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PADRONIZAÇÃO DE METODOLOGIA DE CRIAÇÃO DE *Spodoptera eridania* (Stoll) e *Spodoptera albula* (Walker) VISANDO DETALHAR PARÂMETROS BIOLÓGICOS

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Orientador: Prof. Dr. Alexandre Specht
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RESUMO:

O gênero *Spodoptera*, Guenée 1852, (Lepidoptera: Noctuidae) é representado por 30 espécies de importância por incluir grande parte dos insetos que causam danos significativos a diversas culturas de interesse econômico cultivada pelo homem. Entretanto, existem poucos estudos detalhados de biologia, especialmente relacionados a aspectos reprodutivos. Este estudo objetivou desenvolver e validar uma metodologia que permita detalhar os parâmetros biológicos de representantes de Lepidoptera, para permitir comparações intra e interespecíficas em condições controladas (25 ± 1ºC, 70 ± 10% UR e fotofase de 14 horas) e reunir informações sobre as plantas hospedeiras de suas lagartas. Para tanto foram empregadas e validadas novas metodologias de criação e dieta artificial. Nas fases imaturas observou-se que a viabilidade das fases de ovo, larva, pré-pupa e pupa foram de 94,54; 97,33; 93,84 e 92,34%, para *S. albula*, e de 97,82; 93,62; 96,42 e 97,03% para *S. eridania*, respectivamente. A duração média das fases de ovo, larva, pré-pupa e pupa foi de 4,14; 16,37; 1,69; e 9,34 dias, para *S. albula* e de 4,00; 16,18; 1,58; e 9,17 dias, para *S. eridania*. Na fase de larva observou-se que para ambas as espécies a maioria dos espécimes passaram por seis instares, com protandria larval significativa. Foram relacionadas 55 plantas hospedeiras para *S.albula* e 202 para *S. eridania*. A longevidade das fêmeas foi significativamente maior que a dos machos para ambas as espécies. Os períodos médios de pré, pós e oviposição foram de 2,615; 1,769 e 9,385 dias, respectivamente para *S. albula* e 2,067; 0,600 e 8,133 para *S. eridania*. A fecundidade média foi de 1.417,69 ovos e a fertilidade 1.340,401 lagartas por fêmea para *S. albula* e 1.398.00 e 1.367.50 para *S. eridania*. Em média as fêmeas copularam 1,2 vezes. Observou-se forte correlação positiva entre o número de cópulas e a fecundidade e, forte correlação negativa, entre o número de cópulas e a duração do período de pré-oviposição e a longevidade. O potencial biótico de *S. albula* e *S. eridania* foi estimado em 8,768 x 10^{22} e 1,894 x 10^{25} indivíduos/fêmea/ano respectivamente. A taxa líquida de reprodução (Ro), o tempo médio de geração, e a taxa intrínseca de aumento (rm) para *S. albula* e *S.eridania* foram respectivamente, 353,904; 560,531 vezes por geração, 37,187; 35,807 dias e 1,105; 0,177, com uma razão finita de aumento de (λ) 3,019 e (λ) de 1,193. Tanto a metodologia de criação quanto a dieta larval mostraram-se adequadas, pois permitiram alta sobrevivência, fertilidade e um melhor detalhamento das observações relacionadas ao ciclo biológico, especialmente do estágio larval.

Termos para indexação: Pragas de culturas, lagarta, dieta artificial, desenvolvimento, potencial biótico.

ABSTRACT:

The genus *Spodoptera*, Guenée 1852, (Lepidoptera: Noctuidae) is represented by 30 species of great importance to encompass most of the insects that cause significant damage to several economically important crops cultivated by man. However, there are few detailed studies of biology, especially related to reproductive aspects. This study aimed to develop and validate a methodology to detail the biological parameters of representatives of Lepidoptera, particularly *S. eridania* and *S. albula* to allow comparisons intra and interspecific under controlled conditions (25 ± 1 º C, 70 ± 10% RH and 14h photophase) and gather information about the host plants for their larvae. For both were employed and validated new methods of creation and artificial diet. In the immature stages was observed that the viability of the egg, larva, pupa and pre-pupae were 94.54, 97.33, 93.84 and 92.34% for *S. albula*, and 97.82, 93.62, 96.42 and 97.03% for *S. eridania*, respectively. The average duration of the stages of egg, larva, pupa and pre-pupa was 4.14, 16.37, 1.69, and 9.34 days for *S. albula* and 4.00, 16.18, 1.58, and 9.17 days for *S. eridania*. At the stage of larvae was observed that for both species passed through six instar, with significant larval protandry. 55 host plants were related for *S. albula* and 202 for *S. eridania*. The longevity of females was significantly higher than in males for both species. The average periods of pre, post and oviposition were 2.615, 1.769 and 9.385 days, respectively for *S. albula* and 2.067, 0.600 and 8.133 for *S. eridania*. The average fecundity was 1.417,69 egss 1.340,401 larvae per female for *S. albula* and 1.398.00 and 1.367.50 to *S. eridania*. On average females mated 1.2 times. There was a strong positive correlation between the number of matings and fecundity, and a strong negative correlation between the number of copulations and duration of pre-oviposition and longevity. The biotic potential of *S. albula* and *S. eridania* was estimated at 8,768 x 10^{22} and 1,894 x 10^{25} individuals / female / year respectively. The net reproductive rate (Ro), mean generation time and intrinsic rate of increase (rm) for *S. albula* and *S.eridania* were respectively 353.904, 560.531 times per generation, 37.187, 35.807 days and 1.105, 0.177, with a finite rate of increase (λ) and 3.019 (λ) of 1.193. Both the methodology of creation as the larval diet were suitable, because they enabled high survival, fertility and much more detail of the observations related to the biological cycle, especially the larval stage.

Index terms: annual crop pest, armyworm, artificial diet, development, biotic potential.

1. INTRODUÇÃO

O gênero *Spodoptera* Guenée 1852, (Lepidoptera: Noctuidae) é representado por 30 espécies, importantes por incluir a maior parte dos insetos que causam danos significativos a diversas culturas de interesse econômico cultivada pelo homem.

Espécies de *Spodoptera* incluem as mais expressivas pragas do continente americano, provocando reduções estimadas de 15 a 34% nos rendimentos agrícolas, e 400 milhões de dólares em prejuízos econômicos anuais, devido principalmente a grande voracidade e sua presença em todos os estágios vegetativos.

A maior parte das espécies que ocorrem no continente americano apresenta lagartas polífagas, que atacam especialmente culturas de algodão, arroz, milho, soja e trigo. No Brasil ocorrem as espécies: *Spodoptera albula* (Walker, 1857); *Spodoptera androgea* (Stoll, 1782); *Spodoptera cosmioides* (Walker, 1858); *Spodoptera dolichos* (Fabricius, 1794); *Spodoptera eridania* (Stoll, 1782); *Spodoptera exigua* (Hübner, 1808); *Spodoptera frugiperda* (J.E. Smith, 1797) e *Spodoptera marima* (Schaus, 1904).

As espécies *S. albula* e *S. eridania* são muito similares tanto morfologica quanto filogeneticamente, o que determina que em muitas ocasiões sejam confundidas. As lagartas de ambas as espécies são polífagas, sendo comumente encontradas em diversas plantas cultivadas e de importância crescente em diversas culturas, especialmente algodão e soja. Além do hábito polífago, ambas as espécies podem danificar as plantas consumindo brotos, folhas, flores e frutos.

A maior parte do conhecimento a respeito da biologia e metodologia de criação de representantes de *Spodoptera* restringem-se a *S. cosmioides*, *S. eridania* e *S. frugiperda*. Entretanto as metodologias e dietas são diversas e muitas vezes não permitem comparações devido à falta de detalhamento.

O conhecimento da biologia dessas espécies é de fundamental importância para o desenvolvimento de técnicas de manejo, que só são possíveis com o estabelecimento de metodologias de criação laboratorial que permitam manter diversas gerações em condições padronizadas, obtendo alta viabilidade e sobrevivência dos insetos.

O desenvolvimento destas condições possibilita a adoção de novas ferramentas de estudo e também o conhecimento de aspectos detalhados, como reprodutção dos adultos, extração e análise de feromônios, aspectos comportamentais, entre outros, contribuindo, desta forma para programas de manejo integrado destas pragas.

O presente estudo teve como objetivo desenvolver e validar uma metodologia que permita detalhar os parâmetros biológicos de representantes de Lepidoptera, para serem possíveis comparações intra e interespecíficas.

Os resultados estão apresentados em quatro capítulos: no primeiro são descritos os estágios imaturos de *S. albula* e suas plantas hospedeiras; no segundo são avaliados o potencial biótico, a fertilidade e a tabela de vida de *S. albula* em condições controladas; no terceiro são descritos os estágios imaturos de *S. eridania* e suas plantas hospedeiras e, no quarto, são avaliados, potencial biótico, a fertilidade e a tabela de vida de S. *eridania* em condições controladas.

2. OBJETIVOS

2.1 Objetivo Geral

Desenvolver e validar uma metodologia que permita detalhar os parâmetros biológicos de representantes de Lepidoptera, para serem possíveis comparações intra e interespecíficas.

2.2 Objetivos específicos

- Adaptar, padronizar e validar uma metodologia de criação que permita descrever os parâmetros biológicos em cada fase de desenvolvimento;
- Adaptar, padronizar e validar uma dieta larval artificial que possa ser usada para diferentes espécies de *Spodoptera* visando detalhar os parâmetros biológicos;
- Gerar dados e detalhar parâmetros biológicos que permitam comparar e discutir resultados publicados em estudos anteriores sobre as mesmas espécies e congenéricas;
- Reunir, organizar e disponibilizar informações relativas às plantas hospedeiras nativas e exóticas, cultivadas ou não ocorrentes em todo o Continente Americano.

3. REVISÃO BIBLIOGRÁFICA

3.1 Gênero *Spodoptera* (Gueneé, 1852)

O gênero *Spodoptera* Guenée, 1852 pertence à Noctuidae que é a família mais numerosa da ordem Lepidoptera (Zahiri *et al*. 2010, Lafontaine & Schmidt, 2010). O gênero inclui cerca de 30 espécies das quais pelo menos 15 são consideradas pragas-chave de plantas cultivadas (Tood & Poole 1980, Pogue, 2002, Angulo *et al*. 2006). O grupo é representado por mariposas cujas asas anteriores possuem coloração geral variando de tons de cinza a marrom, com envergadura entre 8 e 22mm e asas posteriores de coloração branca, muitas vezes translúcidas (Pogue, 2002).

Alguns representantes de *Spodoptera* que ocorrem no Brasil e também na região Neártica são relativamente bem estudados em trabalhos sobre a caracterização dos adultos, incluindo a genitália, com o conhecimento da maioria das formas larvais (Tood & Poole, 1980, Passoa, 1991, Heppner, 1998, Pogue, 2002).

Segundo Passoa (1991) muitas espécies são confundidas, especialmente nos estágios larvais, devido a grande variação estrutural e de coloração aliada a descrições incompletas das fases imaturas, não fornecendo elementos que permitam comparações e identificações específicas.

Apesar de existirem várias citações para a maioria das espécies, os conhecimentos biológicos se restringem a *S. cosmioides*, *S. eridania*, *S. exigua* e *S. frugiperda*. Com relação à *S. cosmioides* cabe ressaltar as recentes publicações de Bavaresco et *al*. (2002, 2003, 2004) enquanto que *S. eridania*, *S. exigua* e *S. frugiperda*, distribuídas por todo o Continente Americano, de elevada importância e com alto grau de polifitofagia, contam com diversos estudos documentados em bibliografia nacional e internacional reunidos no trabalho de Pogue (2002).

No Brasil, existe o registro da ocorrência de nove espécies: *Spodoptera albula* (Walker, 1857); *Spodoptera androgea* (Stoll, 1782); *Spodoptera cosmioides* (Walker, 1858); *Spodoptera dolichos* (Fabricius, 1794); *Spodoptera eridania* (Stoll, 1782); *Spodoptera exigua* (Hübner,

1808); *Spodoptera frugiperda* (Smith, 1797), *Spodoptera marima* (Schaus, 1904) e *Spodoptera ornithogalli* (Guenée 1852) (Pogue, 2002), que ocorrem em praticamente todos os Estados.

3.2 *Spodoptera albula* (Walker, 1857)

Até 1989 *S. albula* (Noctuidae, Noctuinae) era erroneamente chamada de *S. sunia* (Guenée, 1852), que atualmente é reconhecida como *Neogalea sunia* (Guenée, 1852) (Poole 1989), representante da subfamília Oncocnemidinae (Lafontaine & Smith, 2010).

A ocorrência de *S. albula* é registrada desde a Florida e sudeste do Texas, por todo o Caribe e América Central, e desde o sul da Venezuela até o Paraguai e sudeste do Brasil (Pogue 2002, Zenker *et al*. 2010), e Chile (Angulo *et al*. 2008).

S. albula compartilha com *S. eridania* inúmeras características biológicas e morfológicas (Pogue, 2002) muitas vezes confundidas, sendo que a identificação específica depende do exame de genitália.

As mariposas adultas medem de 26 a 37 mm de envergadura, as asas anteriores e corpo são acinzentados e as asas posteriores são brancas muitas vezes translúcidas. A característica marcante desta espécie é a presença de uma faixa longitudinal escura na base da asa anterior (Pogue, 2002).

As posturas consistem em massas irregulares, podendo conter até 1.400 ovos (Novo Padrino & Martínez Reyes, 1985), normalmente em duas camadas sobrepostas, mas podendo ocorrer até quatro e geralmente são recobertos por escamas do corpo da fêmea (Pogue, 2002).

Durante os primeiros instares de desenvolvimento as lagartas raspam as folhas, e conforme vão se desenvolvendo as destroem completamente. Essas lagartas têm hábitos noturnos e escondem-se no solo sob as plantas durante o dia.

A coloração das lagartas varia de preto-acinzentada a castanho-acinzentada, com duas fileiras dorsais de manchas triangulares pretas ou escuras, cada uma delas com um ponto branco no centro. Linha subespiracular ausente ou fraca e linha dorsal e subdorsal frequentemente

amarela, vermelha ou laranja, podendo ser fracamente marcada e a cabeça castanha com manchas pretas.

O registro desta espécie no Brasil ocorreu primeiramente em amendoim (*Arachis hypogaea,* L.), com infestações nas safras de 1999/2000, e logo no ano seguinte ocorreu reincidência de infestações, demonstrando assim seu potencial como praga dessa cultura no Estado de São Paulo, onde já houve necessidade de controle químico (Teixeira *et al*. 2001).

S. albula é uma espécie polífaga, registrada na literatura como praga de diversas espécies cultivadas como tomate, soja, milho, sorgo, hortaliças, algodão, ervilha e beterraba, alimentando-se tanto de folhas quanto de frutos, podendo causar alta intensidade de desfolha e, algumas vezes, cortando os caules (Savoie, 1988; Teixeira *et al*. 2001).

Além de polífagas, as lagartas de *S. albula* frequentemente migram para as plantas cultivadas, a partir das várias espécies de ervas daninhas que se desenvolvem nas bordas dos cultivos que servem como plantas hospedeiras (Hallman, 1979, González-B, 1966). Esta espécie representa um risco potencial, em muitos lugares, especialmente na América Central (Stoyan & Machado, 1970, Novo Padrino *et al*. 1984, 1985, Páez Gázquez & Novo Padrino, 1987), podendo inviabilizar o desenvolvimento de importantes culturas, como o tabaco, algodão (Alcaráz-Vieco, 1962, González-B, 1966), tomateiro (Gloria-B, 1975), couve (Armstrong, 1994), soja, gergelim (Hallman, 1979, 1983), amendoim (Teixeira *et al*. 2001), girassol (Pruet & Guaman, 2001), mamão (Semillas del Caribe, 2010) e até mesmo a produção de mudas em viveiros florestais (Vazquez *et al*. 1999).

O manejo dessa espécie precisa ser desenvolvido com um enfoque mais ecológico, pois além de sua voracidade e grande capacidade reprodutiva (Stoyan & Machado, 1970, Martin-Zequeira 1982, Novo Padrino *et al*. 1984, 1985, Novo Padrino & Martínez Reyes, 1985, Páez & Gázquez Novo Padrino, 1987, La Rosa *et al*. 1992), *S. albula* é tolerante a diversos inseticidas químicos (Gloria-B 1975, Savoie, 1988) e também ao gene Cry1Ac de *Bacillus thuringiensis* (Zenner-de-Polanía *et al*. 2008, Amaya *et al*. 2009), sendo o controle biológico uma alternativa

para este manejo. Sua importância como praga e sua tolerância a diversos produtos químicos motiva a identificação dos componentes feromonais para auxiliar no manejo integrado desta espécie em algodão (Bestmann *et al*. 1988) e em culturas de melão (Dunkleblum *et al*. 1995).

Devido à importância econômica desta espécie, vários estudos biológicos foram desenvolvidos para determinar parâmetros biológicos (Stoyan & Machado, 1970, Martin Zequeira 1982, Novo Padrino & Martínez Reyes, 1985, La Rosa *et al*. 1992), e de potencial dano (Novo Padrino *et al*. 1984, 1985, Páez Gázquez & Novo Padrino, 1987).

3.3 *Spodoptera eridania* (Stoll, 1782)

Spodoptera eridania (Stoll, 1782) tem sua ocorrência registrada no sudoeste dos Estados Unidos, do sul de Maryland até a Florida, e do oeste de Kentucky até o Texas. Na região neotropical, vai do México, Caribe, ao sul, passando pela América Central até a Argentina (Pogue, 2002), Chile (Angulo *et al*. 2008) e Uruguai (Betancourt & Scatoni, 2006).

No Brasil, *S. eridania* já foi encontrada em diversos cultivos e é bastante comum em soja desde o início do estágio reprodutivo da cultura, onde, além de se alimentar das folhas ataca também as vagens (Silva *et al*. 1968; Parra *et al*. 1977; Mattana & Foerster 1988, Nora e Reis Filho, 1988; Santos *et al*. 2005; 2010). Nas plantas do algodoeiro, produção de elevado valor econômico no serrado brasileiro, *S. eridania* ocorre desde o início do estagio vegetativo da planta até a maturação de flores e maçãs que também são atacadas, na ausência das maçãs a espécie pode destruir folhas e perfurar hastes (Gallo *et al*. 2002).

S. eridania possui alto grau de polifagia, cujo sucesso de adaptação às mais variadas espécies vegetais provavelmente está associado à sua grande capacidade em desintoxicar ou outras formas de processar a biomassa de plantas ou dietas que contenham altas concentrações de alomônios conhecidos (Brattsten *et al*. 1973, Brattsten, 1977, 1980, Blau *et al*. 1978, Scriber, 1978, 1979, Scriber & Slansky,1981; Manuwoto & Scriber, 1982).

O grande número de informações na literatura com relação a esta espécie indica a importância deste inseto para diferentes culturas como alfalfa, feijão, beterraba, repolho,

mandioca, couve, algodão, cebola, amendoim, quinoa, soja, tabaco, tomate, batata doce, girassol e olerículas, em diversos locais da America (Silva *et al*. 1968, Tietz, 1972, Coto *et a*l. 1995, Maes & Telles Robleto, 1988, Pastrana, 2004, Pogue, 2012).

Adicionalmente, esta espécie tem sido reportada causando surtos em diferentes condições, como em 1989 após a passagem de Furacão Hugo em Porto Rico (Torres, 1992), em reflorestamentos com espécies nativas (Mattana & Foerster, 1988), em culturas de olerículas (Michereff-Filho *et al*. 2008), e atingindo nível de dano econômico em lavouras comercias, especialmente, de alfafa (Hichings & Rabinivich, 1974) algodão e soja (Parra *et al*. 1977, Passos, 1978, Santos *et al*. 2005, 2010, Fontes *et al*. 2006, Sujii *et al*. 2006, Quintela *et al*. 2007, Valverde, 2007).

Além da sua grande voracidade e alta capacidade reprodutiva, (Hichings & Rabinivich, 1974, Parra *et al.* 1977, Valverde-C & Sarmiento, 1987, Mattana & Foerster, 1988, Santos *et al*. 2005) *S. eridania,* como outros representantes do gênero, se desenvolve em espécies de plantas invasoras, que geralmente se constituem a fonte primária de infestação das plantas cultivadas (Tingle *et al*. 1978, Savoie 1988, Sánchez-Aguirré, 1995, Santos *et al*. 2005), apresenta diferentes graus de tolerância a inúmeros inseticidas (González 1966, Campos-S 1972, 1982, Aziz 1973, Aguilera-P & Vasquez-C 1974) extratos vegetais, inseticidas botânicos (Valles & Capinera, 1993, Rosseti *et al*. 2008) e ao gene Cry1Ac de *Bacillus thuringiensis* (Zenner-de-Polanía *et al*. 2008, Amaya *et al*. 2009).

3.4 Importância da Criação Laboratorial de Insetos

O conhecimento da biologia de um inseto é de fundamental importância para desenvolver estratégias eficientes de manejo, dentro dos conceitos do manejo integrado de pragas (Parra, 2002). A criação massal de insetos em laboratório tem múltiplas aplicações, tanto na pesquisa aplicada em entomologia, no estudo de seus ciclos de vida, preferências alimentares entre outros, como na pesquisa aplicada por possibilitar estudos sobre controle biológico, produção de ferômonios, técnica do macho estéril, resistência, controle genético e vetores de doenças entre

outros. Esses estudos são possíveis devido à disponibilidade de meios práticos de criação dos insetos (Kogan, 1980).

O conhecimento dos parâmetros biológicos das espécies é fundamental para solucionar problemas relacionados com a entomologia básica e aplicada e seu posterior emprego em estudos de controle de pragas, e esse conhecimento só é alcançado quando as mesmas são criadas de forma controlada e padronizada.

A criação laboratorial é de fundamental importância para que os trabalhos não sofram falta de continuidade e nem fiquem dependentes da ocorrência natural do inseto, em especial, pragas agrícolas (Parra, 2002). O estudo com esses insetos em dietas artificiais permitiu grandes avanços nos campos da nutrição, toxicologia, endocrinologia, genética, comportamento e ecologia de insetos.

Os trabalhos com *S. albula* e *S. eridania*, assim como de outras espécies tem sido desenvolvidos com diferentes propósitos, diversas metodologias e plantas hospedeiras. As metodologias utilizadas muitas vezes não são detalhadas o suficiente para permitir comparações, ou inferir diferenças no desenvolvimento dessas espécies, principalmente dos estágios imaturos.

A descrição de uma dieta artificial e métodos de criação padronizados que propiciem uma maior sobrevivência, descrição padronizada dos processos de preparação que permitam que a dieta possa ser repetida em outros estudos, com uma descrição mais detalhada dos vários aspectos biológicos e o mínimo de interferência no desenvolvimento, permite a realização de várias inferências desconhecidas, como a duração e a sobrevivência de lagartas e de determinação do sexo, junto com a duração dos estágios de larva e pupa.

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5. RESULTADOS

5.1 CAPÍTULO 1:

Immature stages of *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae): Developmental parameters and host plants.

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Key words: annual crop pest, armyworm, artificial diet, development, life cycle. Short title: Immature stages of *Spodoptera albula*

Section: Biological Sciences

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Abstract

This study aimed to detail the biological parameters of the immature stages of *Spodoptera albula* (Walker, 1857) under controlled conditions (25 ± 1 ° C, 70 ± 10% RH and 14 hour photo phase) and gather information about their larval host plants. For this purpose, a new rearing method and artificial diet was employed and validated. The viability of the egg, larval, pupal and pre-pupal stages was 94.54, 97.33, 93.84 and 92.34%, respectively. The average duration of the egg, larval, pupal and pre-pupal stages was 4.14, 16.37, 1.69, and 9.34 days, respectively. During the larval stage, 80.85% of females and 93.99% of males passed through six and remaining through seven instars, with significant larval protandry. The larvae which developed through six and seven instars exhibited a mean growth rate of 1.58 and 1.48, respectively. Fifty five host plant species belonging to 29 families are listed. The female pupae were significantly larger, exhibiting protogyny. Both the rearing methods as well as the larval diet proved adequate, providing more detailled observations of the biological cycle, especially the larval stage, and resulting in an overall survival of almost 80%.

Introduction

The genus *Spodoptera* Guenée, 1852 (Lepidoptera: Noctuidae: Noctuinae) (Lafontaine & Smith 2010) is cosmopolitan and includes many of the most important agricultural caterpillars (Pogue 2002). *Spodoptera albula* (Walker 1857) has been recorded from Florida and Southern Texas, throughout the Caribbean, Central America, and from Venezuela south to Paraguay and Southern Brazil (Pogue 2002, Zenker *et al*. 2010), and Chile (Angulo *et al*. 2008). *Spodoptera albula* has been erroneously referred to as "*Spodoptera sunia* (Guenée, 1852)" which is currently recognized as *Neogalea sunia* (Guenée, 1852), representative of the Oncocnemidinae (Lafontaine & Smith 2010).

Beside being polyphagous, the larvae of *S. albula* usually migrate to crops, both coming from the various weeds which are between the rows and can be their host plants (Hallman, 1979), as well as along the edges (González-B 1966). This species represents a potential risk, making it unfeasible to develop important crops such as tobacco (Stoyan & Machado 1970, Novo Padrino *et al.* 1984, 1985, Páez Gázquez & Novo Padrino 1987), cotton (Alcaráz Vieco 1962, González-B 1966), tomato (Gloria-B 1975), cabbage (Armstrong (1994), sesame, soybean (Hallman 1979, 1983), peanuts (Teixeira *et al.* 2001), sunflower (Pruet & Guaman 2001), papaya (Semillas del Caribe 2010) and even seedling production in forestry nurseries (Vazquez *et al*. 1999).

Beyond its great voracity and reproductive capacity (Stoyan & Machado 1970, Martin Zequeira 1982, Novo Padrino *et al*. 1984, 1985, Novo Padrino & Martínez Reyes 1985, Páez Gázquez & Novo Padrino 1987, La Rosa *et al.* 1992), *S. albula* is tolerant to several chemical insecticides (Gloria-B 1975, Savoie 1988) and to the *Bacillus thuringiensis* Cry1Ac gene (Zenner-de-Polanía et al. 2008, Amaya *et al.* 2009). Its importance as a pest and its tolerance to several chemical products motivated the identification of pheromonal components to assist the integrated pest management of this species in cotton (Bestmann *et al*. 1988) and in melon crops (Dunkleblum *et al*. 1995).

Due to the importance of this species, especially in Central America and Cuba, several biological studies were developed to determine biological parameters (Stoyan & Machado 1970, Martin Zequeira 1982, Novo Padrino & Martínez Reyes 1985, La Rosa *et al*. 1992), and damage potential (Novo Padrino *et al*. 1984, 1985, Páez Gázquez & Novo Padrino 1987).

Considering the importance of *S. albula* for several crops of economic interest this study aimed to: (a) detail the various biological parameters of the immature stages under controlled conditions, to allow comparisons with previous studies and with other representatives of the same genus; (b) gather and organize information relating to host plants; and (c) validate a rearing method and an artificial larval diet which has already been used to detail the biological parameters of pest noctuids, in the "Laboratório de Controle de Pragas" of the "Universidade de Caxias do Sul".

Material and Methods

Insects

The experiments only used first generation specimens whose progeny initiated with eggs from a single female collected on January 9, 2011, in Jaboticabal, São Paulo (21°16'37.52"S, 48°17'37.54"W, altitude 572m). Species level identification was accomplished by comparing larvae and adults with descriptions in Pogue (2002).

Rearing

All the experiments were preformed in a climate controlled room (25 ±1ºC, 70 ±10% RH and a 14 hour photo phase), with daily observations.

Egg stage

Each egg mass was individually placed in a Petri dish 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 16 egg masses (4,454 eggs) taken randomly from four couples, including the first and last ovipositions. It was observed that the

evaluated egg masses were from couples, whose females presented two spermatophores in the bursa copulatrix, indicating that they had been fertilized during the experiment.

Larval Stage

Soon after hatching, 300 larvae 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 moisture, along with a small dose (~1 cm^3) of artificial diet were included in each cup, as described below. Daily observations were made to verify the survival and development of the larva (with removal of the head capsule), the need to complement or replace the dosage of the diet, and the cotton in order to maintain humidity, always being careful to not interfere and to touch the larva as little as possible. The head capsules were 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.

This methodology allowed us to record the number of larval instars, the survival and the individual duration of each instar / stage and of the 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.

As the method of measuring between the frontal setae of the head capsule (Podole & Klein 1978) is more precise than the traditional method that measures the distance between genas (Perez *et al.* 2005), we chose to measure distances between genas only in the first and last instar to permit comparisons with other studies and between the frontal setae for comparisons among instars, for larvae that developed through six and seven instars.

Composition and preparation of larval diet

The artificial diet (adapted from Greene *et al.*, 1976) was 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.

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 lab table until the temperature reached 25° C.

Then, the pre-baked beans were ground together with the remaining ingredients (wheat germ, powdered milk, yeast extract, soy protein and agar) which were added slowly alongwith the distilled water (1500 mL) in a domestic blender at full power for at least 10 minutes, forming a homogeneous mass. This homogenized mass was transferred to a stainless steel pot and cooked for 5 minutes, counting from the boiling point. After cooking, the mass was removed from the heat, and was cooled to 40 ° C, by manually mixing it.

At the same time, the ascorbic acid, sorbic acid, Nipagim, tetracycline chlorhydrate, vitamin mixture and formaldehyde solution were manually mixed in a 1 L Beaker with 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 gerbox-type boxes (11 x 11 x 3.5 cm) to the maximum height of 2.5 cm of diet. The Gerboxes were immediately transferred to a laminar flow chamber with ultraviolet light, until the temperature of 25° C was reached. After that, the Gerboxes 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 approximately 1 cm^3, 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 was performed, gathering information on the botanical family, specific name, common name and bibliographic reference. The nomenclature of the plants has been updated mainly using Backes & Nardino (2001).

Pupal stage

The pupae were kept without food, under the same conditions and containers of the prepupa. On the second day after pupation, when the cuticle was further hardened, the sex was determined comparing with the drawings of Angulo & Jana-Sáens (1982). In addition to duration, the mass was measured using a semi analytical balance, accurate to one hundredth of a gram. As the gender can only be precisely identified during the pupal stage, the identity number of each larva was maintained until pupation to know whether it was male or female, allowing comparisons between sexes, 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.

Temporal and morphometric parameters

The temporal and morphometric parameters were analyzed using descriptive statistics with the calculation of means and standard deviations. When necessary, the means were compared using a t-test assuming unequal variances, at a significance level of 95%.

Results and Discussion

The duration of the immature stages of *S. albula* (Table 1) resembled many of the results already described for the same species, under similar conditions of temperature and fed with tobacco (Novo Padrino & Martínez Reyes 1985) and tomato (La Rosa et al. 1992). These results also resemble those described for other species of the same genus, reared under similar conditions of temperature and whose larvae were fed certain host plants, such as: *S. eridania* (Stoll, 1782) on sweet potato leaves (Foerster & Dionisio 1989); *Spodoptera frugiperda* (J.E. Smith, 1797) on corn leaves (Pinheiro *et al.* 2008), on manioc leaves (Lopes *et al.* 2008); *S. cosmioides* (Walker, 1858) on artificial diet (Bavaresco *et al.* 2002); and *S. exigua* (Hübner, 1808) on cabbage leaves (Azidah & Sofian-Azirun 2006).

Despite these similarities, it should be noted that several authors have shown a great variation in the duration of the life cycle of the representatives of *Spodoptera*, as a function of the larval diet (i.e. Parra *et al.* 1977, Yoshida & Parrella 1992, Greenberg *et al.* 2001 , Bavaresco *et al.* 2003, Azidah & Sofian- Azirun 2006, Sa et al 2009, Barros *et al.* 2010, Saeed *et al.* 2010, Farahani *et al.* 2011), which may vary even among biotypes of the same species (i.e. Giolo *et al.* 2002, Busato *et al.* 2005).

The incubation period (Table 1) is similar to the 3.5 to 4.0 days described for the same species, under similar temperatures (Novo Padrino & Martínez Reyes 1985, Novo Padrino et al. 1985, La Rosa et al. 1992). However, under mean temperatures of 21.8 and 20.7°C, Martin Zequeira (1982) describes periods of 3.4 and 3.0 days, respectively. Without indicating temperature, Stoyan & Machado (1970) describe an embryonic period of 6.4 days. The

embryonic period of *S. albula* is similar to that described for most of the species of this genus, under similar conditions of temperature (i.e. Foerster & Dionísio 1989, Bavaresco *et al.* 2003, Azidah & Sofian-Azirun 2006, Barros *et al.* 2010).

The relatively high egg viability (Table 1) corresponds to the 94-98% described by Novo Padrino & Martínez Reyes (1985). This viability, above 90%, is only observed in a few studies of representatives of the genus (i.e. Mattana & Foerster 1988 - *S. eridania* ~ 90%, Tisdale & Sappington 2001 - *S. exigua* > 90%; Santos et al. 2005 - *S. frugiperda* ~ 80%,). However, higher rates of fertility for *Spodoptera* are most likely to be observed when using several couples per cage (Milano *et al.* 2008). Along these lines, Saeed *et al.* (2010) even demonstrated that food (host plant) can negatively influence the fecundity and fertility of *S. exigua* during each generation.

Larval stage

The high level of larval survival (Table 1) indicates that both the diet and the rearing conditions were satisfactory for the development of *S. albula* in the laboratory. La Rosa *et al.* (1992) describe a higher larval survival (90.5%) for the same species fed with tomato at a mean temperature of 26.7 °C. However, several authors (Stoyan & Machado 1970, Martin Zequeira 1982, Novo Padrino & Martínez Reyes 1985, Novo Padrino *et al.* 1985, La Rosa *et al.* 1992) have reared this species under controlled conditions. This demonstrates that this species, like other representatives of *Spodoptera* (i.e. Bavaresco *et al.* 2004, Santos *et al.* 2005, Azidah & Sofian-Azirun 2006, Barros *et al.* 2010, Saeed *et al.* 2010, Xue *et al.* 2010, Farahani *et al.* 2011), is adaptable to laboratory conditions.

Most of the larvae (87.226%) developed during six instars and the remainder (12.774%) for seven instars. Published records describe five (Stoyan & Machado 1970) and six (Martin Zequeira 1982, Novo Padrino & Martínez Reyes 1985, Novo Padrino *et al.* 1985, La Rosa *et al.* 1992) larval instars for this species. However, several authors have described the existence of

Spodoptera species larvae having different numbers and proportions of larval instars. Along these lines, Azidah & Sofian-Azirun (2006) after testing host plants for *S. exigua*, found five and six instars for larvae feeding on cabbage (*Brassica oleracea* var. *capitata* variety KK cross) and on long bean (*Vignaun guiculata*), six, seven and eight instar larvae feeding on Shallot (*Allium cepa* var. Indian Rose) and five, six, seven and eight instars feeding on lady's finger (*Abelmoschus esculenta*). Bavaresco *et al.* (2004) discovered the existence of different proportions of *S. cosmioides* larvae which went through six and seven larval instars as a function of three artificial diets. In both studies, the highest proportion of larvae that developed through a greater number of larval instars were in the groups which were fed on plants or less appropriate diets.

Our results (Table 2) indicate that the number of females which developed through seven instars (19.149%) was much higher than that of males (6.015%), an aspect still unexplored for representatives of Noctuidae. According to Esperk et al. (2007), the most common factors influencing instar number include temperature, photoperiod, food quantity and quality, humidity, injuries, inheritance, and sex. Typically, instar number tends to increase under adverse rather than favorable conditions and this conclusion is consistent with the compensations scenario, according to which additional instars are inserted in poor conditions when larvae fail to reach a species-specific threshold-size with the "normal" instar number.

As this study was carried out under controlled conditions, the variation of the number of instars between the sexes can be attributed, at least in part, to the larger size of females (see pupal stage section). In this sense, in species with a pronounced sexual dimorphism and with larger females, the development of larvae which originate females often demands an additional instar (Parra 1991). Thus, considering that the absolute size of caterpillars at the end of their development triggers the process of metamorphosis (Nihout 1975), due to their larger size, some females of *S. albula* require an additional instar to reach the size required for

transformation into a chrysalis.

The duration of the larval stage, including the prepupal period (Table 1) is similar to descriptions for the same species reared under similar temperatures (Novo Padrino & Martínez Reyes 1985, Novo Padrino *et al*. 1985, La Rosa *et al*. 1992). However, several temporal differences were detected between sexes and numbers of larval instars. In general, the duration of the first stage was longer than the subsequent three, this longer duration of the first stage is also described for the same species (Martin Zequeira 1982) and for several noctuids including *S. eridania* (i.e. Santos *et al*. 2005), *S. exigua* (i.e. Azidah & Sofian-Azirun 2006) and *S. frugiperda* (i.e. Santos *et al.* 2003).

Authors such as Novo Padrino & Martínez Reyes (1985), Novo Padrino *et al*. (1985) and La Rosa *et al.* (1992) describe a longer duration for the first, followed by the second, third and last instar. The mean total duration of the larvae which developed through seven instars was significantly higher than through six instars (Table 2). Such differences were also noticed among females, but not among males, probably due to the small number of males which developed through seven instars. The longer duration of larvae that developed through seven instars in this study is consistent with experiments of other *Spodoptera* representatives which associated longer larval duration with the increase in the number of instars (e.g. Santos *et al.* 2005, Azidah & Sofian-Azirun 2006).

The difference in the duration of female and male larvae that developed through six instars was also significant (Table 2). The differences between the duration of the stages was more pronounced (significant) from the fourth instar on, when it was observed that the duration of the larval stages that went through seven instars was reduced compared with those who had six instars. Although there are no studies that individualize the observations by the number of larval instars and by sex, a similar behavior is described in the study by Azidah & Sofian-Azirun (2006) where, in Table 1, the greatest periods of development and differences between *S. exigua* larvae that went through five, six or seven instars, are at the end of their development,

especially during the last instar, including the prepupal period of our results (Table 2).

The mean width of the head capsule ranged from 0.285 ± 0.025 mm, in the first instar, to 2.693 ± 0.121 in the last instar, very similar to descriptions by Martin Zequeira (1982), Novo Padrino & Martínez Reyes (1985) and La Rosa *et al.* (1992) for the same species in Cuba. Also like that of *S. eridania,* which has a similar size (Mayer & Babers 1944 - first instar 0.26 - 0.29 mm; last instar 2.41 - 2.77 mm). However, as demonstrated for several species, depending on the diet, the size of the capsules, especially at the end of development, can vary greatly (eg, Parra *et al.* 1977, Mattana & Foerster 1988, Santos *et al.* 2003).

The measurement between the frontal setae (Table 3) has shown that both in larvae that had six instars, as those which went through seven instars, showed higher growth rates among the first instars, decreasing progressively until the last, especially noticeable in larvae that underwent seven instars. Similar behavior is obtained by analyzing data described for the ame species by Martin Zequeira (1982), Novo Padrino & Martínez Reyes (1985) and La Rosa *et al.* (1992) and for *S. eridania* by (Mayer & Babers (1944) and Parra *et al.* (1977).

The largest mean growth rate recorded for larvae that develop through fewer number of instars (Table 3) is described for other noctuids, including *S. eridania* (Parra *et al.* 1977, Mattana & Foerster 1988), and is certainly related to the principle 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 & Foerster 1988).

During the prepupal period (Tables 1, 2), which corresponds to the time when the larvae do not feed and prepare for metamorphosis into pupae, 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. Nevertheless, the only data referring to prepupal survival in the literature (La Rosa et al. 1992) indicates 100% survival for this period,

regardless of large larval mortality. In any case, *S. albula* was very well adapted to rearing conditions, even during this period, usually considered critical for holometabolous insects due to metamorphosis (Parra 1991).

When observing the number of individuals (N), in Tables 2 and 4, it appears that (during prepupa) many more individuals from larvae that went through seven instars died (28.571%), than those that went through six instars (4.603%). This result is certainly related to the observation that additional instars are inserted in poor conditions when larvae fail to reach a species-specific threshold size with the "normal" instar number (Esperk *et al.* 2007), and that larvae which produced viable adults reached pupation as much as three days earlier than those that eventually failed to successfully complete emergence (Nagoshi 2011).

Examination of different information sources showed that the larvae of *S. albula* already recorded them feeding on at least 55 plant species, from 29 families (Table 4). In addition to the larvae feeding on a wide variety of host plants, they also exhibit some preference for several weeds from which they can migrate to cultivated plants (González-B 1966, Hallman 1979, 1983) and for Fabaceae which can be used as trap plants (Savoie 1988). The behavior of migrating to host plants other than those where they were born, known as polyphagia at the individual level, is relatively unusual among Lepidoptera, although reported for other representatives of the genus, particularly *S. frugiperda* (Bernarys & Singer 2002).

Pupal Stage

The obtained sex ratio was 0.515, which does not differ significantly from a 1:1 ratio (χ^2 = 0.227; $p < 0.05$). In this study, the pupal survival of *S. albula* (Table 1), despite relatively high, was lower than that obtained by La Rosa *et al.* (1992) which indicates 100% pupal survival for the same species whose larvae were fed with tomato at 20°, 25° and 26.7°C and 90.0% at 30°C. Our results are larger than those described for *S. cosmioides*, whose larvae were fed with three artificial diets (Bavaresco *et al.* 2004 to 59.1 to 86.8%). However, studies

that use natural diets, describe very different values (less than 50 to 100%), depending on the suitability of the plant for each species (i.e. Parra *et al.* 1977, Bavaresco *et al.* 2003, Santos *et al.* 2005 Lopes *et al.* 2008, Pinheiro *et al.* 2008).

Pupae of female larvae which underwent six instars had significantly less duration than their respective male larvae (Table 5), presenting a similar behavior among the insects that went through seven instars, but without statistical significance. These observations of protogyny in *S. albula* pupae are consistent with observations reported for several *Spodoptera* representatives, where this phenomenon is well documented (eg Santos *et al.* 1980, Bavaresco *et al.* 2004, Farahani *et al.* 2011, Nagoshi 2011).

However, our results suggest, in a way, that pupal protogyny in *S. albula* emerges as a compensation for larval growth, where the duration of female larvae was significantly longer than male larvae (Table 2). When the data on the duration of the larval and pupal stages is brought together, there are no significant differences for the duration between males and females, both for specimens which had six or seven instars (Table 5). In the same table, one can observe that the duration of larval + pupal development was markedly higher in individuals which had an additional instar, being statistically significant for females. However, when analyzed together, the larval and pupal duration is not significantly different ($p < 0.05$) between females (n = 128. 27614 ± 2.323 days) and males (n = 125. 27064 ± 2.335 days). Thus, these results indicate the importance of biological studies detailing results by sex and by number of larval instars.

The female pupae were significantly heavier than the male, both among individuals who have had six, as with those with seven larval instars. This sexual dimorphism is relatively well documented among the representatives of *Spodoptera* (i.e. Habib *et al.* 1983, Mattana & Foerster 1988, Bavaresco *et al.* 2004, Santos *et al.* 2005, Xue *et al.* 2010).

Several biological parameters described in this study closely resemble those obtained for the same species (Martin Zequeira 1982, Novo Padrino & Martínez Reyes 1985, Novo Padrino

et al. 1985, La Rosa *et al*. 1992) and other *Spodoptera* representatives under specific conditions (i.e. Foerster & Dionísio 1989, Pinheiro *et al.* 2008, Bavaresco *et al.* 2002, Azidah & Sofian-Azirun 2006).

The artificial diet and the proposed rearing methodology allowed an overall survival of almost 80% (Table 1), above the 75% recommended by Singh (1983). A detailed description of the preparation process will permit that the diet can be repeated in many future studies.

The methodology proposed in this study, specifically enabled a more complete detailing of several biological parameters of *S. albula* with minimal interference in its development. This allowed several unknown inferences such as the duration and the survival of larval instars and sex determination, along with the duration of larval and pupal stages. On the other hand, several comparisons with parameters of other species were not possible due to the lack of standardization and, especially, lack of detail in the available information.

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Resumo

Este estudo objetivou detalhar parâmetros biológicos dos estágios imaturos de *Spodoptera albula* (Walker, 1857) em condições controladas (25 ± 1ºC, 70 ± 10% UR e fotofase de 14 horas) e reunir informações sobre suas plantas hospedeiras. Para tanto foram empregadas e validadas novas metodologias de criação e dieta artificial. A viabilidade das fases de ovo, larva, pré-pupa e pupa foi de 94,54; 97,33; 93,84 e 92,34%, respectivamente. A duração média das fases de ovo, larva, pré-pupa e pupa foi de 4,14; 16,37; 1,69; e 9,34 dias, respectivamente. Na fase de larva observou-se que 80,85% das fêmeas e 93,99% dos machos passaram por seis instares e os demais por sete, com protandria larval significativa. As lagartas que passaram por seis e sete instares apresentaram razão média de crescimento de 1,58 e 1,48, respectivamente. Foram relacionadas 55 plantas pertencentes a 29 famílias botânicas. As pupas fêmeass foram significativamente maiores, observando-se protoginia. Tanto a metodologia de criação quanto a dieta larval mostraram-se adequadas, pois permitiram sobrevivência total de praticamente 80% e um maior detalhamento das observações relacionadas ao ciclo biológico, especialmente do estágio larval.

Palavras-chave: desenvolvimento, ciclo de vida, dieta artificial, lagarta-militar, praga de culturas anuais.

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Table 1 – Survival and duration of life cycle of *S. albula* during different developmental stages, under controlled conditions (25 ± 1ºC, 70 ± 10% RH and 14 hour photo phase).

Stage	N initial-final	Survival (%)	Duration (days)	Range (days)
Egg	4454 - 4211	94.544	4.141 ± 0.043	3-5
Larvae	300 - 292	97.333	16.367 ± 0.593	14- 21
Prepupae	292 - 274	93.836	1.691 ± 0.751	1 - 4
Pupae	274 - 253	92.336	9.336 ± 1.051	7 - 12
Total	-----	**79.732**	**31.535**	-----

Table 2 – Mean larval duration (days) of *S. albula*, 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 ± 1ºC, 70 ± 10% RH and 14 hour photo phase).

	Six instars			Seven instars				
	Females (114)	Males (125)	A	Females (27)	Maless (8)	B	C	D
I	2.841 ± 0.368	2.694 ± 0.463	**	2.667 ± 0.480	2.500 ± 0.534	ns	ns	ns
II	2.239 ± 0.449	2.145 ± 0.376	ns	2.185 ± 0.557	2.125 ± 0.641	ns	ns	ns
III	2.522 ± 0.536	2.435 ± 0.574	ns	2.370 ± 0.492	2.250 ± 0.463	ns	ns	ns
IV	2.726 ± 0.448	2.589 ± 0.494	*	2.407 ± 0.501	2.250 ± 0.463	ns	**	*
V	2.920 ± 0.426	2.839 ± 0.467	ns	2.481 ± 0.509	2.250 ± 0.463	ns	**	**
VI	3.336 ± 0.689	3.258 ± 0.901	ns	2.556 ± 0.506	2.625 ± 0.517	ns	**	*
VII	-----	-----		2.667 ± 0.734	2.375 ± 1.061	ns	---	---
Prepupae	1.726 ± 0.848	1.581 ± 0.903	ns	1.963 ± 0.706	2.000 ± 0.756	ns	ns	ns
Total	18.310 ± 1.763	17.540 ± 2.038	**	19.296 ± 1.815	18.375 ± 1.188	ns	*	ns
Total [1]	17.910 ± 1.721			19.085 ± 1.946			**	

1 Mean value including males and females which developed during the same number of instars. Comparisons of means using a Student t-test, considering different variances, at a significance level of 95% (Ns $p > 0,05$; * $p < 0,05$; ** $p < 0,01$) A - comparison between six instar females and males; B - comparison between seven instar females and males; C - comparison between six and seven instar females; D - comparison between six and seven instar males.

Table 3 – Distance between frontal setae of *S. albula* larvae at each instar and their respective growth rates, including larvae which developed for six (15 females and 15 males) and seven instars (15 females and 8 males), fed with an artificial diet, under controlled conditions (25 ± 1ºC, 70 ± 10% RH and 14 hour photo phase).

	Six instars			**Seven instars**	
Instar	**Distance between frontal setae (mm)**	**Growth rate**	**T**	**Distance between frontal setae (mm)**	**Growth rate**
I	0.091 ± 0.015	-----	ns	0.096 ± 0.014	-----
II	0.149 ± 0.022	1.632	ns	0.155 ± 0.025	1.625
III	0.252 ± 0.038	1.688	ns	0.259 ± 0.028	1.664
IV	0.401 ± 0.046	1.592	*	0.379 ± 0.025	1.466
V	0.597 ± 0.060	1.488	**	0.551 ± 0.042	1.453
VI	0.884 ± 0.078	1.481	**	0.817 ± 0.087	1.483
VII	-----	-----	-----	0.953 ± 0.043	1.166
Mean	-----	1.576	-----	-----	1.476

Comparison of means using a Student *t*-test, considering different variances, at a 95% significance level (Ns $p > 0,05$; * $p < 0,05$; ** $p < 0,01$)

Table 4 - Host plants of *Spodoptera albula* larvae from several authors.

Plant Family	Scientific name	Common name	References
1. Aizoaceae	*Trianthema portulacastrum* Linn.	Trianthema	19
2. Amaranthaceae	*Amaranthus dubius* Mart. ex Thell.	Spleen amaranth	6
3.	*Amaranthus spinosus* Linn.	Spiny amaranth	5, 12
4. Apiaceae	*Apium graveolens* Linn.	Celery	2
5.	*Daucus carota* Linn.	Carrot	16
6. Arecaceae	*Elaeis guineensis* J.	Oil palm	14
7. Asteraceae	*Acanthospermum hispidum* DC.	Hispid star bur	6
8.	*Helianthus annuus* Linn.	Sunflower	17
9.	*Lactuca sativa* Linn.	Lettuce	16
10. Bignoniaceae	*Tabebuia* spp.		15
11. Brassicaceae	*Brassica oleracea* var. *capitata* Linn.	Cabbage	8, 11, 13, 16, 18
12. Caricaceae	*Carica papaya* Linn.	Papaya	21
13. Casuarinaceae	*Casuarina* sp.	Casuarina	15
14. Convolvulaceae	*Ipomoea batatas* (Linn.) Lam.	Sweet potato	18
15.	*Ipomoea triloba* Linn.	Littlebell morning glory	6
16. Cucurbitaceae	*Cucumis melo* Linn	Melon	13, 18
17.	*Cucurbita pepo* Linn.	Pumpkin	11, 18
18.	*Citrullus vulgaris* Schrad. Ex Eckl. & Zeyh	Watermelon	11, 18
19. Euphorbiaceae	*Croton hirtus* L'Her	Croton	6
20.	*Manihot esculenta* Crantz	Cassava	18
21. Fabaceae	*Arachis hypogaea* Linn.	Peanut	10, 18
22.	*Cassia tora* Linn.	Tora	5
23.	*Glycine max* (Linn.) Merril.	Soybean	6, 7, 8, 9, 11, 13, 18
24.	*Medicago sativa* Linn.	Alfalfa	2
25.	*Phaseolus vulgaris* Linn.	Bean	3, 9, 10, 11, 12, 13
26.	*Pisum sativum* Linn.	Pea	2, 9, 13, 16, 18

27.	*Vigna unguiculata* (Linn.) Walp.	Cowpea	13
28. Iridaceae	*Cipura campanulata* Ravenna	-----	20
29. Lamiaceae	*Mentha arvensis* Linn. var. *piperacens* Malinvaud.	Peppermint	22
30. Liliaceae	*Allium cepa* Linn.	Onion	13, 16, 18
31.	*Allium porrum* Linn.	Leek	18
32.	*Allium sativum* Linn.	Garlic	16, 18
33.	*Asparagus officinalis* Linn.	Asparagus	2, 13, 16
34. Linaceae	*Linum usitatissimum* Linn.	Flax	8
35. Malvaceae	*Gossypium hirsutum* Linn.	Cotton	2, 3, 5, 8, 10, 11, 13, 18
36.	*Hibiscus* spp.	Hibiscus	15
37. Musaceae	*Musa paradisiaca* Linn.	Banana	18
38. Myrtaceae	*Eucalyptus* sp.	Eucalyptus	15
39. Nyctaginaceae	*Boerhavia erecta* Linn.	Erect spiderling	6, 19
40. Pedaliaceae	*Sesamum indicum* Linn.	Sesame	6, 11, 13
41. Pinaceae	*Pinus caribaea* Morelet (viveiros)	Caribbean pine	15
42.	*Pinus tropicalis* Morelet (viveiros)	Tropical pine	15
43. Poaceae	*Echinochloa colonum* (Linn.) Link	Shama millet	6
44.	*Oryza sativa* Linn.	Rice	8, 11
45.	*Sorghum bicolor* (Linn.) Moench	Sorghum	8, 9, 11, 13, 18
46.	*Zea mays* Linn.	Corn	5, 9, 11, 13, 18
47. Portulacaceae	*Portulaca oleracea* Linn.	Purslane	7, 12, 19
48. Quenopodiaceae	*Beta vulgaris* Linn. var. *cicla* Linn.	Swiss chard	1, 2, 13, 16, 18
49. Scrophulariaceae	*Antirrhinum majus* Linn.	Snapdragons	8
50. Solanaceae	*Capsicum annuum* Linn.	Pepper	11, 13, 16, 18
51.	*Solanum tuberosum* Linn.	Potato	1, 2, 11, 16
52.	*Nicotiana tabacum* Linn.	Tobacco	11, 18
53.	*Solanum melongena* Linn.	Brinjal	11
54.	*Solanum lycopersicum* Linn.	Tomato	2, 8, 9, 10, 11, 13, 16, 18
55. Zygophyllaceae	*Kallstroemia maxima (L.) Hook. & Arn.*	Big caltrop	19

References: 1 - Wolcott 1936; 2 - Wolcott 1951; 3 - González 1959; 4 - Herrera 1961; 5 – Alcaraz Vieco 1962; 6 - Hallman 1979; 7 - Hallman 1983; 8 - Passoa 1983; 9 - Saunders *et al.* 1983; 10 - Rosset *et al*. 1985; 11 - Maes & Tellez Robleto 1988; 12 - Savoie 1988; 13 - Coto *et al*. 1995; 14 - Sául-S & Ortiz-G 1998; 15 - Vázquez *et al*. 1999; 16 - OIRSA 2001; 17- Pruett & Guamán 2001; 18 - Branch et al. 2003; 19 - Lastres 2007; 20 - Janzen & Hallwachs 2009; 21 - Semillas del Caribe 2010; 22 – Mendoza et al. 2011.

Table 5 – *Spodoptera albula* - Mean duration, in days, of pupal stage and larval plus pupal stage and mean weight of the pupae, whose larvae were fed with an artificial diet, under controlled conditions (25 ± 1ºC, 70 ± 10% RH and 14 hour photo phase), arranged by sex and number of larval instars.

	Six instars			**Seven instars**				
	Females (108)	**Males (120)**	**A**	**Females (20)**	**Males (5)**	**B**	**C**	**D**
	Duration							
Pupal	9.037± 1.013	9.517± 0.944	**	9.650± 1.268	10.200± 1.789	ns	*	Ns
Larval + Pupal	27.346 ± 3.425	27.000 ± 2.312	ns	29.050 ± 2.481	28.600 ± 2.302	ns	*	Ns
	Weight							
Pupal	0.217 ± 0.037	0.182 ± 0.431	**	0.221 ± 0.021	0.198 ± 0.031	*	ns	Ns

Comparison of means using a Student *t*-test, considering different variances, at a 95% significance level (Ns $p > 0,05$; * $p < 0,05$; ** $p < 0,01$) A - comparison between six instar females and males; B - comparison between seven instar females and males; C - comparison between six and seven instar females; D - comparison between six and seven instar males.

5. RESULTADOS

5.2 CAPÍTULO 2:

Biotic potential, fertility and life table of *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae), under controlled conditions

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Introduction

The genus *Spodoptera* Guenée, 1852 is cosmopolitan and includes many of the most important agricultural armyworm caterpillars (Pogue 2002). *S. albula* (Walker, 1857) has been recorded from Florida to Southern Texas, throughout the Caribbean, Central America, and from Venezuela south to Paraguay and Southern Brazil (Pogue 2002, Zenker *et al.* 2010), and Chile (Angulo *et al.* 2008). *S. albula* has been erroneously referred to as "*Spodoptera sunia* (Guenée, 1852)", which is currently recognized as *Neogalea sunia* (Guenée, 1852), representative of the subfamily Cuculliinae (Poole 1989).

The larvae of *S. albula* have been recorded as feeding on at least 55 species belonging to 29 plant families (Montezano *et al*, 2013). Generally the larvae move into crops from the invading plants found between the rows and / or along the edges (González-B 1966, Hallman 1979, Savoie 1988).

In many countries, especially in Countries of Central America, *S. albula* makes it unfeasible to develop important crops such as tobacco (Stoyan & Machado 1970, Novo Padrino *et al*. 1984, 1985, Páez Gázquez & Novo Padrino 1987), cotton (Alcaráz Vieco 1962, González-B 1966), tomato (Gloria-B 1975), cabbage (Armstrong (1994), sesame, soybean (Hallman 1979, 1983), peanuts (Teixeira *et al*. 2001), sunflower (Pruet & Guaman 2001), papaya (Semillas del Caribe 2010) and even seedling production in forestry nurseries (Vazquez *et al*. 1999).

The importance of this species is increased by its tolerance to various chemical insecticides and to the *Bacillus thuringiensis* Cry1Ac gene (Zenner de Polanía *et al*. 2008, Amaya *et al*. 2009). Its importance motivated studies on its biology (Stoyan and Machado 1970, Martin Zequeira 1982, Novo Padrino and Martinez Reyes 1985, La Rosa *et al*. 1992), its damage potential (Novo Padrino *et al.* 1984, 1985, Paez Guazquez and Novo Padrino

1987), and on the identification of pheromonal components for behavioral control (Bestmann *et al*. 1988, Dunkleblum *et al*. 1995).

This study complements the previous one on immatures (Montezano *et al,* unpublished data) and aims to evaluate and describe the developmental biological parameters of *S. albula*, with special emphasis on its biotic potential and on its life table and fertility, under controlled conditions.

Material and Methods

All experiments were carried out in a climate controlled room (25 ± 1 ° C, 70 ± 10% RH and a 14 hour photophase), with daily observations. Information on the origin of insects, rearing methodology and data on immature stages are described in detail by Montezano *et al.* (unpublished data).

Considering the previously described incompatibilities between biotypes of the fall armyworm, from different host plants or localities, during copulation (Murúa and Virla 2004, Sadek and Anderson 2007, Murua *et al.* 2008), the insects used in the experiment belong to the first generation obtained from a female collected in the field (see Montezano *et al,* 2013). Adults were kept in pairs (n = 13) within cylindrical plastic containers, 10 cm in diameter and 15 cm high, with tops closed using plastic film, to which container 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 using filter paper.

To avoid the effect of the pupal weight on the reproductive aspects (Tisdale and Sappington 2001), females from pupae weighing 0.19g (n = 6) and 0.20g (n = 7) and males from pupae weighing 0.17g (n = 7) and 0.18g (n = 6) were used. Similarly, to avoid the effects of adults age on their capacity to copulate (Kehat and Gordon 1975, Ellis and Steele, 1982, Rogers and Marti Jr.1994), the couples were formed with adults which emerged on the same date. The food was composed of the diet described by Hoffmann-Campo *et al.* (1985)

which consists of honey (10g), sorbic acid (1g), Methylparaben (1g), sucrose (60g), and distilled water (1000 ml). All components were dissolved in distilled water and the obtained solution was kept under refrigeration (7°C). Pilsen beer was added to the solution at a proportion of ¼, on a daily basis, and made available to the insects in a 5 cm in diameter Petri dish lined with cotton wool. Additionally, distilled water was provided for the hydration of the insects, in another 5 cm cotton lined Petri dish. We calculated 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.

Containers were examined daily to record adult mortality and to remove and record eggs. The fecundity (number of eggs per female), longevity and duration of pre, post and oviposition periods were evaluated. Dead females were dissected to determine the number of spermatophores they received from males while copulating.

To estimate fertility, the viability of 16 postures taken from four couples, including the first and last, totaling 4,454 eggs were evaluated. 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 postures were from couples whose females, after death, had two spermatophores in the bursa copulatrix, proving they had been fertilized during the experiment.

All biological parameters were analyzed using descriptive statistics with the calculation of means and standard deviations. The means were compared using a t-test assuming unequal variances, at a significance level of 95%. The fecundity, longevity of both sexes and the duration of pre, post and oviposition periods were correlated (Pearson Product Moment Correlation) with the number of matings of each couple.

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 * d)^{n} - 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 immature survival; (n) number of generations per year or 365 days divided by total lifespan and (er) environmental resistance, in this case considered as null.

The fertility life table was developed using data from the immature stages of *S. albula* published by Montezano *et al*. (2013) and is presented graphically by plotting the probability of survival values at the midpoint of each interval, or survival (lx), and the total number of eggs per female per week, which became females, or specific fertility (mx).

Using the life table, the values of the different reproductive parameters of *S. albula* were calculated. The net reproductive rate (Ro), the ratio between the number of females in two successive generations; the mean generation time (T), 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 and Discussion

In this study, the longevity of *S. albula* (Table 1) was similar to that described by La Rosa *et al.* (1992) who reported 12.4 days at 25°C and 13.2 days at room temperature (average of 26.7°C). However, these values were higher than those described by Martin Zequeira (1982) (~ 10.8) at approximately 21°C and by Novo Padrino *et al.* (1985) who reported values of 10, 8 and 7 days at 19.60, 23.03 and 25.30°C, respectively.

Considering the Montezano *et al.* (2013) data, which indicates a mean duration of the immature stages as 31.52 days, the average longevity of *S. albula* corresponds to 28.32%, or more than one quarter of their life cycle. These results are similar to other studies involving *Spodoptera* (i.e. Mattana and Foerster 1988, Habib *et al.* 1983, Bavaresco *et al.* 2004, Busato

et al. 2005). These results also indicate that the extended longevity of *S. albula*, like other species of the genus such as *S. dolichos* (Fabricius 1794), *S. eridania* (Stoll, 1782), *S. exigua* (Hübner, 1808), *S. frugiperda* (J.E. Smith, 1797) and *S. ornithogalli* (Guenée, 1852) which have a great 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, Angulo *et al.* 2008, Zenker *et al.* 2010).

On average each female had 1.23 copulations, noting that three (23.08%) did not copulate, four copulated only once (30.77%) and six copulated twice (46.15%). This mean value is within the range described for *S. frugiperda* by Murúa *et al.* (2008), who found very discordant values between different *S. frugiperda* populations in Argentina (0.78 to 2.32 spermatophores per female). Regarding the absence of copulation in some *S. albula* pairs, these same authors reported that in some *S. frugiperda* cohorts more than 20% of the females did not mate, while in other cohorts more than 20% of couples performed more than two copulations. Moreover, considering that Milano *et al.* (2008), using 25 *S. frugiperda* pairs per cage, obtained a mean of over three spermatophores per female with a maximum of eight, at 25°C, it is expected that a greater number of *S. albula* individuals per cage also increases the number of copulations.

The longevity of *S. albula* females was significantly higher than males (Table 1) and was negatively correlated with the number of matings ($r = -0.788$, $P = 0.001$) indicating that *S. albula*, similar to *S. littoralis* (Kehat and Gordon 1975, Ellis and Steele 1982), presents a prolonged longevity as a result of reduced and delayed mating. Roger and Marti Jr. (1997) determined that when there is only a single opportunity of mating, two days after the emergence was the optimum age for mating *S. exigua* females to achieve their maximum reproductive potential, but they lived the fewest number of days. Additionally, Hou and Sheng (1999) describe a reduction in longevity of *Helicoverpa armigera* (Hübner, 1808)

females which have multiple matings. These authors attribute these results to interactions between egg production and metabolism. Multiple matings further stimulate egg production and accelerate energy and material consumption, decreasing resources available for somatic maintenance.

With respect to the different longevity between sexes, in studies with representatives of *Spodoptera*, some authors found greater longevity of females [*i.e.* Santos *et al.* 1980 - *S. cosmioides* (Walker, 1858); Melo and Silva 1987, Garcia and Clavijo 1989, Santos *et al*. 2004 - *S. frugiperda*; Farahani *et al*. 2011 - *S. exigua*], others of males [*i.e.* Parra *et al.* 1977, Mattana and Foerster 1988 - *S. eridania*; Bavaresco *et al.* 2003 - *S. cosmioides*; Xue *et al.* 2010 - *S. exigua*] or some even found no statistical differences between sexes [*i.e.* Habib *et al.* 1983 - *S. cosmioides*, Botton *et al.* 1998 - *S. frugiperda*, Santos *et al*. 2005 - *S. eridania*]. Considering that the longevity of males, was hardly correlated with the number of matings (r= -0.112, P= 0.715), the results of this study allow us to infer that the greater longevity of females with respect to males is due to the reduced number of copulations.

A strong negative correlation between number of copulations and the pre-oviposition period (r = -0.762, P = 0.002) was observed, indicating that *S. albula* presents an extension of the pre-oviposition as a function of the reduced number and absence of mating, which is also reflected as prolonged longevity, similar to *S. littoralis* (Kehat and Gordon 1975, Ellis and Steele 1982), *S. exigua* (Rogers and Marti Jr. 1997), *Helicoverpa armigera* (Hübner, 1808) (Hou and Sheng 1999) and *Trichoplusia ni* (Hübner, [1803]) (Ward and Landolt 1995).

However, there was no significant correlation between the number of copulations and oviposition period (r = -0.300, P = 0.319) and post-oviposition period (r = 0.216, P = 0.479). Nevertheless, the reduction of the oviposition period related to a larger number of copulations, as described by Hou and Sheng (1999), is certainly related to a higher reproductive activity in females which copulated more.

The relatively short pre-oviposition period (Table 1) indicates that *S. albula* adults complete sexual maturity soon after emergence, as occurs with other *Spodoptera* representatives (i.e. Parra *et al*. 1977, Habib *et al.*1983, Mattana and Foerster 1988, Tisdale and Sappington 2001). However, the onset of oviposition, at least in the first days after emergence, is conditioned on the occurrence of the first mating. This initial mating periodshould be near the second day after the emergence of both sexes, as described in Roger and Marti Jr. (1997) for *S. exigua*.

The average fertility of *S. albula*, with approximately 1,400 eggs per female (Table 1) is relatively high when compared with the mean values indicated for the same species in other publications such as: 930 eggs by Alcaraz Vieco (1962); 548, 542 and 995 eggs under mean temperatures of 25, 30 e 26,7°C, by La Rosa *et al.* (1992); and between 800 to 1,400 eggs by Novo Padrino and Martínez Reyes (1985). Such variations are relatively common and reported in studies with *S. cosmioides* (i.e. Habib *et al*. 1983, Bavaresco *et al*. 2003, 2004), *S. eridania* (Parra *et al*. 1977, Mattana and Foerster 1988, Santos *et al*. 2005), *S. exigua* (i.e. Greenberg *et al*. 2001, Tisdale and Sappington 2001, Farahani *et al*. 2011), *S. frugiperda* (i.e. Santos *et al.* 2004, Busato *et al.*2005, Barros *et al*. 2010) and *S. litura* (Fabricius, 1775) (Xue *et al.* 2010). However, the variations can be attributed to several factors such as the conditions of each experiment and the biotypes related to the different host or geographic regions (i.e. Giolo *et al.* 2002, Murúa and Virla 2004, Sadek and Anderson 2007, Busato *et al.*2008, Murúa *et al.* 2008). Nevertheless, the greater number of eggs obtained in this study indicates that the diet and methodology employed to rear the immatures (Montezano *et al.* 2013) and adults were suitable for the development of *S. albula* in the laboratory.

Although high, fertility varied greatly between individuals (Table 1), with a positive correlation ($r = 0.847$, $P < 0.001$) between the number of eggs and number of copulations. The positive relationship between fecundity and number of copulations has been documented for

S. exigua (Rogers and Marti Jr. 1996), *S. frugiperda* (Snow *et al.*1970, Rogers and Marti Jr 1994, Milano *et al.* 2008), *S. littoralis* (Ellis and Steele 1982, Sadek and Anderson 2007), *Spodoptera litura* (Fabricius, 1797) (Chu and Yang 1991) and other noctuids such as *H. armigera* (Hou and Sheng 1999) and *Trichoplusia ni* (Hübner, [1803]) (Ward and Landolt 1995, Landolt 1997). The use of material gained from spermatophores for the production of eggs is one of the demonstrated benefits of "re-mating" which is received by females of other Lepidoptera (not Noctuidae) (i.e. Boggs and Watt 1981, Greenfield 1983). In addition, increases in fecundity are related to hormonal effects in multiple mating females, as showed by Zeng *et al.* (1997) for *Heliothis virescens* (Fabricius, 1977).

Our results, together with the various publications that present a positive relationship between fecundity and fertility, indicate that if somehow the number of copulations were anticipated and increased, by using multiple couples per cage (Milano *et al* . 2008), the fecundity of *S. albula* could be even greater.

The high egg viability (94.54%) is certainly related to the proven fertilization of females who had two spermatophores. This percentage agrees with the 94-98% reported by Novo Padrino and Martínez Reyes (1985) and generally refers to *Spodoptera* representatives 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).

The biotic potential of 8.686×10^{22} individuals per female per year, resulting from the equation $BP= (sr*d)^{n}$ -er $BP= (0{,}515 \times 1{,}130.400)^{8.296}$-0, is obtained when we consider that: 141 female and 133 male immature reached the pupal stage, at a ratio of 0.515 (Montezano *et al*. 2013); on average each female oviposited 1,417.75 eggs and the overall survival was 79.73%, obtaining 1,130.40 viable individuals per female (see Montezano *et al* 2013, Table 1); the average duration of the life cycle (43.99 days), corresponds to 8.29 generations per

year (n); and the environmental resistance as null. In other words, each female could generate more than 86 sextillion offspring.

This relatively high value can also be obtained using published data for other representatives of *Spodoptera*. For example, for *S. exigua*, at 26°C, using data from Greenberg *et al*. (2001), considering an average lifespan of seven days, we getapproximate values of 2.1 x 10^{26}, 3.8 x 10^{33}, 3.6 x 10^{28}, 5.4 x $10^{37}$and 1.6 x 10^{28}, for larvae fed with cabbage, cotton, pepper, pigweed and sunflower, respectively. For *S. eridania*, at 27°C, using data from Parra *et al.* (1977) and considering a sex ratio of 0.5 or 1:1, gives roughly 6.6 x 10^{23}e 6.8 x 10^{18}, for larvae reared on cotton and soybean, respectively.

The maximum rate of population increase occurred between the 36th and 37th day, during the 5th week of life, represented by the crossing of the survival and specific fertility lines (Figure 1). This rate is relatively dislocated towards the beginning of the adult stage, especially driven by the higher fertility and low mortality of imagos shortly after emergence. These observations agree with other studies conducted with representatives of *Spodoptera* where higher values of fecundity are observed during the first few days, from the second or third to the seventh (i.e. Kehat and Gordon 1975, Sadek 2001, Bavaresco *et al.*2004, Murúa and Virla 2004).

The net reproductive rate (Ro) was 353.90 females per generation, similar to values described for other *Spodoptera* representatives on different host plants: for *S. exigua*-377.11 on *Chenopodium album* Linn. -Chenopodiaceae and 342.11 on cabbage -*Brassica napus* Linn. Brassicaceae (Farahani *et al*. 2011); for *S. exigua*-359.3 on cotton -*Gossypiun hirsutum* Linn - Malvaceae, 342.2 on sunflower -*Helianthus annuus* Linn. -Asteraceae, and the maximum value of 596.0 on pigweed -*Amaranthus retroflexus* Linn. -Amaranthaceae (Greenberg *et al*. 2001); for *S. cosmioides*-313.6 on castorbean -*Ricinus communis* Linn. Euphorbiaceae and 380.7 on onion -*Allium cepa* Linn. - 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). Due to the great variability of hosts (Montezano *et al.*2013), it is expected that like 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. albula* varies greatly as a function of the hosts with higher values for preferred plants, both weeds and crops (i.e. Alcaráz Vieco 1962; González-B 1966; Gloria-B 1975; Hallman 1979, 1983; Novo Padrino *et al.*1984, 1985; Páez Gázquez and Novo Padrino 1987; Savoie 1988; Armstrong 1994; Teixeira *et al*. 2001; Montezano *et al*. 2013).

The mean generation time (T) of 37.19 days was above the maximum described for *S. exigua* of ~ 31.6, at 26°C (Greenberg *et al.* 2001; Farahani *et al.* 2001) and for *S. frugiperda* of ~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 (rm) and the daily finite rate of increase (λ) of *S. albula* obtained in the present study were: rm= 0.158 and λ = 1.171, respectively. These relatively low values, resemble those obtained for *S. cosmioides* (Bavaresco *et al.* 2003) which has a higher mean generation time (T), compared with that of *S. exigua* (Greenberg *et al.*2001; Farahani *et al.* 2011) and *S. frugiperda* (Barros *et al.* 2010).

The parameters calculated for *S. albula* 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 great variations between values for the same species, especially in function of temperature and host plant or artificial diet (i.e. Parra *et al.* 1977; Mattana and Foerster 1988; Ali and Gaylor 1992; Greenberg *et al*. 2001; Bavaresco *et al.* 2003, 2004; Busato *et al.* 2005; Santos *et al*. 2005; Azidah and Sofian-Azirun 2006; Sá *et al.* 2009; Barros *et al.* 2010; Farahani *et al*. 2011). Furthermore, Murúa *et al.* (2008) showed huge variations between

biological and reproductive parameters between cohorts of *S. frugiperda* from different locations and host plants in Argentina.

The results obtained in this study, especially related to reproductive aspects, indicate that *S. albula* shares diverse biological characteristics with the other representatives of the genus, considered key pests of various cultures. Among the analyzed parameters, the relatively long duration of the biological cycle is noted and should be further studied to assess whether it is responsible for the greater importance of this species in warmer regions, such as in Central America (i.e. Alcaráz Vieco 1962; González-B 1966; Stoyan and Machado 1970; Gloria-B 1975; Hallman 1979, 1983; Novo Padrino *et al*. 1984, 1985; Páez Gázquez and Novo Padrino 1987; Armstrong 1994; Vázquéz *et al*. 1999; Pruet and Guamán 2001; Semillas del Caribe 2010), where the life cycle is shortened as a function of temperature.

A careful analysis of data from this study indicates the importance of detailing every aspect of the reproductive biology, since many details can underestimate or compromise the data of the reproductive parameters and the full expression of the biotic potential of *S. albula* and other Lepidoptera. Among the observations, the fact that when used single pairs are used, in comparison with single *S. frugiperda* (i.e. Murúa *et al.* 2008) and multiple pairs for cage (Milano *et al.* 2008), there was a reduction in the number of copulations which was associated with an increase in longevity and in the pre-oviposition period, together with the decrease in fecundity and fertility. Consequently, underestimating the biotic potential, reproductive parameters, life table and fertility values obtained.

Our results also indicate concerns for the need of a better understanding of the reproductive parameters of *S. albula* in the field, such as studies which include the collection of adults of other species using light traps (Sadek 2001), in order to compare with data obtained in the laboratory so that more reliable relationships can be inferred.

The results of this study, showing that a reduction, or delay, in the number of copulations negatively influence the population parameters, indicate the relevance of identification studies (Bestmann *et al.* 1988; Dunkleblum *et al.* 1995) and the use of pheromones to retard or prevent the mating of *S. albula* in nature, in mating disruption procedures (Cardéand Minks 1995), as a strategy for the Integrated Management of this species.

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Resumo

Este trabalho objetivou avaliar o potencial biótico e parâmetros da tabela de vida e fertilidade de *Spodoptera albula* (Walker, 1857) em condições controladas (25 ± 1ºC, 70 ± 10% UR e fotofase de 14 horas). Avaliou-se a longevidade, períodos de pré, pós e oviposição, fecundidade e fertilidade de 13 casais. A longevidade das fêmeas (13,500 dias) foi significativamente maior que as dos machos (11,154 dias). Os períodos médios de pré, pós e oviposição foram de 2,615, 1,769 e 9,385 dias, respectivamente. A fecundidade média foi de 1.417,69 ovos e a fertilidade 1.340,401 lagartas por fêmea. Em média as fêmeas copularam 1,231 vezes. Observou-se forte correlação positiva entre número de cópulas e a fecundidade (r = 0,847, P< 0,001) e, forte correlação negativa, entre o número de cópulas e a duração do período de pré-oviposição (r= -0,762, P= 0,002), e a longevidade (r= -0,788, P= 0,001). O potencial biótico de *S. albula* foi estimado em 8,768 x 1022 indivíduos/fêmea/ano. A taxa líquida de reprodução (Ro) foi de 353.904 vezes por geração e o tempo médio de uma geração (T) foi de 37,187 dias. A taxa intrínseca de aumento (rm) foi de 1,105, com uma razão finita de aumento (λ) 3,019.

Palavras-chave: desenvolvimento, espermatóforo, fecundidade, lagarta-militar, reprodução.

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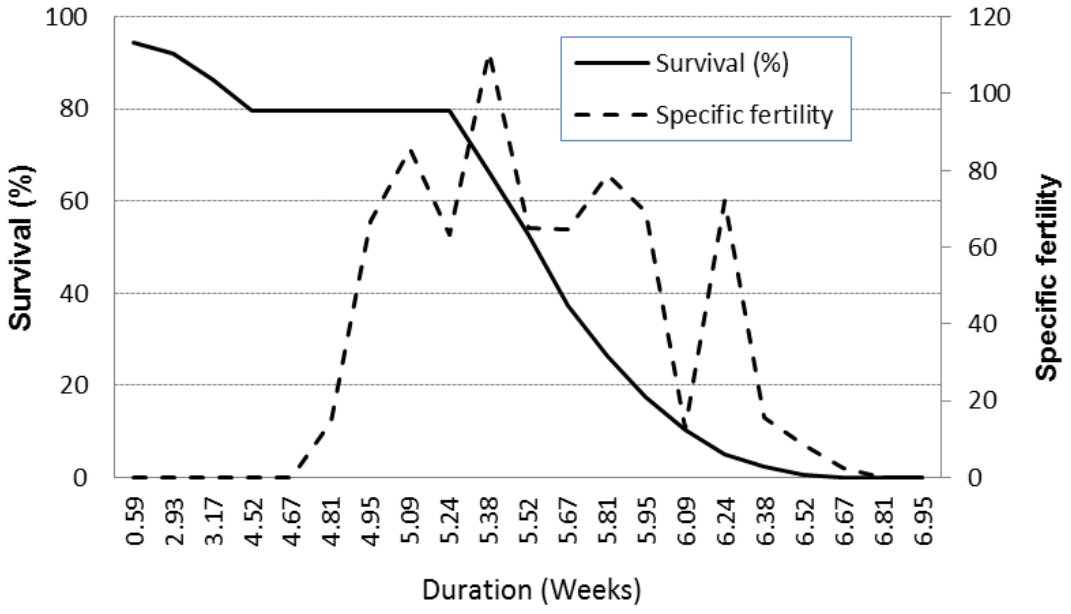

Fig. 1 – Relation between fertility (mx) and survival rate (lx) of *Spodoptera albula* reared on artificial diet at 25 ± 1°C, 70 ± 10% RH and a 14 hour photo phase.

Table 1: Longevity, pre, post and oviposition periods and fecundity of 13 pairs of *Spodoptera albula*, under controlled conditions (25 ± 1°C, 70 ± 10% RH and a 14 hour photo phase).

		Mean	Standard	Range
	Longevity (days)	12.458	2.395	8 - 17
Female	Longevity (days)	13.500	1.732	11 - 17
	Pre-oviposition (days)	2.667	1.303	1 - 5
	Post-oviposition (days)	1.417	1.084	0 - 3
	Oviposition (days)	9.417	1.564	7 - 11
	Fecundity (eggs)	1417.750	55.682	606 - 2298
Male	Longevity (days)*	11.417	2.575	8-16

Comparisons of male and female mean longevity using Student *t* test, considering different variances, at a 95% level of significance (* $p < 0.05$).

5. RESULTADOS

5.3 CAPÍTULO 3

Immature stages of *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae): Developmental parameters and host plants

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ABSTRACT: Immature stages of *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae): Developmental parameters and host plants: This study aimed to detail the temporal and morphological parameters of the immature stages of *Spodoptera eridania* (Stoll, 1782) under controlled conditions (25 ± 1 ° C, 70 ± 10% RH and 14 hour photo phase) and gather information about their larval host plants. For this purpose, a recent rearing method and artificial diet was employed and validated. The viability of the egg, larval, pupal and pre-pupal 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 days, respectively. During the larval stage, 4.44% of females passed through seven instars, with significant larval protandry. The female larvae which developed through six and seven instars exhibited a mean growth rate of 1.52 and 1.44, respectively. Female pupae were significantly larger, exhibiting protogyny. Both rearing methods as well as the larval diet 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 and two host plant species belonging to 58 families are listed, mainly including Asteraceae, Fabaceae, Solanaceae, Poaceae, Amaranthaceae and Malvaceae.

KEYWORDS: armyworm, development, fecundity, reproduction, spermatophore.

RESUMO: Estágios imaturos de *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae): Parâmetros de desenvolvimento e plantas hospedeiras: Este estudo objetivou detalhar os parâmetros biológicos dos estágios imaturos de *Spodoptera eridania* (Stoll, 1782) em condições controladas (25 ± 1 º C, 70 ± 10% UR e fotofase 14 horas) e reunir informações sobre suas plantas hospedeiras. Para tanto foram empregadas e validadas novas metodologias de criação e dieta artificial. A viabilidade das fases de ovo, larva, pré-pupa e foram de: 97,82, 93,62, 96,42 e 97,03%, respectivamente. A duração média das fases de ovo, larva, pré-pupa e pupa foi de 4,00, 16,18, 1,58, e 9,17 dias, respectivamente. Durante a fase larval, 4,44% das fêmeas passaram por sete ínstares, com protandria larval significativa. As lagartas fêmeas que se desenvolveram através de seis e sete ínstares exibiram uma taxa de crescimento médio de 1,52 e 1,44, respectivamente. As pupas fêmeass foram significativamente maiores, exibindo protoginia. Tanto a metodologia de criação, quanto a dieta larval mostraram-se adequadas, proporcionando observações mais detalhadas do ciclo biológico, especialmente na fase de larva, e resultou na sobrevivência global de cerca de 85%. Foram relacionadas 202 espécies de plantas hospedeiras pertencentes a 58 famílias, incluindo principalmente Asteraceae, Fabaceae, Solanaceae, Poaceae, Amaranthaceae e Malvaceae.

PALAVRAS-CHAVE: desenvolvimento, espermatóforo, fecundidade, lagarta-militar, reprodução.

Introduction

The genus *Spodoptera* Guenée, 1852 (Lepidoptera: Noctuidae: Noctuinae) (Lafontaine & Smith 2010) is cosmopolitan and includes many of the most important agricultural caterpillars (Pogue 2002). *Spodoptera eridania* (Stoll, 1782) occurs in the southeastern United States from Maryland south to Florida and West to Kentucky and Texas. Strays have been reported in northeastern Ohio. In the Neotropics, it ranges from Mexico, throughout the Caribbean, and south through Central America to Argentina (Pogue 2002), Chile (Angulo *et al*. 2008) and Uruguay (Bentancourt & Scatoni 2006).

Since the beginning of the last century, *S. eridania* has a high reported degree of polyphagy (i.e. Chittenden & Russel 1909, Crumb 1929, Marques 1932, Fonseca 1934, Monte 1934, Hambleton & Forbes 1935, Babers & Woke 1937, Gross & Howland 1940, Crowell 1941, 1943, Rêgo *et al*. 1945, Biezanko *et al*. 1949, Biezanko & Bertholdi 1951, Corseuil 1955, Bertels 1956, Crumb 1956, Costa 1958). The polyphagy of this species led to important studies on the selection and use of various host plants by polyphagous insects (i.e. Babers & Woke 1937, Crowell 1941, 1943, Soo Hoo & Fraenkel 1966a, 1966b, Scriber 1979, 1981, Manuwoto & Scriber 1982, 1985, Manuwoto *et al.* 1985, Lindroth & Peterson 1988, Puttick & Bowers 1988).

The physiological and ecological success of *S. eridania* is related to its great capability to detoxify, or otherwise process, plant biomass or diets which contain high concentrations of known allelochemicals. This capability is related to the high activity, and capacity for rapid induction, of the mixed function oxidase (MFO) detoxification system after exposure to various allelochemicals (Brattsten et al. 1973, 1977, 1980, Blau *et al.* 1978, Scriber 1978, 1979, 1981, Manuwoto & Scriber 1982). Beside the polyphagous behavior of *S. eridania*, it was hypothesized by Scriber (1986) that pokeweed [*Phytolacca americana* (Linn.)] is its natural host plant. The evidence for this hypothesis came from the report that *Phalaena*

phytolaccae J.E. Smith, 1797, a synonym of the *S. eridania*, was feeding naturally on pokeweed (Smith 1797).

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 (i.e. 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 & Fraenkel (1966a, 1966b) 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 (i.e. Silva *et al.* 1968, Tietz 1972, Coto *et al.*, 1995, Maes & Telles Robleto 1988, Pastrana 2004, 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 & Foerster 1988), in truck crops (Michereff-Filho *et al*. 2008), reaching economic injury levels in commercial crops, especially alfalfa (Hichings & Rabinivich 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 (i.e. Hichings & Rabinivich 1974, Parra *et al.* 1977, Valverde-C & Sarmiento-M 1987, Mattana & 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, Savoie 1988, Sánchez & Vergara 1996, Santos *et al.* 2005), presents different degrees of tolerance to several chemical insecticides (i.e. González 1966, Campos-S 1972, 1982, Aziz 1973, Aguilera-P & Vasquez-C 1974),

botanical insecticides and soap (Valles & Capinera 1993, Rosseti *et al.* 2008), and to the *Bacillus thuringiensis* Cry1Ac gene (Zenner-de-Polanía *et al.* 2008, Amaya *et al.* 2009), as other representatives of the genus.

Considering the importance of *S. eridania* for several crops of economic interest and a possibility of outbreaks, this study aimed to: (a) detail the various temporal and morphological parameters of the immature stages under controlled conditions, to allow comparisons with previous studies and with other representatives of the same genus; (b) gather and organize information relating to host plants, emphasizing South American records; and (c) validate a rearing method and an artificial larval diet which has already been used to detail the biological parameters of *S. albula* (Montezano et al. 2013) and other pest noctuids, in the "Laboratório de Controle de Pragas" of the "Universidade de Caxias do Sul".

Material and Methods

Insects and rearing

These experiments only used first generation specimens whose progeny initiated with 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, 424m height). Identification was accomplished by comparing larvae and adults with descriptions in Pogue (2002).

All the experiments were performed, with daily observations, in a climate controlled room (25 ±1ºC, 70 ±10% RH and a 14 hour photo phase).

Egg stage

Each egg mass was individually placed in a Petri dish 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 couples whose females presented one (n= 2) and two (n= 3) spermatophores in the bursa copulatrix, indicating that they had been fertilized during the experiment.

Larval Stage

Soon after hatching, 298 larvae 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 moisture, along with a small dose (~1 cm^3) of artificial diet were included in 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, in order 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 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.

This methodology allowed us to record the number of larval instars, the survival and the individual duration of each instar / stage and of the 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 capsules was measured, with a micrometer under a microscope. Most of the larvae developed through six instars, of which only fifteen specimens of each sex were measured, and only nine females went through seven instars, which were all measured.

Composition and preparation of larval diet

The artificial diet (adapted from Greene *et al.*, 1976) was 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 lab table until the temperature reached 25° C.

The pre-baked 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 (1500 mL) into a domestic blender at full power for at least 10 minutes, forming a homogeneous mass. This homogenized mass was transferred to a stainless steel pot and cooked for 5 minutes, 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 L 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 x 11 x 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 approximately 1 cm^3, 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 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 & 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 comparing with the drawings in Angulo & Jana-Sáens (1982). In addition to duration, the mass was measured using a semi analytical balance,

accurate to one hundredth of a gram. As the sex can only be precisely identified during the pupal stage, the identity number of each larva was maintained until pupation to know whether it was male or female, allowing comparisons between sexes, 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.

Temporal and morphometric parameters

The temporal and morphometric parameters were analyzed using descriptive statistics with the calculation of means and standard deviations. When necessary, the means were compared using a t-test assuming unequal variances, at a significance level of 95%.

Results

In all the immature stages of *S. eridania*, including the prepupae period, the survival was high, above 90%. The eggs from females which had copulated once or twice have a high viability 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, 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 instar 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 sexes 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 the records of the plants consumed by *S. eridania* in Rio Grande do Sul, provided a list of 202 plants belonging to 58 plant families. In Rio Grande do Sul, 68 host plants were recorded, of which 39 had not been previously reported (Table 4).

The families with the greatest number of species consumed include: Asteraceae (20), Fabaceae (19), Solanaceae (14), Poaceae (10), Amaranthaceae (9), Malvaceae (8), Brassicaceae, Cucurbitaceae, Polygoniaceae, Rubiaceae (7); Lamiaceae, Phytolaccaceae, Rosaceae (6) and both Convolvulaceae and Euphorbiaceae (5) (Table 4). Beside 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 that those who went through six instars (Table 5).

Discussion

Egg stage

Our results (Table 1) indicate that the duration of the incubation period was invariable, similar to that observed by Valverde & Sarmiento (1987) and Mattana & Foerster (1988), under the same temperatures using different host plants. The same incubation period was also observed by Chittenden e Russel (1909), under natural conditions of aproximately 25°C. However, at 27°C, Parra *et al.* (1977) and Santos *et al.* (2005) describe mean incubation periods of aproximately 2.9 and 3.2 days, respectfully.

The relatively high egg viability (Table 1) obtained from fertilized females corresponds to the 94.00-98.84% described by Valverde & Sarmiento (1987), for the first generation of the same species on four host plants. The diferences with respect to other publications (i.e. 82.72 at 89.83% described by Matanna & Foerster (1988), and 47.89 at 58.57% by Parra *et al.* (1977) may be due to eggs from couples which did not copulate. In these cases, high fecundity values are always atributed to representantives 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 high larval survival (Table 1) indicates that the diet and the rearing conditions were satisfactory for the development of *S. eridania* in the laboratory. Our results are consistent with those obtained by Parra *et al.* (1977) on cotton and soybean, Mattana & Foerster (1988) on sweet potato and by Santos *et al.* (2005) on morning glory.

The fact that most of the larvae (96.56%) developed through six instars indicates that diet met the specific needs similarly to that observed with host plants considered as adequate

(i.e. Mayer & Babers 1944, Redfern 1967, Parra *et al.* 1977, Mattana & Foerster 1988, Santos *et al.* 2005). It should be emphasized that the same species had only five instars when reared on the host plant (*Amaranthus hybridus* Linn.) considered as the most appropriate, among the four tested (Valverde-C & Sarmiento-M 1987). 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. eridania*, all subjects which fed on bracatinga, an unsuitable plant, passed through an additional instar (Mattana & Foerster 1988). Though in Parra *et al.* (1977) and Santos *et al.* (2005), approximately 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.

Although diverse factors such as temperature, photoperiod, food quantity and quality, humidity, injuries, inheritance, and sex do influence the number of instars (Esperk *et al.* 2007), the results of this study, and for *S. albula* (Montezano *et al.* 2013), indicate that female representatives of *Spodoptera* are more likely to have an additional instar, probably due to their larger size

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-C & Sarmiento-M 1987, Mattana & 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 & Sarmiento 1987, Mattana & Foerster 1988, Santos *et al.* 2005) and for several *Spodoptera* representatives (i.e. Santos *et al.* 2003, Azidah & Sofian-Azirun 2006, Montezano *et al.* 2013). The temporal differences between sexes is

also described for *S. albula* and probably is 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 & Sofian-Azirun 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 & Foerster (1988), and is slightly larger than that described by Mayer & Babers (1944) and Valverde & Sarmiento (1987) 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 & Babers 1944, Parra *et al*. 1977, Valverde & Sarmiento 1987, Mattana & 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, considered the best food plant, conditions under which the larvae completed their development for only five instars (Valverde & Sarmiento 1987).

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 & Babers 1944, Parra *et al.* 1977, Valverde & Sarmiento 1987, Mattana & Foerster 1988). 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 & 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 (i.e. Chitteneden & Russel 1909, Crumb 1929, Soo Hoo & Fraenkel 1966a, 1966b), Central America (i.e. Maes & Tellez Robleto 1988, Torres 1992, Coto *et al.* 1995) and South America (i.e. 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* (JE 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). Beside 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 Phytolaccacae (Table 4). The fact that this species was initially recorded very early in North (Smith 1797), Central (Puerto Rico) (Chittenden & Russell 1909) and South America (i.e. Lima 1928, 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 relates to the versatility and ability of this species to quickly 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 (i.e. Chittenden & Russel 1909, Lima 1928, Crumb 1929, Marques 1932, Wolcott 1936, 1951, Hambleton 1939, Waterston 1939,1947 Tucker 1939, Corseuil 1955, Olalquiaga 1955, Costa 1958, Nickel 1958, Harris 1959, Kimball 1965, González 1966, McGuire & Crandall 1967, Silva *et al*. 1968, Cantu & Wolfenbarger 1970, Creigton *et al*. 1971, Tietz 1972, Valencia-V & Valdivia-M. 1973, Biezanko *et al*. 1974, Hichings & Rabinovich 1974, Price & Poe 1977, Pena & Waldill 1981, Maes & Tellez Robleto 1988, Ferguson *et al*. 1991, Coto *et al*. 1995, Pastrana 2004, Specht *et al*. 2004, Bentancourt & Scatoni 2006, Angulo *et al*. 2008).

Exemplifying its appearance in more recently explored annual crops of great importance, we can cite the occurrence of *S. eridania* in soybeans since the 1970s after the

expansion of the crop, in the United States (i.e. Tietz 1972), Brazil (i.e. Parra *et al.* 1977) and Argentina (see Pastrana 2004), with a growing importance in other American countries (i.e. Coto et al. 1995, Santos *et al.* 2005, Valverde 2007, Angulo *et al.* 2008).

Similarly, this species has been associated to various weeds of different families (see Table 4). Surely this wide range of weeds, as alternative hosts, is related to their importance as plants used by females for oviposition and to the ability of their larger larvae to migrate to cultivated plants (i.e. Chittenden & Russel 1909, Savoie 1988, Huiza & Loayza 1993, Sanchéz 1996, Sánchez y Vergara 1996, Rodríguez *et al.* 2002, Castillo- Valiente & Castillio-Oliva 2004, Santos *et al*. 2005). According to some authors, these alternative host plants are so important to populations of this and other *Spodoptera* species that in some studies they were treated as sources of parasitoids of other species such as *S. frugiperda* (Tingle *et al*. 1978). Another important aspect of weeds on the development of *S. eridania* is the fact that the slim amaranth is considered the best host plant, where its larval development was completed with only five instars and its shortest life cycle (Valverde & Sarmiento 1986a).

As demonstrated by (Brattsten *et al.* 1973, 1977, 1980, Blau *et al*. 1978, Scriber 1978, 1979, 1981, Manuwoto & Scriber 1982), this species has the great ability to use various host plants as a function of its detoxification mechanisms. However, except for the work of Torres (1992), the majority of records, including the new records in this study (Table 4), for the most part were obtained from ornamentals, truck or extensive annual crops.

Pupal Stage

In this study, the pupal survival of *S. eridania* (Table 1), despite being relatively high, was lower than the 100.0% obtained by Mattana and Foerster (1988) on sweet potato, was similar to the 96.0% obtained on cotton and soybean (Parra et al. 1977) and higher than the 83.3% on bracatinga (Mattana & Foerster 1988), on cotton, on morning glory and on soybean

(Santos *et al.* 2005). The survival of female pupae (95.56% - 129/135) was lower than that of males (98,51% - 132/134). These results are similar to those obtained by Santos *et al.* (2005) for larvae feeding on cotton, morning glory and soybean. These results, together with the observations on *S. albula* (Montezano *et al*. 2013), may indicate that, in general, the female pupae have a greater difficulty in transforming into adults.

Similar to that observed for several *Spodoptera* representatives (i.e. Santos *et al.* 1980, Bavaresco *et al.* 2004, Farahani *et al.* 2011, Nagoshi 2011, Montezano *et al.* 2013), female *S. eridania* pupae from larvae that underwent six instars developed significantly faster than their male counterparts (Table 5), characterizing protogyny. However, our results suggest that pupal protogyny in *S. eridania* and, as documented in *S. albula* (Montezano et al. 2013), may emerge as a compensation for larval growth, where the duration of female larvae was significantly longer than male larvae (Table 2). Thus, when the data on the duration of the larval and pupal stages is brought together, there are no significant differences for the duration of the entire immature period between females and males which had six instars. The duration of larval and 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* (i.e. Habib *et al.* 1983, Mattana & 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 (i.e. Esperk *et al.* 2007, Nagoshi 2011, Montezano *et al.* 2013).

Although there are previously described natural and artificial diets (see Peterson 1953, Soo Hoo & Fraenkel 1964, Redfern 1967, Smilowitz, & Dewey ,1969, Redfern & Raulston

1970) for the mass production of *S. eridania*, we tested 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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Table 1 – Survival and duration of the *Spodoptera eridania* life cycle during different developmental stages, under controlled conditions (25 ± 1ºC, 70 ± 10% RH and 14 hour photophase).

Stage	N initial-final	Survival (%)	Duration (days)	Range (days)
Egg	2383 - 2331	97.818	4.00 ± 0.000	4
Larval	298 - 279	93.624	16.183 ± 1.591	14- 21
Prepupal	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 duration (days) of *Spodoptera 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 ± 1ºC, 70 ± 10% RH and 14 hour photophase).

Developmental Period	Six instars Females (120)		Males (132)		Seven instars Females (9)
Larval Instars	Mean ± SD		Mean ± SD		Mean ± SD
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[1]	5.222 ± 0.667
Prepupal	1.525 ± 0.549	ns	1.629 ± 0.623	ns	1.444 ± 0.527
Total [2]	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 t-test, considering different variances, at a significance level of 95% (Ns $p > 0,05$; * $p < 0,05$; ** $p < 0,01$)
1 – Nine females. 2 - including prepupal period.

Table 3 – Width (mm) of head capsules of *Spodoptera 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 ± 1ºC, 70 ± 10% RH and 14 hour photophase).

	Six instars						**Seven instars**	
	Females (15)			**Males (15)**			**Females (9)**	
Instar	**Mean ± SE**	**Growth rate**	**Sig.**	**Mean ± SE**	**Growth rate**	**Sig.[1]**	**Mean ± SE**	**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	1.546
III	0.783 ± 0.038	1.614	ns	0.785 ± 0.047	1.625	ns	0.747 ± 0.046	1.541
IV	1.183 ± 0.060	1.510	ns	1.189 ± 0.035	1.514	*	1.114 ± 0.066	1.493
V	1.773 ± 0.104	1.499	*	1.664 ± 0.087	1.400	**	1.540 ± 0.101	1.382
VI	2.636 ± 0.105	1.486	*	2.505 ± 0.117	1.505	**	2.096 ± 0.119	1.361
VII	-----	-----		-----	-----	-----	2.720 ± 0.077	1.298
Mean	-----	1.522		-----	1.513	-----	-----	1.437

Comparison of means using a Student *t*-test, considering different variances, at a significance level of 95% (Ns $p > 0,05$; * $p < 0,05$; ** $p < 0,01$)

Table 4 – Host plants of *Spodoptera eridania* larvae described and 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.		*Sanchezia speciosa* Leonard		55, 71
3.		*Teliostachya alopecuroidea* (Vahl) Ness		55, 71
4.	Amaranthaceae	*Achyranthes aspera* Linn.	devil's horsewhip	67
5.		*Amaranthus deflexus* Linn.	red-root amaranth	31, 63, *
6.		*Amaranthus hibridus* Linn.	Slim amaranth	37, 54, 31, 71
7.		*Amaranthus quitensis* Kunth	Ataco	63
8.		*Amaranthus retroflexus.* Linn.	Rough pigweed	54
9.		*Amaranthus spinosus* Linn.	spiny amaranth	1, 2, 6, 29, 51, 67, 71, *
10.		*Amaranthus viridis* Linn.	Callalco	59
11.		*Celosia cristata* Linn.	Cockscomb	*
12.		*Spinacia oleracea* Linn.	spinach	54
13.	Anacardiaceae	*Schinus terebentifolium* Raddi	Brazilian peppertree	*
14.	Apiaceae	*Apium graveolens* Linn.	celery	3, 22, 29, 54, 56, *
15.		*Daucus carota* Linn.	carrot	2, 29, 71
16.		*Hydrocotyle ranunculoides* Linn.	Water pennywort	70
17.	Apocynaceae	*Nerium oleander* Linn.	oleander	2, 29, 71
18.	Araceae	*Xanthosoma* sp.		55, 71
19.	Araliaceae	*Didymopanax morototoni* (Aubl.) Decne & Pl.		55, 71
20.	Asteraceae	*Artemisia absinthium* Linn.	Absinthium	*
21.		*Baccharis trimera* (Less.) DC	Carqueja	*
22.		*Bidens pilosa* Linn.	hairy beggarticks	*
23.		*Chrysanthemum morifolium* Ramat	Chrysanthemum	38, 39, 71
24.		*Clibadium erosum* (Sw.) DC.		55, 71
25.		*Conyza bonariensis* (Linn.) Cron.	Weed	55, 71
26.		*Conyza canadensis* (Linn.) Cron.	hogweed	55, 71
27.		*Eclipta prostrata* (Linn.) Linn.	Eclipta	55, 71
28.		*Erechtites valerianaefolia* (Wolf) DC.	Brazilian fireweed	55, 71
29.		*Gerbera jamesonii* Bolus	Gerbera daisy	*
30.		*Helianthus* sp..		29
31.		*Helianthus annuus* Linn.	Sunflower	2, 43, 71
32.		*Lactuca sativa* Linn.	Lettuce	23, 48, 56, 71, *
33.		*Mikania cordifolia* (Linn.) Willd.	Guaco	55, 71
34.		*Neurolaena lobata* (Linn.) Cass.		55, 71
35.		*Pseudoelephantopus spicatus* (Jussieu ex Aublet) C.F. Baker	Weed	55, 71
36.		*Sonchus* sp.	Sonchus	2, 71
37.		*Sonchus oleraceus* Linn	common sowthistle	29, *

38.		*Taraxacum officinale* Webber	blowball	*
39.		*Vernonia tweedieana* Baker	ironweed	*
40.	Balsaminaceae	*Impatiens sultani* HooK	balsamine	*
41.		*Impatiens wallerana* Hook.		55, 71
42.	Begoniaceae	*Begonia rex* Putz	Begonia	*
43.	Brassicaceae	*Coronopus didymus* (Linn.) Sm.	lesser swinecress	*
44.		*Brassica napus* Linn. var. *oleifera*	Colza	62
45.		*Brassica nigra* (Linn.) W.D.J. Koch	Black mustard	42, 71
46.		*Brassica oleracea* var. *capitata* Linn.	Cabbage	2, 29, 34, 48, 56, 71, *
47.		*Brassica oleracea* Linn. var. *viridis* Linn.	Collard	1, 2, 29, 71, *
48.		*Eruca sativa* Gars.	Garden rocket	*
49.		*Nasturium officinale* R.Br.	Watercress	*
50.	Campanulaceae	*Lobelia portoricensis* (Vatke) Urban		55, 71
51.	Caprifoliaceae	*Lonicera japonica* Thumb.	Japanese honeysuckle	*
52.	Caricaceae	*Carica papaya* Linn.	Papaya	68
53.	Caryophyllaceae	*Dianthus caryophillus* Linn.	Carnation	4, 10, 17, 19, 24
54.	Cecropiaceae	*Cecropia peltata* Linn.	Trumpet-tree	55, 71
55.	Chenopodiaceae	*Beta vulgaris* Linn.	Beet	2, 24, 29, 48, 54, 56, 62, 63, 65, 71, *
56.		*Beta vulgaris vulgaris* Linn.	Sugar beet	31.
57.		*Beta vulgaris* Linn. var. *cicla* Linn.	Swiss chard	16, 62, 65, 71, *
58.		*Chenopodium quinoa* Willdenow	Quinoa	12, 60, 71
59.	Commelinaceae	*Commelina diffusa* Burm.		55, 71
60.		*Tripogandra serrula* (Wahl) Handles		55, 71
61.	Convolvulaceae	*Calonyctium speciosum* Choisy	Good night	*
62.		*Ipomoea batatas* (Linn.) Lam.	Sweet potato	1, 2, 4, 5, 13, 15, 17, 19, 20, 22, 24, 29, 31, 33, 48, 56, 62, 63, 71, *
63.		*Ipomoea grandiflora* Linn.	Moonflower	64
64.		*Ipomea purpurea* Roth	handbell	*
65.		*Ipomea tiliacea* (Willd.) Choisy		55, 71
66.	Cucurbitaceae	*Cayaponia americana* Lam.		55, 71
67.		*Cayaponia racemosa* Mill.		55, 71
68.		*Cucumis melo* Linn	Melon	48, *
69.		*Cucumis sativus* Linn.	Cucumber	24, 48, 56, *
70.		*Cucurbita maxima* Duch	Squash	29
71.		*Citrullus lanatus* var. *lanatus* (Thumb.) Matsum. & Naka	Watermelon	2, 29, 48, 56, 71
72.		*Sechium edule* (Jacq.) Sw.	chayote	*

73.	Dioscoreaceae	*Dioscorea polygonoides* Humb. Bunpl. ex. Willd.	Dioscorea	55, 71
74.		*Rajania cordata* Linn.		55, 71
75.	Ericaceae	*Vaccinium macrocarpum* Aiton	Cranberry	29
76.	Escrofulariaceae	*Antirrhinum majus* Linn.	Snapdragons	*
77.	Euphorbiaceae	*Aleurites fordii* Hemsl.	Tung tree	5, 17, 19, 24, 62.
78.		*Manihot esculenta* Crantz	Cassava	17, 19, 24, 36, 41, 47, 48, 56, 71
79.		*Phyllanthusurinaria* Linn.		55, 71
80.		*Ricinus communis* Linn.	Castor bean	2, 17, 19, 22, 24, 29, 54, 71,72
81.		*Sapium jamaicense* Sw.		55, 71
82.	Fabaceae	*Arachis hypogaea* Linn.	Peanuts	2, 20, 26, 29, 56, 71, *
83.		*Centrosema pubescens* Benth	Spurred butterfly-pea	55, 71
84.		*Cicer arietinum* Linn.	Chick-pea	44, 71
85.		*Crotalaria breviflora* DC	shortflower rattlebox	66
86.		*Crotalaria spectabilis* Roth.	Showy rattlebox	66
87.		*Desmodium adscendens* (Sw.) DC	Tick-clover	55, 71
88.		*Glycine max* (Linn.) Merril.	Soybean	29, 56, 62, 65, 71, *
89.		*Leucaena leucocephala* Lam.		55, 71
90.		*Medicago sativa* Linn.	Alfalfa	24, 28, 30, 31, 62, 63, 65, 71
91.		*Mimosa pudica* Linn.	Sensitive-plant	55, 71
92.		*Mimosa scabrella* Benthan	Bracatinga	49, 52, 71
93.		*Mucuna pruriens* var. Utillis (Wall. Ex Wight) Backer ex. Burk	velvet bean	2, 29, 71
94.		*Phaseolus lunatus* Linn.	Lima bean	44, 71
95.		*Phaseolus polystachios* (Linn.) Britton, Sterns & Poggenb.	Thicket bean	29
96.		*Phaseolus vulgaris* Linn.	Bean	13, 24, 29, 31, 48, 54, 56, 62, 63, 65, 71, *
97.		*Pisum sativum* Linn.	Pea	54, *
98.		*Trifolium sp.*	Clovers	2, 29, 71
99.		*Vicia faba* Linn.	Faba bean	61
100.		*Vignum unguiculata* (Linn.) Walp.	Cowpea	1, 2, 29, 40, 56, 71
101.	Geraniaceae	*Geranium* sp.	Geranium	54
102.		*Pelargonium hortorum* L.H. Bailey	geranium	*
103.	Lamiaceae	*Lavandula angustifolia* Mill.	true lavender	*

104.	*Melissa officinalis* Linn.	common balm	*
105.	*Mentha arvensis* Linn. var. *piperacens* Malinvaud.	Peppermint	69
106.	*Mentha piperita* Linn.		55, 71, *
107.	*Mentha spicata* Linn.	garden mint	*
108.	*Mentha* sp.	Peppermint	24, 62
109.Lauraceae	*Ocotea* sp.		55, 71
110.	*Persea americana* Mill.	Avocado	2, 29, 71
111.Liliaceae	*Allium cepa* Linn.	Onion	23, 24, 31, 48, 56, 71, *
112.	*Allium fistulosum* Linn.	Green Onion	*
113.	*Allium sativum* Linn.	Garlic	48,
114.	*Asparagus officinalis* Linn.	Asparagus	57
115.Linaceae	*Linum usitatissimum* Linn.	Flax	11, 31, 63, 71
116.Litraceae	*Lagerstroemia indica* Linn	crape myrtle	*
117.Lomariopsidaceae	*Elaphoglossum* sp.	--	67
118.Malvaceae	*Abelmoschus esculentus* (Linn.) Moench	okra	1, 2, 29, 31, 63, 71
119.	*Althaea rosea* (Linn.) Cav	Hollyhock	29
120.	*Gossypium herbacium* Linn.	Cotton	2, 7, 8, 17, 20, 24, 25, 29, 48, 56, 62, 71
121.	*Hibiscus cannabinus* Linn.	Brown Indianhemp	56
122.	*Hibiscus rosa-sinensis* Linn.		55, 71
123.	*Malva parviflora* Linn.	Mallow	24, 31, 63,
124.	*Pavonia fruticosa* (Mill.) Fawc. & Rendle		55, 71
125.	*Sida rhombifolia* Linn.	Arrow-leaf sida	55, 71, *
126.Melastomataceae	*Heterotrichum cymosum* (Wendl.) Urban		55, 71
127.Moraceae	*Morus alba* Linn.	Mulberry	16
128.Myrtaceae	*Eucalyptus* sp.	Eucalyptus	24, 65
129.	*Psidium guajava* Linn.	apple guava	*
130.Ochnaceae	*Sauvagesia erecta* Linn		55, 71
131.Onagraceae	*Ludwigia* sp.		55, 71
132.Papaveraceae	*Sanguinaria canadensis* Linn.	Bloodroot	2, 29, 71
133.Passifloraceae	*Passiflora edulis* Sims.	Passion-flower	55, 71
134.	*Passiflora sexflora* Juss.		55, 71
135.Phytolaccaceae	*Phytolacca americana* (Linn.)	pokeweed	1, 2, 29, 45, 71
136.	*Phytolacca decandra* Linn.	Pokeweed	16, *
137.	*Phytolacca dioica* Linn.		*
138.	*Phytolacca rigida* (Small)	pokeweed	2, 45, 71
139.	*Phytolacca rivinoides* Kunth & Bouché		55, 71
140.	*Phytolacca thyrsiflora* Fenz ex Schmidt	pokeweed	*
141.Piperaceae	*Lepianthes umbellatum* (Linn.) Rafinesque		55, 71
142.Plantaginaceae	*Plantago major* Linn.	Common plantain	55, 71

143.Poaceae	*Cynodon nlemfuensis* Vanderyst	African Bermudagrass	67
144.	*Digitaria ischaemum* (Schreb.) Schreb. ex Muhl.	Small crabgrass	29
145.	*Digitaria sanguinalis* (Linn.) Scop.	Large crabgrass	2, 22, 29, 71
146.	*Ichnanthus pallens* (Sw.) Munroe		55, 71
147.	*Lolium perene* Linn.	Ryegrass	46, 71
148.	*Melinis minutiflora* Beauv.	Molassesgrass	24
149.	*Oryza sativa* Linn.	Rice	31, 63,
150.	*Pennisetum purpureum* (Pers.)	elephant grass	*
151.	*Stenopaphrum secundatum* (Walt.) Kunze	Buffalo grass	6, 55, 71
152.	*Zea mays* Linn.	Corn	2, 17, 18, 21, 22, 23, 29, 31, 48, 56, 63, 65, 71, *
153.Polygonaceae	*Persicaria hydropiperoides* (Michx.) Small	false water-pepper	*
154.	*Polygonium* sp.	Polygonium	65
155.	*Polygonium segetum* Kunth	Field Smartweed	67
156.	*Rheum rhabarbarum* Linn.	Rhubarb	29
157.	*Rumex* sp.	Rumex	2, 29, 71
158.	*Rumex crispus* Linn.	curly dock	*
159.	*Rumex obtusifolius* Linn.	Broad Leaved Dock	*
160.Portulacaceae	*Portulaca oleracea* Linn.	Purslane	32, 31, 51, 54, 63, 71, *
161.	*Portulaca grandiflora* Hook	portulaca	*
162.Rosaceae	*Fragaria vesca* Linn.	Strawberry	9, 71, *
163.	*Malus domestica* Borkhausen	Apple	50, 53, 71, *
164.	*Pyrus communis* Linn.	Common Pear	*
165.	*Rosa* spp.	Rose	58, *
166.	*Rubus idaeus* Linn.	rasberry	*
167.	*Rubus rosifolius* Smith	Mauritius rasberry	55, 71
168.Rubiaceae	*Coffea arabica* Linn.	Coffe	56
169.	*Diodia ocimifolia* (Willd. ex. Roem. & Schult.) Bremek.	Weed	55, 71
170.	*Gonzalagunia spictata* (Lam.) Maza		55, 71
171.	*Hamelia ptlens* Jacq		55, 71
172.	*Pentas sp.*	Pentas	54
173.	*Psycotria berteriana* DC		55, 71
174.	*Spermacoce ocymifolia* Willd. Ex Roem. & Schult.	Slender Buttonweed	67
175.Rutaceae	*Citrus sp.*	Citrus trees	2, 14, 71
176.	*Citrus limon* (Linn.) Burm	Lemon tree	29
177.	*Citrus grandis* (Linn.) Osbeck	Grapefruit	29
178.	*Citrus sinensis* (Linn.) Osbeck	Orange	29
179.Salicaceae	*Salix* sp.	Willow	2, 29, 71

180.Scrophulariaceae	*Bacopa stricta* (Schrad.) Robins		55, 71
181.Solanaceae	*Capsicum annuum* Linn.	Pepper	1, 2, 6, 16, 29, 31, 63, 71, *
182.	*Cestrum macrophyllum* Vent	Galán del monte	55, 71
183.	*Lycopersicum esculentum* Mill.	Tomato	1, 2, 6, 15, 16, 17, 19, 22, 23, 24, 27, 29, 30, 31, 35, 48, 54, 56, 62, 63, 65, 67, 71, *
184.	*Nicotiana alata* Link & Otto	Jasmine tobacco	31, 63,
185.	*Nicotiana tabacum* Linn.	Tobacco	2, 6, 16, 24, 29, 31, 48, 63, 71
186.	*Solanum acerosum* Sendt.	Arrebenta-cavalo	*
187.	*Solanum americanum* Schultz	American nightshade	55, 71
188.	*Solanum andigenum* Juz.&Bukasov	Andigena	30
189.	*Solanum jamaicense* Mill.	Jamaica nightshade	67
190.	*Solanum melongena* Linn.	Eggplant	1, 2, 29, 56, 63, 71, *
191.	*Solanum peruvianum* Linn.	Peruvian nightshade	30
192.	*Solanum rugosum* Dunal	tabacon aspero	55, 71
193.	*Solanum torvum* Sw.	Turkey Berry	6, 16, 55, 71
194.	*Solanum tuberosum* Linn.	Potato	1, 2, 6, 9, 13, 16, 19, 22, 24, 29, 30, 31, 48, 54, 56, 62, 63, 71, *
195.Teaceae	*Camelia japonica* Linn.	Camellia	24
196.Urticaceae	*Laportea aestuans*(Linn.) Chew	West Indian woodnettle	67
197.	*Urera bacifera* (L.) Gaudich. ex Wedd.	Scratchbush	*
198.Verbenaceae	*Citharexylum fruticosum* Linn.	Fiddlewood	55, 71
199.Violaceae	*Viola tricolor* Linn.	Pansy	*
200.Vitaceae	*Vitis labrusca* Linn.	fox grape	*
201.	*Vitis vinifera* Linn.	wine grape	*
202.Zingiberaceae	*Alpinia purpurata* Vieill ex k. Schum.	Red ginger	55, 71

1 - Chittenden & Russel 1909, 2 - Crumb 1929, 3 - Stoner & Wisecup 1930, 4 - Marques 1932, 5 - Monte 1934, 6 - Wolcott 1936, 7 - Hambleton 1939, 8 - Tucker 1939, 9 - Waterston 1939, 10 - Brandão Filho 1942, 11 - Wille & Garcia Rada 1942, 12 - Alberts 1947, 13 - Waterston 1947, 14 - Bedford 1949, 15 - Biezanko & Bertholdi 1951, 16 - Wolcott 1951, 17 - Corseuil 1955, 18 - Olalquiaga Faure 1955, 19 - Costa 1958, 20 - Nickel 1958, 21 - Harris

1959, 22 - Kimball 1965, 23 - McGuire & Crandall 1967, 24 - Silva *et al*. 1968, 25 - Cantu & Wolfenbarger 1970, 26 - Briceno-V. 1971, 27 - Creigton et al. 1971, 28 - Cortés et al. 1972, 29 - Tietz 1972, 30 - Valencia-V & Valdivia-M. 1973, 31 - Biezanko et al. 1974, 32 - Figueiroa 1976, 33 - Habeck 1976, 34 - Link 1977, 35 - Price & Poe 1977, 36 - Bellotti & Schoonhoven 1978, 37 - Tingle et al. 1978, 38 - Schuster & Engelhard 1979, 39 - Price *et al*. 1980, 40 - Silva & Magalhães 1980, 41 - Pena & Waddill 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 & Tellez Robleto 1988, 49 - Mattana & Foerster 1988, 50 - Nora & Reis 1988, 51 - Savoie 1988, 52 - Foerster & Dionisio 1989, 53 - Nora *et al*. 1989, 54 - Ferguson *et al*. 1991, 55 – Torres 1992, 56 - Coto *et al*. 1995, 57 - Sanchés-V & Vergana-C 1995, 58 - Sánchez-Aguirre 1996, 59 - Clarke-Harris *et al*. 1998, 60 - Rasmussen et al 2003, 61 - Nuassly *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 & Hallwachs 2009, 68 - Semillas del Caribe 2010, 69 - Mendoza *et al*. 2011, 70 - Walsh & Maestro 2011, 71 - Pogue 2012, 72 – Berger 1920 * new record.

Table 5 – Pupal weight (mg) of *Spodoptera eridania* reared on artificial diet, including pupae whose larvae developed for six and seven instars (only females), under controlled conditions (25 ± 1ºC, 70 ± 10% RH and 14 hour photo phase).

Larval instars	**Gender**	**N**	**Mean ± SE**	**Range**
Six	Female	120	377.533 ± 51.654	253 - 538
	Male	132	329.447 ± 41.427	205 - 399
	Significance[1]		**	---
Seven	Female	9	435.111 ± 41.619	389-528
	Significance[2]		*	---

Comparison of means using a Student *t*-test, considering different variances, at a significance level of 95% (* $p < 0,01$; ** $p < 0,001$).
1 comparisons between females/males – six larval instars.
2 comparisons between females/females – six and seven larval instars.

RESULTADOS

5.4 CAPÍTULO 4

Potencial biótico, fertilidade e tabela de vida de *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae), em condições controladas

(Artigo a ser submetido à Revista Brasileira de Entomologia)

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ABSTRACT: Biotic potential, fertility and life table of *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae), on controlled conditions: This study aimed to evaluate the biotic potential, life table parameters and fertility of *Spodoptera eridania* (Stoll, 1782) under controlled conditions (25 ± 1 ° C, 70 ± 10% RH and 14 hour photophase). The longevity, pre, post and oviposition periods, fecundity and fertility of 15 couples was evaluated. The longevity of females (10.80 days) wasn't 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 was 1,398.00 eggs and mean fertility was 1,367.50 larvae, per female. On average, females copulated 1,133 times. A strong positive correlation was observed between the number of copulations and fecundity ($r = 0.881$, $P < 0.001$), as well as a strong negative correlation between the number of copulations and the duration of the pre-oviposition period ($r = -0.826$, $P = 0.002$), and longevity ($r = -0.823$, $P = 0.001$). The biotic potential of *S. eridania* was estimated at 1.894×10^{25} 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 (λ) of 1.193, per week.

KEY WORDS: armyworm, development, fecundity, reproduction, spermatophore.

RESUMO: Potencial biótico, tabela de vida e fertilidade de *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae), em condições controladas: Este trabalho objetivou avaliar o potencial biótico e parâmetros da tabela de vida e fertilidade de *Spodoptera eridania* (Stoll, 1782) em condições controladas (25 ± 1ºC, 70 ± 10% UR e fotofase de 14 horas). Avaliou-se a longevidade, períodos de pré, pós e oviposição, fecundidade e fertilidade de 15 casais. A longevidade das fêmeas (10,80 dias) não diferiu significativamente da dos machos (9,27 dias). Os períodos médios de pré, pós e oviposição foram de 2.067, 0,600 e 8,133 dias, respectivamente. A fecundidade média foi de 1.398,00 ovos e a fertilidade 1.367,50 lagartas por fêmea. Em média as fêmeas copularam 1.133 vezes. Observou-se forte correlação positiva entre número de cópulas e a fecundidade (r = 0.881, P< 0.001) e, forte correlação negativa, entre o número de cópulas e a duração do período de pré-oviposição (r= -0,826, P= 0,001), e a longevidade (r= -0,823, P= 0,001). O potencial biótico de *S. eridania* foi estimado em 1,893 x 10^{25} indivíduos/fêmea/ano. A taxa líquida de reprodução (Ro) foi de 560,531 vezes por geração e o tempo médio de uma geração (T) foi de 35,807 dias. A taxa intrínseca de aumento (r_m) foi de 0,177, com uma razão finita de aumento (λ) 1,193, por semana.

PALAVRAS-CHAVE: lagarta-militar, desenvolvimento, fecundidade, reprodução, espermatóforo.

Introdução

O gênero *Spodoptera* Guenée, 1852 é cosmopolita e abriga grande parte das lagartas militares de importância agrícola (Pogue, 2002). Entre as espécies de maior importância destaca-se *Spodoptera eridania* (Stoll, 1782) que ocorre em todo o Continente Americano (Pogue, 2002, Montezano *et al.* in press) e representa risco potencial para diferentes culturas como alfalfa, feijão, beterraba, repolho, mandioca, couve, algodão, cebola, amendoim, quinoa, soja, tabaco, tomate, batata doce, girassol e olerículas, em diversos locais da America (Hichings & Rabinivich 1974, Parra *et al*. 1977, Passos 1978, 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, Montezano *et al.* in press).

Atribui-se o alto grau de polifagia, relatado desde o começo do último século (Chittenden & Russel, 1909, Crumb, 1929), à grande capacidade de desintoxicar ou outras formas de processar a biomassa de plantas ou dietas que contenham altas concentrações de alomônios conhecidos (Brattsten *et al*. 1973, 1977, 1980, Blau *et al*. 1978, Scriber 1978, 1979, Manuwoto & Scriber 1982).

Além da grande voracidade e capacidade reprodutiva (ex. Hichings & Rabinivich 1974, Parra *et al*. 1977, Valverde & Sarmiento 1987a, Mattana & Foerster 1988, Santos 2005) lagartas de *S. eridania*, como as de outros representantes do gênero, desenvolve-se em plantas invasoras que geralmente constituem a fonte primária de infestação das plantas cultivadas (Tingle *et al*. 1978, Valverde & Sarmiento 1987a, Savoie 1988, Sánchez & Vergara 1996, Santos *et al*. 2005). *S. eridania* ainda apresenta diferentes graus de tolerância a diversos inseticidas químicos (González 1966, Campos 1972, 1982, Aziz 1973, Aguilera & Vasquez 1974, Valverde & Sarmiento 1987b), extratos vegetais e inseticidas botânicos (Valles & Capinera 1993, Rosseti *et al*. 2008) e ao gene Cry1Ac de *Bacillus thuringiensis* (Zenner-de-Polanía *et al*. 2008, Amaya *et al*. 2009).

Este estudo complementa o realizado anteriormente sobre imaturos de *S. eridania* (Montezano *et al.* in press) e objetiva avaliar e descrever os parâmetros biológicos de *S. eridania* com especial ênfase no potencial biótico e na tabela de vida, em condições controladas.

Materiais e Métodos

Os experimentos foram desenvolvidos em sala climatizada (25 ± 1 ° C, 70 ± 10% UR e fotofase de 14 horas), com observações diárias. A procedência dos insetos, metodologia de criação e dados de imaturos encontram-se descritos detalhadamente em Montezano *et al*. (in press).

Para descartar possíveis incompatibilidades de cópula, descritas anteriormente, entre biotipos provenientes de plantas hospedeiras de localidades distintas (Murúa & Virla 2004, 2008, Sadek & Anderson 2007), os insetos utilizados no experimento correspondem a primeira geração obtida a partir de lagartas coletadas em uma lavoura de soja (Montezano *et al.* in press). Adultos foram mantidos em pares (n = 15) em recipientes plásticos cilíndricos, com 10 cm de diâmetro e 15 cm de altura, tendo sua parte superior fechada com filme plástico, na qual foram aderidas fitas de papel filtro com o comprimento do frasco para estimular a oviposição. A porção inferior foi fechada com uma placa de Petri (10.5 cm de diâmetro), com o fundo forrado com papel filtro.

Para evitar o efeito do peso das pupas sobre os aspectos reprodutivos (Tisdale & Sappington 2001), no segundo dia após a metamorfose as mesmas foram pesadas, sendo utilizados para o experimento adultos fêmeas provenientes de pupas com peso entre 0,322 a 0,341g e adultos machos provenientes de pupas com peso entre 0,263 a 0,288g. Da mesma forma para evitar efeitos da idade dos adultos sobre a capacidade de cópula (Kehat & Gordon

1975, Ellis & Steele, 1982, Rogers & Marti Jr.1994), os casais foram formados com adultos emergidos na mesma data.

A alimentação foi baseada na dieta artificial descrita por Hoffmann-Campo *et al*. (1985) que consta de mel (10g), ácido sórbico (1g), methilparaben (1g), sacarose (60g), e água destilada (1000 ml). Todos componentes foram dissolvidos em água destilada e a solução obtida foi mantida sob refrigeração (7°C). Diariamente foi adicionada à solução, cerveja Pilsen na proporção de ¼, sendo a mistura disponibilizada aos insetos em uma placa de Petri de 5cm, forrada com algodão hidrófilo. Adicionalmente, em outra placa de Petri de 5cm também forrada com algodão disponibilizou-se água destilada para eventual hidratação dos insetos.

Avaliou-se fecundidade (numero de ovos por fêmeas), fertilidade (número de lagartas eclodidas por fêmea), longevidade e duração de períodos de pré e pós oviposição.

Os frascos foram analisados diariamente para anotar dados da mortalidade de adultos, remover e contar os ovos. Fêmeas mortas foram dissecadas para determinar o número de espermatóforos recebidos dos machos durante as cópulas.

Para estimar a fertilidade foram analisadas 32 posturas retiradas de quatro cópulas, incluindo as primeiras e as últimas, totalizando 3.782 ovos avaliados. Para isso, cada postura foi individualizada em placa de Petri, cujo fundo foi forrado com papel filtro umedecido com água destilada, onde permaneceram até a eclosão das lagartas. Todas as posturas avaliadas foram provenientes de cópulas de casais cujas fêmeas, após a morte, apresentaram pelo menos um espermatóforo na bolsa copulatória, comprovando terem sido fertilizadas no decorrer do experimento.

Todos os parâmetros biológicos foram analisados através de estatística descritiva com o cálculo das médias e desvio padrão. A fecundidade, longevidade para ambos os sexos e a duração de pré e pós oviposição foram correlacionados (Pearson Product Moment

Correlation) com o número de cópulas de cada casal. Em função da alta correlação dos parâmetros em relação ao número de cópulas, apenas as médias gerais da longevidade foram comparada utilizando o teste *t* presumindo variâncias diferentes ao nível de significância de 95%. A média de cada parâmetro, considerando o número de cópulas foi comparada utilizando Análise de Variância Univariada (LSD) com significância ao nível de 95% de probabilidade.

A partir da reunião de parâmetros biológicos, o potencial biótico (PB) foi calculado considerando nula a capacidade de suporte do ambiente, utilizando a equação descrita em Silveira Neto *et al.* (1976), $PB = (rs * d)^n - re$, onde: (re) razão sexual é o número de fêmeas dividido pelo número de fêmeas mais o número de machos; (d) indivíduos viáveis por fêmea, consistindo do número de ovos por fêmea (ou fecundidade) multiplicado pelo total de sobrevivência de lagartas. (n) número de gerações por ano (ou 365 dias) dividido pelo total tempo total de vida. (re) A capacidade de suporte do ambiente nesse caso foi considerada nula.

A tabela de vida de fertilidade foi elaborada empregando dados dos estágios imaturos de *S. eridania* Montezano *et al* (in press) e é representada graficamente traçando a probabilidade dos valores de sobrevivência no ponto médio de cada intervalo de tempo (taxa de sobrevivência - lx) e o número total de ovos por fêmeas por semana que originarão fêmeas (fertilidade específica - mx).

Utilizando a tabela de vida, os valores dos diferentes parâmetros reprodutivos de *S. eridania* foram calculados. A taxa líquida de reprodução (Ro), dada pela relação entre o número de fêmeas em duas gerações sucessivas; o tempo médio de uma geração (T), que compreende o período médio de dias do nascimento dos pais ao nascimento dos descendentes; taxa intrínsica de aumento diário (rm) e a razão finita de aumento diário (λ), seguindo as fórmulas constantes em Silveira Neto *et al.* (1976).

Resultados

A tabela 1 apresenta a longevidade de 15 casais, fêmeas e machos, a duração média de pós, pré e oviposição bem como a fecundidade média. Utilizando os dados de viabilidade dos ovos, (97,81%) (Montezano, *et al.* in press) a fertilidade média foi de 1,367.50 lagartas por fêmea de *S. eridania*.

Em média cada fêmea copulou 1,13 vezes, sendo que quatro (26,67%) não copularam, seis copularam apenas uma vez (40,00%), uma copulou duas vezes (6,66%) e quatro copularam três vezes (26,67%). Foi observada uma forte correlação positiva entre o número de cópulas e a fecundidade ($r = 0,881$, $P < 0,001$), bem como uma forte correlação negativa entre o número de cópulas e a duração do período de pré-oviposição ($r = -0,826$; $P = 0,002$), e longevidade ($r = -0,823$; $P = 0,001$).

A análise dos parâmetros reprodutivos em função do número de cópulas revelou diferenças entre fecundidade e duração, especialmente com relação às fêmeas que não foram fecundadas (Figuras 1-5). O número diário médio de ovos de fêmeas não fecundadas foi muito menor que as fêmeas fecundadas uma ou mais vezes, verificando-se, também, o prolongamento do período de pré-oviposição (Figura 1). Os períodos de pré e oviposição foram significativamente maiores para as fêmeas que não foram fecundadas (Figuras 2 e 3).

Tais diferenças foram responsáveis pela maior longevidade das fêmeas não fecundadas com relação às fecundadas. De forma similar observou-se uma redução na longevidade dos machos (Figura 4).

A fecundidade foi positivamente afetada pelo número de cópulas, observando-se que as fêmeas não fecundadas ovipositaram menos da metade do que as fecundadas, com

diferenças significativas entre fêmeas não fecundadas, fecundadas uma e duas vezes (Figura 5).

O potencial biótico de 5.800 x 10^{24} indivíduos por fêmea por ano, resultantes da equação $BP = (sr * d)^n - er \therefore BP = (0,502 \times 1.797,709)^{8,911}-0$, é obtido quando considerado que: 135 fêmeas e 134 machos imaturos atingiram a fase de pupa, a uma razão de 0,502 (Montezano *et al* in press); em média, cada uma das fêmeas ovipositaram 1.398,000 ovos, e a sobrevivência global foi de 85,673%, obtendo-se 1.197,709 indivíduos viáveis por fêmea (Montezano *et al* in press Tabela 1), a duração média do ciclo de vida (40,96 dias), corresponde a 8,911 gerações por ano (n), considerando-se nula a capacidade de suporte do ambiente.

A taxa máxima de crescimento da população ocorreu entre os dias 34 e 35, durante a 5ª semana de vida, representado pelo cruzamento das linhas de sobrevivência específica e fecundidade (Figura 6). Esta taxa é relativamente deslocada para o início da fase adulta, especialmente impulsionado pela maior fecundidade e a baixa mortalidade de imaturos logo após a emergência.

A taxa líquida de reprodução (Ro) foi de 560,53 fêmeas por geração, o tempo médio de geração (T) foi de 35,81 dias, a taxa diária intrínseca de aumento (rm) e razão finita diária de aumento (λ) foram rm = 0,177 e λ = 1,193, respectivamente.

Discussão

Neste estudo, a longevidade de *S. eridania* (Tabela 1) foi semelhante ao descrito por Valverde & Sarmiento (1987a) quando alimentadas com quatro diferentes tipos de plantas e Mattana & Foerster (1988) em duas diferentes plantas hospedeiras, ambos a 25 °C. Da mesma forma, estes valores são semelhantes aos descritos por Parra *et al.* (1977), quando as lagartas

foram alimentadas com soja, mas, estes valores foram inferiores quando as lagartas foram alimentadas com algodão, a 27 °C.

No experimento realizado por Mattana & Foerster (1988), não foi verificada diferença significativa entre a longevidade media de machos e fêmeas. Entretanto a maior longevidade (numérica) para fêmeas (Tabela 1) também é descrita por Valverde & Sarmiento (1987a) e Santos *et al*. (2005) para adultos provenientes de lagartas alimentadas com quatro plantas hospedeiras, diferindo dos resultados obtidos por Parra *et al*. (1977) que relacionam maior longevidade para os machos.

Contudo, a análise dos resultados comparando a longevidade em função do número de cópulas (Figura 4) indica que este é um fator importante a ser incluído em análises de longevidade, especialmente em função do prolongamento dos períodos de pré oviposição e oviposição das fêmeas que não foram fertilizadas (Figuras 2-3).

Com base nos dados de Montezano *et al.* (in press), que indicam uma duração média dos estágios imaturos de 30,927 dias, a longevidade média dos adultos de *S. eridania* corresponde a 24,495%, ou quase um quarto do seu ciclo de vida. Estes resultados são semelhantes aos de outros estudos envolvendo *S. eridania* (Parra *et al*. 1977, Mattana & Foerster 1988) e outros representantes de *Spodoptera* (Habib *et al*. 1983, Bavaresco *et al.* 2004, Busato *et al*. 2005). Estes resultados também indicam que a maior longevidade de *S. eridania*, assim como outras espécies do gênero, que possuem uma grande capacidade de dispersão e até mesmo de migração (Ferguson *et al*. 1991), está relacionada à sua ampla distribuição no continente americano, estendendo-se entre os paralelos 30 º de Norte a Sul (Montezano *et al* in press).

O número de cópulas obtido neste estudo é similar ao obtido *S. albula* (1,23) criadas nas mesmas condições (Montezano *et al* 2013b). Este valor médio está dentro da variação

descrita para *S. frugiperda* por Murúa *et al*. (2008), que observaram valores muito discordantes entre diferentes populações de *S. frugiperda* na Argentina (0,78-2,32 espermatóforos por fêmea). No que diz respeito à ausência de cópula em alguns pares de *S. eridania*, estes mesmos autores relataram que, em alguns grupos de *S. frugiperda*, mais de 20% das fêmeas não acasalaram, para *S. albula* relatou-se que 23,08% das fêmeas não copularam Montezano *et al*. (2013b). Além disso, considerando que Milano *et al*. (2008), utilizando 25 pares de *S. frugiperda*, por gaiola, obteve uma média de mais de três espermatóforos por fêmea, com um máximo de oito, a 25 ° C, espera-se que um número maior de indivíduos *S. eridania* por gaiola também aumente o número de cópulas.

A forte correlação negativa observada entre o número de cópulas e o período pré oviposição (Figura 2) indicam que a *S. eridania* apresenta um aumento da pré-oviposição em função do número reduzido ou ausência de acasalamento, o que também se reflete como longevidade prolongada, semelhante a *S. albula* (Montezano *et al*. 2013b), *S. littoralis* (Kehat & Gordon 1975, Ellis & Steele, 1982) e *S. exigua* (Rogers & Marti Jr. 1997).

Do mesmo modo, a correlação negativa significativa entre o número de cópulas e período de postura (Figura 3) está relacionada com a interação entre a produção de ovos e o metabolismo (Hou & Sheng, 1999). Estes autores postulam que múltiplas fecundações estimulam a produção de ovos e aceleram o consumo de energia e de material, diminuindo os recursos disponíveis para a manutenção somática. No entanto, a redução do período de postura relacionada com um maior número de cópulas, como descrito por Hou e Sheng (1999) certamente relaciona-se com o aumento da atividade reprodutora nas fêmeas que copularam mais.

O período relativamente curto de pré-oviposição (Tabela 1), especialmente em fêmas fecundadas (Figura 2) indica que os adultos atingem a maturidade sexual em *S. eridania* logo

após a emergência, como acontece com outros representantes de *Spodoptera* (Habib *et al.* 1983, Tisdale e Sappington, 2001, Montezano *et al.* 2013b). No entanto, a primeira oviposição, nos primeiros dias após a emergência, pressupõe a ocorrência de fertilização. Nossos resultados indicam que o período inicial de fertilização de *S. eridania* deve estar entre o primeiro e segundo dia após a emergência, de ambos os sexos, conforme descrito em Roger e Marti Jr. (1997) para *S. exigua.*

A fertilidade média de *S. eridania*, com cerca de 1.400 ovos por fêmea (Tabela 1) é semelhante aos valores médios indicados para a mesma espécie quando as lagartas foram alimentadas com folhas da soja, apresentando 1.346,08 ovos (Parra *et al.* 1977). Porém é relativamente elevada quando comparada com lagartas alimentadas com algodão, corda de viola e soja, que foi de: 680,5, 823,9 e 839,6, respectivamente (Santos *et al.* 2005). Entretanto, foi relativamente menor que o observado quando as lagartas foram alimentadas com folhas de batata-doce e bracatinga, 1.859,64 e 2.082,73 ovos respectivamente (Mattana & Foerster 1988); com algodão, 2.922,91 (Parra *et al* 1977) e quando alimentadas com tomate, batata doce, amaranto e Portulaca, 1.863,7 a 2.211,7 ovos (Valverde & Sarmiento 1987a).

Atribui-se dois fatores fundamentais as diferenças de fecundidade encontradas entre os diversos estudos: a - adequação da dieta, uma vez que as pupas dos exemplares mais fecundos relatados em bibliografia eram mais pesados, pelo menos em Parra *et al*. (1977) com lagartas alimentadas com algodão e Valverde & Sarmiento (1987a) com lagartas alimentadas com tomate e batata doce e, b – A fertilização das fêmeas (Figura 5), quando computados apenas os dados das fêmeas que acasalaram a fecundidade variou de mais de 1.500 até quase 1.800, assemelhando-se muito ao máximo apresentado para adultos provenientes de pupas com peso semelhante ao utilizado no presente estudo (Parra *et al*. 1977, Valverde & Sarmiento 1987a, Mattana & Foerster 1988).

No entanto essa variação pode ser atribuída a diversos fatores como as condições de

cada experimento, biótipos relacionados a diferentes plantas hospedeiras ou diferentes regiões geográficas (Giolo *et al.* 2002, Murúa & Virla 2004, Sadek & Anderson 2007, Busato *et al.* 2008, Murúa *et al.* 2008). O número de ovos obtidos no presente estudo indica que a dieta e a metodologia de criação dos imaturos (Montezano in press) e dos adultos foram adequados para o desenvolvimento de *S. eridania* em laboratório. Estes resultados ressaltam a importância de que em estudos futuros sejam indicados o número de cópulas (ou pelo menos se as fêmeas foram fecundadas ou não) e o peso das pupas que deram origem aos adultos.

A alta viabilidade de ovos (97,818%) está certamente, relacionada à fertilização comprovada das fêmeas que tinham um ou dois espermatóforos. Isto está de acordo com a porcentagem de 96,00-98,84% relatada por Valverde & Sarmiento (1987a) e, geralmente, estudos com representantes do gênero *Spodoptera* em que são relatados múltiplos acasalamentos demonstram um aumentam na capacidade reprodutiva e na fertilidade (Kehat & Gordon 1975, Sadek 2001, Sadek & Anderson, 2007, Busato *et al*. 2008, Milano *et al*. 2008, Montezano *et al.* 2013a).

O alto valor do potencial biótico (5.800×10^{24}) de *S. eridania* indica que cada fêmea pode gerar mais de 5,8 quadrilhões de descendentes. Este resultado é semelhante ao obtido a partir dos dados de Parra *et al*. (1977) com lagartas alimentadas com algodão a 27° C e razão sexual de 0,5 ou 1:1, o potencial calculado foi de aproximadamente $6,6 \times 10^{23}$. Este resultado também se aproxima aos obtidos para *S. albula* (8.768×10^{22}) criada nas mesmas condições (Montezano *et al*. 2013a, 2013b).

De forma similar ao observado para *S. albula*, nas mesma condições (Montezano *et al*, 2013b), a taxa máxima de aumento da população de *S. eridania* (Figura 6) está relativamente deslocada para o início da fase adulta, especialmente impulsionado pela maior fecundidade e baixa mortalidade de imaturos logo após a emergência. Estas observações também são similares as observadas em outros estudos realizados com representantes de

Spodoptera onde os valores mais elevados de fecundidade são observados durante os primeiros dias, a partir do segundo ou terceiro até o sétimo (Kehat & Gordon 1975, Sadek 2001, Bavaresco *et al*. 2004, Murúa & Virla 2004).

A taxa líquida de reprodução (Ro = 360,53) foi semelhante aos valores descritos por *S. albula* nas mesmas condições (353,90) e também para outros representantes de *Spodoptera* em diferentes plantas hospedeiras. Por exemplo: 377,11 para *S. exigua* em *Chenopodium album* Linn. - Chenopodiaceae e 342,11 em repolho - *Brassica napus* Linn. Brassicaceae (Farahani *et al*. 2011), ainda para *S. exigua*, 359,3 em algodão - *Gossypiun hirsutum* Linn - Malvaceae, 342,2 no girassol - *Helianthus annuus* Linn. - Asteraceae, e o valor máximo de 596,0 em Caruru - *Amaranthus retroflexus* Linn. - Amaranthaceae (Greenberg *et al*. 2001); Para *S. cosmioide,* 313,6 em mamona - *Ricinus communis* Linn. - Euphorbiaceae e 380,7 em cebola - *Alliun cepa* Linn. - Liliaceae (Bavaresco *et al*. 2003), e para *S. frugiperda*, 372,2 no algodão (folha), 363,2 (folha e botão floral), 330,5 em milheto (folha), 421,8 em soja (folha) e 501,7 em milho (folha) (Barros *et al*. 2010). Devido à grande variabilidade de hospedeiros (Montezano *et al.* in press), espera-se que, tal como outros representantes do mesmo gênero (Greenberg *et al*. 2001, Bavaresco *et al*. 2003, Barros *et al.* 2010, Farahani *et al.* 2011), a taxa líquida de reprodução (Ro) de *S. eridania* varie muito em função das plantas com valores mais elevados para as espécies preferenciais, tanto cultivadas como invasoras (Parra *et al*. 1977, Valverde & Sarmiento 1987a, Mattana & Foerster 1988, Santos *et al*. 2005, Montezano *et al*. in press).

O tempo médio de geração (T = 35,81 dias) de *S. eridania* foi semelhante ao observado para *S. albula* nas mesmas condições (T = 37,19 dias) e foi acima do máximo descrito para *S. exigua* ~ 31,6, a 26 ºC (Greenberg *et al.* 2001, Farahani *et al.* 2001) e para *S. frugiperda* ~ de 30,8, a 25 ºC (Barros *et al.* 2010). No entanto, foi menor do que o mínimo observado para *S. cosmioides* de ~ 47,2, a 26 ºC (Bavaresco *et al*. 2003).

Os valores da taxa diária intrínseca de crescimento (rm = 0,177) e a razão finita diária de aumento (λ = 1,193) de *S. eridania* foram semelhantes aos valores obtidos para *S. albula* (rm = 0,158; λ = 1,171) nas mesmas condições (Montezano *et al.* In press). Estes valores, relativamente baixos, assemelham-se aos obtidos para *S. cosmioides* (Bavaresco *et al.* 2003) que tem um tempo de geração (T) superior, em comparação com o de *S. exigua* (Greenberg *et al.* 2001; Farahani *et al.* 2011) e *S. frugiperda* (Barros *et al*. 2010).

Os parâmetros calculados para *S. eridania* são semelhantes aos obtidos para *S. albula* nas mesmas condições (Montezano *et al.* 2013) e assemelham-se a alguns dos valores obtidos com certas plantas hospedeiras de *S. cosmioides* (Bavaresco *et al.* 2003), *S. exigua* (Greenberg *et al.* 2001, Farahani *et al.* 2011), e *S. frugiperda* (Barros *et al.* 2010). No entanto, deve-se considerar que existem grandes variações entre os valores para as mesmas espécies, especialmente em função da temperatura, da planta hospedeira ou dieta artificial (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). Além disso, devem ser consideradas variações populacionais, neste sentido Murúa *et al.* (2008) demonstraram enormes variações entre os parâmetros biológicos e reprodutivos entre acasalamentos de *S. frugiperda* de diferentes locais e plantas hospedeiras na Argentina.

Uma análise dos dados deste estudo e do realizado com *S. albula* (Montezano *et al.* 2013a, 2013 in press) indicam a importância de detalhar todos os aspectos da biologia reprodutiva dessas espécies, uma vez que muitos detalhes podem subestimar ou comprometer os dados dos parâmetros reprodutivos e a expressão completa do potencial biótico.

Os resultados indicam também preocupações para a necessidade de uma melhor compreensão dos parâmetros reprodutivos de *S. eridania* no campo, tais como estudos que incluam a coleta de adultos de outras espécies, utilizando armadilhas de luz (Sadek, 2001), a

fim de comparar com os dados obtidos em laboratório para que relações possam ser inferidas com mais confiança.

Os resultados do presente estudo, demonstram que uma redução, ou o atraso, no número de cópulas influenciam negativamente os parâmetros populacionais, indicando a relevância dos estudos de identificação e do uso de feromônios (Jacobson *et al*. 1970, Redfern *et al*. 1971, Mitchell & Doolittle 1976, Teal *et al*. 1985, Mitchell & Tumlinson 1994) para retardar ou evitar o acasalamento de *S. eridania* na natureza, em procedimentos de interrupção de acasalamento (Cardé & Minks 1995), como uma estratégia para o Manejo Integrado desta espécie-praga.

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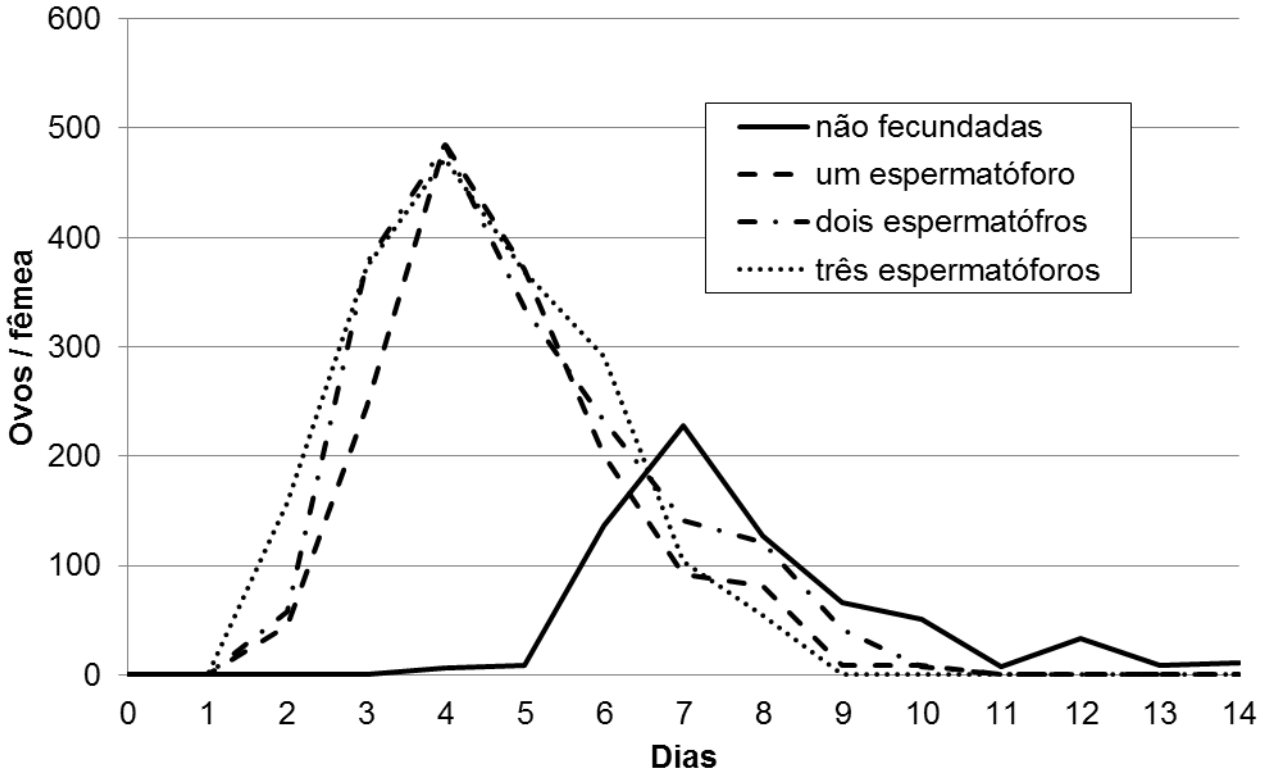

Figura 1. Número médio diário de ovos por fêmea de *Spodoptera eridania*. Fêmeas não fertilizadas (n= 4), com um (n= 6), dois (n= 4) ou três (n= 1) espermatóforos. Um casal por gaiola 25 ± 1°C, 70 ± 10% UR e 14 horas fotofase.

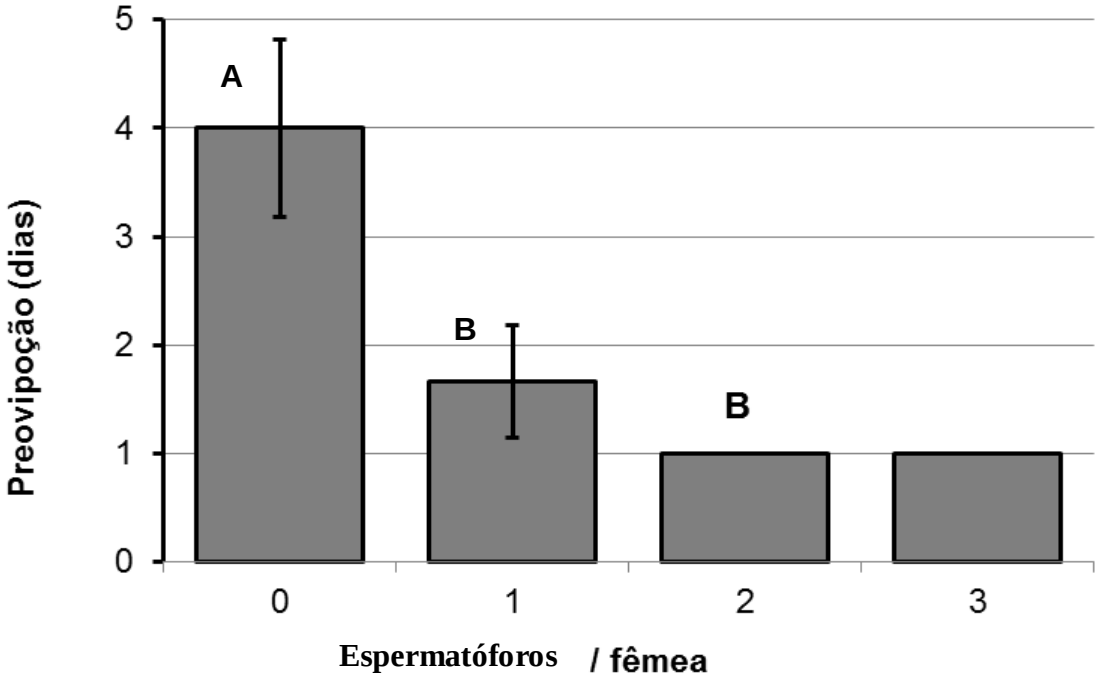

Figura 2. Período de pré-oviposição de *Spodoptera eridania*. Fêmeas não fertilizadas (n= 4), com um (n= 6), dois (n= 4) ou três (n= 1) espermatóforos. Um casal por gaiola 25 ± 1°C, 70 ± 10% UR e 14 horas fotofase. Médias seguidas pela mesma letra não diferem significativamente (Tukey HSD, $P < 0,05$).

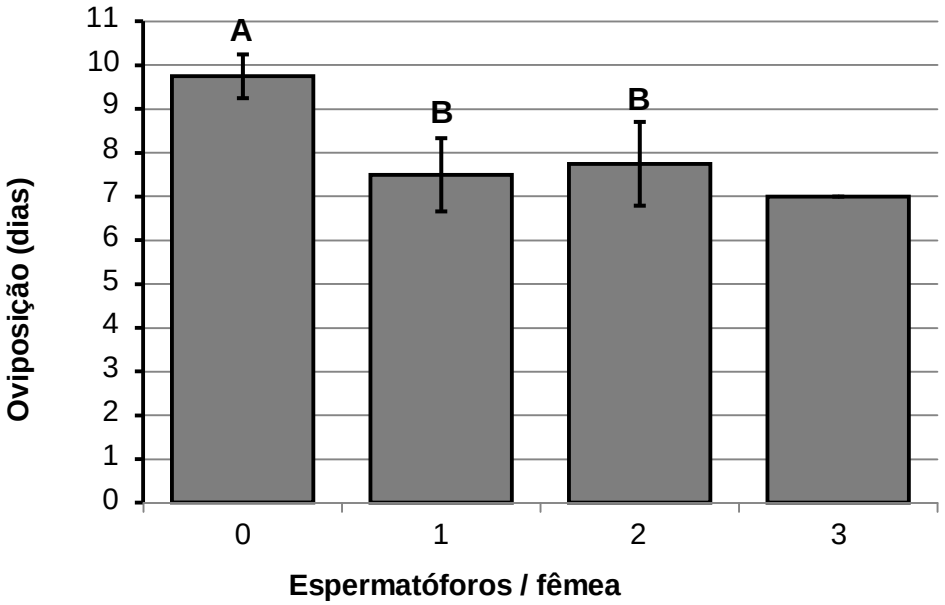

Figura 3 – Período de oviposição de *Spodoptera eridania*, fêmeas não fertilizadas (n= 4), com um (n= 6), dois (n= 4) ou três (n= 1) espermatóforos. Um casal por gaiola 25 ± 1°C, 70 ± 10% UR e 14 horas fotofase. Médias seguidas pela mesma letra não diferem significativamente (Tukey HSD, $P < 0,05$).

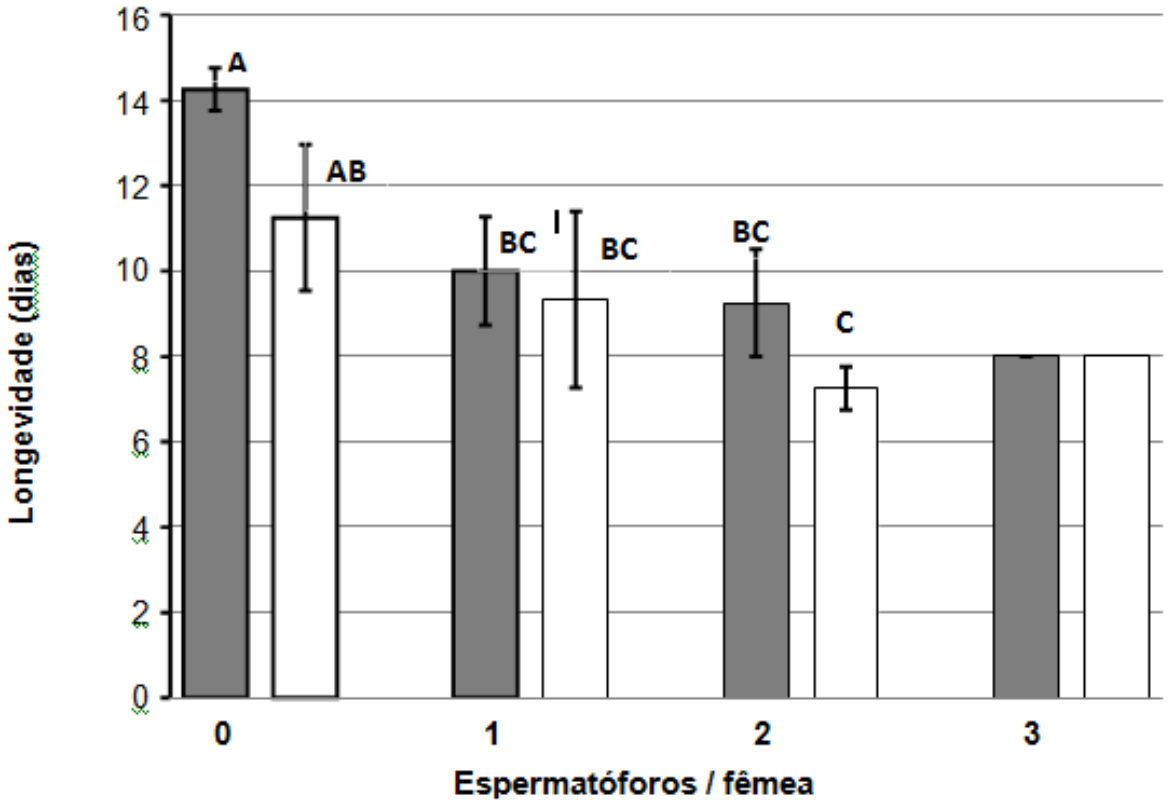

Figura 4. Longevidade de *Spodoptera eridania*. Fêmeas não fertilizadas (barras escuras) e machos (barras vazias). Não fertilizadas (n= 4), com um (n= 6), dois (n = 4) ou três (n= 1) espermatóforos. Um casal por gaiola 25 ± 1°C, 70 ± 10% UR e 14 horas fotofase. Médias seguidas pela mesma letra não diferem significativamente (Tukey HSD, P < 0,05).

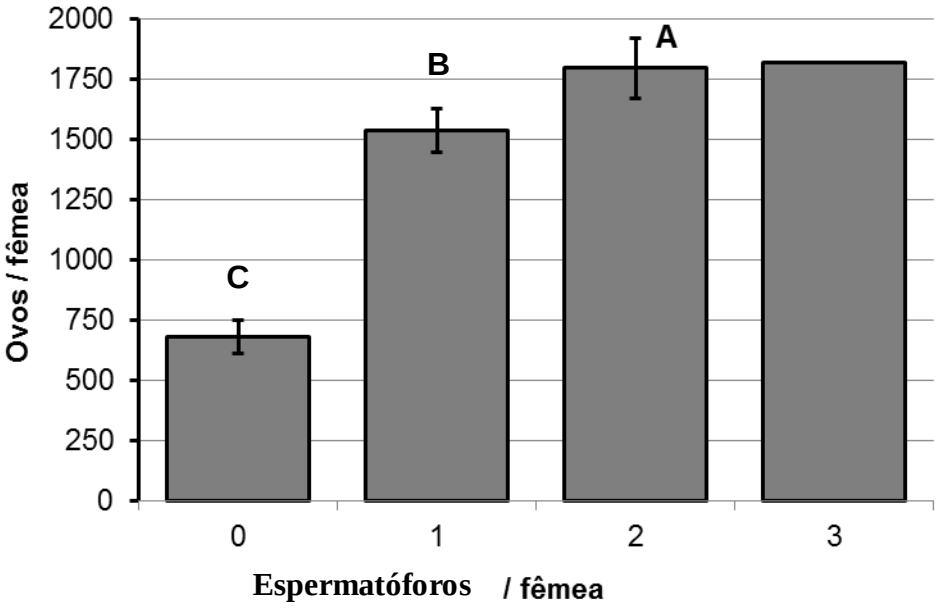

Figura 5. Fecundidade media de *Spodoptera eridania*. Fêmeas não fertilizadas (n= 4), com um (n= 6), dois (n= 4) ou três (n= 1) espermatóforos. Um casal por gaiola 25 ± 1°C, 70 ± 10% UR e 14 horas fotofase. Médias seguidas pela mesma letra não diferem significativamente (Tukey HSD, $P < 0,05$).

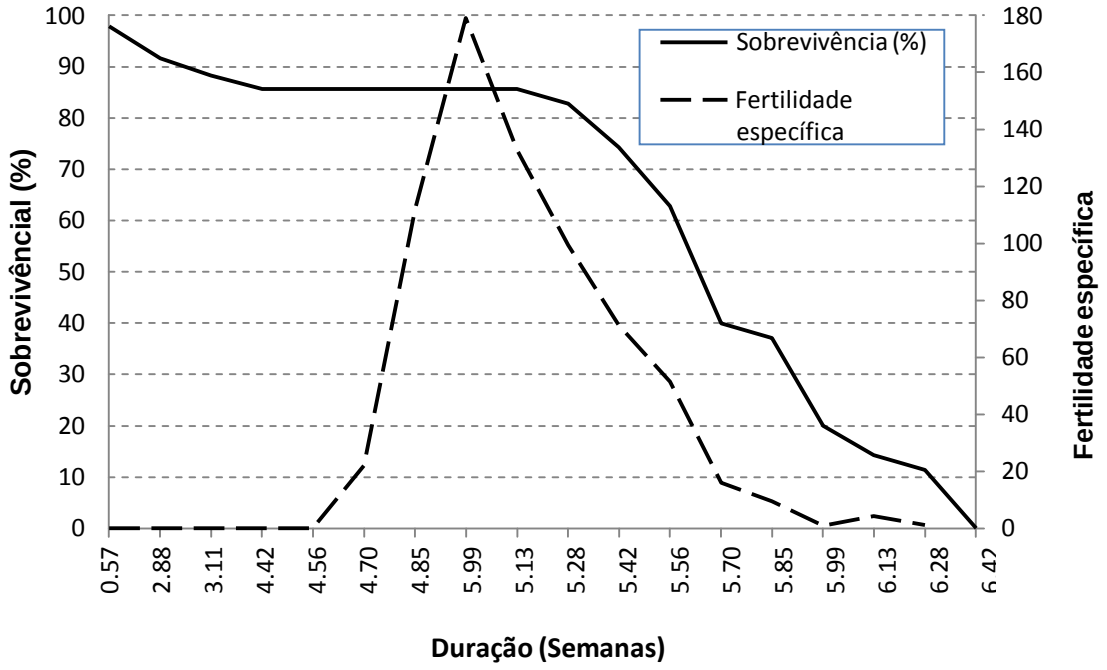

Figura 6. Relação entre fertilidade (mx) e taxa de sobrevivência (lx) de *Spodoptera eridania* criada em dieta artificial a 25 ± 1°C, 70 ± 10% UR e 14 horas de fotofase.

Tabela 1: Longevidade, períodos de pré, pós e oviposição e fecundidade de 15 casais de *Spodoptera eridania*, em condições controladas (25 ± 1°C, 70 ± 10% UR e 14 horas de fotofase).

Sexo	Parâmetro	Média	Desvio padrão	Variação
Ambos	**Longevidade (dias)**	10,033	2,371	6 - 14
Fêmea	**Longevidade (dias)**	10,800	2,426	8 - 14
	Pré - oviposição (dias)	2,067	1.335	1 - 5
	Pos - oviposição (dias)	0,600	0,507	0 - 1
	Oviposição (dias)	8,133	1,246	6 - 10
	Fecundidade (ovos)	1.398,000	470,289	634 - 1900
Macho	**Longevidade (dias)**	9,267	2,120	6 - 13

Comparação entre a longevidade média de fêmeas e machos usando teste *t* de Student, bicaudal, considerando variâncias diferentes, a 95% de significância, revelou p= 0,076.

6. DISCUSSÃO GERAL

A dieta artificial e a metodologia de criação propostas nesse estudo foram satisfatórias para o desenvolvimento de *S. albula* e *S. eridania* em laboratório, proporcionando sobrevivência de mais de 90% das fases imaturas de ambas as espécies. Além disso, permitiu comparações de todas as fases de desenvolvimento.

O fato de a maioria dos espécimes terem se desenvolvido em seis ínstares (87.226% em *S. albula* e 96.56% em *S. eridania*), indica que a dieta supriu as necessidades específicas, de forma semelhante ao observado quando as lagartas foram alimentadas com plantas hospedeiras consideradas adequadas para o desenvolvimento dessas espécies (Mayer & Babers, 1944, Redfern, 1967, Parra *et al*. 1977, Mattana & Foerster, 1988, Santos *et al*. 2005). A porcentagem de indivíduos que passaram por sete instares foi maior nas fêmeas, embora diversos fatores, como temperatura, fotoperíodo, quantidade e qualidade dos alimentos, umidade, entre outros, influenciem no número de instares (Esperk *et al*. 2007). Os resultados deste estudo, indicam que os representantes do sexo feminino de *Spodoptera* são mais propensos a ter um instar adicional, provavelmente devido ao seu maior tamanho.

Foram obtidas informações complementares às constantes no banco de dados sobre as plantas hospedeiras dessas espécies (Pogue, 2012) sendo registradas 55 plantas hospedeiras para *S. albula* e 202 para *S. eridania*. Esses números de plantas hospedeiras relacionam-se ao alto grau de polifagia dessas espécies, já relatado por diversos autores na America do Norte (Chitteneden & Russel, 1909, Crumb, 1929, Soo Hoo & Fraenkel, 1966a, 1966b), America Central (Maes & Tellez Robleto, 1988, Torres, 1992, Coto *et al*. 1995) e América do Sul (Silva *et al*. 1968, Biezanko *et al*. 1974, Pastrana, 2004). Esta polifagia também relaciona-se à versatilidade e a rápida capacidade das espécies deste gênero em se adaptar nas diversas regiões do continente alimentando-se de plantas cultivadas como alfafa, feijão, beterraba,

repolho, mandioca, milho, algodão, batata, batata doce, tomate, (Chittenden & Russel, 1909, Lima, 1928, Crumb, 1929, Marques, 1932, Wolcott, 1936, Hambleton, 1939, Waterston, 1939, Tucker, 1939, Waterston, 1947, Wolcott, 1951, Corseuil, 1955, Olalquiaga, 1955, Costa, 1958, Nickel, 1958, Harris, 1959, Kimball, 1965, González, 1966, McGuire & Crandall, 1967, Silva *et al*. 1968, Cantu & Wolfenbarger, 1970, Creigton *et al.* 1971, Tietz, 1972, Valencia-V & Valdivia-M., 1973, Biezanko *et al*. 1974, Hichings & Rabinovich, 1974, Price & Poe, 1977, Pena & Waldill, 1981, Maes & Tellez Robleto 1988, Ferguson *et al*. 1991, Coto *et al.* 1995, Pastrana, 2004, Specht *et al*. 2004, Bentancourt & Scatoni 2006, Angulo et *al*. 2008).

A longevidade média dos adultos de *S. albula* e *S. eridania* correspondeu a 28.32% e 24,50% respectivamente, ou quase um quarto de seu ciclo de vida. Estes resultados são semelhantes aos de outros estudos envolvendo *S. eridania* (Parra *et al*. 1977, Mattana & Foerster, 1988) e outros representantes de *Spodoptera* (Habib *et al*. 1983, Bavaresco *et al.* 2004, Busato *et al*. 2005). Estes resultados também indicam que a maior longevidade dessas espécies, assim como outras espécies do gênero, que possuem uma grande capacidade de dispersão e até mesmo de migração (Ferguson *et al*. 1991), está relacionada à sua ampla distribuição no continente americano, estendendo-se entre os paralelos 30º de Norte a Sul (Pogue, 2002).

A longevidade dos adultos foi maior em fêmeas tanto para *S. albula* quanto para *S. eridania* e apresentou correlação negativa com o número de cópulas, indicando que essas espécies, de forma similar a outras do gênero como *S. littoralis* (Kehat & Gordon, 1975, Ellis & Steele, 1982), apresentam um prolongamento da longevidade em função da redução do número de cópulas.

Observou-se um prolongamento dos períodos de pré e oviposição das fêmeas que não foram fertilizadas em ambas as espécies, assim como mostrado para *S. littoralis* (Kehat &

Gordon 1975, Ellis e Steele, 1982) e *S. exigua* (Rogers & Marti Jr., 1997) A análise dos resultados, comparando a longevidade em função do número de cópulas, indica que este é um fator importante a ser incluído em análises de longevidade. Esta constatação está relacionada com a interação entre a produção de ovos e o metabolismo (Hou e Sheng, 1999). Estes autores postulam que múltiplas fecundações estimulam a produção de ovos e aceleram o consumo de energia e de material, diminuindo os recursos disponíveis para a manutenção somática. No entanto, a redução do período de postura relacionada com um maior número de cópulas, como descrito por Hou e Sheng (1999) certamente relaciona-se com o aumento da atividade reprodutora nas fêmeas que copularam mais.

Os números médios de cópulas obtidos neste estudo foram similares para *S. albula* (1,23) e *S. eridania* (1,13), e estão dentro da variação descrita para *S. frugiperda* por Murúa *et al*. (2008), que observaram valores muito discordantes entre diferentes populações de *S. frugiperda* na Argentina (0,78 - 2,32 espermatóforos por fêmea).

A fecundidade média de 1.400 ovos por fêmea para ambas as espécies mostrou forte correlação positiva entre com o número de cópulas, e quando comparado com outros estudos com as mesmas espécies apresentou valores elevados (Alcaraz-Vieco, 1962, La Rosa *et al.* 1992, Novo Padrino & Martínez Reyes 1985, Parra *et al.* 1977, Santos *et al.* 2005) e também bastante variação comparado com demais trabalhos para espécies do mesmo gênero (Habib *et al*. 1983, Bavaresco *et al*. 2003, 2004, Mattana & Foerster 1988, Santos *et al.* 2005, Greenberg *et al*. 2001, Tisdale & Sappington, 2001, Farahani *et al*. 2011, Santos *et al.*2004, Busato *et al.*2005, Barros *et al.* 2010, Xue *et al.*2010). Essas diferenças podem ser atribuídas a muitos fatores (Giolo *et al.* 2002, Murúa & Virla 2004, Sadek & Anderson 2007, Busato *et al.* 2008, Murúa *et al.* 2008), no entanto, a alta fecundidade obtida no presente estudo indica que a dieta e a metodologia de criação dos imaturos e dos adultos foram adequados para o desenvolvimento das espécies em laboratório. Estes resultados ressaltam a importância de que

em estudos futuros sejam indicados o número de cópulas (ou pelo menos se as fêmeas foram fecundadas ou não).

O potencial biótico de *S. albula* e *S. eridania* foi estimado em 8,768 x 10^{22} e 1.894 x 10^{25} indivíduos/fêmea/ano respectivamente. A taxa máxima de aumento da população dessas espécies está relativamente deslocada para o início da fase adulta, especialmente impulsionado pela maior fecundidade e baixa mortalidade de imaturos logo após a emergência. Estas observações também são similares às observadas em outros estudos realizados com representantes de *Spodoptera* onde os valores mais elevados de fecundidade são observados durante os primeiros dias, a partir do segundo ou terceiro até o sétimo (Kehat & Gordon, 1975, Sadek, 2001, Bavaresco *et al*. 2004, Murúa & Virla, 2004).

Este estudo iniciou com a descrição da biologia de *S. albula* e *S. eridania*, duas espécies que compartilham muitas caracteríscas (Pogue, 2002) que foram comprovadas com a aplicação da metodologia de estudo proposta.

Uma análise dos dados deste estudo indica a importância de detalhar todos os aspectos da biologia reprodutiva dessas espécies, uma vez que muitos detalhes podem subestimar ou comprometer os dados dos parâmetros reprodutivos e a expressão completa do potencial biótico.

A metodologia deste estudo, com mais detalhes do que as existentes na bibliografia, permite realizar experimentos com parâmetros passíveis de repetição fornecendo dados mais precisos a estudos que necessitem os dados da biologia dessas espécies, como testes com novos produtos químicos, estudos com feromônios, estudos genéticos entre outros.

7. CONCLUSÕES

7.1 A análise dos de dados de biologia indicam a importância de detalhar todos os aspectos reprodutivos das espécies pertencentes a *Spodoptera*, uma vez que muitos detalhes podem subestimar ou comprometer os dados dos parâmetros reprodutivos e a expressão completa do potencial biótico.

7.2 A metodologia proposta no presente estudo, permite um detalhamento dos vários parâmetros biológicos de *S. albula e S. eridania* com o mínimo de interferência no seu desenvolvimento. Isto permitiu realizar várias observações desconhecidas, como a duração e a sobrevivência de lagartas considerando o sexo.

7.3 Os resultados indicam a importância de uma melhor compreensão dos parâmetros reprodutivos dessas espécies no campo, tais como estudos que incluam a coleta de adultos, utilizando armadilhas luminosas a fim de comparar com os dados obtidos em laboratório para que relações possam ser inferidas com mais confiança.

7.4 Nos estudos relacionados ao potencial reprodutivo, especialmente relacionados a duração, fecundidade e fertilidade, deve-se ter o cuidado de verificar se efetivamente as fêmeas foram fecundadas, caso contrário os resultados podem ser subestimados.

7.5 A redução, ou o atraso, no número de cópulas influenciam negativamente os parâmetros populacionais.

8. PERSPECTIVAS

8.1 Aplicar a metologia e dieta de criação para os demais representantes do gênero que ocorrem no país visando comparar efetivamente diferenças específicas em condições idênticas;

8.2 Utilizar esta metodologia de criação para obtenção de indivíduos de diferentes espécies e biótipos de *Spodoptera* visando a comparação intra e interespecífica de feromônios;

8.3 Desenvolver estudo visando determinar a capacidade máxima reprodutiva de pelo menos uma espécie comparando a presença de um casal e de mais de um casal por gaiolas para aumentar o número de cópulas;

8.4 Desenvolver estudos para comparar o efeito do tamanho dos adultos na fecundidade, empregando como parâmetro o peso pupal;

8.5 Desenvolver estudos de identificação e de uso de feromônios para retardar ou evitar os acasalamentos na natureza, em procedimentos de interrupção de acasalamento, como uma estratégia para o Manejo Integrado destas espécies-praga;

8.6 Realizar complementação de estudos já descritos na literatura sobre a biologia de outras espécies com a finalidade de padronização dos dados.

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