinium macrocarpum Aiton | Cranberry | 29 |
| 75. | Euphorbiaceae | Phytolacca americana | Pokeweed | 1, 2, 29, 31, 48, 54, 56, 62, 63, 65, 71, a |
| 76. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 77. | Fabaceae | Phaseolus polystachios | Thicket bean | 29 |
| 78. | Fabaceae | Phaseolus lunatus | Bean | 13, 24, 29, 31, 48, 54, 56, 62, 63, 65, 71, a |
| 79. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 80. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 81. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 82. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 83. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 84. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 85. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 86. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 87. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 88. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 89. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 90. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 91. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 92. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 93. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 94. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 95. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 96. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 97. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 98. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 99. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 100. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 101. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 102. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 103. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 104. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 105. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 106. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 107. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 108. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 109. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 110. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 111. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 112. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 113. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 114. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 115. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 116. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 117. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 118. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 119. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 120. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 121. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 122. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 123. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 124. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 125. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 126. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 127. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 128. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 129. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 130. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 131. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 132. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 133. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 134. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 135. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 136. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 137. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 138. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 139. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 140. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 141. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 142. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |
| 143. | Fabaceae | Phaseolus vulgaris | Lima bean | 44, 71 |

(continued)
Table 4. Continued

| Botanic family       | Scientific name               | Common name          | References |
|----------------------|-------------------------------|----------------------|------------|
| 144. Polygonaceae    | Digitaria ischaemum (Schreb.) Schreber ex Muhltenberg | Small crabgrass      | 29         |
| 145. Digitaria sanguinalis (L.) Scopoli | Large crabgrass | 2, 22, 29, 71         |
| 146. Ichnanthus pallens (Sw.) Munroe | Ryegrass | 55, 71       |
| 147. Loliwm perenne L. | Melinis minutiflora Beauverie | Molassesgrass       | 24         |
| 148. Oryza sativa L. | Pennisetum purpureum (Persoon) | Elephant grass      |            |
| 149. Stenopaphrum secundatum (Walter) Kunze | Buffalo grass | 6, 55, 71       |
| 150. Zea mays L.     | Link (1977); 35, Price and Poe (1977); 36, Bellotti and Schoonhoven (1978); 37, Tingle et al. (1978); 38, Schuster and Engelhard (1979); 39, Price et al. (1980); 40, Silva and Magalhães (1980); 41, Pena and Wadill (1981); 42, Wolfson (1982); 43, Mitchell (1984); 44, Anderson et al. (1986); 45, Scriber (1986); 46, Ahmad et al. (1987); 47, Jones (1987); 48, Maes and Tellez (1988); 49, Mattana and Foerster (1988); 50, Nora and Reis (1988); 51, Savoie (1988); 52 - Foerster and Link (1977); 53, Price and Poe (1977); 54, Bellotti and Schoonhoven (1978); 55, Tingle et al. (1978); 56, Schuster and Engelhard (1979); 57, Price et al. (1980); 58, Silva and Magalhães (1980); 59, Clarke-Harris et al. (1998); 60, Rasmussen et al. (2003); 61, Nuesly et al. (2004); 62, Pastrana (2004); 63, Specht et al. (2004); 64, Santos et al. (2005); 65, Angulo et al. (2008); 66, Dias et al. (2009); 67, Janzen and Hallwachs (2009); 68, Semillas del Caribe (2010); 69, Mendoza et al. (2011); 70, Walsh and Maestro (2011); 71, Pogue (2012); 72, Bortoli et al. (2012). |

1. Chittenden and Russell (1909); 2. Crumb (1929); 3. Stoner and Wisecup (1930); 4. Marques (1932); 5. Monte (1934); 6. Wolcott (1935); 7. Hambleton (1939); 8. Tucker (1939); 9. Waterston (1939); 10. Brandão Filho (1942); 11. Wille and Garcia (1942); 12. Nickel (1942); 13. Waterston (1942); 14. Bedford (1949); 15. Biezanko and Bertholdi (1951); 16. Wolcott (1951); 17. Corseuil (1955); 18. Olalquiaga (1955); 19. Costa (1958); 20. Nickle (1958); 21. Harris (1959); 22. Kimbal (1965); 23. McGuire and Crandal (1967); 24. Silva et al. (1968); 25. Cantu and Wolfenbarger (1970); 26. Brandaño Filho (1971); 27. Creighton et al. (1972); 28. Cortés and Campos (1972); 29. Tietz et al. (1972); 30. Valencia and Valdivia (1973); 31. Biezanko et al. (1974); 32. Figueroa (1976); 33. Habeck (1976); 34. Link (1977); 35. Price and Poe (1977); 36. Bellotti and Schoonhoven (1978); 37. Tingle et al. (1978); 38. Schuster and Engelhard (1979); 39. Price et al. (1980); 40. Silva and Magalhães (1980); 41. Peña and Wadill (1981); 42. Wolfson (1982); 43. Mitchell (1984); 44. Anderson et al. (1986); 45. Scriber (1986); 46. Ahmad et al. (1987); 47. Jones (1987); 48. Maes and Tellez (1988); 49. Mattana and Foerster (1988); 50. Nora and Reis (1988); 51. Savoie (1988); 52 - Foerster and Dionisio (1989); 53. Nora et al. (1989); 54. Ferguson et al. (1991); 55. Torres (1992); 56. Coto et al. (1995); 57. Sánchez and Vergara (1996); 58. Sánchez-Aguirre R (1996); 59. Clarke-Harris et al. (1998); 60. Rasmussen et al. (2003); 61. Nuesly et al. (2004); 62. Pastrana (2004); 63. Specht et al. (2004); 64. Santos et al. (2005); 65. Angulo et al. (2008); 66. Dias et al. (2009); 67. Janzen and Hallwachs (2009); 68. Semillas del Caribe (2010); 69. Mendoza et al. (2011); 70. Walsh and Maestro (2011); 71. Pogue (2012); 72. Bortoli et al. (2012).
Table 5. Pupal weight (mg) of S. eridania 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 | Mean ± SD | Range |
|---------------|--------|---|-----------|-------|
| Six           | Female | 120 | 377.533 ± 51.654 | 253–538 |
|               | Male   | 132 | 329.447 ± 41.427 | 205–399 |
| Seven         | Female | 9   | 435.111 ± 41.619 | 389–528 |

*Comparison of means using Student’s t-test, considering different variances, at a significance level of 95% (*P < 0.01; **P < 0.001).
*Significance difference for the duration of the entire immature period between females and males which had six instars. The duration of larval + pupal development was markedly higher in females which had an additional instar (Table 2).

The sexual dimorphism, represented by the weight during the pupal phase, is relatively well documented among representatives of Spodoptera (e.g., Habib et al. 1983, Mattana and Foerster 1988, Bavaresco et al. 2004, Santos et al. 2005, Xue et al. 2010, Montezano et al. 2013) and other Lepidoptera. The larger size of the females which went through seven instars (Table 5) should be attributed to the additional instar (e.g., Esper et al. 2007, Nagoshi 2011, Montezano et al. 2013).

Although there are previously described natural and artificial diets (Peterson 1953, Soo Hoo and Fraenkel 1964, Redfern 1967, Smilowitz and Dewey 1969, Redfern and Raulston 1970) for the mass production of S. eridania, we used the artificial diet and the proposed rearing method, which was previously described for S. albula (Montezano et al. 2013). This methodology resulted in an overall survival of almost 85% (Table 1), above the 75% recommended by Singh (1983) and permitted a more complete detailing of several biological parameters of S. eridania, with minimal interference in its development. Moreover, the artificial diet allows the introduction of different substances and concentrations such as toxins for experiments, which evaluate toxicity, in a more standardized manner.

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