

Development and Leaf Consumption by *Spodoptera cosmioides* (Walker) (Lepidoptera: Noctuidae) Reared on Leaves of Agroenergy Crops

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Abstract

Spodoptera cosmioides (Walker) (Lepidoptera: Noctuidae) is a polyphagous pest that threatens more than 24 species of crop plants including those used for biodiesel production such as *Ricinus communis* (castor bean), *Jatropha curcas* (Barbados nut), and *Aleurites fordii* (tung oil tree). The development and leaf consumption by *S. cosmioides* reared on leaves of these three species were studied under controlled laboratory conditions. The egg-to-adult development time of *S. cosmioides* was shortest when reared on castor bean leaves and longest when reared on tung oil tree leaves. Larvae reared on castor bean and Barbados nut leaves had seven instars, whereas those reared on tung oil tree leaves had eight. Females originating from larvae reared on castor bean and Barbados nut leaves showed greater fecundity than did females originating from larvae reared on tung oil tree leaves. Insects fed on castor bean leaves had shorter life spans than those fed on tung oil tree and Barbados nut leaves although the oviposition period did not differ significantly. The intrinsic and finite rates of increase were highest for females reared on castor bean leaves. Total leaf consumption was highest for larvae reared on tung oil tree leaves and lowest for those reared on Barbados nut leaves. We conclude that castor bean is a more appropriate host plant for the development of *S. cosmioides* than are Barbados nut and tung oil tree.

Introduction

The Brazilian government initiated an ambitious program in 2004 to develop biodiesel for the internal market (Suarez *et al* 2006, Pousa *et al* 2007). This occurred principally because of the exponential increase in petroleum prices and the environmental pollution caused by burning fossil fuels, which generates the emission of greenhouse gases into the atmosphere.

Among the plant species used for the production of biodiesel in Brazil, planting of the Euphorbiaceae castor bean (*Ricinus communis*), Barbados nut (*Jatropha curcas*), and tung oil tree (*Aleurites fordii*) has been encouraged (Leite &

Leal 2007, Franco & Gabriel 2008, Oliveira *et al* 2009). Since these are not traditional crops, certain problems have limited their production, including the damage caused by insect pests, which can cause extensive losses and render their production impractical (Franco & Gabriel 2008). *Spodoptera cosmioides* (Walker) (Lepidoptera: Noctuidae) is an important pest of castor bean (Carvalho 2005), and has been recently observed damaging tung oil tree and Barbados nut crops (Nava D.E., personal observation). *Spodoptera cosmioides* is restricted to South America, except for the southern part of Argentina, Chile, and parts of Peru west of the Andes (Silvain & Lalanne-Cassou 1997).

In Brazil, more than 24 commercial plant species have been reported as hosts of *S. cosmioides* (Habib et al 1983, Bavaresco et al 2003, 2004, Specht et al 2004). However, despite the large number of potential hosts, *S. cosmioides* is considered a key pest only for certain crops, and its infestation is generally associated with imbalances caused by excessive use of broad-spectrum insecticides and the consequences, such as suppression of natural biological control. Although *S. cosmioides* is a pest of castor bean and is also reported to attack Barbados nut and tung oil trees, there is little information on basic aspects of its biology and ecology on these crops. Knowledge of the biology of *S. cosmioides* on different hosts may assist in establishing control strategies, such as reducing the number of insecticide applications to hosts that are less suitable for the development of the pest or indicating the defoliation tolerance of a particular crop plant and the possibility of using compatible control methods. Therefore, the development and leaf consumption on castor bean, tung oil tree, and Barbados nut of *S. cosmioides* was studied under laboratory conditions in order to determine the most suitable host plant for its development.

Material and Methods

Spodoptera cosmioides colony

Eggs of *S. cosmioides* were collected from castor bean trees grown in the experimental area of the Empresa Brasileira de Pesquisa Agropecuária, Centro de Pesquisa Agropecuária de Clima Temperado located in the city of Pelotas, state of Rio Grande do Sul, Brazil. Eggs were disinfected by immersion in 1% copper sulfate for 5 min and the eclosed larvae were transferred to flat-bottomed glass tubes (2.7 cm in diameter by 8.5 cm high) containing an artificial diet consisting of wheat germ, beans (*Phaseolus vulgaris*), and brewer's yeast (Burton & Perkins 1972), and reared following Parra (2009). After pupation, the insects were separated by gender and placed in general-purpose polystyrene boxes. After emergence, mating pairs were placed in individual cages made of PVC tubes (10 cm in diameter by 13 cm high) lined with newsprint, which served as the oviposition substrate. Adults were fed a 10% honey solution supplied on cotton rolls in plastic vials (3.0 cm in diameter by 6.0 cm high) and the rolls were replaced every 2 days. Eggs were removed daily and stored under controlled conditions.

Spodoptera cosmioides development

Eighty, 0- to 12-h-old larvae of *S. cosmioides* were placed individually in flat-bottomed glass tubes (2.5 cm in diameter by 8.0 cm high) and fed pieces of leaves of castor bean,

Barbados nut, or tung oil tree, all of the same age and taken from the upper third of the plants. The food was replaced and larval excrement was removed from the vials daily. At 24 h after pupation, the pupae were weighed and separated by gender. Pupae were placed individually in plastic cups (5.3 cm in diameter by 7.3 cm high), where they remained until adult emergence. We assessed the duration and survival of the larval, prepupal, and pupal stages, as well as the duration and survival of the egg-to-adult development, together with the number of instars, pupal weight, and sex ratio [$sr = \frac{\text{♀}}{(\text{♀} + \text{♂})}$].

To analyze the number of instars, the head capsules of 20 individuals per study group (i.e., per host plant species) were measured daily with an ocular micrometer attached to a stereomicroscope. Measurements were taken until the prepupal stage, when feeding was terminated.

After emergence, 20 mating pairs of *S. cosmioides* were placed in cages and fed as earlier described. For the adult stage, we evaluated the following biological parameters: male and female life spans, daily and total fecundity, duration and survival of the egg stage, and duration of the preoviposition and oviposition periods. In order to determine the survival rates and the duration of the egg stage, we used the second clutch from each pair. All experiments were conducted at $25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH, and a photoperiod of 14:10 h (light/dark).

The life table parameters described by Southwood (1978), including the mean number of eggs per female (mx) on each date of oviposition (x), the total number of females, the cumulative survival rate of females (lx) during the oviposition period, and the number of descendants that survived to age (x) in the next generation ($lx.mx$), were also calculated for *S. cosmioides* by using the biological data collected on each host plant.

Leaf consumption

Third instars were individually placed in Petri dishes (9.0 cm in diameter by 1.5 cm high) and fed castor bean, Barbados nut, or tung oil tree leaves. We used healthy, tender leaves of the same age, which were taken from the upper third of the plants. Leaves from the three host plants were collected daily, washed with distilled water, dried with absorbent paper, and cut into pieces with a circular punch (ranging from 20 to 150 cm², depending on the instar). The pieces of leaves were replaced daily. A sample of pieces of each leaf (10 per host-plant species) was individually placed into Petri dishes under the same conditions as those that were offered to the larvae in order to determine the change in leaf area due to the loss of moisture. The leaf remnants were removed every 24 h, their area was measured with a Leaf Area Meter (LI-COR model LI-3000, Lincoln, NE, USA). Leaf consumption per larva was obtained by subtracting the remaining leaf area

from the initial leaf area after correcting the value obtained by the index determined by the gain or loss of area as a function of the variation in temperature and humidity.

The instars were determined by measuring the head capsule with the aid of an ocular micrometer attached to a stereomicroscope. Measurements were taken until the larvae reached the prepupal stage. Leaf consumption was considered to begin at the third instar, because first- and second-instar larvae only scrape the leaves, and their leaf consumption is negligible in relation to the total leaf consumption (Crócomo & Parra 1985). The experiments were conducted under the same environmental conditions as earlier described.

Statistical analyses

The experiments were carried out with a fully randomized block design. The data for duration and survival of the egg, larva, prepupa, and pupa stages, egg–adult period, pupal weight, fecundity, and leaf consumption were examined by analysis of variance and the means compared by Tukey’s test ($p \leq 0.05$), carried out in the SAS (PROC: GLM) (SAS Institute 2002).

The sex ratio (sr) was evaluated by Chi-square test ($p \leq 0.05$), which was calculated taking into consideration the expected frequencies (one male for one female) in relation to the frequency observed on each host. To evaluate longevity, survival curves were constructed by means of the Kaplan–Meier estimator, and these curves were then compared by the log-rank test with the aid of the R statistical software package (R Development Core Team 2011).

For determination of the number of instars on each host plant, the multimodal curve of frequencies for the widths of the cephalic capsules was used in the formulation of hypotheses, which were tested in the linear model of Dyar’s rule using the MOBAE (Modelos Bioestatísticos para a Entomologia) software (Haddad *et al* 1995).

Life table parameters and the respective standard errors were estimated using the Jackknife method (Meyer *et al* 1986) as described by Maia *et al* (2000). Statistical analyses were performed using the SAS computer program “lifetable.sas” developed in the SAS System environment (SAS Institute 2002).

Results

Spodoptera cosmioides development

The biological parameters of *S. cosmioides* varied with the host plant employed (Tables 1 and 2; Fig 1). The three host species had no significant effect on the duration of the egg stage ($F = 1.98$; $df = 2, 35$; $p = 0.15$) (Table 1). The host effect on the larval stage was significant ($F = 5381.38$; $df = 2, 178$; $p < 0.01$): insects fed on tung oil tree leaves showed the longest developmental time in relation to those fed on castor bean and Barbados nut, which also differed from one another. Larvae reared on tung oil tree leaves had eight instars ($y = -1.4995 + 0.3038x$, $R^2 = 0.9999$, $K = 1.35$), whereas those reared on castor bean or Barbados nut leaves had seven instars ($y = -0.9309 + 0.3016x$, $R^2 = 0.9999$, $K = 1.35$ and $y = -0.6701 + 0.2470x$, $R^2 = 0.9999$, $K = 1.28$, respectively; Table 1).

No differences were observed in the duration of the prepupal stage ($F = 0.97$; $df = 2, 157$; $p = 0.38$; Table 1). However, the host plant had a significant effect on the duration of the pupal period ($F = 59.57$; $df = 2, 142$; $p < 0.01$). Larvae fed on tung oil tree leaves showed the longest pupal development time, differing significantly from the values observed for pupae originating from larvae fed on castor bean and Barbados nut leaves (Table 1).

The differences observed in the larval and pupal stages significantly influenced the duration of the egg–adult period ($F = 1759.35$; $df = 2, 142$; $p < 0.01$): insects reared on castor bean leaves showed the shortest development time in

Table 1 Duration (mean±SE) of the egg, larval, prepupal, and pupal stages and the egg-to-adult development time, as well as the number of instars and pupal weight of *Spodoptera cosmioides* reared on castor bean, Barbados nut, or tung oil tree leaves at controlled conditions (25±1°C; 70±10% RH; 14:10 h).

Host plant	Duration (d)					Instars ^B			Pupal weight (g) ^a
	Egg stage	Larval stage ^a	Prepupal stage	Pupal stage ^a	Egg-to-adult development time ^a	N	K	R ²	
Castor bean	3.3±0.12	14.3±0.07 c	2.7±0.08	14.4±0.22 b	31.4±0.31 c	7	1.35	0.999	0.5±0.005 a
Barbados nut	3.7±0.11	27.4±0.13 b	2.8±0.07	15.1±0.25 b	45.3±0.32 b	7	1.28	0.999	0.4±0.005 b
Tung oil tree	3.6±0.15	36.6±0.78 a	2.8±0.07	18.6±0.26 a	58.0±0.28 a	8	1.35	0.999	0.3±0.006 c

N number of instars, K growth rate, R² coefficient of determination.

^a Values followed by the same letter in the same columns are not significantly different by Tukey’s test ($p > 0.05$).

^b Values determined by means of the MOBAE program.

Table 2 Means (\pm SE) for sex ratio, preoviposition period, oviposition period, daily fecundity, and total fecundity of *Spodoptera cosmioides* males and females reared on castor bean, Barbados nut, or tung oil tree leaves at controlled conditions ($25\pm 1^\circ\text{C}$; $70\pm 10\%$ RH; 14:10 h).

Host plant	Sex ratio ^a	Preoviposition period (days) ^b	Oviposition period (days) ^b	Fecundity ^b	
				Daily	Total
Castor bean	0.4 a	3.4 ± 0.23 b	7.7 ± 0.85 a	711.7 ± 56.20 a	$4,951.3\pm 344.77$ a
Barbados nut	0.6 a	6.8 ± 0.28 a	8.6 ± 0.52 a	507.3 ± 28.53 b	$4,218.6\pm 240.79$ a
Tung oil tree	0.6 a	5.6 ± 0.65 a	8.6 ± 0.74 a	331.7 ± 41.33 c	$2,173.5\pm 209.36$ b

^a Sex ratio of progeny of *S. cosmioides* reared on each host species and compared individually in the proportion 1:1, χ^2 ($p < 0.05$).

^b Means followed by the same letter in a column do not differ significantly by Tukey's test ($p > 0.05$).

relation to those reared on tung oil tree and Barbados nut leaves, and these groups in turn differed from one another (Table 1).

The host plant had a significant effect on the weight of the pupa ($F = 339.92$; $df = 2, 157$; $p < 0.01$): insects reared on castor bean leaves were heavier than the others (Table 1).

Survival was significantly affected by the host plant for the egg stage ($F = 8.20$; $df = 2, 36$; $p < 0.01$), larva ($F = 6.26$; $df = 2, 237$; $p < 0.01$), prepupa ($F = 4.93$; $df = 2, 178$; $p < 0.01$), and pupa ($F = 8.28$; $df = 2, 157$; $p < 0.01$) of *S. cosmioides* (Fig 1). Females originating from larvae fed on leaves of Barbados nut produced eggs with higher survival rates (71.7%) than those fed on castor bean leaves (47.0%), while those from tung oil tree leaves displayed intermediate values (61.5%; Fig 1). Survivorship of larvae fed on castor bean leaves was significantly higher (88.8%) than those fed on Barbados nut (71.3%) or tung oil tree leaves (66.3%). In the prepupa stage, the highest survivorship was observed for the tung oil tree (98.1%) and the lowest for the castor bean (80.3%; Fig 1). The host effect on the survival of the pupal stage was similar to that recorded for the prepupal stage, with a higher survivorship on tung oil tree (100%) and Barbados nut (94.1%) than on

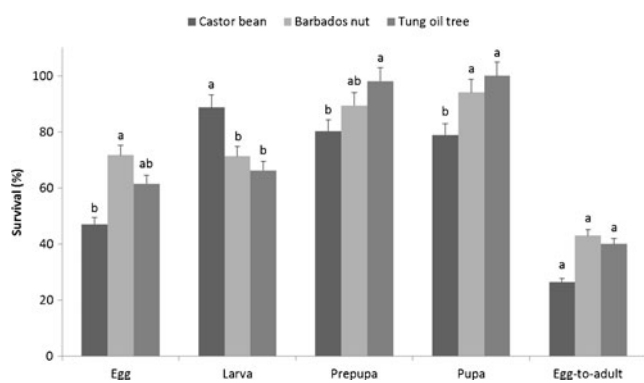


Fig 1 Survival rates for the different stages of development and the egg-to-adult development time of *Spodoptera cosmioides* reared on castor bean, Barbados nut, or tung oil tree leaves at controlled conditions ($25\pm 1^\circ\text{C}$; $70\pm 10\%$ RH; 14:10 h). Means followed by the same letter within the stages of development are not significantly different, as assessed by Tukey's test ($p > 0.05$).

castor bean (79.0%). No significant effect of the hosts was observed for the egg-to-adult period ($F = 1.17$; $df = 2, 237$; $p = 0.31$; Fig 1).

The sex ratio was not affected by the host plant, and was close to 1:1 on castor bean ($\chi^2 = 2.96$; $p = 0.08$), Barbados nut ($\chi^2 = 1.59$; $p = 0.21$), and tung oil tree ($\chi^2 = 1.92$; $p = 0.17$; Table 2).

The preoviposition period was significantly affected ($F = 19.74$; $df = 2, 36$; $p < 0.01$) by the host plant. Females of *S. cosmioides* reared on castor bean had a shorter preoviposition period than females reared on tung oil tree and Barbados nut (Table 2). However, the oviposition period was not affected by the host plant ($F = 0.58$; $df = 2, 36$; $p = 0.56$; Table 2).

The daily ($F = 18.75$; $df = 2, 36$; $p < 0.01$) and total fecundity ($F = 24.90$; $df = 2, 36$; $p < 0.01$) were significantly affected by the host plant used for larval development (Table 2). Females reared on castor bean displayed the highest daily fecundity,

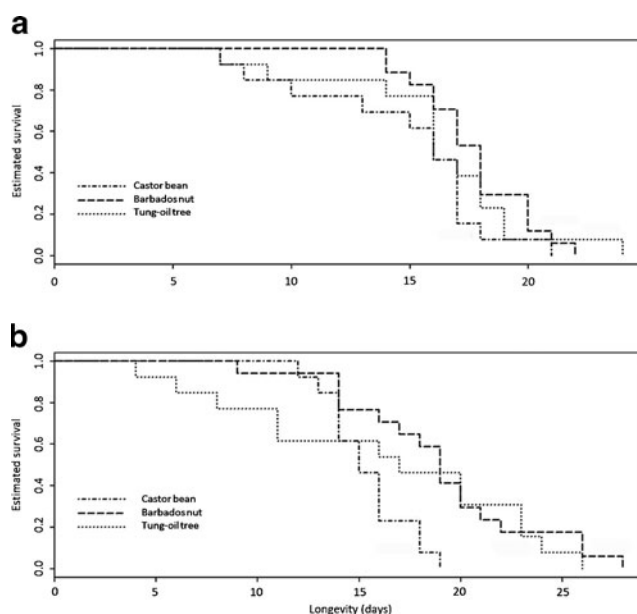


Fig 2 Longevity of females (a) and males (b) of *Spodoptera cosmioides* reared in the larval stage on leaves of castor bean, Barbados nut, or tung oil tree ($25\pm 1^\circ\text{C}$; $70\pm 10\%$ RH; 14:10 h).

Table 3 Mean interval between generations, net reproductive rate, intrinsic rate of increase, doubling time, and finite rate of increase for *Spodoptera cosmioides* reared on castor bean, Barbados nut, or tung oil tree leaves at controlled conditions (25±1°C; 70±10% RH; 14:10 h).

Host plant	T (days)	R _o	r _m	T _d (days)	λ
Castor bean	39.9±0.20 c	444.1±30.92 b	0.2±0.002 a	4.4±0.05 c	1.2±0.002 a
Barbados nut	56.0±0.22 b	1070.3±61.09 a	0.1±0.001 b	5.6±0.05 b	1.1±0.001 b
Tung oil tree	69.3±0.22 a	521.7±50.25 b	0.1±0.001 c	7.7±0.11 a	1.1±0.001 c

Values followed by the same lowercase letter in the same column are not significantly different, as assessed by the t test (p > 0.05). T mean interval between generations, R_o net reproductive rate, r_m intrinsic rate of increase, T_d doubling time, λ finite rate of increase.

differing significantly from those fed with leaves of Barbados nut and tung oil tree, which in turn differed from one another. With respect to the total fecundity, females from castor bean and Barbados nut were more fecund than those from tung oil tree leaves.

Female longevity did not differ among treatments (χ² = 3.30; df = 2; p = 0.192), but male longevity did (χ² = 7.80; df = 2; p = 0.02). Males from Barbados nut lived the longest, while those from castor bean had the shortest life spans (Fig 2).

The host plants differed significantly in their impact on the *S. cosmioides* life table parameters (Table 3). The net reproductive rate was significantly higher for adult females that originated from larvae reared on Barbados nut leaves than for those from larvae reared on castor bean or tung oil tree leaves (t ≤ 0.05). The intrinsic and finite rates of increase were highest for insects reared on castor bean leaves (t ≤ 0.05; Table 3). Also, the mean interval between generations and the doubling time were shortest for the insects reared on castor bean leaves (t ≤ 0.05). The maximum rates of increase of *S. cosmioides* populations fed on castor bean, Barbados nut, and tung oil tree leaves were observed on days 38, 54, and 67, respectively.

Leaf consumption

Leaf consumption by *S. cosmioides* was affected by both the host plant (F = 56.32; df = 2, 495; p < 0.01) and instar (F = 401.69; df = 4, 495; p < 0.01), and by the interaction of these

factors (F = 6.45; df = 8, 495; p < 0.01; Table 4). Leaf consumption increased linearly for all host plants (Table 4). Third instars fed on tung oil tree leaves consumed more leaf area than those fed on castor bean and Barbados nut. Fourth, fifth, sixth, and seventh instars all consumed the largest leaf area on castor bean, and these values were significantly higher than those recorded on Barbados nut and tung oil tree leaves, with the exception of the consumption of tung oil tree leaves by fifth instars (Table 4).

The host plant had a significant effect on the total leaf consumption (F = 57.67; df = 2, 99; p < 0.01). The highest consumption occurred when *S. cosmioides* was fed on tung oil tree leaves, followed by leaves of castor bean and Barbados nut (Table 4). Larvae reared on Barbados nut leaves and those reared on castor bean leaves had seven instars, and the sixth and seventh instars consumed the largest amount of leaf material (75% of the total leaf consumption; Table 4). In contrast, larvae reared on tung oil tree leaves had eight instars, and the seventh and eighth instars consumed the largest amount of leaf material (64% of the total leaf consumption).

Discussion

We demonstrate here that immature and adult stages of *S. cosmioides* tend to develop better when larvae are fed on leaves of castor bean as compared to leaves of Barbados nut

Table 4 Consumption (mean ± SE) of castor bean, Barbados nut, and tung oil tree leaves by different instars of *Spodoptera cosmioides* at controlled conditions (25±1°C; 70±10% RH; 14:10 h).

Instar	Leaf consumption (cm ²)					
	Castor bean		Barbados nut		Tung oil tree	
		(%)		(%)		(%)
3rd	3.9±0.33 bD	1.9	2.2±0.25 bD	1.5	10.8±1.62 aE	3.5
4th	25.9±1.48 aC	12.4	8.5±0.87 cCD	5.5	20.8±1.49 bDE	6.8
5th	31.0±2.95 aC	14.8	20.6±1.41 bC	13.5	31.0±1.90 aCD	10.1
6th	60.0±5.10 aB	28.6	43.3±6.06 aB	28.3	46.7±3.90 aC	15.2
7th	98.7±5.54 aA	48.0	78.3±5.60 bA	51.2	78.1±6.54 bB	25.4
8th	–	–	–	–	120.3±9.86 A	39.1
Total	219.5±4.83 b		152.9±5.92 c		307.7±14.44 a	

Values followed by the same lowercase letter on the same line or by the same uppercase letter in the same column are not significantly different, as assessed by Tukey's test (p > 0.05).

and tung oil tree. Moreover, larvae consumed a smaller leaf area of castor bean as compared to tung oil tree.

The longer duration of the larval and pupal stages and consequently the life cycle (egg–adult) and the lower pupal weight of *S. cosmioides* when larvae were fed on leaves of Barbados nut and tung oil tree indicate that some secondary substance or non-nutritional compounds may affect the growth and development of *S. cosmioides*, as observed for other hosts of *Spodoptera* species in the family Euphorbiaceae (Ghumare & Mukherjee 2005, Sintim et al 2009, Ramos-Lopez et al 2012, Rossi et al 2012). The three hosts used in this study belong to the family Euphorbiaceae, which is comprised of approximately 321 genera and 7,550 species (Kirkbride et al 2006). Several of these plants are characterized by synthesizing tri and diterpenes, many of which with known insecticidal activity (Devappa et al 2010).

The Euphorbiaceae *R. communis*, *J. curcas*, and *A. fordii* possess tannins and saponins in leaves and seeds that are toxic to insects, as for other species of *Spodoptera* (Phowichit et al 2008, Sakthivadivel & Daniel 2008, Ramos-López et al 2012). So probably, these substances should also be active against *S. cosmioides*, especially in tung, where the worst development was observed. Moreover, the greatest number of instar observed for larvae reared on tung oil tree leaves suggests that this food source is the least appropriate for *S. cosmioides* development. The effects of food suitability on the number of instars is a well-known phenomenon (Parra 2009), and although more easily observed in monophages, there are several examples demonstrating the effects of the quality of food on the number of instars in polyphages, including *S. cosmioides* (Santos et al 1980, Habib et al 1983, Bavaresco et al 2003, 2004).

The effect of the host plant used by insects in the larval stage also influences the biological attributes of the adult (Wedell et al 1997). In the case of *S. cosmioides*, there was an increase in the preoviposition period and a reduced daily and total fecundity for insects fed on Barbados nut and tung oil tree leaves. The total fecundity of females fed on leaves of castor bean did not differ from those fed with Barbados nut, indicating an effect of allelochemicals during larval feeding. However, there was no effect of food consumed in the larval stage on the longevity of females of *S. cosmioides*, probably because females feed during the adult stage and thus can compensate for any nutritional deficiency incurred during the larval stage. The use of carbohydrates in the adult stage is common for species of Lepidoptera; for representatives of Noctuidae, it is key to increase longevity (Gilbert & Singer 1975, Milano et al 2010).

The higher leaf consumption of *S. cosmioides* in tung oil tree was not reversed in further development, probably because it incurs in a higher metabolic cost, so that the pupal weight and fecundity of these insects were lower than those observed on castor bean and Barbados nut. Rossi et al (2012)

found a higher metabolic cost for larvae of *S. frugiperda* fed on artificial diet with a higher concentration of extracts of leaves of castor beans, indicating that a substance with an insecticidal effect must be present.

Analysis of the combined biological data obtained for the different stages of development by analyzing the fertility life table showed that castor bean is the best host for the development of *S. cosmioides*, probably due to the fact that this species is already adapted to this host, being considered a major pest of this crop (Carvalho 2005).

Life tables are of a great value in understanding the population dynamics of a species because they provide an integrated view of the biological characteristics of a given population under certain environmental conditions (Coppel & Mertins 1977). Although the present study was conducted under controlled conditions, insects in nature experience adverse biotic and abiotic factors that affect their fitness, so that life table studies are useful in evaluating these ecological factors (Nava et al 2008).

Understanding the differences among the three host plants in terms of their nutritional quality has practical implications for the management of *S. cosmioides*. The present study suggests that the larvae reared on tung oil tree leaves required a longer feeding time because of the low nutritional quality of these leaves. This leads to higher levels of leaf consumption and consequently greater damage to tung oil tree crops in comparison with the damage seen in castor bean and Barbados nut crops.

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