Special Supplement: Pulses

Resistance of chickpea genotypes to *Spodoptera frugiperda* (Lepidoptera: Noctuidae)¹

Frederico Landim Teixeira², André Cirilo de Sousa Almeida³, Márcio da Silva Araújo², Warley Marcos Nascimento⁴, Flávio Gonçalves de Jesus³

ABSTRACT

The fall armyworm, Spodoptera frugiperda (J. E. Smith, 1797) (Lepidoptera: Noctuidae), is a globally distributed polyphagous pest that threatens several crops, including chickpea. This study aimed to assess the antixenosis and antibiosis to S. frugiperda in chickpea genotypes (BRS Aleppo, BRS Cícero, BRS Kalifa, BRS Toro, Flip 10328C, Flip 10329C, Flip 10370C, Flip 10379C, and Flip 10161C). Antixenosis was evaluated using free-choice and no-choice tests with third-instar larvae, and antibiosis through biological and nutritional parameters. BRS Kalifa and Flip 10379C exhibited antixenosis to S. frugiperda, possibly associated with trichome density. The genotypes also influenced the larval and pupal duration, pupal weight, and total immature development, which were the most affected biological parameters. The larvae fed on Flip 10329C, Flip 10161C, Flip 10379C, BRS Cícero, BRS Toro, BRS Aleppo, and BRS Kalifa exhibited a longer larval duration, whereas the pupae from BRS Cícero, BRS Aleppo, BRS Kalifa, BRS Toro, and Flip 10161C showed a longer pupal duration. The larvae fed on BRS Kalifa, BRS Aleppo, BRS Toro, BRS Cícero, and Flip 10379C had the longest immature development time. Overall, Flip 10379C and BRS Aleppo negatively affected the development of S. frugiperda.

KEYWORDS: Cicer arietinum, plant resistance to insects, fall armyworm.

INTRODUCTION

Chickpea (*Cicer arietinum* L.) (Fabaceae) is one of the legumes most widely cultivated globally, with substantial economic and nutritional relevance in several countries, particularly in Asia and the Middle East (Kaur & Prasad 2021).

RESUMO

Resistência de genótipos de grão-de-bico a Spodoptera frugiperda (Lepidoptera: Noctuidae)

A lagarta-do-cartucho, Spodoptera frugiperda (J. E. Smith, 1797) (Lepidoptera: Noctuidae), é uma praga polífaga de distribuição global que ameaça diversas culturas, incluindo o grão-de-bico. Objetivou-se avaliar a antixenose e antibiose a S. frugiperda em genótipos de grão-de-bico (BRS Aleppo, BRS Cícero, BRS Kalifa, BRS Toro, Flip 10328C, Flip 10329C, Flip 10370C, Flip 10379C e Flip 10161C). A antixenose foi avaliada utilizando-se testes com e sem chance de escolha com larvas de terceiro instar, e a antibiose por meio de parâmetros biológicos e nutricionais. BRS Kalifa e Flip 10379C exibiram antixenose a S. frugiperda, possivelmente associada à densidade de tricomas. Os genótipos também influenciaram na duração larval e pupal, peso da pupa e desenvolvimento imaturo total, que foram os parâmetros biológicos mais afetados. As larvas alimentadas com Flip 10329C, Flip 10161C, Flip 10379C, BRS Cícero, BRS Toro, BRS Aleppo e BRS Kalifa apresentaram maior duração larval, enquanto as pupas provenientes de BRS Cícero, BRS Aleppo, BRS Kalifa, BRS Toro e Flip 10161C mostraram maior duração pupal. As larvas alimentadas com BRS Kalifa, BRS Aleppo, BRS Toro, BRS Cícero e Flip 10379C apresentaram maior tempo de desenvolvimento imaturo. De modo geral, Flip 10379C e BRS Aleppo afetaram negativamente o desenvolvimento de S. frugiperda.

PALAVRAS-CHAVE: Cicer arietinum, resistência de planta a inseto, lagarta-do-cartucho.

In Brazil, chickpea cultivation is expanding as a second-season crop option in the Cerrado (Brazilian Savanna), and consumer demand has increased, largely due to the introduction of cultivars adapted to this region (Nascimento et al. 2017, Avelar et al. 2018). However, the national production remains limited and relies heavily on imports from countries

¹Received: Sep. 05, 2025. Accepted: Nov. 03, 2025. Published: Dec. 04, 2025. DOI: 10.1590/1983-40632025v5583867. Universidade Estadual de Goiás, Ipameri, GO, Brazil. *E-mail/ORCID*: fredericolt@gmail.com/0009-0004-3707-7957; marcio.araujo@ueg.br/0000-0002-0811-960X.

Instituto Federal Goiano, Urutaí, GO, Brazil. *E-mail/ORCID*: andre.almeida@ifgoiano.edu.br/0000-0001-9786-2990; flavio.jesus@ifgoiano.edu.br/0000-0001-6881-5431.

Empresa Brasileira de Pesquisa Agropecuária (Embrapa Hortaliças), Brasília, DF, Brazil. *E-mail/ORCID*: warley.nascimento@embrapa.br/0000-0002-6235-0917.

such as Mexico and Argentina (Nascimento et al. 2016).

Insect pests, especially lepidopteran larvae, can significantly reduce chickpea yields and increase quantitative and qualitative grain losses (Correa et al. 2021, Borella Junior et al. 2022). *Helicoverpa armigera* (Hbn.) (Lepidoptera: Noctuidae) is the primary chickpea pest worldwide and has been reported in several regions as a damaging agent of immature grains (Sharma et al. 2020). *Chloridea virescens* (F.), *Helicoverpa zea* (Boddie), *H. armigera*, and *Chloridea subflexa* (Guenee) (Lepidoptera: Noctuidae) are the main key pests of chickpea in Brazil (Borella Junior et al. 2022, Reyes et al. 2023).

Because chickpea is increasingly incorporated into crop-rotation systems in Brazil, additional insect pests have become associated with yield losses in this crop, including Spodoptera frugiperda (J. E. Smith, 1779) (Lepidoptera: Noctuidae). S. frugiperda is a major pest of several crops in Brazil, including corn, soybean, bean, cotton, rice, and sorghum (Paiva et al. 2018, Correa et al. 2021, Silva et al. 2021). With the expansion of chickpea cultivation in the Cerrado, S. frugiperda has emerged as a secondary chickpea pest (Correa et al. 2021). Other species such as Spodoptera eridania (Cramer) and Spodoptera cosmioides (Walker) (Lepidoptera: Noctuidae) have also been observed feeding on chickpea, and damages caused by the Spodoptera complex is primarily associated with plant defoliation during both vegetative and reproductive stages (Correa 2019).

Given this scenario, pest populations in chickpea crops in the Cerrado tend to increase, and control methods aligned with integrated pest management are required to reduce the reliance on synthetic insecticides. Moreover, only a few synthetic insecticides are currently registered in Brazil for controlling *S. frugiperda* in chickpea (Agrofit 2025).

Plant resistance to insects is a promising strategy in this context, because it is compatible with other control tactics, including biological and chemical control. Additionally, the effects of resistant plants are persistent and cumulative, impairing pest biological performance without adverse environmental impacts (Seifi et al. 2013, Baldin et al. 2019).

Plant resistance to insects encompasses three mechanisms: antixenosis, antibiosis, and tolerance (Baldin et al. 2019). Antixenosis is typically

associated with the plant's ability to prevent or reduce pest colonization, expressed through physical, morphological, or chemical defenses. Resistant plants may negatively affect insect host-selection behavior, reducing oviposition, feeding, or sheltering (Seifi et al. 2013, Baldin et al. 2019). Antibiosis occurs when the plant negatively affects insect biological traits, such as prolonging developmental stages, causing deformities, altering sex ratios, and reducing larval and pupal weight, survival, adult longevity, or fertility (Sharma et al. 2005, Almeida et al. 2017). Tolerance refers to a plant's genetic capacity to withstand pest infestation and recover after injury by producing new vegetative or reproductive tissues (Seifi et al. 2013, Paiva et al. 2018) or by improving physiological parameters such as reactive oxygen species detoxification, gasexchange rates, and chlorophyll content (Jesus et al. 2018, Almeida et al. 2021).

Sources of resistance in chickpea have been linked to the presence of glandular trichomes, as observed in BRS Kalifa and BRS Toro, which exhibit high trichome density (Correia et al. 2021), and to chemical exudates containing organic acids (Narayanamma et al. 2013, Rachappa et al. 2019), such as the higher oxalic and malic acid content found in Jamu 96 and BRS Toro (Borella Junior et al. 2022).

Antibiosis has also been documented as a resistance mechanism in chickpea genotypes. For instance, Nacional 29 caused high larval and pupal mortality of *S. frugiperda*, whereas BRS Aleppo led to extended larval development, reduced larval weight, and prolonged pupal duration (Correa et al. 2021). *Chloridea virescens* larvae exhibited the lowest weights when fed on BRS Cícero, BRS Toro, and BRS Kalifa (Borella Junior et al. 2022).

Plant resistance to insects is therefore a key tool in chickpea integrated pest management because of its compatibility with other management tactics (Bueno et al. 2011, Baldin et al. 2019). However, few studies have screened chickpea genotypes for resistance to insect pests, and available research predominantly focuses on pod borers such as *H. armigera* and *C. virescens* (Narayanamma et al. 2013, Rachappa et al. 2019, Borella Junior et al. 2022). In this context, antixenosis (attractiveness) and antibiosis were evaluated in chickpea genotypes in response to the fall armyworm *S. frugiperda*, assessing larval growth, survival, nutritional performance through consumption, and their association with resistance expression.

MATERIAL AND METHODS

The experiments were conducted at the integrated pest management laboratory of the Instituto Federal Goiano (Urutaí, Goiás state, Brazil). The chickpea cultivars BRS Aleppo, BRS Cícero, BRS Kalifa, and BRS Toro had been previously screened as potentially resistant to *S. frugiperda* and *C. virescens* (Correa et al. 2021, Borella Junior et al. 2022), with BRS Aleppo considered the standard susceptible genotype. The genotypes Flip 10-328C, Flip 10-329C, Flip 10-370C, Flip 10-379C, and Flip 10-161C were included to evaluate resistance to *S. frugiperda*. All chickpea genotypes were obtained from the germplasm bank of the breeding program at the Embrapa Hortaliças (Brasília, Federal District, Brazil).

Seeds were sown in 5-L pots containing a substrate (soil, sand, and organic compost at a 3:1:1 ratio) corrected and fertilized according to chickpea cultivation guidelines (Nascimento et al. 2016). Plants were maintained in a greenhouse under natural conditions and irrigated as needed.

Adults of S. frugiperda were maintained in polyvinyl chloride (PVC) tubes (10 cm in diameter × 21.5 cm in height) internally lined with white paper as an oviposition substrate. Adults were fed a 10 % honey solution and a vitamin solution containing 1 % methylparaben as an antifungal agent. Eggs were collected and transferred to plastic pots (14 cm in diameter × 9 cm in height), and hatched larvae were individually reared on artificial diet (Greene et al. 1976) in tray cells (CM & CM Comércio de Plásticos, São Paulo, SP, Brazil) until pupation. Pupae were sexed, separated into pairs (15 males and 15 females), and placed back into PVC cages for adult emergence and mating. Colony maintenance was conducted under controlled laboratory conditions (25 \pm 2 °C, 70 ± 10 % of relative humidity, and 12:12 h light/ dark photoperiod).

For the free-choice test, an arena containing equidistant whole chickpea plants (30 days after emergence - DAE) was placed inside a plastic cage (14 cm in diameter × 20 cm in height; 32 L in volume) covered with voile fabric to prevent insect escape (Correia et al. 2021). Nine third-instar *S. frugiperda* larvae were released at the center of the arena, and the number of larvae feeding on each genotype was recorded at 1, 5, 10, 15, 30, 60, 120, 360, 720, and 1,440 min to assess feeding non-preference. A mean

reference value was calculated from all evaluation times. The experiment followed a randomized block design, with 9 treatments (genotypes) and 10 replicates (arenas).

In the no-choice test, plants of each genotype were grown individually in containers (Correia et al. 2021) and infested with one third-instar *S. frugiperda* larva. The containers were kept under the same laboratory conditions used for the colony. The number of insects feeding on each plant was recorded at the same times used in the free-choice test. The experiment followed a completely randomized design, with 9 treatments and 10 replicates (pots).

The preference index (PI) was calculated according to Kogan & Goeden (1970), using the equation: PI = 2C/(C + S), where C is the number of insects located on the evaluated genotype and S the number of insects on the standard susceptible genotype (BRS Aleppo in the free-choice test and Flip 10161C in the no-choice test).

Glandular and non-glandular trichomes were quantified at 30 DAE (Borella Junior et al. 2022), using a fully randomized design with 9 treatments and 10 replicates.

Newly hatched S. frugiperda larvae were placed in Petri dishes (9 cm in diameter) containing moistened filter paper and sealed with polyethylene film. The larvae were fed leaves from the apical region of each genotype, replaced daily or after consumption, and remained in the Petri dishes until pupation, after which leaf supply was terminated. After adult emergence (adults were not fed), the insects were transferred to 150-mL plastic containers until completing their life cycle. The following biological variables were evaluated: a) larval stage: duration, survival, and larval weight at 10 days; b) pupal stage: duration, weight at 24 h, and survival; c) total cycle: duration and survival; d) adult stage: longevity. The experiment followed a completely randomized design with 9 treatments (cultivars and genotypes) and 30 replicates.

Spodoptera frugiperda larvae (3rd instar) were weighed, individualized in Petri dishes (1.5 × 9.0 cm in diameter), and supplied daily with leaf tissue from each chickpea genotype for 7 days. Nutritional indices of *S. frugiperda* were measured following the methodology of Correia et al. (2021).

The quantitative nutritional indices of the larval phase were calculated according to Waldbauer (1968) and Scriber & Slansky Junior (1981).

The following indices were evaluated: relative consumption rate (RCR = $I/\overline{B} \times T$ - g/g/d); relative metabolic rate (RMR = $M/\overline{B} \times T$ - g/g/d); relative growth rate (RGR = $B/\overline{B} \times T$ - g/g/d); approximate digestibility [AD = (I - F)/I × 100]; conversion efficiency of ingested food [EIF = (B/I) × 100]; and conversion efficiency of digested food [EDF = $B/(I - F) \times 100$]. In these equations: T is the feeding period (days); I the food consumed during T (g); B the larval weight gain during T (g); F the feces produced during T (g); M the food used in metabolic processes [M = (I - F) - B]; and \overline{B} the mean larval weight during T (g). The experiment followed a completely randomized design, with 9 treatments and 10 replicates.

An analysis of variance model was fitted to the data from each experiment. Residual normality and homoscedasticity were verified using the Shapiro-Wilk and Bartlett tests. When assumptions were not met, the Box-Cox method was applied to identify an optimal transformation. Transformed data were then used to fit the analysis of variance models, and means were compared using the Scott-Knott test (α = 0.05) (R Core Team 2023; Scott-Knott package). Means were back-transformed for presentation. Hierarchical cluster analysis (unweighted pair group method with arithmetic mean - UPGMA, using Euclidean distance) was conducted to determine resistance patterns among the chickpea genotypes (R Core Team 2023; biotools package).

The preference index and standard error for each genotype were calculated and then compared to 1.0 [neutral - susceptible genotype - BRS Toro (free-choice test) and Flip 10161C (no-choice test)], using the Student's t test ($\alpha = 0.05$). The genotypes

that presented indices statistically different from 1.0 were classified as either deterrent (< 1.0) or stimulating (> 1.0).

RESULTS AND DISCUSSION

The analysis of the free-choice test did not detect significant differences among the chickpea genotypes, regarding non-preference to *S. frugiperda* (Table 1). In the no-choice test, *S. frugiperda* was less attracted to BRS Kalifa, Flip 10328C, Flip 10329C, Flip 10379C, BRS Aleppo, Flip 10370C, and Flip 10161C, when compared with BRS Toro and BRS Cícero (Table 1). No significant differences were observed in the preference index for either the free-choice or no-choice tests among the chickpea genotypes, when compared with the standard susceptible genotypes (Table 1).

The number of glandular trichomes differed significantly among the evaluated genotypes. BRS Kalifa (33.4), BRS Toro (33.3), Flip 10379C (30.4), and BRS Aleppo (30.7) exhibited the highest trichome densities, whereas BRS Cícero (19.1) showed the lowest one (Table 1).

Our results indicate antixenosis in BRS Kalifa, Flip 10328C, Flip 10329C, Flip 10379C, Flip 10370C, Flip 10161C, and BRS Aleppo. Antixenosis is commonly associated with morphological traits such as trichome density, leaf coloration, and physical or chemical attributes that influence insect behavior related to oviposition, feeding, and shelter (Seifi et al. 2013).

The chickpea cultivars BRS Kalifa and BRS Aleppo were among the least attractive to

Table 1. Preference (mean ± SE) and preference index in free-choice and no-choice tests, and trichome densities (counts within 9 mm ²).

Genotypes	Free-choice test		No-choice test —		Glandular trichome
	Preference	Index (p-value)	Preference	Index (p-value)	Giandular tricnome
Flip 10328C	0.6 ± 0.1	1.1(0.49)	$0.7 \pm 0.1 \text{ b*}$	0.9(0.45)	$26.8 \pm 1.0 \text{ b}$
BRS Cícero	0.5 ± 0.1	1.1(0.55)	$1.3 \pm 0.2 \text{ a}$	1.2(0.13)	$19.2 \pm 1.8 c$
BRS Toro	0.5 ± 0.1	1.00	1.1 ± 0.1 a	1.1(0.34)	$33.3 \pm 1.3 \text{ a}$
BRS Aleppo	0.5 ± 0.1	1.0(0.94)	$0.9 \pm 0.1 \text{ b}$	1.1(0.38)	$30.7 \pm 1.4 a$
Flip 10161C	0.5 ± 0.1	0.9(0.67)	$0.9 \pm 0.1 \text{ b}$	1.00	$26.8 \pm 1.1 \text{ b}$
Flip 10329C	0.4 ± 0.1	1.9(0.68)	$0.6 \pm 0.1 \text{ b}$	0.8(0.36)	$26.2 \pm 1.4 \text{ b}$
Flip 10370C	0.4 ± 0.1	0.9(0.83)	$0.7 \pm 0.1 \text{ b}$	0.9(0.45)	$27.6 \pm 1.3 \text{ b}$
BRS Kalifa	0.4 ± 0.1	0.9(0.66)	$0.6 \pm 0.1 \text{ b}$	0.8(0.25)	$33.4 \pm 1.0 a$
Flip 10379C	0.4 ± 0.1	0.8(0.33)	$0.6 \pm 0.9 \text{ b}$	0.9(0.86)	$30.4 \pm 0.8 a$
F (treatment)	0.29	-	2.59	-	11.92
p-value	0.965	-	0.008	-	0.001

^{*} Means followed by the same letter within a column do not differ by the Scott-Knot test at 5 %. SE: standard error. ** Calculated according to Kogan & Goeden (1970).

S. frugiperda, likely due to their higher densities of glandular trichomes. Trichomes are a welldocumented defensive trait in several crops and constitute an important mechanism of resistance against insect pests (Rachappa et al. 2019). In chickpea, a high trichome density acts as a physical barrier that reduces caterpillar feeding (Golla et al. 2018, Borella Junior et al. 2022). Helicoverpa armigera larvae exhibit reduced feeding on plants with high pubescence, and both glandular and nonglandular trichomes have been associated with antixenosis against C. virescens oviposition and attractiveness (Golla et al. 2018, Borella Junior et al. 2022). However, trichomes alone may not fully explain antixenosis to S. frugiperda in chickpea, as other factors such as leaf color, tissue hardness, or chemical compounds including malic and oxalic

acids may also contribute (Borella Junior et al. 2022).

Previous studies also support the presence of antixenosis in chickpea. For example, the genotypes Jamu 96, BRS Cícero, BRS Toro, BRS Aleppo, and FLIP 02-23C were less preferred by *S. frugiperda* larvae, whereas Nacional 29, BRS Cícero, BRS Toro, and 003UP exhibited antixenosis to *Spodoptera eridania* (Correa 2019, Correa et al. 2021).

The development of *S. frugiperda* was significantly influenced by the chickpea genotypes. Larval and pupal development time, pupal weight, and the overall immature development period were affected (Tables 2 and 3). The larval development time was longer in larvae fed on Flip 10329C, Flip 10161C, Flip 10379C, BRS Cícero, BRS Toro, BRS Aleppo, and BRS Kalifa, and the pupal development

Table 2. Larval and pupal development time (mean \pm SE) and longevity of adult (days), and larval and pupal weight (g) of *Spodoptera frugiperda* fed on the chickpea genotypes.

	Larval		Pupal		T '4 C 1 14
Genotypes	Development time	Weight	Development time	Weight	Longevity of adults
Flip 10328C	$12.5 \pm 0.2 \text{ b}$	0.23 ± 0.02	$10.5 \pm 0.1 \text{ b}$	0.15 ± 0.02 b	7.3 ± 0.6
BRS Cícero	13.6 ± 0.7 a	0.27 ± 0.02	11.8 ± 0.3 a	$0.16 \pm 0.01 \text{ b}$	8.7 ± 1.4
BRS Toro	$14.5 \pm 1.2 a$	0.29 ± 0.03	11.2 ± 0.3 a	$0.15 \pm 0.01 \text{ b}$	8.3 ± 0.9
BRS Aleppo	15.3 ± 1.7 a	0.26 ± 0.01	11.8 ± 0.3 a	$0.12 \pm 0.01 \text{ b}$	9.0 ± 1.5
Flip 10161C	13.1 ± 0.3 a	0.33 ± 0.01	11.1 ± 0.2 a	0.17 ± 0.01 a	7.5 ± 0.7
Flip 10329C	13.0 ± 0.1 a	0.27 ± 0.02	$10.8 \pm 0.7 \text{ b}$	$0.15 \pm 0.01 \text{ b}$	6.6 ± 0.7
Flip 10370C	$12.1 \pm 0.1 \text{ b}$	0.23 ± 0.02	$10.1 \pm 0.5 \text{ b}$	0.17 ± 0.01 a	6.1 ± 1.3
BRS Kalifa	$16.3 \pm 1.5 a$	0.31 ± 0.02	11.9 ± 0.4 a	$0.12 \pm 0.01 \text{ b}$	8.3 ± 0.6
Flip 10379C	$13.3 \pm 0.8 \text{ a}$	0.27 ± 0.02	$10.8 \pm 0.2b$	$0.15 \pm 0.01 \text{ b}$	7.6 ± 0.5
F (treatment)	2.13	1.60	2.88	3.09	1.10
p-value	0.048	0.118	0.004	0.003	0.380

^{*} Means followed by the same letter within a column do not differ by the Scott-Knot test at 5 %. SE: standard error.

Table 3. Larval (mean ± SE), pre-pupal and pupal viability (%) and total cycle (days) of *Spodoptera frugiperda* fed on chickpea genotypes.

Genotypes	Larval survival	Pre-pupal survival	Pupal survival	Immature development time
Flip 10328C	80.0 ± 13.3	60.0 ± 16.3	30.0 ± 15.2	$31.8 \pm 10.7 \text{ b}$
BRS Cícero	80.0 ± 13.3	60.5 ± 16.3	60.5 ± 16.3	$36.3 \pm 1.0 \text{ a}$
BRS Toro	80.0 ± 13.3	80.0 ± 13.3	70.0 ± 15.2	$36.2 \pm 1.4 \text{ a}$
BRS Aleppo	90.0 ± 10.0	60.0 ± 16.3	33.3 ± 15.2	$37.3 \pm 2.4 \text{ a}$
Flip 10161C	90.0 ± 10.0	90.0 ± 10.0	66.7 ± 16.3	$33.9 \pm 0.8 \text{ b}$
Flip 10329C	60.0 ± 16.3	40.0 ± 16.3	30.0 ± 15.2	$32.7 \pm 0.4 \text{ b}$
Flip 10370C	90.0 ± 10.0	80.0 ± 13.3	33.3 ± 16.3	$30.9 \pm 1.3 \text{ b}$
BRS Kalifa	95.0 ± 08.3	90.0 ± 10.0	60.0 ± 16.3	$38.8 \pm 3.2 \; a$
Flip 10379C	90.0 ± 10.0	60.0 ± 16.3	55.5 ± 16.6	$34.5 \pm 0.9 \text{ b}$
F (treatment)	0.95	1.36	1.08	24.13
p-value	0.474	0.225	0.386	0.001

^{*} Means followed by the same letter within a column do not differ by the Scott-Knot test at 5 %. SE: standard error.

time was shorter in larvae fed on Flip 10370C, Flip 10328C, Flip 10329C, and Flip 10379C. All genotypes resulted in lower pupal weights, when compared with Flip 10161C and Flip 10370C (Table 2).

The genotypes also influenced the immature development time of *S. frugiperda*. Larvae fed on BRS Kalifa, BRS Aleppo, BRS Toro, and BRS Cícero had the longest immature development periods. No significant differences were detected among the genotypes for survival of *S. frugiperda* (Table 3).

The biology of *S. frugiperda* was negatively affected when the larvae fed on Flip 10329C, Flip 10161C, Flip 10379C, BRS Cícero, BRS Toro, BRS Aleppo, and BRS Kalifa. Notably, BRS Cícero, BRS Toro, BRS Aleppo, and BRS Kalifa prolonged the larval and pupal phases and the overall immature development period. Extended larval development, and consequently longer immature stages, typically indicates inadequate nutritional quality or presence of chemical compounds that confer resistance to the plant (Almeida et al. 2017, Silva et al. 2021).

Antibiosis has been reported in chickpea genotypes. For instance, IG 70012, IG 70022, IG 70018, IG 70006, PI 599046, PI 599066 (Cicer bijugum), IG 69979 (C. cuneatum), PI 568217, PI 599077 (C. judaicum), and ICCW 17148 (C. microphyllum) have demonstrated antibiosis to H. armigera (Golla et al. 2018). Likewise, the chickpea accessions ICC 17257, IG 70002, IG 70003, IG 70012 (C. bijugum), IG 69948 (C. pinnatifidum), IG 69979 (C. cuneatum), IG 70032, IG 70033, IG 70038, and IG 72931 (C. judaicum) reduced the larval weight in H. armigera (Sharma et al. 2005).

Antibiosis occurs when normal plant feeding causes adverse biological effects that directly or indirectly impair insect development and/or reproductive potential (Silva et al. 2021). This mechanism results from secondary metabolites or physical and structural barriers such as trichomes. Chickpea plants contain organic acids including oxalic, malic, and citric acids, and both oxalic and malic acids have been associated with antibiosis in this crop (Narayanamma et al. 2013, Golla et al. 2018, Borella Junior et al. 2022).

The chickpea genotypes significantly influenced the following nutritional indices of *S. frugiperda*: weight gain (mg), ingested food (mg), relative growth rate (mg mg⁻¹ day⁻¹), relative consumption rate (mg mg⁻¹ day⁻¹), approximate digestibility (%), efficiency of ingested food (%), efficiency of digested food (%), and metabolic cost (%) (Tables 4 and 5).

The lowest weight gain (F = 3.80; df = 8; p = 0.001) occurred in larvae fed on Flip 10379C, Flip 10329C, BRS Aleppo, BRS Cícero, and BRS Toro, whereas the remaining genotypes yielded higher values. The lowest food intake (F = 9.73; df = 8; p = 0.001) was recorded for BRS Aleppo, Flip 10379C, Flip 10161C, and Flip 10370C, whereas the highest values were obtained for BRS Toro, BRS Kalifa, and Flip 10329C. Feeding on Flip 10379C, Flip 10329C, BRS Aleppo, and BRS Cícero resulted in reduced relative growth rate (F = 4.85; df = 8; p = 0.001). In addition, larvae fed on BRS Aleppo, Flip 10328C, Flip 10161C, BRS Cícero, and Flip 10379C exhibited the lowest relative consumption rate values (F = 2.74; df = 8; p = 0.010) (Table 4).

Table 4. Nutritional indices ((mean \pm SE) of <i>Spodoptera</i>	<i>i frugiperda</i> (Lepidoptera	: Noctuidae) fed o	n chickpea genotypes.

Genotypes	WG	IF	RGR	RCR
Flip 10328C	$14.78 \pm 1.6 a$	$74.63 \pm 7.5 \text{ b}$	0.12 ± 0.01 a	$0.61\pm0.03\;b$
BRS Cícero	$8.83 \pm 1.5 \text{ b}$	$70.78 \pm 4.9 \; b$	$0.08\pm0.01\;b$	$0.67\pm0.05\;b$
BRS Toro	$10.81 \pm 1.5 \text{ b}$	$106.73 \pm 2.7 \text{ a}$	$0.10\pm0.01~a$	$1.09\pm0.02~a$
BRS Aleppo	$8.17 \pm 1.3 \text{ b}$	$46.43 \pm 4.5 \text{ c}$	$0.08 \pm 0.01~b$	$0.48 \pm 0.04 \; b$
Flip 10161C	13.01 ± 1.6 a	$52.86 \pm 7.7 \text{ c}$	$0.14\pm0.01~a$	$0.66\pm0.05\;b$
Flip 10329C	$8.56 \pm 1.1 \text{ b}$	$88.89 \pm 7.2~a$	$0.08\pm0.02\;b$	$0.91\pm0.04~a$
Flip 10370C	$14.86 \pm 0.9 \ a$	$57.04 \pm 3.8 \text{ c}$	0.13 ± 0.01 a	0.87 ± 0.06 a
BRS Kalifa	$13.13 \pm 1.3 a$	$100.54 \pm 6.8 a$	0.11 ± 0.01 a	$0.87\pm0.05~a$
Flip 10379C	$6.04\pm1.8\;b$	$52.09 \pm 9.8 \text{ c}$	$0.07\pm0.01\;b$	$0.74 \pm 0.05 \; b$
F (treatment)	3.80	9.73	4.85	2.74
p-value	0.001	0.001	0.001	0.010

^{*} Means followed by the same letter within a column do not differ by the Scott-Knot test at 5 %. SE: standard error. WG: weight gain (mg); IF: ingested food (mg); RGR: relative growth rate (mg mg⁻¹ day⁻¹); RCR: relative consumption rate (mg mg⁻¹ day⁻¹).

Approximate digestibility (F = 18.49; df = 8; p = 0.001) was lower for Flip 10370C, BRS Aleppo, Flip 10379C, Flip 10161C, and Flip 10328C. Efficiency of ingested food (F = 3.50; df = 8; p = 0.002) was lower in Flip 10329C, Flip 10379C, BRS Toro, and BRS Cícero. Efficiency of digested food (F = 8.12; df = 8; p = 0.001) was higher in all genotypes, except BRS Aleppo and Flip 10161C. The larvae fed on Flip 10161C and BRS Aleppo exhibited the lowest metabolic cost (%) values (F = 13.84; df = 8; p = 0.001) (Table 5).

The chickpea genotypes were clustered into four resistance groups by UPGMA (Euclidian distance) (Figure 1). Group I (BRS Aleppo and BRS Kalifa) was classified as resistant; group II (BRS Cícero and BRS Toro) as moderately resistant; group III (Flip 10161C, Flip 10329C, and Flip 10379C) as susceptible; and group IV (Flip 10328C and Flip 10370C) as highly susceptible. All evaluated biological parameters were used to define these groups.

The reduced consumption and nutritional indices (weight gain, ingested food, relative growth

Table 5. Nutritional indices (mean ± SE) of Spodoptera frugiperda (Lepidoptera: Noctuidae) fed on chickpea genotypes.

Genotypes	AD	EIF	EDF	MC
Flip 10328C	$42.02 \pm 3.84 \ c^*$	19.99 ± 1.26 a	$48.60 \pm 4.47 \ b$	$51.4 \pm 4.47 \text{ b}$
BRS Cícero	$55.49 \pm 6.25 b$	$11.92 \pm 3.86 \ b$	$21.07 \pm 2.38 \ b$	$78.9 \pm 2.38 \; a$
BRS Toro	$67.70 \pm 2.80 \text{ a}$	$9.48 \pm 1.53 \ b$	$13.50 \pm 1.73 \text{ b}$	$86.4 \pm 1.73 \ a$
BRS Aleppo	$21.84 \pm 1.92 d$	$17.34 \pm 2.00 a$	64.80 ± 17.50 a	$39.8 \pm 17.50 \ d$
Flip 10161C	$30.63 \pm 3.84 d$	19.77 ± 1.69 a	$67.40 \pm 8.97 a$	$41.4\pm8.97\ d$
Flip 10329C	63.44 ± 3.67 a	$9.04 \pm 1.09 \ b$	$14.80 \pm 1.59 \text{ b}$	$85.1 \pm 1.59 a$
Flip 10370C	$19.13 \pm 3.65 d$	$15.34 \pm 1.30 a$	$45.70 \pm 3.51 \text{ b}$	$54.2 \pm 3.51 \text{ b}$
BRS Kalifa	$52.30 \pm 3.36 b$	$13.92 \pm 1.30 a$	$22.90 \pm 2.68 \ b$	$77.0 \pm 2.68 \ a$
Flip 10379C	$28.64 \pm 1.86 \ d$	$9.38 \pm 1.71 \ b$	$26.50 \pm 3.52 \ b$	$73.4 \pm 3.52 \text{ a}$
F (treatment)	18.49	3.50	8.12	13.84
p-value	0.001	0.002	0.001	0.001

^{*} Means followed by the same letter within a column do not differ by the Scott-Knot test at 5 %. SE: standard error. AD: approximate digestibility (%); EIF: efficiency of ingested food (%); EDF: efficiency of digested food (%); MC: metabolic cost (%).

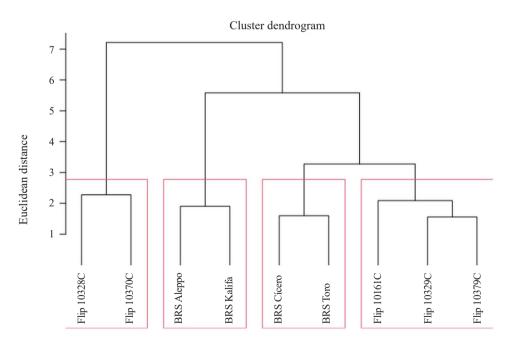


Figure 1. Dendrogram based on biological variables of *Spodoptera frugiperda* larvae in different chickpea genotypes. Hierarchical cluster analysis was performed using the unweighted pair group method with arithmetic mean (UPGMA) with Euclidean distance as the dissimilarity measure.

rate, and relative consumption rate) in larvae fed on Flip 10379C and BRS Aleppo indicate that these genotypes contain compounds that inhibit the S. frugiperda development. Antibiosis in Flip 10379C and BRS Aleppo was evidenced by poor insect performance and an extended immature stage. Generally, reduced food intake decreases the insect size and weight and prolongs the life cycle (Hemati et al. 2012). Plants containing allelochemicals or insufficient nutrient availability can negatively affect insect development. The low relative consumption rate values observed in larvae feeding on Flip 10379C and BRS Aleppo may reflect allelochemical presence or interactions between nutrients and allelochemicals, suggesting that these genotypes are less suitable hosts for S. frugiperda. The multivariate analysis (UPGMA cluster analysis) effectively grouped the genotypes by resistance level, corroborating the univariate analysis (Pitta et al. 2010).

CONCLUSIONS

- 1. Among the chickpea genotypes exhibiting resistance traits, BRS Aleppo showed the lowest efficiency of digested food values, suggesting that it likely contains metabolic compounds that inhibit the *Spodoptera frugiperda* development;
- 2. Flip 10379C and BRS Aleppo possess resistance characteristics that negatively affect the development of *S. frugiperda*.

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