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Biology of *Spodoptera eridania* and *Spodoptera cosmioides* (Lepidoptera: Noctuidae) on different host plants

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Abstract

The moths *Spodoptera eridania* (Stoll) and *Spodoptera cosmioides* (Walker) are pests of increasing importance in various grain production systems, causing defoliation and damage to reproductive structures of plants. This fact underscores the need for studies that analyze the nutrition and development of pests on different hosts. The objective of this study was to evaluate the development of *S. eridania* and *S. cosmioides* feeding on different host species. To this end, newly hatched larvae were separated individually into waxed cups and fed soybean, cotton, maize, wheat, oat leaves, or an artificial diet as control. The evaluated parameters were: duration of larval, pre-pupal, and pupal development (days), pupal weight (g), sex ratio (%), larvae-adult survival (%), oviposition preference, larval feeding performance, and weight gain on different hosts. Soybean and cotton were found to be more suitable hosts for development and oviposition of *S. eridania* and *S. cosmioides* than oat, wheat, and maize, all of which negatively affected larval development and survival. The maize cultivar 'DKB 390' did not allow for larvae to develop to adults and therefore proved to be inadequate for both studied *Spodoptera* species.

Key Words: insect-plant interactions; food preference; oviposition preference; feeding behavior; host susceptibility; polyphagous pest adaptation

Resumen

Spodoptera eridania (Stoll) y *Spodoptera cosmioides* (Walker) son plagas de creciente importancia en diferentes sistemas de producción de granos, causan daños a las estructuras reproductivas de las plantas y defoliación. Esto realza la necesidad de estudios que evalúen su desarrollo y nutrición en diferentes huéspedes. El objetivo de este trabajo fue evaluar el desarrollo de *S. eridania* y *S. cosmioides* alimentándose de diferentes plantas huéspedes y de dieta artificial. Larvas recién nacidas se separaron individualmente en vasos de cartón encerados y se alimentaron con folíolos de soja, algodón, maíz, trigo, avena, o con dieta artificial. Los parámetros evaluados fueron: duración (días) de las fases larval, de prepupas y pupas, peso de pupas (g), proporción de sexos (%), supervivencia de larva a adulto (%), preferencia de oviposición, rendimiento nutricional de las larvas y aumento de peso en diferentes huéspedes. Los substratos soja y algodón fueron mejores huéspedes que avena, trigo y maíz para el desarrollo y oviposición de *S. eridania* y *S. cosmioides*. La alimentación sobre gramíneas afectó negativamente el desarrollo larval y la supervivencia. El maíz 'DKB 390' no permitió la formación de adultos, y este cultivar resultó ser inadecuado para ambas especies de *Spodoptera*.

Palabras Clave: interacciones planta-insecto; preferencia alimentaria; preferencia de oviposición; comportamiento alimentario; susceptibilidad del huésped; adaptación de plagas poligáceas

Introduction

Agriculture has intensified worldwide. Some areas, mainly in the tropics, allow for the completion of more than 1 crop cycle per year. Continuous land use with successive crops throughout the year can lead to a 'green bridge' (Pedigo 2002), i.e., it can increase the availability of green plants throughout the year and facilitate the persistence of pests in agricultural areas (Bueno et al. 2012). The increase in food sources available to insects also encourages pest outbreaks, allowing polyphagous insect species once considered secondary pests to gain greater economic significance and become key pests of various agroecosystems (Pedigo 2002).

Food quality plays an important role for herbivore insects because their foraging strategies are ultimately aimed at optimizing the correct blend and balance of nutrients. Therefore, understanding the diversity of insect responses to different host species represents a key challenge for the development of durable pest control strategies (Karowe & Martin 1989; Després et al. 2007; Hemati et al. 2012; Cabezas et al. 2013; Kianpour et al. 2014.). In this context, it is important to point out that the polyphagous nature of some insects contributes to their rapid adaptation to different agroecosystems (Barros et al. 2010; Bortolotto et al. 2014). The management of polyphagous and mobile pests requires pest management systems that focus not only on 1 major seasonal crop on a single field or farm, but also on wide-area cropping systems (Abel

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et al. 2007; Wu 2007; Herde 2009). The availability of nearby crops as food sources and crop rotation sequences play important roles in population dynamics and outbreaks of polyphagous herbivores. Therefore, the identification of insect feeding preferences, biology, and behavior is crucial in order to find economically and ecologically sustainable solutions to the problems caused by these herbivores (Behmer 2009).

The genus *Spodoptera* includes pest species with increased economic importance in the intensive agriculture of tropical areas such as Brazil (Bueno et al. 2010). The moths *Spodoptera eridania* (Stoll) and *Spodoptera cosmioides* (Walker) (Lepidoptera: Noctuidae) are 2 species important in this context. They have a very broad host range, including crops such as soybean (*Glycine max* [L.] Merrill [Fabaceae]), cotton (*Gossypium hirsutum* L. [Malvaceae]), and maize (*Zea mays* L. [Poaceae]) (Michereff-Filho et al. 2008; Santos et al. 2010). The polyphagy of these pest species may contribute to their rapid adaptation to different agroecosystems and landscape modifications. They also have the capacity to produce successive generations throughout the year, which emphasizes their relevance for integrated pest management (IPM).

Spodoptera cosmioides, previously considered a synonym of the North and Central American species *Spodoptera latifascia* (Walker) (Lepidoptera: Noctuidae), is now known to be a separate species restricted to South America (Silvain & Lalanne-Cassou 1997) threatening more than 24 species of crop plants (Cabezas et al. 2013). It occurs both on cultivated plants and weeds and can severely reduce the yield in various crops of economic importance (Habib et al. 1983).

Both *S. eridania* and *S. cosmioides* are recognized as key pests in Brazil (Bueno et al. 2011) with a high tolerance to the Cry1Ac protein, which is expressed in some Bt crops (Bernardi et al. 2014). Larvae are defoliators and feed gregariously between the first and third instars, often skeletonizing leaves. As they mature, they become solitary and may injure reproductive tissues and fruit, such as soybean pods and cotton bolls. When stressed by a lack of food, they will eat the apical parts of branches, bore into stem tissues, and attack plant roots that are near the soil surface (Redfern 1967; Bavaresco et al. 2004; Santos et al. 2005). The occurrence of both pests, which cause defoliation and significant yield reduction in soybean and cotton crops, recently has been reported in Brazil (Quintela et al. 2007; Bueno et al. 2011).

Despite the increasing importance of *S. eridania* and *S. cosmioides*, basic information about their biology, including host adaptation, is scarce (Scriber & Slansky 1981). However, in order to establish pest management strategies it is crucial to understand survival, population dynamics, and infestation of these species throughout the year. These traits, including their migration patterns, contribute to changes in the population dynamics of *S. eridania* and *S. cosmioides* in agricultural landscapes (Tisdale & Sappington 2001).

The management of *S. eridania* and *S. cosmioides* relies on understanding their host use within and between crop seasons. Consequently, in addition to studies on host preferences, basic biological studies on their use of different food sources are important for assessing the effects of the nutritional composition of different crops on these pests (Scriber & Slansky 1981; Sarfraz et al. 2007; Barros et al. 2010). In this work we studied the development of *S. eridania* and *S. cosmioides* using different food sources under laboratory conditions including hosts cultivated in summer such as soybean, cotton, and maize as well as hosts cultivated in fall and winter such as maize, wheat (*Triticum aestivum* L. [Poaceae]), and oat (*Avena strigosa* Schreb. [Poaceae]). An artificial diet (Greene et al. 1976) was used as control treatment. We also studied oviposition preference of adults in the field. To the best of our knowledge, this is the first study in which different life history traits of *S. eridania* and *S. cosmioides* are compared when fed on hosts grown in different seasons. The results of our study help to improve our knowledge on the susceptibility of several important crops in Brazilian agriculture to these pests.

Materials and Methods

We evaluated how different host plants (soybean, cotton, maize, wheat, and oat) affect the biology of *S. eridania* and *S. cosmioides* in order to better understand host susceptibility to these pests. Host plants used in our trials were soybean ('BRS 284'), cotton ('FMT 701'), maize ('DKB390'), wheat ('BRS Pardela'), and oat ('Embrapa 139'). These representative cultivars are planted during summer, fall, and winter seasons in southern and west-central Brazil.

SPODOPTERA ERIDANIA AND *SPODOPTERA COSMIOIDES* COLONIES

Spodoptera eridania and *S. cosmioides* specimens were obtained from insect colonies maintained at Embrapa Soybean, Londrina, State of Paraná, Brazil. Both species were originally collected in 2010 from soybean plants growing in the State of Goiás, and maintained in the laboratory for approximately 32 generations. New field insects were introduced on a yearly basis to maintain insect quality. Perkins (1979) reported successful rearing of *Spodoptera frugiperda* (Smith 2005) (Lepidoptera: Noctuidae) in the laboratory for more than 18 years without any indication of degeneration. Both species were reared under laboratory-controlled conditions (25 ± 2 °C, 70 ± 10% RH, photoperiod of 14:10 h L:D) and fed on an artificial diet (Greene et al. 1976).

DEVELOPMENT OF *SPODOPTERA ERIDANIA* AND *SPODOPTERA COSMIOIDES* ON DIFFERENT FOOD SOURCES

This experiment was conducted separately for each species in a Biochemical Oxygen Demand climate chamber (ELETROLab®, model EL 212, São Paulo, São Paulo, Brazil) under controlled laboratory conditions (25 ± 2 °C, 70 ± 10% RH, photoperiod of 14:10 h L:D) using a randomized block design with 6 treatments (5 crop plants plus the artificial diet) and 6 replicates. Each replicate contained 10 individual larvae (a total of 60 larvae per treatment). The different shelves of the climate chamber were considered as blocks in order to control for a possible temperature gradient. Host plants were grown in the greenhouse in pots (capacity 20 L) filled with soil up to 15 cm from the top, sown at a density of 5 plants per pot.

Trials were initiated when plants had 8 to 10 completely expanded leaves. Then, on a daily basis, 1 leaf from the top was removed from each plant. Leaf positioning varied from the first to the third completely expanded leaf depending on leaf availability. Then, plant leaves were cleaned by immersion in 0.1% sodium hypochlorite, and rinsed in distilled water for 3 to 5 s. Excess water was removed with paper towels before offering the leaves to the experimental insects. The artificial diet (8 g per replicate) was replaced daily to avoid dehydration.

Initially, eggs of *S. eridania* and *S. cosmioides* were isolated into waxed cups containing different food sources. Temperature, humidity, and photoperiod were controlled until hatching. After that, first instar larvae were individualized in new, waxed cups with plant leaves, which were replaced on a daily basis to avoid excessive water loss. The insects were maintained in the same climate chamber (25 ± 2 °C, 70 ± 10% RH, photoperiod of 14:10 h L:D) for daily assessment of the following biological traits: duration (days) of larval period (first to sixth instar), pre-pupal period (nonfeeding stage between the larval and pupal period), pupal period, larva-adult period (total period from the hatching of larvae to the emergence of adults), pupal weight (g) measured 24 h after pupation, larvae-adult survival (%), and sex ratio.

The results were subjected to exploratory analysis to test for normality and independence of the residuals (Shapiro & Wilk 1965), homogeneity of variance of errors in the treatments (Burr & Foster 1972),

and non-additivity of the model (Tukey 1949). Where necessary, data were transformed in order to meet the assumptions of the analysis of variance (ANOVA) (SAS Institute 2009). Thus, sex ratio was transformed by $\sqrt{X + 0.5}$. Treatment means were compared using Tukey's test ($P \leq 0.05$) with the SAS statistical analysis program (SAS Institute 2009).

OVIPOSITION PREFERENCE OF *SPODOPTERA ERIDANIA* AND *SPODOPTERA COSMIOIDES* ON DIFFERENT HOSTS

Two experiments (no-choice and free-choice tests) for each pest species were conducted to evaluate oviposition preferences of *S. eridania* and *S. cosmioides* adults between soybean, cotton, maize, wheat, and oat in the field without environmental control. Host plants were grown in pots (capacity 20 L) filled with soil up to 15 cm from the top, sown at a density of 5 plants per pot. Plants were used in the trials when they had 8 to 10 completely expanded leaves. The experiments were performed inside screened cages (5 × 4 × 2.5 m, length, width, and height) in a randomized block design, with 5 treatments (soybean 'BRS 284', cotton 'FMT 701', maize 'DKB390', wheat 'BRS Pardela', and oat 'Embrapa 139') and 5 replicates.

In the no-choice test, each replicate was a screened cage with 50 pots (250 plants) of the same host. A total of 25 screened cages were used in the trial (5 blocks and 5 hosts). In the free-choice test each replicate consisted of 10 pots with 5 plants each (50 plants of each host) that were arranged at a distance of 15 cm between pots, at equal distance to the other host plants inside the same screened cage (1 block with 250 plants, 50 plants of each host). A total of 5 screened cages (5 blocks) were used in the trial.

For all experiments, the moths were reared in the laboratory on an artificial diet (Greene et al. 1976) until reaching the adult stage. After the start of oviposition in the laboratory (age 3 d), the moths were released into the cages at the beginning of the scotophase at a density of 100 pairs (100 males and 100 females) per cage and maintained for 3 d for egg-deposition on the plants. All detected egg masses were removed 72 h after the release of the moths and taken to the laboratory, where the number of eggs and egg position on the plant (bottom, middle, and upper sector of the canopy) were evaluated. Canopy sectors were identified by measuring plants of each species and equally dividing them into 3 parts. Therefore, the size of each part is different for each host species. Even though some of the host species might be small at the time of oviposition, canopy division data is able to provide further insight into this biological parameter. Understanding the oviposition preference for each part of the plant canopy is important for growers to help them find eggs in the field. This is crucial to forecast pest outbreaks as well as to devise necessary biological control strategies such as the release of egg parasitoids.

The total number of eggs on each host and the number of eggs in each section of the plant canopy per host were submitted to exploratory analysis to test for normality and independence of the residuals (Shapiro & Wilk 1965), homogeneity of variance of the errors of the treatments (Burr & Foster 1972), and the non-additivity of the model (Tukey 1949) in order to apply ANOVA (SAS Institute 2009). Treatment means were compared between hosts for the whole plant (total of eggs) as well as plant canopy section by Tukey's test ($P \leq 0.05$) using the SAS statistical analysis program (SAS Institute 2009).

FEEDING PERFORMANCE AND WEIGHT GAIN OF *SPODOPTERA ERIDANIA* AND *SPODOPTERA COSMIOIDES* ON DIFFERENT FOOD SOURCES

The experiment was repeated for each pest species and conducted in the same chamber and environmental conditions as the experiment on *S. eridania* and *S. cosmioides* development on different food sources. It had a completely randomized design with 30 replicates for each host plant. Plants were cultivated in the greenhouse and their leaves removed and cleaned in 0.1% sodium hypochlorite to eliminate any possible contamination, as described for the previous experiment. First, *S. eridania* and *S. cosmioides* larvae were maintained on leaves of the 5 different hosts until the third larval instar, determined by head capsule morphology. We used an artificial diet (Greene et al. 1976) as control. After reaching the third larval instar, 30 insects were weighed to obtain their initial weight, individually isolated in waxed cups and placed under the same laboratory conditions as before. The provided food (host leaves) was weighed daily on an analytical balance (Shimadzu®, model AUY220, Shimadzu do Brasil, Barueri, São Paulo, Brazil) accurate to 0.0001 grams. Any food remaining, as well as feces were removed and stored. Finally, after reaching the sixth instar, larvae were weighed, killed by freezing, and subsequently dried in an oven. The remaining food and feces were maintained at 55 to 60 °C for 72 h until a constant weight indicated complete dehydration.

The evaluated variables were: initial weight of the third larval instar (mg), final weight of the sixth larval instar (mg), food consumed (mg), weight of feces (mg) and feeding time (d). At the same time, fresh and dry weights of 10 larvae were recorded to obtain the correction factor for initial dry weight, which was calculated from the average dry weight divided by the average fresh weight, and multiplied by all the initial fresh weights of the larvae used in the experiment. The water loss of the hosts was calculated similarly to the water loss of the larvae. All weight values were converted to dry weight values for analysis.

Initial weight of larvae (mg), final weight of larvae (mg), food consumed (mg), weight of feces (mg), feeding time (d), and digested food were submitted to exploratory analysis separately for each species to test for normality and independence of the residuals (Shapiro & Wilk 1965), homogeneity of variance of the errors of the treatments (Burr & Foster 1972), and non-additivity of the model (Tukey 1949) in order to apply ANOVA (SAS Institute 2009). Treatment means were compared using Tukey's test ($P \leq 0.05$) with the SAS statistical analysis program (SAS Institute 2009).

Results

DEVELOPMENT OF *SPODOPTERA ERIDANIA* AND *SPODOPTERA COSMIOIDES* ON DIFFERENT FOOD SOURCES

Larval, pre-pupal, pupal and larval-adult development times of *S. eridania* were similar when fed on soybean, cotton, oat leaves, or on an artificial diet. Wheat and maize leaves did not permit development of *S. eridania*, resulting in 100% mortality (Table 1).

Larval, pre-pupal, and pupal development times of *S. cosmioides* were shortest when fed on maize leaves. Soybean and cotton leaves allowed faster total larvae-adult development time than maize, oat leaves, and the artificial diet. Wheat leaves did not allow for the development of *S. cosmioides*, resulting in 100% mortality. Maize leaves allowed for only 1.7% of larvae-adult survival (Table 1). Pupal weight of *S. eridania* and *S. cosmioides* was higher for larvae fed on soybean and cotton leaves, as well as on the artificial diet. The lowest value was observed for larvae fed on oat leaves (Table 1).

Spodoptera eridania had the highest larvae-adult survival rate when fed on soybean or cotton leaves (45.5% and 40.0%, respectively) and the lowest rate when fed on the artificial diet or oat leaves (21.7% and 5.0%, respectively). Similar results were observed for *S. cosmioides*, in which the larva-adult survival rate was highest when fed on soybean or cotton leaves (76.7% and 78.3%, respectively) and lowest when fed on the artificial diet or oat leaves (45.0% and 40.0%, respectively) (Table 1).

Table 1. Biological characteristics (mean ± SD) of *Spodoptera eridania* and *Spodoptera cosmioides* fed on different food sources.

S. eridania							
	Duration (days)						
Treatment	Larva[a]	Pre-pupa[a]	Pupa[a]	Larvae-Adult[a,b]	Pupal weight (g)[a]	Larvae - adult survival (%)[a]	Sex ratio (%)[a,c]
Soybean	23.7 ± 2.5[ns]	1.5 ± 0.1[ns]	11.8 ± 0.5[ns]	36.3 ± 2.5[ns]	0.25 ± 0.02a	45.5 ± 6.6a	0.52 ± 0.02[ns]
Cotton	22.8 ± 1.9	1.9 ± 0.2	10.9 ± 0.2	33.6 ± 1.5	0.20 ± 0.00a	40.0 ± 13.2a	0.49 ± 0.07
Diet[d]	22.1 ± 1.7	2.0 ± 0.1	8.9 ± 0.6	33.0 ± 1.7	0.25 ± 0.02a	21.7 ± 1.7b	0.48 ± 0.09
Oat	22.8 ± 1.1	1.6 ± 0.2	10.3 ± 1.3	33.5 ± 1.1	0.10 ± 0.00b	5.0 ± 3.4c	—[f]
Wheat	—[e]	—[e]	—[e]	—[e]	—[e]	—[e]	—[e]
Maize	—[e]	—[e]	—[e]	—[e]	—[e]	—[e]	—[e]
p-value	0.9423	0.1313	0.1060	0.6343	<0.0001	<0.0001	0.0170
R^2	0.2899	0.5354	0.5371	0.4106	0.7718	0.8746	0.5243
S. cosmioides							
	Duration (days)						
Treatment	Larva[a]	Pre-pupa[a]	Pupa[a]	Larva-Adult[a,b]	Pupal weight (g)[a]	Larva - adult survival (%)[a]	Sex ratio (%)[a,c]
Soybean	18.9 ± 0.6c	2.2 ± 0.3a	12.3 ± 0.2a	33.5 ± 0.9c	0.37 ± 0.02b	76.7 ± 7.6a	0.64 ± 0.11[ns]
Cotton	20.4 ± 0.7bc	2.2 ± 0.2a	12.59 ± 0.2a	35.2 ± 0.9bc	0.46 ± 0.01ab	78.3 ± 3.1a	0.53 ± 0.08
Diet[d]	23.2 ± 0.9bc	2.4 ± 0.1a	12.4 ± 0.7a	38.0 ± 1.2ab	0.54 ± 0.02a	45.0 ± 7.2b	0.37 ± 0.15
Oat	25.0 ± 0.6b	2.0 ± 0.0a	12.6 ± 0.1a	39.6 ± 0.5ab	0.24 ± 0.00c	40.0 ± 5.8b	0.62 ± 0.11
Wheat	—[e]	—[e]	—[e]	—[e]	—[e]	—[e]	—[e]
Maize	31.3 ± 0.0a	1.0 ± 0.0b	10.0 ± 0.0b	42.3 ± 0.0a	0.20 ± 0.00c	1.7 ± 1.7c	—[f]
p-value	<0.0001	0.0282	0.0227	0.0011	<0.0001	<0.0001	0.2507
R^2	0.8154	0.6076	0.5614	0.7052	0.9403	0.9076	0.5205

[a]Means (±SE) followed by the same letter in the columns for each species did not differ statistically (Tukey test, $p \leq 0.05$). [b]Larvae-Adult period comprises the entire juvenile period (larvae + pre-pupae + pupa). [c]Statistical analysis performed on transformed data ($\sqrt{X + 0.5}$). [d]Artificial diet (Greene et al. 1976). [e]There were no survivors. [f]There was no emergence of adults from the pupae (no survivors). [ns]Not significant.

OVIPOSITION PREFERENCE OF *SPODOPTERA ERIDANIA* AND *SPODOPTERA COSMIOIDES* ON DIFFERENT HOSTS

In the no-choice preference experiment (Fig. 1a, b), the highest number of *S. eridania* eggs when considering the whole plant was found on soybean followed by cotton (Fig. 1b). The number of eggs found in the bottom and middle sectors of the canopy was highest for soybean (Fig. 1a). Regarding the upper canopy, the highest number of eggs was found on cotton (Fig. 1a). The lowest number of eggs, both on the entire plant (Fig. 1b) and by canopy section was found on maize (Fig. 1a).

Oviposition preference of *S. eridania* in the free-choice test (Fig. 1c, d) was highest for cotton and soybean, with the highest number of eggs deposited in the bottom section of the canopy (Fig. 1c). In the middle and upper canopy sections, the highest number of eggs was found on soybean (Fig. 1c). With regard to the whole plant, soybean hosted the highest number of eggs, while there was little difference between the numbers of eggs found on the other host plants (Fig. 1d).

In the no-choice preference test the number of *S. cosmioides* eggs found at the bottom and middle sectors of the canopy was highest for cotton (Fig. 2a, b). In the upper canopy, the highest number of eggs was found on oat (Fig. 2a). Similar observations were made for *S. eridania.* The lowest number of eggs was found on maize, both regarding the whole plant (Fig. 2b) and the 3 canopy sectors (Fig. 2a). With regard to the whole plant (Fig. 2b), the highest number of eggs was found on cotton followed by soybean and oat (Fig. 2b).

In the free-choice preference test (Fig. 2c, d), the number of *S. cosmioides* eggs found at the bottom of the canopy was higher for cotton and soybean plants than for the other hosts (Fig. 2c). In the middle sector of the canopy, the numbers of eggs were similar for all hosts, with the exception of maize, which had the lowest values (Fig. 2c). The highest number of eggs on cotton, soybean and wheat were found in the upper sector of the canopy. Regarding whole plants, maize had the lowest number of eggs (Fig. 2c). The highest total numbers of eggs (Fig. 2d) were observed for cotton and soybean.

FEEDING PERFORMANCE AND WEIGHT GAIN OF *SPODOPTERA ERIDANIA* AND *SPODOPTERA COSMIOIDES* ON DIFFERENT FOOD SOURCES08

For *S. eridania*, results differed for the initial weight of the third larval instar, final weight of the sixth larval instar, amount of food consumed, feces weight, and digested food (Table 2). Wheat, oat, and maize were not included in the analysis due to insect mortality rates of 100%. Larvae fed on cotton and the artificial diet had the highest values for consumption, feces weight, and digested food. The highest larval weights were observed under the artificial diet (Table 2). Initial weight of third instar larvae was highest when fed on soybean (Table 2).

Similar results were obtained for *S. cosmioides*. Results differed in final weight of sixth instar larvae, amount of food consumed, feces weight, feeding time, and digested food (Table 2). Larvae feeding on

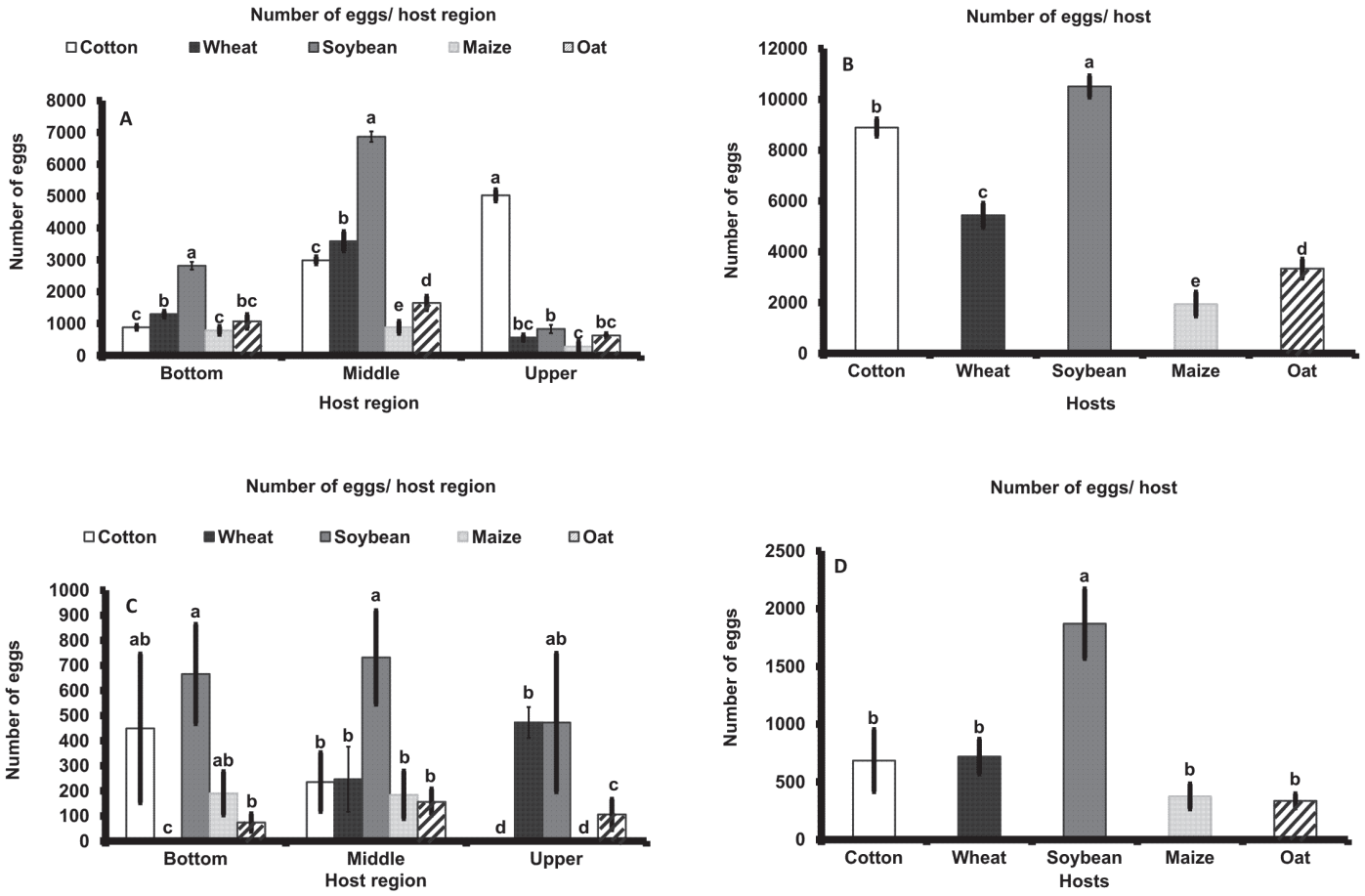

Fig. 1. Number of eggs (mean ± SE) of *Spodoptera eridania* on different sectors of the host canopy (**a** and **c**) and host species (**b** and **d**) in no-choice (**a** and **b**) and free-choice (**c** and **d**) tests. Means followed by the same letter did not differ between canopy sectors (bottom, middle, and upper) or different hosts (Tukey's HSD test, $p \leq 0.05$).

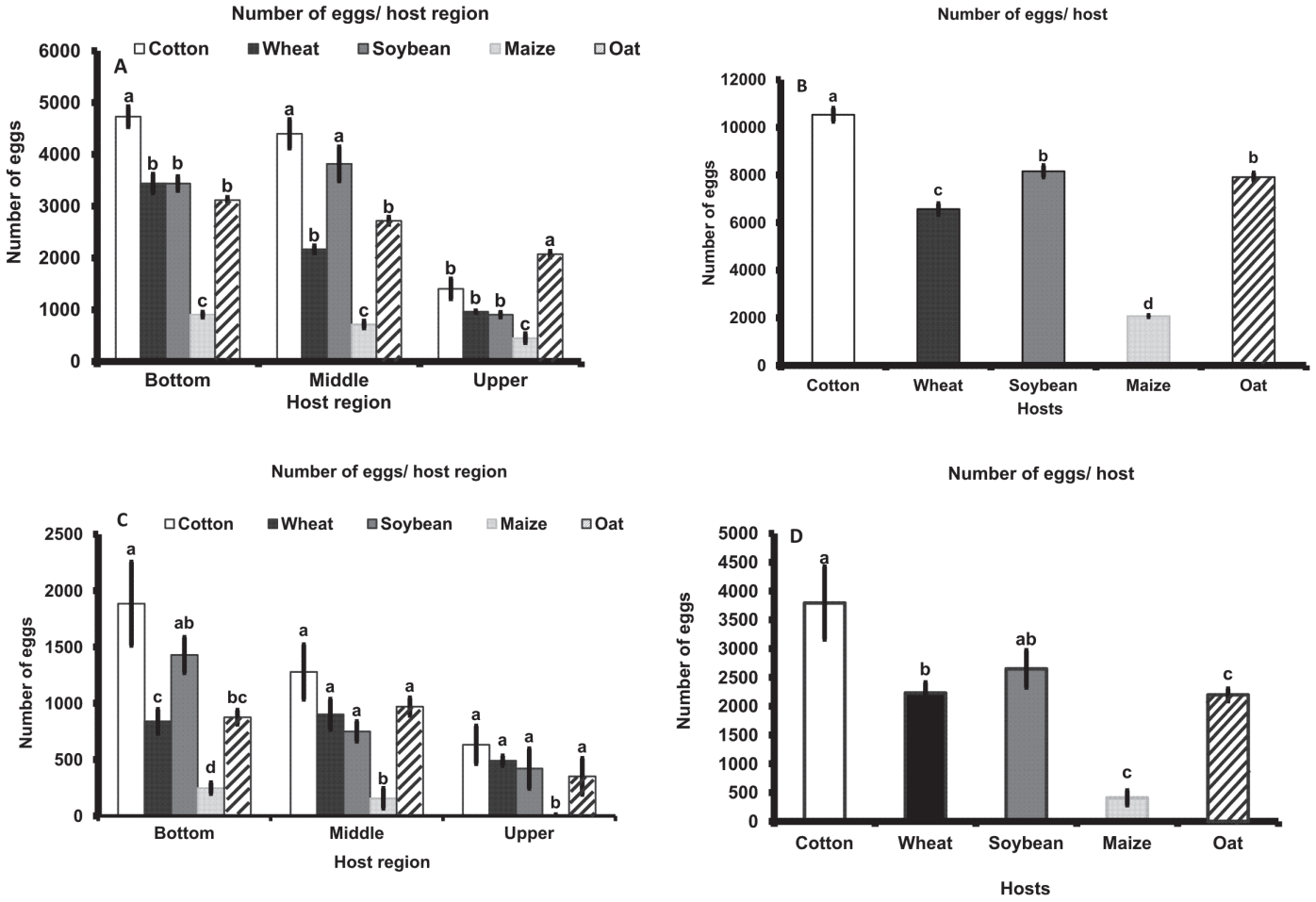

Fig. 2. Number of eggs (mean ± SE) of *Spodoptera cosmioides* on different sectors of the host canopy (**a** and **c**) and host species (**b** and **d**) in no-choice (**a** and **b**) and free-choice (**c** and **d**) tests. Means followed by the same letter did not differ between canopy sectors (bottom, middle, and upper) or different hosts (Tukey's HSD test, $p \leq 0.05$).

wheat, oat, and maize was not included in the analysis because of the low insect survival rates. Larvae fed on cotton and the artificial diet had a higher final weight of sixth instar larvae with shorter feeding time and lower food consumption than larvae fed on soybean. In contrast, soybean had a negative influence on the final weight of the sixth instar larvae and prolonged the feeding period. Although *S. cosmioides* consumption rate was highest on soybean, it was not converted to the final weight of the larvae (Table 2). The initial weight of the third instar larvae was not affected by the treatments.

Discussion

Soybean and cotton leaves were more suitable hosts for the development of *S. eridania* and *S. cosmioides* larvae than oat, maize, wheat,

Table 2. Initial weight of larvae of third instar (mg), body weight of larvae (mg), consumption (mg), feces weight (mg), feeding time (d) (mean ± SE) of *Spodoptera eridania* and *Spodoptera cosmioides* fed different foods (25 ± 2 °C, 70 ± 10% RH and photoperiod of 14:10 L:D).

	Treatment	Initial weight of caterpillar (mg)[a]	Final weight of the caterpillar (mg)[a]	Food consumed (mg)[a]	Feces weight (mg)[a]	Feeding time (d)[a]	Digested food[a]
S. eridania	Soybean	2.60 ± 0.09a	70.50 ± 6.03b	1032.50 ± 41.67b	125.45 ± 12.51b	11.35 ± 0.16[ns]	907.10 ± 39.19b
	Cotton	1.40 ± 0.06c	84.48 ± 5.94b	1550.40 ± 65.91a	177.48 ± 12.55a	11.29 ± 0.10	1372.90 ± 65.89a
	Diet[b]	2.09 ± 0.06b	131.94 ± 6.44a	1756.30 ± 99.51a	211.53 ± 14.99a	11.47 ± 0.17	1544.80 ± 99.06a
	p-value	<0.0001	<0.0001	<0.0001	0.0003	0.6800	<0.0001
	R^2	0.6961	0.4357	0.4384	0.2300	0.0122	0.3834
S. cosmioides	Soybean	1.20 ± 0.12[ns]	72.79 ± 7.07 b	1427.82 ± 28.41a	175.08 ± 11.63b	10.96 ± 0.03a	1252.73 ± 25.62a
	Cotton	1.35 ± 0.12	112.70 ± 11.18 a	1179.86 ± 30.03b	235.37 ± 21.00a	9.34 ± 0.10b	944.48 ± 23.42b
	Diet[b]	1.31 ± 0.09	131.52 ± 9.03 a	431.93 ± 13.92c	157.62 ± 13.13b	8.12 ± 0.13c	274.30 ± 13.92c
	p-value	0.6479	<0.0001	<0.0001	0.0020	<0.0001	<0.0001
	R^2	0.0121	0.2407	0.9251	0.1600	0.8604	0.9391

[a]Means (±SE) followed by the same letter in the columns for each species did not differ statistically (Tukey test, $p \leq 0.05$). [b]Artificial diet (Greene et al. 1976). [ns]Not significant.

and the artificial diet. Larvae fed on both soybean and cotton leaves had the highest survival rate (close to 50% and 80% for *S. eridania* and *S. cosmioides*, respectively). Both *S. eridania* and *S. cosmioides* fed on oat, wheat, and maize had low or zero survival rates, suggesting that the nutritional composition of these hosts is unfavorable for the development of the 2 lepidopteran species. Quality and quantity of food consumed by species directly influence their host preferences and affect their biological, physiological, and behavioral characteristics (Nation 2002; Golizadeh et al. 2009; Cabezas et al. 2013). In this context, insects fed on hosts of low nutritional value can have compensatory strategies such as an extension of the feeding period or an increase of food intake (Behmer 2009). Such strategies were observed for *S. cosmioides* fed on maize, which had the longest larva-adult period (Table 1) but lower pupal weight and survival rate than when fed on cotton and soybean leaves. In contrast, the larva-adult period (d) of *S. eridania* was not influenced by the food source. However, none of its larvae survived on maize and pupal weight was lowest when larvae were fed on oat leaves.

Carbohydrate and protein content are important for the full development of insects and can vary depending on the host plant and its phenological stage. Compared with other leaf components, older leaves generally have higher concentrations of proteins as well as carbohydrates, while younger leaves generally only have higher protein concentrations (Mattson 1980; Lincoln et al. 1993). Concentrations of these components can also depend on environmental conditions (soil nutrient, light, and water level) (Behmer 2009). Larvae provided with low quality proteins and carbohydrates may be able to develop, but their efficiency in converting food to biomass is generally low. Thus, the food conversion efficiency (the amount of food consumed minus the amount of feces produced) estimates the energy that can be allocated for growth or to convert it to other metabolic pathways (Karowe & Martin 1989; Lincoln et al. 1993; Elser et al. 2000; Throop & Lerdau 2004).

Host-plant adaptation also can be viewed in terms of physiological, biochemical, and evolutionary adaptations to host-plant allelochemicals (Caprio & Tabashnik 1992; Ahmad et al. 1986; Slansky 1992; Sorensen & Dearing 2006). Several authors report the importance of allelochemicals as deterrents, repellents, and stimulants present in plants (Berenbaum & Neal 1985; Vendramim & Guzzo 2009), which may explain the results of our study and should be considered further in future research. Our results on their development on different hosts suggest that *S. eridania* and *S. cosmioides* may be more adapted to chemical compounds of cotton and soybean given their faster development and higher survival rates on these hosts. Considering that cotton is harvested a couple of months later than soybean, high pest survival rates can have serious implications for resistance management and tactical control because the pest can be continuously selected on both crops. Therefore, using the same Bt proteins (for OGM plants) or the same active ingredient (for insecticide management) in both crops can cause severe problems for pest resistance management (Roush 1989; Scott 1990; Scott 1995). In addition, the coexistence of diverse crops in the agroecosystem allows polyphagous species such as *S. eridania* and *S. cosmioides* to feed on alternative plant species in the absence of their preferred host, ensuring their survival (Nagoshi & Meagher 2008).

It is also important to consider alternative explanations to understand the better adaptation of *S. eridania* and *S. cosmioides* to soybean and cotton, including ecological factors that determine host use (Veenstra et al. 1995). With insects of the order Lepidoptera, host plant selection for larvae is commonly associated with adult female choice of the site of oviposition (Singer 1984; Leal & Zucoloto 2008). Accounting for this behavioral pattern, many studies have investigated the relationship between host preference of adult females and performance of their offspring (Damman & Feeney 1988; Nylin & Janz 1993; Singer et al. 1994), known as the 'preference-performance hypothesis' or as the 'mother-knows-best hypothesis' (Jaenike 1978; Gripenberg et al. 2010). It is possible that different regulation mechanisms of food intake may have influenced *S. eridania* and *S. cosmioides* feeding on the studied hosts. Host preferences of insects seem to be triggered by plant characteristics that affect the insects' performance, including nutritional composition, allelochemicals, and even physical characteristics such as hardness, size, shape, and texture (Renwich 1983; Tabashinik & Slansky 1987; Bruce et al. 2005). These factors may determine host recognition (Scriber & Slansky 1985; Thompson & Pellmyr 1991; Dodds et al. 1996) and may play an important role for the biology and ecology of *S. eridania* and *S. cosmioides*.

The moths in the no-choice tests laid eggs on all hosts. However, the non-preference for oviposition on maize was more pronounced and corroborates the low suitability of this host for the development of this species. Furthermore, larvae were not able to complete their development feeding on maize leaves. Other mechanisms involved in host selection, such as color and presence of trichomes on the leaves, were not considered in this study, but may contribute to the mechanisms of choice (Vendramim & Guzzo 2009).

In conclusion, based on larval development, preferable oviposition sites, and survival of *S. eridania* and *S. cosmioides*, preference for the studied hosts was determined as soybean > cotton > oat > wheat > maize, and the nutritional value as cotton > soybean > oat > wheat > maize. Thus, the present study demonstrated that host plants are selected to optimize development and survival of *S. eridania* and *S. cosmioides*. Our results contribute to understanding the biology of these pests and assist in their control, particularly on soybean and cotton. Future studies should focus on testing other hosts of *S. eridania* and *S. cosmioides* and on evaluating the chemical composition of these hosts for additional insights of host suitability to these pests.

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