Biotic potential and reproductive parameters of *Spodoptera eridania* (Stoll) (Lepidoptera, Noctuidae) in the laboratory

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ABSTRACT. Biotic potential and reproductive parameters of Spodoptera eridania (Stoll) (Lepidoptera, Noctuidae) in the laboratory: This study aimed to evaluate the biotic potential and reproductive parameters of Spodoptera eridania (Stoll, 1782) under controlled conditions (25 ± 1°C, 70 ± 10% RH and 14 h photophase). The longevity, pre-, post- and oviposition periods, fecundity and fertility of 15 couples was evaluated. The longevity of females (10.80 days) was not significantly higher than those of males (9.27 days). The mean durations of the pre, post and oviposition periods were 2.067, 0.600 and 8.133 days, respectively. The mean fecundity per female was 1.398 eggs and the mean fertility was 1.367.50 larvae. On average, females copulated 1.133 times. A strong positive correlation was observed between the number of mating and fecundity (r = 0.881, P < 0.001). However a strong negative correlation was observed between the number of copulations and the duration of the pre-oviposition period (r = -0.823, P < 0.001). The biotic potential of S. eridania was estimated at 1.894 x 10^5 individuals/female/year. The net reproductive rate (Ro) was 560.531 times per generation and the mean generation time (T) was 35.807 days. The intrinsic rate of increase (rm) was 0.177, with a finite rate of increase (l) of 1.193, per week.

KEYWORDS. Armyworm; development; Insecta; reproduction; spermatophore.

The genus Spodoptera Guenée, 1852 is cosmopolitan and includes many of the most important agricultural armyworm caterpillars (Pogue 2002). Spodoptera eridania (Stoll, 1782) stands among the most important species that occurs throughout the American continent (Pogue 2002) and represents a potential risk for different crops like alfalfa, beans, beets, cabbage, cassava, cotton, onion, peanuts, quinoa, soybeans, tobacco, tomato, sweet potato, sunflower and vegetables in different parts of America (Hichings & Rabinovich 1974; Parra et al. 1977; Mattana & Foerster 1988; Coto et al. 1995; Santos et al. 2005, 2010; Sujii et al. 2006; Quintela et al. 2007; Valverde 2007; Michereff-Filho et al. 2008; Bortoli et al. 2012).

In addition to their great voracity and reproductive capacity (i.e. Hichings & Rabinovich 1974; Parra et al. 1977; Valverde & Sarmiento 1987a; Mattana & Foerster 1988; Santos et al. 2005), caterpillars of S. eridania, as other representatives of the genus, develop on invasive weeds which generally constitute the primary source of infestation of cultivated plants (Savoie 1988; Sánchez & Vergara 1996; Santos et al. 2005). S. eridania even has varying degrees of tolerance to various synthetic insecticides (Aziz 1973; Aguilera & Vasquez 1974; Valverde & Sarmiento 1987b), to plant extracts and botanical insecticides (Valles & Capinera 1993; Rosseti et al. 2008) and to the Cry1Ac gene of Bacillus thuringiensis (Polania et al. 2008; Amaya et al. 2009).

Due to the importance of S. eridania, studies have been developed comparing its biology in several host plants (Parra et al. 1977; Valverde & Sarmiento 1987a; Mattana & Foerster 1988; Santos et al. 2005; Bortoli et al. 2012), but obtaining contrasting results. Such differences may be attributed to the methodologies employed, the host plants, and the differences among populations, as observed for S. frugiperda (Smith, 1797) (Busato et al. 2005, 2008; Murúa et al. 2008). The present work is part of a series of studies which compare different aspects of the biology of S. albula (Walker, 1857) (Montezano et al. 2013), S. cosmioides (Walker, 1858), S. dolichos (Fabricius, 1794), S. eridania, and S. frugiperda under the same conditions. Thus, this study aims to evaluate and describe the biological parameters of S. eridania with special emphasis on its biotic potential and reproductive parameters, under controlled conditions, in order to allow comparisons with trials that evaluated the same species in different host plants as well as with future studies involving other populations and species.

MATERIAL AND METHODS

The experiments were carried out in a climate-controlled room (25 ± 1°C, 70 ± 10% RH and a 14-h photophase), with daily observations. The insects used belong to the first generation obtained from 32 caterpillars collected in a soybean field crop in Jataizinho/Ibiporã municipalities, Paraná State, Brazil (23°11’11.9”S, 51°01’58.3”W, 424 m.a.s.l.), to rule out possible mating incompatibilities, as previously described.
between biotypes from host plants from different locations (Murúa & Virla 2004; Murúa et al. 2008; Sadek & Anderson 2007).

To avoid the effect of the pupal weight on reproductive characteristics (Tisdale & Sappington 2001), they were weighed on the second day after metamorphosis, and only adult females from pupae weighing between 0.322 to 0.341 g and adult males from pupae weighing between 0.263 to 0.288 g were used in the experiments. Likewise, to avoid the effects of the adult age on their capacity to copulate (Kehat & Gordon 1975; Ellis & Steele 1982; Rogers & Marti Jr. 1994), the couples were formed with adults which emerged on the same date.

Adults were kept in pairs (n = 15) within cylindrical plastic containers, 10 cm in diameter and 15 cm high with tops closed using plastic film, to which long filter paper strips were attached to stimulate oviposition. The bottom part of the container was closed with a Petri dish (10.5 cm diameter), and its bottom was lined with filter paper. The food was composed of the diet described by Hoffmann-Campo et al. (1985) which consists of honey (10 g), sorbic acid (1 g), Methylparaben (1 g), sucrose (60 g), and distilled water (1000 ml). All components were dissolved in distilled water and the resulting solution was kept under refrigeration (7°C). Pilsen beer was added, on a daily basis, to the solution at a proportion of one-quarter, and made available to the insects in a 5 cm Petri dish lined with cotton wool. Furthermore, distilled water was provided for the hydration of the insects, in another 5 cm cotton lined Petri dish. Containers were examined daily to record adult survival and to remove and count the number of eggs. Dead females were dissected to determine the number of spermatophores they had received from males during copulation.

The fecundity (number of eggs per female), the fertility (number of hatched larvae per female), the longevity and the duration of the pre-oviposition, post-oviposition and oviposition periods were calculated. To estimate fertility, the viability of 32 egg masses taken from four couples that mated, including the first and the last ones, totaling 2,383 evaluated eggs. To this end, each egg cluster was individualized in a Petri dish, whose bottom was lined with filter paper moistened with distilled water, where it remained until the eclosion of the larvae. All the evaluated egg masses were from copulations of couples whose females, after death, had at least one spermatophore in the bursa copulatrix, proving they had been inseminated during the experiment.

All the biological parameters were analyzed using descriptive statistics with the calculation of means and standard deviations. The fecundity, longevity of both sexes and the duration of pre and post oviposition periods were correlated (Pearson Product Moment Correlation) with the number of copulations for each couple. Due to the high correlation of the parameters with respect to the number of copulations, only the overall averages of longevity were compared using the t-test assuming unequal variances, at a significance level of 5%. Between couples comparisons of the pre-oviposition, oviposition, longevity and fecundity were performed using ANOVA, with number of spermatophores as factor, and the means were separated by Tukey’s test at 5% probability. The data of the single pair that copulated only once are presented in figures but could not be included in the analysis.

After gathering the biological parameters, the Biotic Potential (BP) was calculated considering the resistance of the environment as being null, using the equation described in Silveira Neto et al. (1976), BP = (sr * dp) – er, where: (sr) sex ratio is number of females divided by number of females plus number of males; (d) viable individuals per female consisting of the number of eggs per female (or fecundity) multiplied by total survival; (n) number of generations per year or 365 days divided by the total lifespan; and (er) environmental resistance, in this case considered as null.

The biotic potential and the fertility life table was developed using data from the immature stages of S. eridania reared in accordance with the methodology of Montezano et al. (2013) and is graphically presented by plotting the probability of survival values at the midpoint of each time interval, (survival rate- lx), and the total number of eggs per female per week, which became females (specific fertility – mx).

Using the life table, the values of the different reproductive parameters of S. eridania were calculated. The net reproductive rate (Ro), given by the ratio between the number of females in two successive generations; the mean generation time (T), which is composed by the mean number of days from the birth of the parents to the birth of offspring; the daily intrinsic rate of increase (rm); and the daily finite rate of increase (λ), followed the formulas contained in Silveira Neto et al. (1976).

RESULTS

Table I shows the longevity of 15 couples, females and males, the average length of post-, pre- and oviposition as well as the average fertility. Using the data of egg viability (97.81%) of 2,383 eggs, the mean fertility was 1,367.50 caterpillars per female of S. eridania.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Biological parameter</th>
<th>Mean</th>
<th>Standard Deviation</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both</td>
<td>Longevity (days)</td>
<td>10.033</td>
<td>2.371</td>
<td>6 – 14</td>
</tr>
<tr>
<td>Female</td>
<td>Longevity (days)</td>
<td>10.800</td>
<td>2.426</td>
<td>8 – 14</td>
</tr>
<tr>
<td></td>
<td>Pre-oviposition (days)</td>
<td>2.067</td>
<td>1.335</td>
<td>1 – 5</td>
</tr>
<tr>
<td></td>
<td>Post-oviposition (days)</td>
<td>0.600</td>
<td>0.507</td>
<td>0 – 1</td>
</tr>
<tr>
<td></td>
<td>Oviposition (days)</td>
<td>8.133</td>
<td>1.246</td>
<td>6 – 10</td>
</tr>
<tr>
<td>Female</td>
<td>Fecundity (eggs)</td>
<td>1,398,000</td>
<td>470,289</td>
<td>634 – 1900</td>
</tr>
<tr>
<td>Male</td>
<td>Longevity (days)</td>
<td>9.267</td>
<td>2.120</td>
<td>6 – 13</td>
</tr>
</tbody>
</table>

Comparisons of male and female mean longevity using a Student t-test, considering different variances, at 5% level of significance (ns – p = 0.076).

On average each female copulated 1.13 times, while four (26.67%) did not copulate, six copulated only once (40%), four copulated twice (26.67%) and one copulated three times.
There was a strong positive correlation between the number of copulations and fecundity \((r = 0.881, P < 0.001)\), along with a strong negative correlation between the number of copulations and the duration of pre-oviposition period \((r = -0.826, P = 0.002)\), and longevity \((r = -0.823, P = 0.001)\).

The average daily number of eggs of uniseminated females was much smaller than females which were inseminated one or more times, along with an increase in the length of the pre-oviposition period (Fig. 1). The pre- and oviposition periods were significantly higher for females that were not inseminated (Figs. 2 and 3). Such differences were responsible for the increased longevity of the uniseminated females with respect to those which were inseminated. Similarly, a reduction in the longevity of males was observed (Fig. 4). The fecundity was positively affected by the number of copulations, as females which were not inseminated oviposited less than half of those which were inseminated, with significant differences between uniseminated females, and those inseminated once and twice (Fig. 5).
The biotic potential of $5.800 \times 10^{24}$ individuals per female per year, resulting from the equation $BP = (sr \times d^n - er \times BP = (0,502 \times 1,197,709)^{891.0}$, is obtained when we consider that: 135 females and 134 immature males reached the pupal stage, at a ratio of 0.502; on average each female oviposited 1,398 eggs and the overall survival was 85.673%, obtaining 1,197.71 viable individuals per female, the average duration of the life cycle (40.96 days), corresponds to 8.9 generations per year (n), considering the environmental resistance as null.

The maximum rate of population growth occurred between days 34 and 35, during the 5th week of life, represented by the intersection of the specific survival and fecundity lines (Fig. 6). This rate is relatively shifted towards the beginning of the adult phase, especially driven by the higher fertility and low mortality of immature individuals, soon after emergence.

The net reproductive rate (Ro) was 560.53 females per generation, the mean generation time (T) was 35.81 days, the daily intrinsic rate of increase (rm) and the daily finite rate of increase ($\lambda$) were $rm = 0.177$ and $\lambda = 1.193$, respectively. 

![Fig. 6. Relation between fertility (mx) and survival rate (lx) of females of Spodoptera eridania reared on an artificial diet at 25 ± 1°C, 70 ± 10% RH and a 14 hour photophase.](image)

### DISCUSSION

In this study, the longevity of *S. eridania* (Table I) was similar to that described by Valverde & Sarmiento (1987a) when fed with four different types of plants and by Mattana & Foerster (1988) in two different host plants, both at 25 °C. Likewise, these values are similar to those described by Parra et al. (1977) when the larvae were fed with soybeans, but these values were lower when the larvae were fed with cotton at 27 °C. However, the values were intermediate compared with those found for the same species raised at 22 °C when the larvae were fed with strawberry and grape (Bortoli et al. 2012). These results indicate that both larval and adult artificial diets provided the individuals with adequate nutrition, similar to that supplied by the most appropriate plants.

In the experiments conducted by Mattana & Foerster (1988) and Bortoli et al. (2012), there was no significant difference between the average longevity of males and females. However, a higher longevity for females (Table I) is also described by Valverde & Sarmiento (1987a) and Santos et al. (2005) for adults obtained from larvae fed on four host plants, differing from results obtained by Parra et al. (1977) that present a higher longevity for males.

Nevertheless, as it has been shown for other species in the genus (Kehat & Gordon 1975; Ellis & Steele 1982; Rogers & Marti Jr. 1997), the analysis of results comparing longevity as a function of the number of copulations (Fig. 4) indicates that this is an important factor to be included in analyses of longevity, especially considering the prolonged pre-oviposition and oviposition periods of the females that are not inseminated (Figs. 2–3).

Considering the data of the immature stages (30,927 days), the average longevity of adults of *S. eridania* corresponds to 24.495%, or more than one quarter of their life cycle. These results are similar to those of other studies involving *S. eridania* (Parra et al. 1977; Mattana & Foerster 1988) and other representatives of *Spodoptera* (Habib et al. 1983; Bavaresco et al. 2004; Busato et al. 2005). These results also indicate that the greater longevity of *S. eridania*, like other species of the genus, which have a strong ability for dispersal and even migration (Ferguson et al. 1991), is related to its wide distribution within the American continent, extending between the parallels 30° north and south (Pogue 2002).

The number of copulations obtained in this study is within the range described for *S. frugiperda* by Murúa et al. (2008), who found very discordant values between different populations of *S. frugiperda* in Argentina (0.78 to 2.32 spermatozoa per female). Regarding the absence of copulation in some couples of *S. eridania*, these same authors reported that in some groups of *S. frugiperda* more than 20% of the females did not mate. Moreover, considering that Milano et al. (2008), using 25 pairs of *S. frugiperda* per cage, obtained a mean of over three spermatozoa per female with a maximum of eight, at 25°C, it is expected that a higher number of individuals of *S. eridania* per cage would also increase the number of copulations.

The strong negative correlation observed between the number of copulations and the pre-oviposition period (Fig. 2) indicates that *S. eridania* presents an increase of the pre-oviposition period as a function of the reduced number or absence of mating, which is also reflected as prolonged longevity, similar to *S. littoralis* (Kehat & Gordon 1975; Ellis & Steele 1982) and *S. exigua* (Rogers & Marti Jr. 1997).

Similarly, the significant negative correlation between the number of copulations and egg laying period (Fig. 3) is related to the interaction between egg production and metabolism (Hou & Sheng 1999). These authors postulate that multiple fertilizations stimulate egg production and accelerate the consumption of energy and body reserves, reducing the resources available for somatic maintenance. However, the reduction of the egg laying period associated with a higher number of copulations, as described by Hou and Sheng (1999), certainly relates to the increase of the reproductive activity in females which copulated more.

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The relatively short pre-oviposition period (Table I), especially in inseminated females (Fig. 2) indicates that in adults of *S. eridania* reach sexual maturity soon after emergence, as occurs with other representatives of *Spodoptera* (Habib et al. 1983; Tisdale & Sappington 2001). However, the first oviposition, during the first days after emergence, presumes the occurrence of insemination. Our results indicate that the initial mating period of *S. eridania* must be between the first and second day after emergence, of both sexes, as described in Roger and Marti Jr. (1997) for *S. exigua*.

The average fertility of *S. eridania*, with close to 1,400 eggs per female (Table I) is similar to values indicated for the same species when the larvae were fed on soybean leaves, specifically 1,346.08 eggs (Parra et al. 1977). But it is relatively high when compared with larvae fed on cotton, morning glory and soybeans, which was: 680.5, 823.9 and 839.6, respectively (Santos et al. 2005). However, it was relatively lower than that observed when the larvae were fed with of sweet potato and bracatinga leaves, 1,859.64 and 2,082.73 respectively (Mattana & Foerster 1988), with cotton, 2,922.91 (Parra et al. 1977), with tomato, sweet potato, amaranth and *Portulaca*, 1,863.7 to 2,211.7 eggs (Valverde & Sarmiento 1987a) and when fed with strawberry and grape, 1,747.5 and 1,764.9 eggs (Bortoli et al. 2012).

Two fundamental factors are attributed to the differences in fertility found among the various studies: (a) adequacy of the diet, since the pupae of the most fertile specimens reported in literature were heavier, at least in Parra et al. (1977) with caterpillars fed on cotton and Valverde & Sarmiento (1987a) with caterpillars fed on tomato and sweet potato; and (b) fertilization of females (Fig. 5), when considering only the data from females that mated, the fecundity ranged from more than 1,500 to nearly 1,800, very much resembling the maximum indicated for adults emerging from pupae with a weight similar to that used in the present study (Parra et al. 1977; Valverde & Sarmiento 1987a; Mattana & Foerster 1988; Bortoli et al. 2012).

However, this variation can be attributed to several factors such as the conditions of each experiment, the biotypes related to the different host plants or different geographical regions (Giolo et al. 2002; Murúa and Virla 2004; Sadek and Anderson 2007; Busato et al. 2008; Murúa et al. 2008). The number of eggs obtained in this study indicates that the diet and the methodology employed to rear the immature stages and the adults were suitable for the development of *S. eridania* in the laboratory. These results underscore the importance that future studies should indicate the number of copulations (or at least if the females were inseminated or not) and the weight of pupae that gave rise to the adults.

The high egg viability (97.818%) is certainly related to proven insemination of females that had one or two spermatophores. This percentage agrees with the 96.00 to 98.84% reported by Valverde & Sarmiento (1987a) and generally agrees with studies on representatives of the genus *Spodoptera* where it is demonstrated that multiple matings result in an increase in reproductive capacity and in fertility (Kehat & Gordon 1975; Sadek 2001; Sadek & Anderson 2007; Busato et al. 2008; Milano et al. 2008).

The high value of the biotic potential (5.800 x 10^24) of *S. eridania* indicates that each female can produce more than 5.8 quadrillion descendants. This result is similar to that obtained from the data of Parra et al. (1977) for larvae reared on cotton at 27°C, considering a sex ratio of 0.5 or 1:1, where the calculated potential was approximately 6.6 x 10^23. The value of the biotic potential obtained in this study also indicates that diets and rearing conditions propitiated laboratory results very close to the maximum observed for the same species in the best conditions of the host plant in nature.

The maximum rate of population increase of *S. eridania* (Fig. 6) is relatively dislocated towards the beginning of the adult stage, especially driven by the higher fertility and low mortality of the immature individuals shortly after emergence. These observations are similar to those observed in other studies conducted with representatives of *Spodoptera* where the highest fertility values are observed during the first days, from the second or third to the seventh (Kehat & Gordon 1975; Sadek 2001; Bavaresco et al. 2004; Murúa & Virla 2004).

The net reproductive rate (Ro = 360.53) in artificial diet was similar to values reported in strawberry (Ro = 394.89) but was different to that described in grape (Ro = 213.98) (Bortoli et al. 2012). The result in artificial diet also was similar to values described for other representatives of *Spodoptera* in different host plants. For example: 377.11 for *S. exigua* on *Chenopodium album* L. (Chenopodiaceae), and 342.11 on canola, *Brassica napus* L. (Brassicaceae) (Farahani et al. 2011); also for *S. exigua*, 359.3 on cotton, *Gossypium hirsutum* L. (Malvaceae), 342.2 on sunflower, *Helianthus annuus* L. (Asteraceae), and the maximum value of 596.0 on pigweed, *Amaranthus retroflexus* L. (Amaranthaceae) (Greenberg et al. 2001); for *S. cosmioides*, 313.6 on castorbean, *Ricinus communis* L. (Euphorbiaceae) and 380.7 on onion, *Allium cepa* L. (Liliaceae) (Bavaresco et al. 2003); and for *S. frugiperda*, 372.2 on cotton (leaf), 363.2 (leaf and boll), 330.5 on millet (leaf), 421.8 on soybean (leaf) and 501.7 on corn (leaf) (Barros et al. 2010).

As demonstrated between two host plants for *S. eridania* (Bortoli et al. 2012) and observed in other representatives of the same genus (Greenberg et al. 2001; Bavaresco et al. 2003; Barros et al. 2010; Farahani et al. 2011), the net reproductive rate (Ro) of *S. eridania* varies widely depending on the plants with higher values for the preferred species, both cultivated crops and invasive weeds (Parra et al. 1977; Valverde & Sarmiento 1987a; Mattana & Foerster 1988; Santos et al. 2005).

The mean generation time (T = 35.81 days) of *S. eridania* was shorter than that observed at 22°C with larvae feed on strawberry (T = 59.1) and grape (T = 48.8) (Bortoli et al. 2012). It was similar to the maximum value obtained for *S. exigua* ~ 31.6 at 26°C (Greenberg et al. 2001; Farahani et al. 2011) and for *S. frugiperda* ~ 30.8 at 25°C (Barros et al. 2010). However, it was less than the minimum observed for *S. cosmioides* of ~ 47.2 at 26°C (Bavaresco et al. 2003).
The daily intrinsic rate of increase ($\lambda = 0.177$) and the daily finite rate of increase ($\lambda = 0.119$) was higher than that observed on strawberry ($\lambda = 0.101$, $\lambda = 1.100$) and grape ($\lambda = 0.110$, $\lambda = 1.120$) (Bortoli et al. 2012). These relatively low values are similar to those obtained for $S.\ cosmioides$ (Bavaresco et al. 2003) which has a higher generation time (T) compared with $S.\ exigua$ (Greenberg et al. 2001; Farahani et al. 2011) and $S.\ frugiperda$ (Barros et al. 2010).

The parameters calculated for $S.\ eridania$ resemble some of the values obtained with certain host plants of $S.\ cosmioides$ (Bavaresco et al. 2003), $S.\ exigua$ (Greenberg et al. 2001; Farahani et al. 2011), and $S.\ frugiperda$ (Barros et al. 2010). However, one must consider that there are large variations between the values for the same species, especially as a function of temperature, of host plant or of an artificial diet (Parra et al. 1977; Mattana & Foerster 1988; Ali & Gaylor 1992; Greenberg et al. 2001; Bavaresco et al. 2003, 2004; Busato et al. 2005; Santos et al. 2005; Azidah & Sofian-Azirun 2006; Sá et al. 2009; Barros et al. 2010; Farahani et al. 2011). Moreover, population variations should be considered, and in this sense Murúa et al. (2008) indicated large variations between biological and reproductive parameters between cohorts of $S.\ frugiperda$ from different locations and host plants in Argentina.

The analysis of data from this study indicate the importance of detailing all aspects of the reproductive biology of these species, since many details can underestimate or compromise data of reproductive parameters and complete expression of their biotic potential. Similarly, many aspects of the reproductive parameters of $S.\ eridania$ could not be compared with those of other studies due to lack of information, such as the average weight of pupae that originated the couples, the number of copulations for each couple, among others.

The results also indicate concerns with the need for a better understanding of the reproductive parameters of $S.\ eridania$ in the field, such as studies that include collecting adults of other species, using light traps (Sadek 2001), in order to compare with the data obtained in the laboratory so that relationships can be inferred with greater confidence. Also, the results of this study demonstrate that a reduction, or delay, in the number of copulations negatively influence the population parameters, indicating the relevance of the studies on the identification and use of pheromones (Jacobson et al. 1970; Redfern et al. 1971; Mitchell & Doolittle 1976; Teal et al. 1985; Mitchell & Tumlinson 1994) to delay or prevent the mating of $S.\ eridania$ in nature, in mating disruption procedures (Cardé & Minks 1995), as a strategy for the Integrated Management of this pest species.

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