

Role of nutritional composition in the development and survival of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on artificial diet and natural hosts

Research Paper

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Abstract

Helicoverpa armigera is a pest of several crops causing significant economic impact. We evaluated the insect development on different vegetative and reproductive structures of cotton, maize, and soybean compared to artificial diet. One hundred individuals were evaluated per structure (cotton leaves and bolls; maize leaves, grains, and silk; soybean leaves and pods) and artificial diet. Centesimal analyses were performed on quantifiable nutrient contents in diets. The viability of immatures (eggs, larvae, and pupae) ranged from 30% on maize leaf to 74% on cotton bolls, while on the artificial diet, it was 70%. Maize, cotton, and soybean leaves provided viability of 30, 37, and 42%, respectively, revealing these leaves tissues are less favorable to the development of *H. armigera* immatures compared to 'reproductive tissues'. Centesimal composition of diets compared 14 common components in all diets, which correlated significantly with larval and pupal stages and/or pupal weight. Of the 12 dietary components that significantly affected larval development time, half were negatively correlated, indicating a decrease in developmental time from their increments. In general, when insects were confined separately to substrates, the artificial diet was the most suitable for *H. armigera* development compared to the evaluated natural diets. However, in natural conditions, the variability of available hosts must be considered. In addition, it is acceptable for moths to select more suitable hosts for oviposition, while their larvae move to other more suitable tissues of the same plant or even migrate to other plants.

Introduction

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is a polyphagous species with great destructive capacity (e.g. Zalucki *et al.*, 1986; Liu *et al.*, 2004) and wide geographical distribution (Zalucki and Furlong, 2005). It causes economic losses in various agriculturally important crops around the world (Naseri *et al.*, 2011; Cunningham and Zalucki, 2014). Losses from the attack of this insect on crops worldwide are estimated to reach US\$ 4 billion a year (Kriticos *et al.*, 2015), including damage to plants and costs related to management tactics. *H. armigera* larvae move around and can feed on different plant structures. They have been found on leaves and stems of host plants, but they prefer reproductive structures such as flower buds, bolls, pods, silk, and inflorescences (Perkins *et al.*, 2009; Yamasaki and Fujisaki, 2010).

Due to individual's polyphagia (Bernarys and Singer, 2002) and large capacity to move between plants and within the same plant, *H. armigera* larvae consume diets with varying nutritional values, which determine different development (Ruan and Wu, 2001; Schellhorn *et al.*, 2008). Qualitative and quantitative nutritional variations in food directly influence insect performance, leading to changes in developmental time, size, and weight (Yamasaki and Fujisaki, 2010). Hence, host availability and quality impact insect population outbreaks (Awmack and Leather, 2002) and are related to pest population dynamics in production systems (Maelzer and Zalucki, 1999; Kennedy and Storer, 2000; Krishnareddy and Hanur, 2015).

In Brazil, *H. armigera* was officially registered in 2013 (Czepak *et al.*, 2013) but has been in Brazil since 2008 (Sosa-Gómez *et al.*, 2016). The main attacks were reported in the Cerrado (Czepak *et al.*, 2013; Specht *et al.*, 2013), especially where the intensive production system includes three preferred insect hosts: cotton, maize, and soybeans (Reigada *et al.*, 2016). For cotton, the largest insect damage is observed in bolls (Kumar and Saini, 2008). In maize, *H. armigera* larvae concentrate their attack on cobs (Bentivenha *et al.*, 2016), and in soybeans,

they mainly damage the pods (Naseri *et al.*, 2009). These hosts are cultivated extensively and sequentially with planting and harvesting windows that overlap between seasons (Paula-Moraes *et al.*, 2017). Although this continuous rotation allows for maximum exploitation of cultivated areas and improves soil quality, this system also offers continuous food for the pest.

To investigate the suitability of artificial and natural diets for *H. armigera* in the old world, several studies have been conducted in the last decade (Soleimannejad *et al.*, 2010; Hemati *et al.*, 2012; Naseri and Razmjou, 2013; Rahimi Namin *et al.*, 2014; Hosseinejad *et al.*, 2015; Yue *et al.*, 2016). After its detection in Brazil, some studies evaluated biological parameters of the insect under different diets (Azambuja *et al.*, 2015; Reigada *et al.*, 2016), but none correlated nutritional aspects of the hosts to *H. armigera* performance.

Thus, this study aimed to compare biological parameters of *H. armigera* on plants that represent the three main 'commodities' (cotton, maize, and soybeans) of the Brazilian Cerrado and on artificial diet. Considering that *H. armigera* can develop in the various structures of the host plant, vegetative (leaves from the three hosts) and reproductive tissues (cotton boll, soybean pod, maize silk, and grains) were evaluated. Centesimal composition was performed of plant tissues to establish correlations between the nutritional variables of each plant tissue and the biological parameters of *H. armigera* (Analytical Quality Center (CQA[®])).

Considering the number of publications about this species on artificial diets (Krishnareddy and Hanur, 2015; Barbosa *et al.*, 2016), for data analysis, we also included previous results obtained with the same population on artificial diet (Silva *et al.*, 2018), to compare pest performance on natural host plants and artificial diet. The information may broaden the understanding of the interactions between the insect and the three host plants. In addition, the discovery of differential performance on the plant structures may help to predict significant insect outbreaks, with a direct impact on IPM strategies in cotton, maize, and soybean crops.

Materials and methods

Insect origin and maintenance in laboratory

During 2017, larvae of *H. armigera* were collected in citrus fruits, at Faculdade de Ciências Agrônomicas, Universidade Estadual Paulista, FCA-UNESP, Botucatu, SP, Brazil (22°53'09"S; 48°26'42"W). The collected larvae were placed in plastic containers (4.5 liters, 9 cm height × 26.6 cm width × 26.6 cm length) and fed on an artificial diet and kept under controlled conditions (25 ± 2 °C, 70 ± 10% RH, and 14 h photophase). Adults that emerged were kept in cylindrical polyvinyl chloride (PVC) cage (20 cm diameter × 30 cm height) and fed via capillarity with a 10% aqueous honey solution on absorbent cotton. The hydration of the insects was kept with another cotton piece containing only autoclaved water inside the cages. The species identification of the adults was performed by examining the adult male genitalia morphology (Pogue, 2004) at the Entomology Laboratory of Embrapa Cerrados, Planaltina, DF, Brazil.

The *H. armigera* colony was established and kept at the Laboratório de Resistência de Plantas a Insetos e Plantas Inseticidas (LARESPI) of the Department of Plant Protection for eight generations (Silva *et al.*, 2018). The larvae and adults used in the experiments were from the mass rearing fed on artificial diet maintained, to avoid larval preconditioning (Petit *et al.*,

2018). Details of the breeding procedures are described in Silva *et al.* (2018).

Host plants and dietary structures

The host plants were conventional cultivars of cotton (FMT 709), maize (AL Bandeirante), and soybean (BRS 284) adapted to the edaphoclimatic conditions of the State of São Paulo, SP, Brazil. The seeds of the three materials were purchased from Fundação de Apoio à Pesquisa Agropecuária de Mato Grosso (Fundação MT), Coordenadoria de Assistência Técnica Integral (CATI), and Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), respectively.

The host plants were grown in plastic pots with capacities of 8, 11, and 5 liters, for cotton, maize, and soybean, respectively. The substrate used was a mixture of soil – Distroferric Red Nitosol (Embrapa, 1999), washed sand (granules between 2 and 4 mm), and matured cattle manure (Huang *et al.*, 2017), in the proportions of 2:1:1. All plants were kept in a greenhouse, grown free of chemical application and insect infestation. Maize plants received a cover of nitrogen fertilization (urea) at 40 days after germination (Coelho and França, 1995). The plants were cultivated under irrigation and following the agronomic recommendations to the region.

The plant structures (leaves, pods, bolls, grains, and silk) used to perform the feeding studies were obtained by different crop planting times. Cotton, maize, and soybean leaves were harvested when the plants were at the beginning of the vegetative stage (V3 to V5) (Marur and Ruano, 2001), (V2 to V4) (Ritchie and Hanway, 1989), and (V2 to V5) (Ritchie *et al.*, 1982), respectively. Cotton bolls were harvested at stage B3 (flower buds of the third visible reproductive branch) (Marur and Ruano, 2001). The maize silk was collected when the plant was at the R1 stage (beginning of 'feathering' or before pollination and kernel formation) and the ears to supply the kernels were harvested at R3 and R4 ('milky and/or pasty' grains) (Ritchie and Hanway, 1989). Soybean pods were used at the R6 stage (beans green and filling the entire pod cavity) (Ritchie *et al.*, 1982).

Centesimal composition of diets

Centesimal composition of the diets was performed by the Analytical Quality Center (CQA[®]), in Campinas, SP, Brazil. The analysis methodology proposed by the AOAC (2010) and FDA (2010) was used, following Resolution RCD #360 (RCD 360/2003-Brazil). To enable comparisons between natural and artificial diets, data were used on components that had detectable values in most diets. Thus, values related to carbohydrates, ashes, iron, total dietary fiber, phosphorus, unsaturated fats, saturated fats, magnesium, manganese, potassium, total protein, sodium, energy value, zinc, and free fatty acids were considered.

Comparative biology assays and life table construction

Comparative biology assays were performed at LARESPI under controlled conditions ($T = 25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ RH, and 14 h photophase). For each diet, we followed the development of 100 newborn *H. armigera*, which were individualized and identified in Petri dishes, using eight treatments: T1 = (cut up) cotton leaves; T2 = (cut up) cotton boll; T3 = (cut up) maize leaves; T4 = maize grains; T5 = maize silk; T6 = (cut up) soybean leaves; T7 = (cut up) soybean pods; T8 = artificial diet (Silva *et al.*, 2018).

The Petri dish was internally lined with moist germitest paper (Cienlab®, Campinas, SP, Brazil) to maintain the turgidity of plant materials. Portions of the diet were added or replaced as needed. The plates were cleaned daily, removing the droppings and food debris, thus avoiding possible contamination. During the assays, the larval instars were confirmed by analyzing the ecdyses (cephalic capsule and larval exuviae) of each individual under observation. Feeding ceased as soon as the larvae entered the pre-pupal period, characterized by feeding interruption and size reduction. At this time, 0.5 cm³ of water-moistened vermiculite was added to each plate to provide moisture. After pupal metamorphosis (48 h), the individuals were weighed on semi-analytical scales accurate to one-thousandth of a gram and examined to identify sex (Queiroz-Santos *et al.*, 2018). The daily maintenance of the pupae was restricted to maintaining the humidity of the vermiculite, by applying a few drops of water until the emergence of adults. All daily observations were made in the morning between 8:00 and 10:00.

This bioassay with *H. armigera* larvae on different plant structures was carried out simultaneously with those already described on artificial diet (Silva *et al.*, 2018). Thus, the biological parameters both with different plant tissues and with artificial diet could be compared statistically. The original (raw) data were included in all comparative analyses. All analyses were performed considering only the immature insects that became adults without apparent malformation. In cases in which the pupae or pupae died, the larval data were also disregarded. The assays were evaluated daily from egg hatching to the end of the pupal stage or death, to obtain the following biological parameters: viability (%); larval, pre-pupal, pupal duration (days); and pupal weight (mg).

Subsequently, couples adult ($n = 15$) from larvae fed on the same host plant were kept in 'honeymoon cages' containers of cylindrical PVC (10 cm in diameter and 15 cm in height) with long strips of paper attached to stimulate oviposition (Silva *et al.*, 2018). To avoid the effects of adult age on their ability to mate, the mating pairs were formed by adults who emerged on the same date. The tops of the containers were covered with voile fabric (Corttex®, Divinópolis, MG, Brazil) and the bottoms were closed with Petri dishes (10.5 cm in diameter) coated with filter paper. The adult diet consisted of honey (10 g), sorbic acid (1 g), methylparaben (1 g), sucrose (60 g), and distilled water (1000 ml) (Hoffmann-Campo *et al.*, 1985). All components were dissolved in distilled water, and the resulting solution was refrigerated (7°C) until use. In addition, distilled water was supplied in a 5 cm cotton-lined Petri dish. The containers were examined daily to record adult survival and to remove and count the number of eggs.

The following reproductive parameters of *H. armigera* were estimated: fecundity (number of laid eggs per female), fertility (number of hatched larvae per female), longevity and duration of preoviposition, postoviposition and oviposition periods. The estimation of the fertility was based on the viability of eggs from the pairs of each host evaluated at the beginning and end of the oviposition period. The eggs were placed in Petri dishes coated with filter paper, which was moistened with distilled water, until the larvae hatched. Each adult couple cage was a replication, with a total of 15 per population, in a completely randomized design.

After the estimation of the biological parameters, biotic potential (BP) was calculated considering the environmental resistance as null, using the following equation described by Silveira Neto

et al. (1976), $BP = (sr \times d)^n - er$. Where the sex ratio (sr) is the number of females divided by the number of females plus the number of males; the viable individuals per female (d), considering the observed fecundity multiplied by the total survival of the immature; the number (n) of generations per year, or 365 days divided by the total lifetime (egg to adult); and environmental resistance (er), in this case considered null.

The BP as well as the life and fecundity table were developed using data from immature stages of *H. armigera* reared according to the methodology of Silva *et al.* (2018). Data are presented graphically, representing the probability of survival values at the midpoint of each time interval (survival rate- 1_x) and the total number of eggs per female per week that became female (specific fertility- m_x).

The life table parameters were estimated based on the calculation of the values of the different reproductive parameters of the *H. armigera* groups. The net reproductive rate (R_0), given by the relationship between the number of females in two successive generations; the average generation time (T), which is the average number of days from birth of parents to birth of offspring; the daily intrinsic rate of increase (r_m); and the daily finite growth rate (λ), following the formulas contained in Silveira Neto *et al.* (1976).

Statistical analysis

The data were tested and did not meet the normality assumption. Non-parametric tests were applied to test whether two independent samples come from the same population, and to compare the weight of pupae between sexes on each type of diet using the Mann-Whitney test. The difference to compare three or more independent groups of the following response variables was a test: larval, pre-pupal, pupal, and total period as well as pupal weight using the Kruskal-Wallis test (Siegel and Castellan, 2006). The ordering of treatments considered the order of magnitude of the medians, using a matrix of 'P' values.

The relationship between the non-normally distributed biological parameters (verified with Shapiro-Wilk test) and the main components of the vegetal tissues of each diet, Spearman correlation tests were applied using the FactoMineR package in the R statistical software, freely available at the website: <http://www.r-project.org>. The temporal parameters (in days) of larval, pre-pupal, pupal, and total immature stages were correlated with pupal weight and the free acidity, carbohydrate, ash, iron, total dietary fiber, phosphorus, unsaturated fats, saturated fat, magnesium, manganese, potassium, total protein, sodium, energy value, zinc, and free fatty acid content. Spearman correlation was used as a function of data deviation for normality, the presence of ordinal variables, and the lack of linearity between the studied variables.

A principal component analysis and Pearson correlation were also performed to identify among the variables studied, which contributed most to the linear combination of the first two principal components. The x and y axes, called principal components, can be seen as 'super variables', constructed by combining the correlation between the analyzed variables. These are extracted in descending order of importance according to their contribution to the total variation of data. The principal components, arranged in a two-dimensional space, represent sufficient variability that may indicate some pattern to be interpreted. To help interpret the results, besides the unitary circle of correlations between the eigenvectors of the variables, diagrams of natural diets consisting

Table 1. Centesimal composition of natural and artificial diets used as food sources for *Helicoverpa armigera* larvae under controlled conditions ($25 \pm 2^\circ\text{C}$, $70 \pm 10\%$ RH, and 14 h photophase).

Components	Cotton		Maize			Soybean		Artificial diet
	Leaf	Boll	Leaf	Grain	Silk	Leaf	Pods	
Carbohydrates $\text{g } 100 \text{ g}^{-1\text{a}}$	4.00	16.50	1.00	29.70	8.00	6.00	1.70	8.10
Ashes $550^\circ\text{C } \text{mg } 100 \text{ g}^{-1\text{a}}$	2.70	1.20	1.50	0.30	0.90	2.00	2.20	0.70
Total dietary fiber $100 \text{ g}^{-1\text{a}}$	<0.01	<0.01	2.60	1.60	4.70	8.00	13.80	1.60
Phosphorus $\text{mg } 100 \text{ g}^{-1\text{b}}$	82.62	84.55	145.78	284.38	13.74	830.00	18.00	145.03
Unsaturated fats $\text{g } 100 \text{ g}^{-1\text{a}}$	0.77	0.93	0.58	1.04	0.61	0.51	2.20	0.70
Saturated fats $\text{g } 100 \text{ g}^{-1\text{a}}$	0.23	0.27	0.52	0.29	0.18	0.29	1.30	0.02
Magnesium $\text{mg } 100 \text{ g}^{-1\text{b}}$	118.30	34.13	50.00	62.17	33.71	110.00	111.00	36.10
Manganese $\text{mg } 100 \text{ g}^{-1\text{b}}$	1.38	0.20	1.89	1.76	1.97	3.00	0.96	9.95
Potassium $\text{mg } 100 \text{ g}^{-1\text{b}}$	883.44	749.17	477.20	258.82	290.03	290.00	5000.00	192.50
Total protein $\text{g } 100 \text{ g}^{-1\text{a}}$	4.30	4.10	2.40	1.30	0.50	4.00	6.40	5.30
Sodium $\text{mg } 100 \text{ g}^{-1\text{a}}$	27.48	18.50	57.20	49.08	44.80	12.00	13.00	13.20
Energy value $\text{kcal } \text{g}^{-1\text{c}}$	42.00	93.00	32.00	136.00	41.00	47.00	64.00	60.00
Zinc $\text{mg } 100 \text{ g}^{-1\text{b}}$	0.21	0.36	0.60	0.69	0.37	1.60	2.40	1.05
Free fatty acids $\text{g } 100 \text{ g}^{-1\text{a}}$	0.25	0.30	0.40	0.60	0.10	<0.01	<0.01	5.61

^aAOAC – A.O.A.C. INTERNATIONAL, Official Methods of Analysis, 18th edition, Maryland/USA; Current Through – Revision 3, 2010.

^bFDA – Food And Drug Administration. Elemental Analysis Manual. United States of America. Section 4.4 Inductively Coupled Plasma-Atomic Emission Spectrometric Determination of Elements in Food Using Microwave Assisted Digestion, August 2010.

^cRDC360/2003 – BRAZIL. RCD Resolution No. 360 of 23 December 2003. Approves Technical Regulation on Nutritional Labeling of Packaged Food, nutrition labeling becoming mandatory, the Brazilian Health Regulatory Agency. Official Gazette, Brasília, December 26, 2003.

of cotton (leaf and boll), maize (leaf, grain, and silk), soybean (leaf and pod), and artificial diet. All analyses were performed by the R Statistical software, version 3.2.2. The life table was prepared as described by the equations of Silveira Neto *et al.* (1976).

Results

Centesimal composition of diets

The centesimal composition revealed large variations between the parameters, with significant differences (up to more than 30 times) between diets, especially related to free fatty acids, carbohydrates, phosphorus, and potassium (table 1). Values ranged from $1 \text{ g } 100 \text{ g}^{-1}$ of carbohydrates present (maize leaf) to close to $30 \text{ g } 100 \text{ g}^{-1}$ (maize grains). Phosphorus contents found in maize silk ($13.74 \text{ mg } 100 \text{ g}^{-1}$) were lower than those found in soybean leaves ($830 \text{ mg } 100 \text{ g}^{-1}$). The lowest value detected for potassium was $258.82 \text{ mg } 100 \text{ g}^{-1}$ (maize grains), while the highest value was found in soybean pods ($5000 \text{ mg } 100 \text{ g}^{-1}$). Large variations in the energy value were observed of the different tissues, with the lowest value detected in maize leaf ($32.00 \text{ kcal } \text{g}^{-1}$) and the highest value in maize grains ($136.00 \text{ kcal } \text{g}^{-1}$). Total protein values were relatively similar between food sources ($4.00\text{--}6.40 \text{ g } 100 \text{ g}^{-1}$), except for corn tissues (0.50 in silk, 1.30 in grains, and 2.40 in leaves) (table 1).

Comparative biology when fed on natural and artificial diets

The duration of the *H. armigera* larval period significantly depended on the offered food source (table 2). Longer larval phases were observed when individuals were fed on artificial diet, soybean pods, maize grains, and cotton bolls ($P \leq 0.001$),

differing from diets based on cotton, maize, and soybean leaves ($P \leq 0.05$). Different diets did not cause any difference in the incubation period, pre-pupa, and pupa stages. The highest percentages of *H. armigera* eggs-to-adult viability were observed when insects fed on cotton bolls ($\sim 73\%$), artificial diet ($\sim 70\%$), and soybean pods ($\sim 66\%$) (fig. 1). Maize, cotton, and soybean leaves provided the lowest viability indexes ($< 42\%$). Regardless of sex, the highest average pupae weight was obtained when immature fed on cotton bolls and artificial diet ($> 0.320 \text{ mg}$) ($P \leq 0.05$) (fig. 2).

The BP of *H. armigera* calculated from the equation $\text{BP} = (\text{sr} \times \text{d}) \text{ n-er}$ resulted in higher values of crude reproduction rate (R_0), daily intrinsic rate of increase (r_m), and daily finite growth rate (λ) in individuals fed with cotton bolls (table 3), followed by individuals fed with artificial diet and soybean pods. The average higher indices of generation time (T) were found in individuals feeding on cotton leaves, followed by feeding on maize, and soybean leaves. The shortest generation time (T) duration was found in insects feeding on artificial diet (table 3).

Large variations in insect-specific fertility and respective viability of eggs obtained from pairs of each host were detected and depend on the diet offered to larvae (fig. 3 – dashed line). The maximum population growth rate, represented by the intersection of specific survival and fertility lines in most progenies feeding on different hosts, occurred between the 4th and 5th day of life (fig. 3), except for individuals feeding on other diets, which maximum occurred later, beginning on the 7th day of life (fig. 3).

Principal component analysis

Principal component analysis using the component data for each diet revealed that the first (dimension 1 – or horizontal axis)

Table 2. Mean duration (days ± SD) of the larval, pre-pupal, pupal, and total phases of *Helicoverpa armigera* fed natural and artificial diets under controlled conditions (25 ± 2°C, 70 ± 10% RH, and 14 h photophase).

Diet	Egg	Larvae		Pre-pupae	Pupae
Cotton leaf	2.91 ± 0.04	23.32 ± 0.32*	c	3.19 ± 0.17	10.82 ± 0.21
Cotton boll	2.87 ± 0.03	19.32 ± 0.38*	a	2.89 ± 0.15	10.58 ± 0.23
Maize leaf	2.93 ± 0.03	23.40 ± 0.29*	c	3.20 ± 0.19	10.77 ± 0.25
Maize grain	2.88 ± 0.04	19.29 ± 0.35*	a	2.97 ± 0.16	10.67 ± 0.17
Maize silk	2.89 ± 0.05	20.52 ± 0.41*	ab	3.00 ± 0.21	10.48 ± 0.22
Soybean leaf	2.91 ± 0.04	21.82 ± 0.31*	bc	3.24 ± 0.23	10.52 ± 0.26
Soybean pod	2.90 ± 0.03	19.28 ± 0.33*	a	3.13 ± 0.26	10.58 ± 0.21
Artificial diet	2.89 ± 0.03	18.63 ± 0.37*	a	3.21 ± 0.21	10.46 ± 0.19
P	0.243	<0.001		0.161	0.073

*Means followed by the same letter within the column do not differ from each other by the Kruskal-Wallis test (P > 0.05).

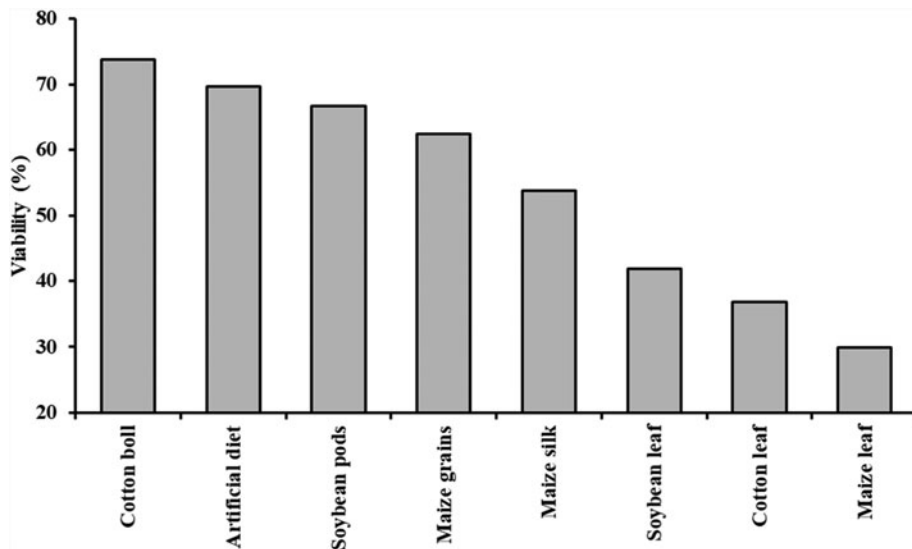


Figure 1. Viability (%) of *Helicoverpa armigera* immatures (egg to pupa) on natural and artificial diets under controlled conditions (25 ± 2°C, 70 ± 10% RH, and 14 h photophase).

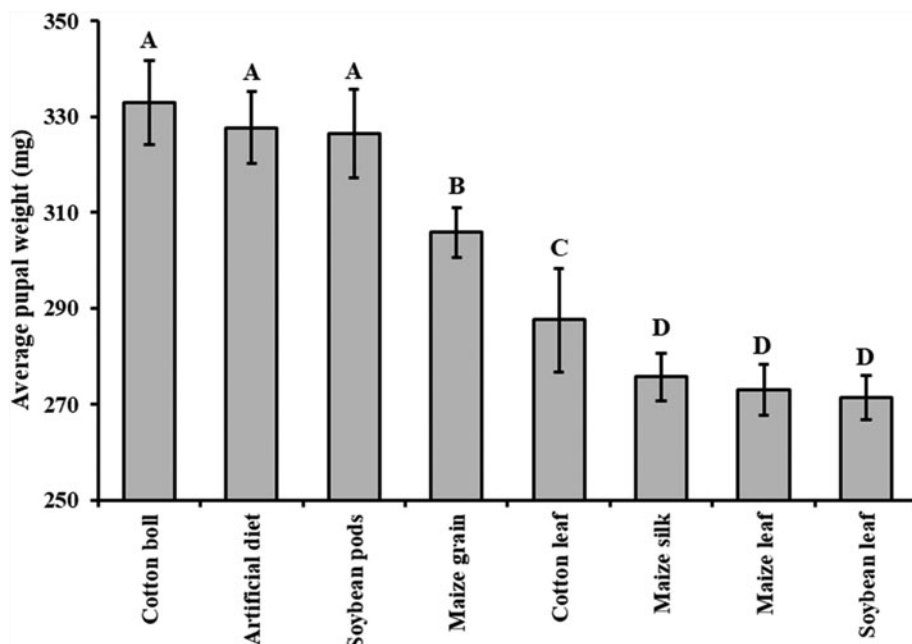


Figure 2. Average pupal weight (mg) and standard deviation of *Helicoverpa armigera* with larvae fed on natural and artificial diets, under controlled conditions (25 ± 2°C, 70 ± 10% RH, and 14 h photophase).

Table 3. Life table for *Helicoverpa armigera* larvae fed with different diets, under controlled conditions (25 ± 1°C, 70 ± 10% RH, 14 h photophase).

Diet	BP	R_0	r_m	λ	T
Cotton leaf	5.663×10^{17}	149.764	0.103	1.108	48.796
Cotton boll	9.709×10^{23}	536.336	0.147	1.158	42.802
Maize leaf	2.719×10^{18}	124.838	0.102	1.108	47.164
Maize grain	1.233×10^{22}	310.501	0.134	1.143	42.900
Maize silk	5.274×10^{19}	153.608	0.118	1.125	42.655
Soybean leaf	4.970×10^{19}	226.434	0.118	1.125	45.942
Soybean pod	8.377×10^{22}	397.560	0.138	1.148	43.327
Artificial diet	1.147×10^{24}	456.413	0.144	1.155	42.441

Biotic potential (BP), net reproductive rate (R_0), mean generation time (T), daily intrinsic rate of increase (r_m), and daily finite rate of increase (λ).

together with the second (dimension 2 – or vertical axis) explained 73.41, 71.47, and 71.48% of the total data variability for the duration of the larval and pupal stages, and pupal weight, respectively (table 4, fig. 4).

Correlation circles (figs 4A, C and E) illustrate great variation between the three biological parameters of *H. armigera* in relation to dietary components. Correlations between dietary components remained very similar. In the horizontal axes, the variables that most influenced (closest to the axis) positively were phosphorus, potassium, saturated fats, dietary fiber, unsaturated fats, magnesium, and zinc; negatively were free fatty acids and manganese. In the vertical axes, the variables that most positively influenced were manganese, free fatty acids, and total protein and negatively were sodium and energy value (table 4).

The dietary sorting diagrams, as a function developmental components and parameters of immature *H. armigera* (figs 4B, D and F), are similar to the correlation circles, and the dietary dispositions remained similar to development parameters. Notice that in fig. 4, the artificial diet and soybean pod diet were very far from the other diets. There was also great proximity between maize leaves and cotton bolls, and a relative proximity between soybean and cotton leaves, and between maize silk and grain.

Correlation between diet components and biological parameters

A significant correlation was found between the parameter values of each studied diet (except carbohydrates and magnesium) and the duration of the larval phase of *H. armigera* (table 5). The duration of the pupal period was significantly influenced by the parameters: ash, saturated fat, manganese, potassium, and free fatty acids. Pupal weight (mg) correlated significantly with changes in carbohydrate, ash, dietary fiber, unsaturated and saturated fat, total protein, sodium, and free fatty acids parameters (table 5).

Discussion

Biological performance studies of Noctuidae under different hosts are important to better understand aspects related to their survival and dispersal (Kennedy and Storer, 2000; Silva et al., 2017). This is particularly relevant in the agroecosystem, which the knowledge of the variations in the developmental period and migratory flow of lepidopterans is fundamental to understand

the population dynamics of species (Tisdale and Sappington, 2001) and support management decisions. Although studies have already evaluated the development of *H. armigera* on different hosts (Razmjou et al., 2014; Hosseinejad et al., 2015; Honnakerappa and Udikeri, 2018), few studies have related larval performance of this species with different host plant tissues (e.g. Sarate et al., 2012; Suzana et al., 2015). Additionally, there is little information about the correlation between the biological performance of *H. armigera* with nutritional composition of potential hosts or nutritional quality of diets (Sarate et al., 2012; Wang et al., 2019).

The present feeding study was performed with preferred host plants of *H. armigera* (Cunningham and Zalucki, 2014). However, the results revealed that the different vegetative and reproductive structures of cotton, maize, and soybean significantly affect *H. armigera* performance, causing changes in development time, weight, and viability of immatures. These variations were associated with differences related to the nutritional constitution of the different plant tissues (diets), since each diet has a specific composition.

Insects that fed on maize or cotton leaves had longer larval development time, indicating that these leaves are less suitable for the insect. For some Lepidoptera species, prolongation in the developmental time indicates a compensatory action, where larvae subjected to a poorer nutritional source tend to compensate for food stress by lengthening the immature stage (Silva et al., 2017). The lengthening of the larval period would allow the larvae to reach the ideal (or minimum) weight for pupation, a stage with nutritional/energy expenditure for the insect (Parra et al., 2009). In general, insect development is affected by its food source and the quality, relationship between protein/carbohydrate available to insects, which are factors that influence the small or large variations throughout the life cycle (e.g. Barros et al., 2010; Sarate et al., 2012; Suzana et al., 2015; Bisht et al., 2018; Wang et al., 2019). These previously listed components could be the explanation of the differences in *H. armigera* larval development time and variation of approximately 6 days in the mean generation time, performed with no choice experiments. These developmental time variations would be possibly minimized in field conditions due to the *H. armigera* larvae being able to maximize their development moving between plants and between different tissues of the same plant (e.g. Zalucki et al., 1986, 1994; Cunningham and Zalucki, 2014; Wang et al., 2019).

Based on the well-recognized preference of *H. armigera* to plant reproductive tissues, this study demonstrated that, except for maize silk, the other diets (cotton bolls, maize grains, and soybean pods) provided faster development time, higher survival, and greater pupal weight. The calculation of the life table parameters is influenced by these variations, resulting in the highest rates of BP, with values over 10^{22} individuals from one female in a year. The artificial diet provided values similar to those obtained with reproductive tissues, indicating although it is artificial it provides results very similar to those obtained with plant tissues most suitable for the full development of the studied species. These results indicate that the use of artificial diet allows reproducibility study comparisons of *H. armigera* development similar to that observed in more suitable host plants. The greater adequacy of reproductive tissues for *H. armigera* development results in the high probability of outbreaks of this species during the reproductive stages of host plants (Maelzer and Zalucki, 1999; Scott et al., 2006; Fefelova and Frolove, 2008). However, even in the vegetative stages, high population of this species can occur.

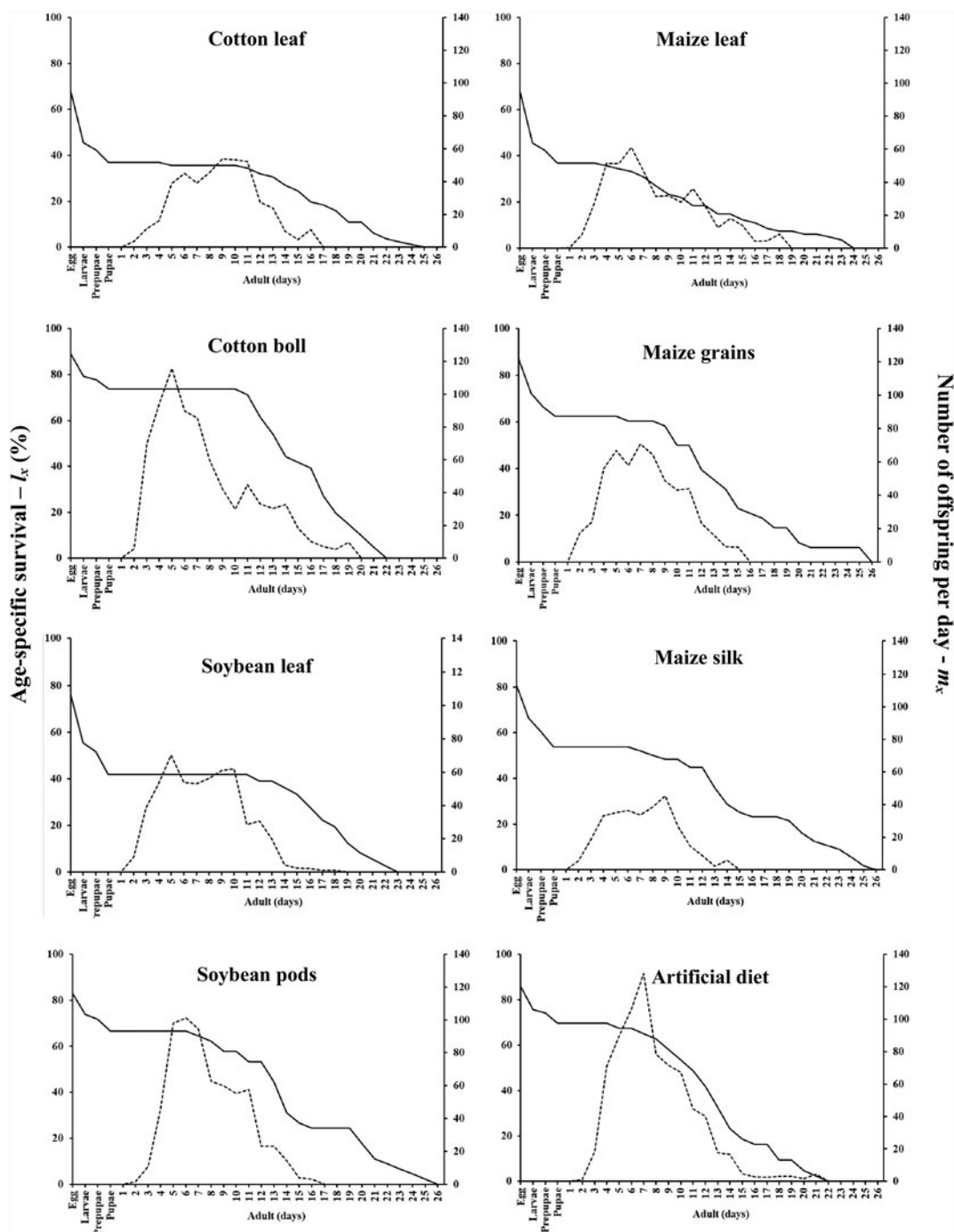


Figure 3. Relationship between age-specific survival - l_x (left axis and continuous line) and number of offspring per day - m_x (right axis and dashed line) of *Helicoverpa armigera* whose larvae were reared with different vegetal tissues and artificial diet ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH, 14 h photophase).

The great mobility of larva and their ability to find plants and structures most suitable for larval development (e.g. flower buds, flowers, or invasive plants) is critical to maximize their viability and development, even in not so appropriate or with adverse conditions of host plants (Cunningham and Zalucki, 2014).

Despite the high values for BP obtained in this study, especially with reproductive structures of maize (grains), soybeans (pods), and cotton (bolls), larval viability of lepidopterans is generally low in the natural environment due to high mortality rate in early instars (Zalucki *et al.*, 2002; Kumar *et al.*, 2009). In addition

to the nutritional aspects discussed here, other important factors on lepidopteran mortality in the field are related to predation, parasitism, disease, and canopy microclimate (e.g. Pereira *et al.*, 2018). The present study indicates *H. armigera* had better conditions for development when feeding on reproductive tissues (cotton bolls, soybean pods, maize silk, and grains) instead of vegetative tissues, such as leaves (fig. 1).

In addition to differences in *H. armigera* immature development time, qualitative and quantitative factors of the nutrients ingested also influenced pupal weight as reported in several

Table 4. Pearson correlation between the main components identifying the contribution of each dietary component in dimensions 1 (horizontal axis) and 2 (vertical axis) on the duration of the larval and pupal phases and on the pupal weight of *Helicoverpa armigera*.

Dietary component	Biological parameter					
	Larval phase (days)		Pupal phase (days)		Pupal weight (mg)	
	1	2	1	2	1	2
Variance	7.16	4.59	7.14	4.29	7.13	4.30
Variance%	44.74	28.67	44.65	26.82	44.59	26.89
Cumulative variance%	44.74	73.41	44.65	71.47	44.59	71.48
Carbohydrates	-0.388	-0.468	-0.402	-0.460	-0.402	-0.442
Ashes	0.704	0.023	0.703	0.017	0.700	0.001
Total dietary fiber	0.899	0.180	0.907	0.136	0.907	0.125
Phosphorus	0.946	0.175	0.952	0.136	0.954	0.129
Unsaturated fats	0.831	0.039	0.831	0.017	0.834	0.021
Saturated fat	0.927	-0.104	0.925	-0.140	0.924	-0.147
Magnesium	0.774	-0.071	0.772	-0.102	0.770	-0.115
Manganese	-0.486	0.844	-0.459	0.850	-0.452	0.854
Potassium	0.933	0.125	0.936	0.101	0.938	0.098
Total protein	0.490	0.760	0.509	0.769	0.516	0.768
Sodium	-0.319	-0.699	-0.335	-0.718	-0.343	-0.720
Energy value	0.154	-0.776	0.131	-0.782	0.127	-0.771
Zinc	0.788	0.459	0.804	0.419	0.808	0.412
Free fatty acids	-0.515	0.813	-0.490	0.828	-0.482	0.836
Biological parameter	0.189	-0.598	-0.130	0.123	0.083	0.171

studies with natural/artificial diets and non-larval feeding choice (e.g. Barros *et al.*, 2010; Sarate *et al.*, 2012; Suzana *et al.*, 2015; Bisht *et al.*, 2018; Wang *et al.*, 2019). Highest weights were found in individuals feeding on cotton bolls, soybean pods, and artificial diet, while lowest pupal weights (<0.270 mg) were found in individuals feeding on soybean leaves, maize silk, and maize leaves. A lower suitability of these tissues for *H. armigera*, which could lead to nutritional and adaptive disadvantages during pupal metamorphosis and even during adulthood due to lower nutritional reserve would be expected (Liu *et al.*, 2009; Yamasaki and Fujisaki, 2010). Studies have shown that higher pupal weight is generally related to higher fecundity (e.g. Awmack and Leather, 2002; Specht *et al.*, 2016; Montezano *et al.*, 2019). The same pattern was documented in the present study, based on R_0 values [net reproductive rate] and number of offspring per day (m_x), represented graphically in fig. 4.

The relationship between higher fecundity and oviposition period usually results from greater reproductive compatibility and copulation soon after emergence (Specht *et al.*, 2016). The present study documented that in addition to the higher specific fertility in individuals from artificial diet and reproductive plant tissue (except maize grains), there was a tendency to have a pronounced oviposition peak between the 5th and 6th day. This better reproductive performance (observed fecundity) is associated with the adequacy of plant tissues consumed in the larval stage, which in turn provided heavier larvae and consequently more suitable adults (Hemati *et al.*, 2012).

The adequacy of a host is directly related to the balance of its nutrients (amino acids, carbohydrates, lipids, fatty acids, vitamins, and minerals) and water, fundamental components for the proper performance of insects (Cohen and Crittenden, 2004; Behmer, 2009). In our study, the centesimal composition investigated the presence of 50 components, not common to all of them. Many of these components were detected below $0.01 \text{ g } 100 \text{ g}^{-1}$; nevertheless, their role in the biological development of *H. armigera* cannot be ruled out, as discussed in the literature (Parra *et al.*, 2009). Among the components found above $0.01 \text{ g } 100 \text{ g}^{-1}$, 14 were common to all diets, which significantly correlated with larval and pupal stage development times and/or pupal weight, except for magnesium.

Correlations between dietary components and insect development have been made only with artificial diets, in which composition can be estimated as a function of the ingredients used (Parra *et al.*, 2009; Cohen, 2015; Bisht *et al.*, 2018), without assessing denaturation losses and processing changes, especially during cooking (Cohen and Crittenden, 2004). Thus, the contribution of our study is to document that the centesimal composition analysis makes possible to correlate the development of *H. armigera* immatures with various components in natural and artificial diets. The most significant correlations (12) were found between dietary components and the duration of the larval development time. The correlations found are associated with digestion, absorption, and assimilation of nutrients and histogenesis of the larval stage (Scriber and Slansky, 1981; Moreau *et al.*, 2006). On the other hand, the lower number of significant correlations (5) in the pupal

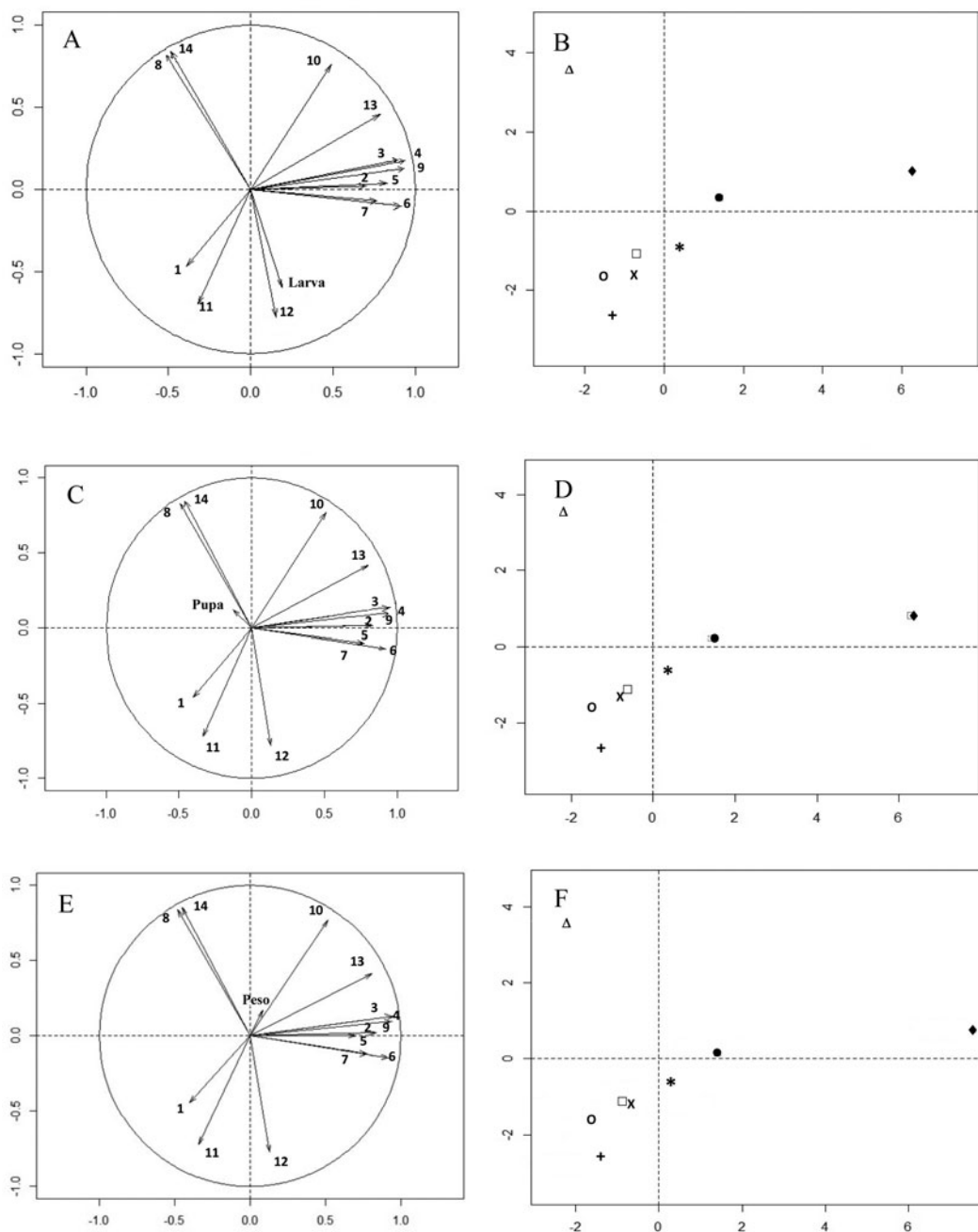


Figure 4. Correlation circles between dietary components (1–14) and length larval (A), pupal (C) and pupal weight (E) phases of *Helicoverpa armigera* and respective diet sorting diagrams (B, D, and F). Dietary parameters: 1 – carbohydrates, 2 – ashes, 3 – total dietary fiber, 4 – phosphorus, 5 – unsaturated fats, 6 – saturated fats, 7 – magnesium, 8 – manganese, 9 – potassium, 10 – total protein, 11 – sodium, 12 – energy value, 13 – zinc, 14 – free fatty acids. Diets: *cotton leaf, x – cotton boll, □ – maize leaf, + – maize grains, ○ – maize silk, • soybean leaf, ◆ – soybean pod, and Δ – artificial diet.

stage is associated with the fact that nutrients have already been assimilated and participate only in histolysis and non-histogenesis processes (Awmack and Leather, 2002; Moreau *et al.*, 2006).

Out of the 12 dietary components that significantly affect larval stage development time, half were negatively correlated, indicating a decrease in developmental time from their increments. Although they are a type of carbohydrate, dietary fibers have β-glycosidic bonds and promote intestinal mobility, helping to remove toxins from the body. Phosphorus is important for bioenergetic activities such as ATP formation. Manganese is an

enzymatic cofactor of hydrolysis, kinases, decarboxylases, and transferases reactions, as well as constituent of metalloenzymes. Zinc assists the enzymes responsible for protein synthesis and carbohydrate metabolism. Regarding the total proteins, obtained from various sources, in general, insects need adequate nitrogen for tissue development and maintenance of vital activities. Free fatty acids are associated with insect lipid metabolism, and because they have polar and non-polar parts, they can dissolve in water and other lipid compounds, influencing digestion, transport, and metabolism (Parra, 2009; Cohen, 2015).

Table 5. Spearman correlation between *Helicoverpa armigera* biological parameters and the main dietary components

Components	Length (days)				Weight (mg)	
	Larva		Pupa		Pupa	
	Correlation	Sig	Correlation	Sig	Correlation	Sig
Carbohydrates	0.035	0.514	0.086	0.104	0.244	<0.001
Ashes at 550°C	0.211	<0.001	-0.114	0.032	-0.142	0.007
Total dietary fiber	-0.158	0.003	-0.046	0.392	-0.186	<0.001
Phosphorus	-0.109	0.040	-0.040	0.456	-0.026	0.619
Unsaturated fats	0.246	<0.001	-0.077	0.151	0.345	<0.001
Saturated fat	0.245	<0.001	-0.110	0.038	-0.144	0.007
Magnesium	0.076	0.152	-0.100	0.060	-0.057	0.286
Manganese	-0.600	>0.001	0.122	0.022	-0.102	0.055
Potassium	0.490	>0.001	-0.147	0.005	-0.048	0.372
Total protein	-0.207	>0.001	-0.028	0.598	0.284	>0.001
Sodium	0.204	>0.001	-0.015	0.778	-0.157	0.003
Energy value	0.487	>0.001	-0.063	0.239	0.056	0.295
Zinc	-0.403	>0.001	0.015	0.781	0.098	0.064
Free fatty acids	-0.357	>0.001	0.106	0.047	0.167	0.003

The other components, in which a positive correlation occurred between their quantities and the duration of the larval period, six components stood out. The main saturated fats in vegetables are triacylglycerols, a glycerol molecule linked to three fatty acids. Because triacylglycerols are large molecules, insects need to expend more energy to metabolize them, affecting their development. The presence of double bonds in unsaturated fat molecules makes them more easily metabolized for use in insect metabolism. On the other hand, they can affect the stability of fats leading to oxidation and the formation of undesirable toxic substances (Cohen and Crittenden, 2004). Sodium and potassium act together to regulate water inside the cell and values of these elements higher than the metabolic needs of insects promote an imbalance of the homeostatic system.

As ashes include several elements, energy value is associated with different dietary components, making it difficult to understand their relationship, which can be individual or joint (Moreau *et al.*, 2006; Parra *et al.*, 2009; Cohen, 2015). The ashes are composed of oxides, sulfates, and phosphates, consisting of a combination of minerals whose isolated identification of the components is difficult, especially since they are not detectable by conventional analytical methods. Thus, it is not possible to identify which ash elements benefit or hinder insect development, with no exact determination of the need for each mineral and its influence on the insect organism. Finally, the joint action of these minerals is complex and there may have synergistic, antagonistic, or neutral behavior (Cohen and Crittenden, 2004).

A significant correlation between pupal weight with eight dietary components was observed, including carbohydrates, which had not correlated with larval and pupal duration. The dietary components that positively correlated with the pupae weight were carbohydrates, unsaturated fats, total protein, and free fatty acids. These components are associated with quantitative insect nutrition, meaning they are important for insects for both basic

nutritional requirements and the amount of food ingested, digested, assimilated, and converted into growth tissues (Behmer, 2009; Parra *et al.*, 2009; Cohen, 2015; Bisht *et al.*, 2018). On the other hand, ashes, dietary fiber, phosphorus, saturated fat, and sodium were negatively correlated with pupal weight. The negative correlation of ashes, dietary fiber, phosphorus, saturated fat, and sodium with pupal weight may be associated with a lower water content stored during the larval stage. The correlations enable an analysis of how the contents of each component influence in the biology of *H. armigera*, through centesimal composition. However, attention should be paid to all interactions between the components of different diets, including those not detected in the analyses and known to be essential for insect development (Scriber and Slansky, 1981; Moreau *et al.*, 2006; Behmer, 2009; Parra *et al.*, 2009; Cohen, 2015).

Cumulative percentages of variance (over 70%) demonstrated, through principal component analysis, the influence of each constituent on insect biological variables. In the correlation circles, the influential variables were the same ones highlighted by Pearson's correlation. The results presented in the sorting diagrams of *H. armigera* biological parameters demonstrate that the artificial diet and soybean pods differed greatly from the other diets. Considering the greater larval viability on the artificial diet, the proportions found of the main constituents of this substrate should be considered more adequate than the other diets (Behmer, 2009; Parra *et al.*, 2009). This nutrient balancing is essential for good insect development in laboratory rearing (Behmer, 2009; Bisht *et al.*, 2018).

In Lepidoptera, the major problems in nutrient conversion and assimilation efficiency are related to the amount of water present in different diets. Water is the most important component as it is a solvent for most compounds. The average moisture content required for most insects is approximately 70% (Moreau *et al.*, 2006; Cohen, 2015), and the three ways that insects obtain

water are through food, the environment, and metabolic water production. In general, the greater the amount of water disponible during the oxidation of protein, carbohydrate, and fat, the greater the efficiency of the conversion of these nutrients to insect development (Cohen, 2015). This could explain why some diets such as soybean pod and artificial diet differ from others in relation to the different biological parameters of *H. armigera*. For example, in soybean pods, an imbalance of the homeostatic system may have occurred due to the high potassium content found in this diet.

The unprecedented approach of this study consisted of identifying and quantifying the main components present in natural and artificial diets, in order to allow simultaneous comparisons with each other and with the development of insects. In addition, these associations expand knowledge about the relationship between diet composition and insect performance. Although correlations between the components evaluated and the development of *H. armigera* have been verified, other undetectable components, especially micronutrients, may have played a significant role in the evaluated diets. In general, the artificial diet was the most suitable substrate for the development of *H. armigera* compared to natural diets. However, under natural conditions, the variability of available plants should be considered. In addition, moths can select the most suitable hosts for oviposition, and their larvae can move to more suitable tissues on the same plant or even move between plants.

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