SOCIEDADE BRASILEIRA DE ENTOMOLOGIA
FUNDADA EM 1937

REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

Resistance of rice genotypes to fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae)

Cinthia Luzia Teixeira Silva[1], Fernanda Correa[1], André Cirilo de Sousa Almeida[2], Márcio da Silva Araújo[1], José Alexandre de Freitas Barrigossi[3], Flávio Gonçalves de Jesus[2]*

[1]*Universidade Estadual de Goiás, Campus de Ipameri, Ipameri, GO, Brasil.*
[2]*Instituto Federal Goiano, Campus Urutaí, Urutaí, GO, Brasil.*
[3]*Embrapa Arroz e Feijão, Santo Antônio de Goiás, GO, Brasil.*

ARTICLE INFO

Article history:
Received 23 February 2021
Accepted 20 September 2021
Available online 18 October 2021
Associate Editor: Ricardo Siqueira da Silva

Keywords:
Oryza sativa
Host plant resistance
Antixenosis
Antibiosis

ABSTRACT

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is an important rice pest which consumes leaf area during all phases of plant development. The objective of this study was to identify rice genotypes that provide antixenosis and antibiosis to fall armyworm. Antixenosis was investigated by measuring non-preference in free-choice and no-choice tests while antibiosis was determined by measuring biological parameters and nutritional indices of *S. frugiperda* in twelve rice genotypes. The genotype Miúdo Branco showed antixenosis to *S. frugiperda*, whereas the genotypes IR 64 and Bacaba Branco showed antibiosis to *S. frugiperda* by affecting insect development and prolonging insect life cycle. Insects that fed on Bacaba Branco genotype demonstrated the lowest nutritional indices. Since Miúdo Branco, IR 64 and Bacaba Branco showed moderate resistance, rice producers could use these genotypes as part of a control strategy for *S. frugiperda*.

Introduction

Rice (*Oryza sativa* L.) is an important cereal that feeds a significant part of the world population (Stout et al., 2009). Rice yield and quality are severely affected by insect pests (Jiang et al., 2014). The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is native to tropical and subtropical America; however, it has spread rapidly to other continents, and became an invasive pest in African countries in 2016 (Goergen et al., 2016) and has since been confirmed in Asian countries such as India (Mallapur et al., 2018) and China (Jing et al., 2020). Consequently, it is considered one of the most important agricultural pests in the world (Wang et al., 2020). *Spodoptera frugiperda* is a polyphagous pest that feeds on as many as 353 plant species and is a key pest in maize, rice, sorghum, cotton, and sugarcane (Montezano et al., 2018).

Spodoptera frugiperda is a sporadic pest in rice fields that mainly appears during the early season in unflooded systems (Kraus and Stout, 2019). The pest damages rice crops by destroying or weakening new plants, cutting culms to the ground, defoliating and damaging flowers and panicles and severely injuring small seedlings that may necessitate replanting (Busato et al., 2005; Nascimento et al., 2014; Kraus and Stout, 2019).

The main methods for controlling *S. frugiperda* in rice crops are synthetic insecticides (Busato et al., 2006). Nevertheless, alternative methods can be used such as flooding the rice crop (flooded systems), increasing natural agents such as parasitoids and predators, applications of *Beauveria bassiana* as a biological insecticide and applications of insecticidal proteins produced by *Bacillus thuringiensis* (Barrigossi and Martins, 2015).

Excessive use of chemical insecticides has selected resistant *S. frugiperda* that have become a significant challenge to integrated pest management - IPM (Bernardi et al., 2016; Viteri et al., 2018). In addition, pesticides add toxic residues to food crops, eliminate natural enemies, may bring about pest resurgence, present risks to the applicator,

* Corresponding author.
E-mail: flavio.jesus@ifgoiano.edu.br (F.G. Jesus).

https://doi.org/10.1590/1806-9665-RBENT-2021-0020

cause environmental contamination and increase costs associated with repeated applications (Bueno et al., 2010; Negrisoli et al., 2010).

Among the alternative control methods that have been studied, plant resistance to insects - PRI has become an important component of IPM in rice (Correa et al., 2018; Almeida et al., 2020; Almeida et al., 2021). PRI is compatible with other control tactics, such as biological control, cultural practices and chemical control, and can minimize insecticide use (Kartohardjono and Heinrichs, 1984; Rashid et al., 2005). PRI keeps pest populations below economic thresholds and does not adversely affect the environment or entail additional costs (Smith and Clement, 2012; Seifi et al., 2013; Ta-Liao and Chen, 2017).

There are three types of PRI: antixenosis, antibiosis and tolerance (Paiva et al., 2018). Antixenosis occurs when insects reduce feeding, oviposition, or shelter in a genotype (Queiroz et al., 2020). Antibiosis negatively affects an insect's biology/physiology by reducing weight, increasing mortality, prolonging life cycle, and reducing fertility (Smith and Clement, 2012; Seifi et al., 2013). Tolerance reflects a plant's ability to recover from insect damage by producing new vegetative or reproductive structures (Smith, 2005; Baldin et al., 2019).

Screening of resistant rice genotypes has become an important component of IPM. Nevertheless, pest resistance in the rice genotypes of Brazil is limited and has only been identified for the stalk borer *Diatraea saccharalis* Fabricius (Lepidoptera: Crambidae) and rice stalk stink bug *Tibraca limbaventris* Stål (Hemiptera: Pentatomidae) (Nascimento and Barrigossi, 2014; Nascimento et al., 2015; Correa et al., 2018; França et al., 2018; Almeida et al., 2020). There are currently no rice genotypes that are characterized as resistant to *S. frugiperda*.

The genotype Ku 94-2 showed antibiosis to *D. saccharalis* due to high larval mortality, while BR IRGA 417, MTU 15 and IR 40 showed tolerance due to greater tiller production in plants damaged by *D. saccharalis* (Nascimento and Barrigossi, 2014; Nascimento et al., 2015). The cultivars Bonança, Caripuna, IR 42, Canela de Ferro, SWA Norte, BR IRGA 409, Pepita, Serra Dourada, Araguaia, Xingú, Tangará, and Soberana showed antibiosis and/or antixenosis to *D. saccharalis* (Correa et al., 2018).

The objective of this study was to identify resistance in rice genotypes by antixenosis (non-preference) and antibiosis (biological parameters and nutritional indices) to *S. frugiperda*.

Material and methods

Spodoptera frugiperda *colony*

The experiments were conducted at the Integrated Pest Management Laboratory of the Goiano Federal Institute, Urutaí Campus (Urutaí, GO, Brazil). The *S. frugiperda* colony was established using caterpillars obtained from the Laboratory of Plant Resistance to Insects at UNESP, Jaboticabal, SP, Brazil.

The pupae were sexed and separated into couples (15 males and 15 females) and kept in polyvinyl chloride (PVC) cages (15 cm diameter × 20 cm height) for emergence and adult mating. The cages were lined with paper that served as an oviposition substrate. Adults were fed a 10% honey solution containing methylparaben and vitamins (Armes et al., 1992) and kept in the same PVC cages.

Spodoptera frugiperda eggs were collected and transferred to plastic pots (14 cm in diameter and 9 cm height) until larval hatching. Second instar caterpillars were then placed individually in B16 PET trays (CM&CM Comercio de Plásticos, São Paulo, SP, Brazil) and fed an artificial diet (Greene et al., 1976) until the pupal phase.

The insects were maintained under controlled conditions (25 ± 2 °C, 70 ± 10% relative humidity, and a 12:12 h light/dark photoperiod) during all phases of development.

Plant material

The rice genotypes were obtained from the active gene bank of the Brazilian Agricultural Research Corporation – Embrapa, National Research Center for Rice and Beans (Santo Antônio de Goiás, GO, Brazil) (Table 1). These genotypes were chosen based on historical resistance to different rice pests from different geographic regions and their potential as sources of resistance to *S. frugiperda* (Correa et al., 2018; Almeida et al., 2020).

The seeds were sown in containers (3.5 cm in diameter by 14 cm in depth) with a substrate (3:1 – soil and sand) and kept in a greenhouse under natural light and temperature conditions. The soil was chemically amended and fertilized as recommended for rice cultivation (Sousa and Lobato, 2004) and irrigated daily at field soil levels. The rice plants used in the experiment were 45 days old. The plants were selected at the end of tillering since pest damage to rice crops is greatest at this critical stage (Barrigossi and Martins, 2015).

Non-preference for feeding and preference index

In the free-choice test, a perforated polystyrene plate (arena) containing equidistantly distributed whole rice plants was placed in a plastic cage (14 cm Ø x 20 cm high and 32 L vol.) and covered with voile fabric. Twelve *S. frugiperda* larvae (3rd instar) were released in the center of each arena and non-preference was determined by counting the number of insects feeding on each genotype at 1, 3, 5, 10, 15, 30,

Table 1
Rice accessions screened for resistance to *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae). Urutaí, GO, Brazil.

Genotypes	ID no.	Colletion	Origin
Pela Mão	BGA 012512	Traditional variety	Brasil-Região Nordeste-Maranhão-Lima Campos
Gojobinho	BGA 011304	Traditional variety	Brasil-Região Nordeste -Maranhão-Caxias
Lageado Ligeiro	BGA 011384	Traditional variety	Brasil-Região Nordeste-Maranhão-Tuntum
IR 64	BGA 018794	Breeding line	Filipinas-Luzon
Guabirú	BGA 011324	Traditional variety	Brasil-Região Nordeste-Maranhão-Caxias
Miúdo Branco	BGA 012626	Traditional variety	Brasil-Região Nordeste-Maranhão-Esperantinópolis
Arroz do Governo	BGA 011335	Traditional variety	Brasil-Região Nordeste-Maranhão-São João do Soter
Branco Tardão	BGA 011318	Traditional variety	Brasil-Região Nordeste-Maranhão-Caxias
Nenenzinho	BGA 011585	Traditional variety	Brasil-Região Nordeste-Maranhão
Trinca Ferro	BGA 011391	Traditional variety	Brasil-Região Nordeste-Maranhão-Presidente Dutra
Bacaba Branco	BGA 011352	Traditional variety	Brasil-Região Nordeste-Maranhão-Timbira
Bico Ganga	BGA 000412	Traditional variety	Brasil

ID: identification code

60, 120, 360, 720 and 1440 min. A mean reference value was calculated from all evaluation times. The data were generated from a randomized block design with 12 treatments (genotypes) and 10 replicates (arenas).

In the no-choice test, 20 rice plants from each genotype were grown individually in containers (3.5 cm in diameter by 14 cm in depth) and infested with one larvae of *S. frugiperda* (3rd instar). The containers were arranged in a plastic tray (38 cm × 58 cm) and maintained under laboratory conditions at 25 ± 2 °C, 60 ± 10% RH, and 12:12 h (L:D). The number of insects feeding on each genotype was recorded at the same intervals used in the free-choice test. The data were generated from a completely randomized design with 12 treatments (genotypes) and 20 replicates (pots).

The preference index (AI) was calculated according to Kogan and Goeden (1970) with the following formula: AI = 2C/(C+S), where C = the number of insects attracted to a given genotype and S = the number of insects attracted to the standard susceptible genotype (Guabirú - BGA 011324). The standard susceptible genotype was obtained from the average number of larvae attracted to the genotypes at all assessment times.

Biological parameters and nutritional indices

Antibiosis was measured for each newly hatched *S. frugiperda* larva, which were kept in individual cells (5.5 cm x 3.5 cm and 2 cm height) of a plastic tray (27.5 cm x 20 cm) (CM & CM Comercio de Plásticos, Pinheiros, SP, Brazil) containing moistened filter paper and fed with leaves from the rice genotypes. The larvae remained in the plastic container until the pupal stage when feeding was interrupted.

The emerged adults were separated and caged to measure longevity without feeding. The following biological parameters were evaluated: a) larval phase: duration and viability of the larval stage and weight of larvae at 10 days; b) pre-pupal phase: duration and viability; c) pupal stage: duration, weight of pupa after 24 hours and viability; d) adult: longevity and sex ratio, and e) total cycle: period and viability. Each replication (a single larva in a plastic container) was set up in a completely randomized design with 12 treatments (genotypes) and 32 replicates.

After abstaining from food for 3 hours, a separate group of *S. frugiperda* larvae (3rd instar) were weighed and then segregated in petri dishes (1.5 × 9.0 cm diameter) that were lined with moistened filter paper and supplied with leaf tissue from each genotype for 7 days. The leaf sections were replaced daily. After 7 days, the feces and remaining unconsumed leaf sections were separated and dried in an oven (Nova Ética, Vargem Grande Paulista, SP, Brazil) at 60°C for 48h and weighed on an analytic scale (Marter, Santa Rita do Sapucaí, MG, Brazil). The dry weights were used to calculate the nutritional indices.

The following nutritional indices were determined according to Waldbauer (1968) and Scriber and Slansky Junior (1981): relative consumption rate (RCR; g/g/d), relative metabolic rate (RMR = M/Bm by T; g/g/d), relative growth rate (RGR = B/Bm by T; g/g/d), conversion efficiency of ingested food (ECI = [B/I] × 100; %), conversion efficiency of digested food (ECD = B/[I − F] × 100; %), and approximate digestibility (AD = [I − F]/I × 100; %), where T = feeding period, I = food consumption during T, B = larval weight gain during T, F = feces produced during T, M = food used in metabolic processes during T (M = [I − F] − B), and Bm = mean larval weight during T. The experiment was conducted in a completely randomized design with 12 treatments and 10 replicates.

Statistical analysis

An analysis of variance model was fit to the data from each experiment. Residual normality and homoscedasticity were determined by the Shapiro-Wilk and Bartlett tests. When data did not meet these assumptions, the Box-Cox method was used to find an optimal transformation. The transformed data were then used to fit the analysis of variance models and the means were compared by the Scott-Knott test (α = 0.05) (R Core Team 2017 – ScottKnott package). The means were back transformed for presentation purposes. Hierarchical Cluster Analysis – UPGMA (based on the Euclidian distance) was used to determine resistance patterns among the rice genotypes (R Core Team 2017 - biotools package). The preference index (AI) and standard error for each genotype were calculated and then compared to 1.0 (neutral - susceptible genotype - Guabirú - BGA 011324) using the Student's t test (α = 0.05). The genotypes that presented indices statistically different from 1.0 were classified as either deterrent (<1.0) or stimulating (>1.0).

Results

The free-choice test showed no significant differences among rice genotypes regarding non-preference to *Spodoptera frugiperda* (F = 1.03; df = 11; P = 0.4283). According to the preference indexes, the genotypes Pela Mão (0.56; P = 0.0688), Lageado Ligeiro (0.42; P = 0.0166), Miúdo Branco (0.60; P = 0.0231), and Branco Tardão (0.50; P = 0.0408) were the most preferred by *S. frugiperda* (Table 2).

Table 2
Non-preference (mean±SE) and preference index in free-choice and no-choice tests of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on 12 rice genotypes. Urutaí, GO, Brazil.

Genotypes*	Free-choice test		No-choice test	
	Preference	Index (P value)	Preference	Index (P value)
Pela Mão	0.22±0.07	0.56 (0.0688)	0.77±0.04a	1.08 (0.4983)
Gojobinho	0.40±0.18	1.14 (0.1388)	0.80±0.06a	1.11 (0.1490)
Lageado Ligeiro	0.25±0.06	0.42 (0.0166)	0.62±0.06a	0.95 (0.8099)
IR 64	0.47±0.16	1.01 (0.9452)	0.71±0.04a	1.04 (0.6729)
Guabirú	0.30±0.09	1.00	0.69±0.05a	1.00
Miúdo Branco	0.18±0.06	0.60 (0.0231)	0.47±0.08b	0.85 (0.1575)
Arroz do Governo	0.22±0.07	0.67 (0.1484)	0.49±0.06b	0.85 (0.2514)
Branco Tardão	0.32±0.16	0.50 (0.0408)	0.64±0.06a	0.96 (0.9468)
Nenenzinho	0.17±0.06	0.68 (0.1287)	0.50±0.05b	0.84 (0.2075)
Trinca Ferro	0.26±0.08	0.83 (0.4306)	0.70±0.05a	1.02 (0.6544)
Bacaba Branco	0.56±0.08	1.07 (0.7434)	0.67±0.06a	0.99 (0.7996)
Bico Ganga	0.47±0.10	1.23 (0.1408)	0.72±0.07a	1.02 (0.5547)
F treatments	1.03	-	2.97	-
P value	0.4283	-	0.0017	-

Means followed by the same letter do not differ statistically according to the Scott-Knott test at 5% probability.

The no-choice test showed that *S. frugiperda* was least attracted to Miúdo Branco (0.47), Arroz do Governo (0.49) and Nenenzinho (0.50). The other genotypes were equally more attractive. The preference index from the non-choice test showed no significant differences among rice genotypes relative to the standard susceptible genotype – Guabirú (Table 2).

Spodoptera frugiperda development was influenced by the rice genotypes. The larval period was longest (F = 13.47; df = 11; P <0.0001) when caterpillars were fed on the IR 64 genotype and shorter for the other genotypes (Table 3).

The pre-pupal period was longest in caterpillars fed on IR 64 and Bacaba Branco and shortest in Nenenzinho, Miúdo Branco, Pela Mão and Trinca Ferro (F = 2.75; df = 11; P = 0.0002). The pupal period was longest for insects feeding on Bacaba Branco and Branco Tardão and shortest in the other genotypes, except Guabirú, IR 64 and Bico Ganga (F = 1.62; df = 11; P = 0.0562).

The longevity of adult *S. frugiperda* was greatest in the genotypes Bico Ganga, Bacaba Branco, Nenenzinho, Branco Tardão, Trinca Ferro, Arroz do Governo and Miúdo Branco and shortest in the remaining genotypes (F = 3.12; df = 11; P < 0.0001). The total *S. frugiperda* cycle was longest in insects fed on IR 64 and Bacaba Branco and shortest in Pela Mão, Nenenzinho and Gojobinho (F = 7.93; df = 11; P <0.0001). *Spodoptera frugiperda* fed on the genotypes Bacaba Branco, Arroz do Governo, Branco Tardão, Trinca Ferro and Nenenzinho showed the lowest total viability (F = 19.14; df = 11; P <0.0001).

The nutritional indices of *S. frugiperda* were influenced by the rice genotypes (Table 4 and Table 5). Consumption was lowest in Bico Ganga, Bacaba Branco, Arroz do Governo, Gojobinho, Branco Tardão, Nenenzinho, Guabirú, Lageado Ligeiro and Miúdo Branco genotypes (F = 9.31; df = 11; P <0.0001). Larval weight gain was highest in Pela Mão (F = 7.71; df = 11; P <0.0001) and lowest in the remaining 11 rice genotypes. The lowest RCR was observed in the genotypes Miúdo Branco, Arroz do Governo, Branco Tardão, Bico Ganga, Gojobinho, Pela Mão and Bacaba Branco (F = 3.37; df = 11; P <0.0001). The lowest RMR values were found in Arroz do Governo, Gojobinho, Miúdo Branco, Lageado Ligeiro, Bico Ganga, Pela Mão, Nenenzinho and Bacaba Branco (F = 2.95; df = 11; P = 0.0002). The remaining genotypes provided the lowest RGR values, except Pela Mão (F = 5.99; df = 11; P <0.0001) (Table 4).

The AD of *S. frugiperda* was lowest in Arroz do Governo, Gojobinho, Nenenzinho, Lageado Ligeiro and Trinca Ferro (F = 6.18; df = 11; P <0.0001), while ECI was lowest in Nenenzinho, Trinca Ferro and Guabirú (F = 3.53; df = 11.108; P <0.0001). ECD was lowest in IR 64, Guabirú, Trinca Ferro, Branco Tardão, Nenenzinho and Bacaba Branco (F = 2.70; df = 11; P = 0.0042) and MC was lowest in Arroz do Governo,

Table 3
Duration (mean±SE) of the larval, pre-pupal and pupal periods (days), adult longevity (days), total cycle (days) and total viability (%) of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on 12 rice genotypes. Urutaí, GO, Brazil.

Genotypes*	Larval	Pre-pupal	Pupal	Longevity	Total cycle	Viability
Pela Mão	19.50±0.19b	1.28±0.11c	13.00±0.19c	4.75±0.21b	38.53±0.35d	98.12±6.5a
Gojobinho	20.36±0.41b	1.43±0.13b	12.85±0.34c	4.59±0.19b	39.00±0.60d	84.37±6.2a
Lageado Ligeiro	20.72±0.58b	1.48±0.24b	13.11±0.51c	4.77±0.68b	39.88±1.40c	84.37±8.7a
IR 64	24.10±0.77a	1.70±0.22a	13.57±0.71b	4.65±0.21b	43.00±1.26a	81.25±7.4a
Guabirú	20.74±0.29b	1.51±0.14b	13.64±0.23b	4.80±0.39b	40.52±0.54b	78.12±6.5a
Miúdo Branco	19.59±0.39b	1.09±0.11c	13.14±0.19c	5.71±0.22a	39.57±0.45c	65.62±7.4b
Arroz do Governo	19.28±0.28b	1.50±0.09b	12.60±0.23c	5.60±0.20a	39.60±0.45c	15.62±6.4c
Branco Tardão	20.00±0.29b	1.50±0.10b	14.33±0.15a	5.33±0.15a	41.00±0.39b	18.75±6.2c
Nenenzinho	18.75±0.36b	1.00±0.27c	13.45±0.26c	5.27±0.26a	38.54±0.55d	34.37±6.5c
Trinca Ferro	20.10±0.29b	1.33±0.06c	13.33±0.18c	5.44±0.18a	39.88±0.38c	28.12±6.8c
Bacaba Branco	21.66±0.19b	1.80±0.10a	14.20±0.38a	5.20±0.38a	42.80±0.38a	15.62±7.2c
Bico Ganga	20.36±0.47b	1.54±0.15b	13.70±0.16b	5.15±0.16a	40.55±0.60b	62.50±7.0b
F treatments	13.47	2.75	1.62	3.12	7.93	19.14
P value	< 0.0001	0.0002	0.0562	< 0.0001	< 0.0001	< 0.0001

Means followed by the same letter do not differ statistically according to the Scott-Knott test at 5% probability.

Table 4
Nutritional indices (mean±standard error) of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) fed on 12 rice genotypes. Urutaí, GO, Brazil.

Genotypes*	Consumption	Weight gain	RCR	RMR	RGR
Pela Mão	0.171±0.004a	0.030±0.001a	1.25±0.06b	0.29±0.02b	0.22±0.00a
Gojobinho	0.117±0.017c	0.017±0.002b	1.24±0.07b	0.22±0.02b	0.17±0.01b
Lageado Ligeiro	0.128±0.007c	0.018±0.001b	1.37±0.10a	0.27±0.05b	0.19±0.01b
IR 64	0.138±0.006b	0.020±0.000b	1.35±0.07a	0.43±0.05a	0.20±0.01b
Guabirú	0.124±0.006c	0.016±0.002b	1.39±0.05a	0.37±0.05a	0.17±0.01b
Miúdo Branco	0.130±0.006c	0.022±0.002b	1.17±0.07b	0.26±0.03b	0.18±0.01b
Arroz do Governo	0.111±0.005c	0.017±0.001b	1.22±0.09b	0.21±0.04b	0.18±0.01b
Branco Tardão	0.118±0.004c	0.018±0.001b	1.22±0.03b	0.34±0.02a	0.18±0.01b
Nenenzinho	0.120±0.004c	0.012±0.000b	1.59±0.07a	0.29±0.03b	0.16±0.00b
Trinca Ferro	0.137±0.007b	0.017±0.001b	1.46±0.07a	0.34±0.03a	0.17±0.01b
Bacaba Branco	0.110±0.004c	0.016±0.001b	1.25±0.06b	0.30±0.02b	0.17±0.01b
Bico Ganga	0.101±0.005c	0.015±0.000b	1.23±0.03b	0.27±0.03b	0.18±0.01b
F treatment	9.37	7.71	3.37	2.95	5.99
P value	< 0.0001	< 0.0001	< 0.0001	0.0002	< 0.0001

Means followed by the same letter do not differ statistically according to the Scott-Knott test at 5% probability. Consumption (g/larvae), Weight gain (g/larvae), RCR (relative consumption rate - g/g/d), RMR (relative metabolic rate - g/g/d), RGR (relative growth rate - g/g/d).

Table 5
Nutritional indices (mean ± standard error) of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) fed on 12 rice genotypes. Urutaí, GO, Brazil.

Genotypes*	AD (%)	ECI (%)	ECD (%)	MC (%)
Pela Mão	41.46±1.94a	17.90±0.84a	43.61±2.07a	56.38±2.07b
Gojobinho	32.61±1.11b	14.85±1.41a	45.29±3.19a	54.70±3.19b
Lageado Ligeiro	34.74±2.11b	15.14±1.75a	44.70±5.08a	55.29±5.08b
IR 64	45.77±1.75a	14.76±0.94a	32.90±2.92b	67.09±2.92a
Guabirú	39.82±2.75a	12.95±1.02b	33.69±2.94b	66.30±2.94a
Miúdo Branco	38.82±1.82a	16.63±1.57a	42.66±3.25a	57.32±3.25b
Arroz do Governo	32.60±1.96b	15.45±1.21a	48.69±4.43a	51.30±4.43b
Branco Tardão	43.23±1.03a	15.26±0.76a	35.35±1.68b	64.64±1.68a
Nenenzinho	28.40±1.86b	10.39±0.50b	37.96±3.06b	62.03±3.06a
Trinca Ferro	35.60±1.52b	12.25±0.73b	34.68±2.03b	65.31±2.03a
Bacaba Branco	39.16±2.71a	14.63±0.89a	37.96±2.02b	62.03±2.02a
Bico Ganga	37.43±1.60a	14.84±0.49a	40.44±2.61a	59.54±2.61b
F treatment	6.18	3.53	2.70	2.71
P value	< 0.0001	< 0.0001	0.0042	0.0043

**Means followed by the same letter do not differ statistically according to the Scott-Knott test at 5% probability. AD (approximate digestibility), ECI (efficiency of conversion of ingested food), ECD (efficiency of conversion of digested food), MC (metabolic cost).*

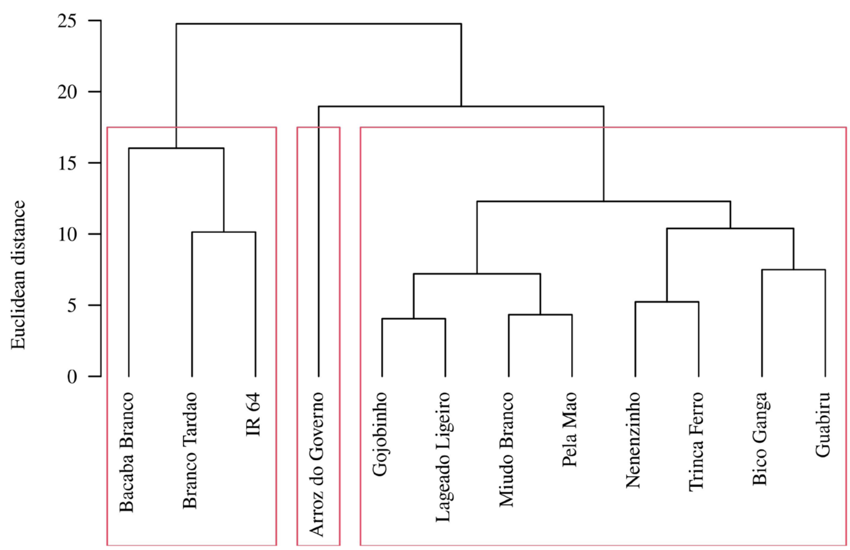

Figure 1 Dendrogram resulting from UPGMA multivariate cluster analysis (Euclidian distance), based on the length of larval, pre-pupal, pupal periods and total cycle (days) and total viability (%) and parameters of nutritional indices (Table 4 and Table 5) on rice genotypes for resistance to *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Urutaí, GO, Brazil.

Gojobinho, Lageado Ligeiro, Pela Mão, Miúdo Branco and Bico Ganga (F = 2.71; df = 11; P = 0.0043).

The rice genotypes were grouped into three resistance levels according to UPGMA (Euclidian distance) (Figure 1). Group I consisted of one susceptible genotype: Arroz do Governo, group II contained moderately resistant genotypes (Bacaba Branco, Branco Tardão and IR 64) and group III had the highly susceptible genotypes Gojobinho, Lageado Ligeiro, Miudo Branco, Pela Mão, Nenenzinho, Trinca Ferro, Bico Ganga and Guabirú.

Discussion

Resistance to *S. frugiperda* in rice genotypes has been little studied in Brazil. Some studies on rice and *S. frugiperda* have examined the induction response to silicon and its negative effects on insect biology (Nascimento et al., 2017; França et al., 2018). Other studies have looked at creating resistance to *S. frugiperda* by inserting *Bacillus thuringiensis* (cry1Aa and cry1B) in rice (Pinto et al., 2013). Thus, selecting for PRI in rice genotypes via classical methods is an important component of IPM in rice crops (Baldin et al., 2019).

Our results showed that the Miúdo Branco genotype exhibited antixenosis to *S. frugiperda*. Antixenosis is related to insect preference for hosts regarding feeding, oviposition and/or shelter. The deterrence attributes of these rice genotypes can be mediated by chemical substances or morphological characteristics of the plants (Smith and Clement, 2012; Seifi et al., 2013; Baldin et al., 2019).

Spodoptera frugiperda biology was negatively affected by feeding on IR 64 and Bacaba Branco (Table 3). Specifically, IR 64 prolonged the larval and pre-pupal phases and overall life cycle of *S. frugiperda*, while Bacaba Branco prolonged insect development (larval and pre-pupal periods and total cycle) and produced lower *S. frugiperda* viability. Longer larval phases suggest inadequate nutrition resulting from chemical compounds that confer insect resistance to the plant (Silva et al., 2017; Almeida et al., 2017).

The lower consumption and nutrition indices (weight gain, RCR, RMR and RGR) of insects fed on Gojobinho, Miúdo Branco, Arroz do Governo, Bacaba Branco and Bico Ganga indicate that these genotypes have compounds that may have inhibited the larval development of *S. frugiperda*.

Antibiosis in Bacaba Branco was indicated by the poor performance of *S. frugiperda* and consequent prolongation of the immature phase of this insect. Usually, reductions in food consumption decrease the size and weight and prolong the life cycle of an insect (Hemati et al., 2012). Plants with allelochemicals and insufficient nutrients can influence insect development. The low RCR levels in the insects feeding on Bacaba Branco may be associated with the presence of allelochemicals or interactions among nutrients and allelochemicals in the plant, suggesting that this genotype may not be a preferred host for *S. frugiperda* (Ramalho et al., 2011).

Among the rice genotypes with resistance characteristics, IR64, Bacaba Branco and Branco Tardão produced the lowest ECD values. ECD represents the conversion rate of digested food and lower values suggest that *S. frugiperda* larvae spent more time feeding on these genotypes. These results indicate that the IR64, Bacaba Branco and Branco Tardão genotypes probably have metabolic compounds that inhibit the development of *S. frugiperda*.

Multivariate analysis (UPGMA cluster analysis) grouped the rice genotypes by resistance levels, which complemented the results of the univariate analysis (Pitta et al., 2010). This study showed that the IR 64, Bacaba Branco and Branco Tardão genotypes presented resistance characteristics that negatively affected the development of *S. frugiperda*. The resistant rice genotypes IR 64, Bacaba Branco and Branco Tardão could be incorporated into an IPM strategy for managing *S. frugiperda*.

Acknowledgments

The authors recognize the Federal Goiano Institute – Campus Urutaí for support and Embrapa Rice and Beans (Santo Antônio de Goiás, Goiás, Brazil) for providing the rice genotypes. This study was partially supported by the National Council of Research and Technology of Brazil (CNPq), grant 406904/2016-2. The University of Goiás State (UEG) Campus Ipameri for the scholarship granted to CLTS.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Author contribution statement

This work was carried out in collaboration between the authors. FGJ and CLTS designed and performed the trials with the help of FC, ACSA, MSA and JAFB. FGJ and CLTS analyzed the data and wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

References

Almeida, A.C.S., Silva, C.L.T., Paiva, L.A., Araújo, M.S., Jesus, F.G., 2017. Antibiosis in soybean cultivars to *Heliothis virescens* (Lepidoptera: noctuidae). Fla. Entomol. 100, 334–338. https://doi.org/10.1653/024.100.0231.

Almeida, A.C.S., Dierings, C.A., Borella Junior, C., Jesus, F.G., Barrigossi, J.A.F., 2020. Resistance of rice genotypes to *Tibraca limbativentris* (Hemiptera: pentatomidae). J. Econ. Entomol. 20, 1–7. https://doi.org/10.1093/jee/toz277.

Almeida, A.C.S., Jesus, F.G., Heng-Moss, T.M., Lanna, A.C., Barrigossi, J.A.F., 2021. Evidence for rice tolerance to *Tibraca limbativentris* (Hemiptera: pentatomidae). Pest Manag. Sci. 77(9), 4181–4191. https://doi.org/10.1002/ps.6455.

Armes, N.J., Bond, G.S., Cooter, R.J., 1992. The laboratory culture and development of *Helicoverpa armigera*. Natural Resources Inst. Bull. 57. Natural Resources Institute, Chatham, United Kingdom.

Baldin, E.L.L., Vendramim, J.D., Lourenção, A.L., 2019. Resistência de plantas a insetos: fundamentos e aplicações. FEALQ, Piracicaba, 493 p.

Barrigossi, J.A.F., Martins, J.F., 2015. Manejo de Pragas. In: Borém, A., Rangel, P.H.N (Eds.), Arroz do plantio a colheita. Editora UFV, Viçosa, pp. 178–198.

Bernardi, O., Bernardi, D., Horikoshi, R.J., Okuma, D.M., Miraldo, L.L., Fatoretto, J., Medeiros, F.C.L., Burd, T., Omoto, C., 2016. Selection and characterization of resistance to the Vip3Aa20 protein from *Bacillus thuringiensis* in *Spodoptera frugiperda.* Pest Manag. Sci. 72, 1794-1802. https://doi.org/10.1002/ps.4223.

Bueno, R.C.O., Carneiro, T.R., Bueno, A.F., Pratissoli, D., Fernandes, O.A., Vieira, S. S., 2010. Parasitism capacity of *Telenomus remus* Nixon (Hymenoptera: Scelionidae) on *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) eggs. Braz. Arch. Biol. Technol. 53, 133–139. https://doi.org/10.1590/S1516-89132010000100017.

Busato, G.R., Grützmacher, A.D., Garcia, M.S., Zotti, M.J., Nörnberg, S.D., Magalhães, T.R., Magalhães, J.B., 2006. Susceptibilidade de lagartas dos biótipos milho e arroz de *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae) a inseticidas com diferentes modos de ação. Cienc. Rural 36, 15–20. https://doi.org/10.1590/S0103-84782006000100003.

Busato, G.T., Grützmacher, A.D., Garcia, M.S., Giolo, F.P., Zotti, M.J., Stefanello Júnior, G.J., 2005. Biologia comparada de populações de *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) em folhas de milho e arroz. Neotrop. Entomol. 34, 743–750. https://doi.org/10.1590/S1519-566X2005000500005.

Correa, F., Silva, C.L.T., Pelosi, A.P., Almeida, A.C.S., Heinrichs, E.A., Barrigossi, J.A.F., Jesus, F.G., 2018. Resistance in 27 rice cultivars to sugarcane borer (Lepidoptera: crambidae). J. Econ. Entomol. 111, 422–427. https://doi.org/10.1093/jee/tox291.

França, L.L., Dierings, C.A., Almeida, A.C.S., Araújo, M.S., Heinrichs, E.A., Silva, A.R., Barrigossi, J.A.F., Jesus, F. G., 2018. Resistance in rice to *Tibraca limbaventris* (Hemiptera: Pentatomidae) infuenced by plant silicon contente. Fla. Entomol. 101, 587–591. https://doi.org/10.1653/024.101.0419.

Goergen, G., Kumar, P.L., Sankung, S.B., Togola, A., Tamò, M., 2016. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. PLoS One 11 (10), e0165632. https://doi.org/10.1371/journal.pone.0165632.

Greene, G.L., Leppla, N.C., Dickerson, W.A., 1976. Velvetbean caterpillar: a rearing procedure and artificial medium. J. Econ. Entomol. 69, 487–488.

Hemati, S.A., Naseri, B., Ganbalani, G.N., Dastjerdi, H.R., Golizadeh, A., 2012. Effect of different host plants on nutritional indices of the Pod Borer, *Helicoverpa armigera.* J. Insect Sci. 12, 1–15. https://doi.org/10.1673/031.012.5501.

Jiang, L.B., Cheng, J., Zhu, Z.F., Ge, L.Q., Yang, G.Q., Wu, J.C., 2014. Impact of day intervals on sequential infestations of the rice Leaffolder *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae) and the white backed rice Planthopper *Sogatella furcifera* (Horváth) on rice grain damage. Int. J. Insect Sci. 6, 23–31. https://doi.org/10.1177/IJIS.S13536.

Jing, D., Guo, F., Jiang, Y., Zhao, J., Sethi, A., He, K., Wang, Z., 2020. Initial detections and spread of invasive *Spodoptera frugiperda* in China and comparisons with other noctuid larvae in cornfields using molecular techniques. Insect Sci. 27, 780–790. https://doi.org/10.1111/1744-7917.12700.

Kartohardjono, A., Heinrichs, E.A., 1984. Populations of the brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), and its predators on rice varieties with different levels of resistance. Environ. Entomol. 13, 359–365. https://doi.org/10.1093/ee/13.2.359.

Kogan, M., Goeden, R.D., 1970. The host-plant ranger of *Lema trilineata daturaphila* (Coleoptera: chrysomelidae). Ann. Entomol. Soc. Am. 63, 1175–1180.

Kraus, E.C., Stout, M.J., 2019. Effects defoliation on the resistance and tolerance of rice, *Oryza sativa*, to root injury by the rice water weevil, *Lissorhoptrus oryzophilus*. Entomol. Exp. Appl. 167, 350–359. https://doi.org/10.1111/eea.12789.

Mallapur, C.P., Naik, A.K., Hagari, S., Prabhu, S.T., Patil, P.K., 2018. Status of alien pest fall armyworm, *Spodoptera frugiperda* (J.E. Smith) on maize in Northern Karnataka. J. Entomol. Zool. Stud. 6, 432–436.

Montezano, D.G., Specht, A., Sosa-Gómez, D.R., Roque-Specht, V.F., Sousa-Silva, J.C., Paula-Moraes, S.V., Peterson, J.A., Hunt, T.E., 2018. Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. Afr. Entomol. 26, 286–300. https://doi.org/10.4001/003.026.0286.

Nascimento, A.M., Assis, F.A., Moraes, J.C., Sakomura, R., 2014. Não preferência a *Spodoptera frugiperda* (Lepidoptera: Noctuidae) induzida em arroz pela aplicação de silício. Agraria 9, 215–218.

Nascimento, A.M., Assis, F.A., Moraes, J.C., Souza, B.H.S., 2017. Silicon application promotes rice growth and negatively affects development of *Spodoptera frugiperda* (J. E. Smith). J. Appl. Entomol. 142, 241–249. https://doi.org/10.1111/jen.12461.

Nascimento, J.B., Barrigossi, J.A.F., 2014. Responses of rice mini-core collection accessions to damage by *Diatraea saccharalis* (Fabricius) stem borer. Agric. Sci. 5, 776–784. https://doi.org/10.4236/as.2014.59082.

Nascimento, J.B., Barrigossi, J.A.F., Borba, T.C.O., Martins, J.F.S., Fernandes, P.M., Mello, R.N., 2015. Evaluation rice genotypes for sugarcane borer resistance using phenotypic methods and molecular markers. Crop Prot. 67, 43–51. https://doi.org/10.1016/j.cropro.2014.09.018.

Negrisoli, A.S., Garcia, M.S., Negrisoli, C.R.C.B., 2010. Compatibility of entomopathogenic nematodes (Nematoda: Rhabditida) with registered insecticides for *Spodoptera frugiperda* (Smith, 1797) (Lepidoptera: Noctuidae) under laboratory conditions. Crop Prot. 29, 545–549. https://doi.org/10.1016/j.cropro.2009.12.012.

Paiva, L.A., Resende, W.C., Silva, C.L.T., Almeida, A.C.S., Cunha, P.C.R., Jesus, F.G., 2018. Resistance of common bean (*Phaseolus vulgaris*) cultivars to *Spodoptera frugiperda* (Lepidoptera: noctuidae). Rev. Colomb. Entomol. 44, 2–18.

Pinto, L.M.N., Fiuza, L.M., Ziegler, D., Oliveira, J.V., Menezes, V.G., Bourrié, I., Meynard, D., Guiderdoni, E., Breitler, J.C., Altosaar, I., Gantet, P., 2013. Indica rice cultivar IRGA 424, transformed with cry genes of *B. thuringiensis*, provided high resistance against *Spodoptera frugiperda* (Lepidoptera: noctuidae). J. Econ. Entomol. 106, 2585–2594. https://doi.org/10.1603/ec13163.

Pitta, R.M., Boiça Júnior, A.L., Jesus, F.G., Tagliari, S.R., 2010. Seleção de genótipos resistentes de amendoinzeiro a *Anticarsia gemmatalis* Hübner (Lepidoptera: Noctuidae) com base em análises multivariadas. Neotrop. Entomol. 39, 260–265. https://doi.org/10.1590/S1519-566X2010000200018.

Queiroz, E.B., Miranda, D.S., Silva, F.C., Borella Junior, C., Almeida, A.C.S., Hirose, E., Jesus, F.G., 2020. Antibiosis in soybean genotypes to *Spodoptera cosmioides* (Lepidoptera: noctuidae). Rev. Bras. Entomol. 64, 20200010. https://doi.org/10.1590/1806-9665-RBENT-2020-0010.

R Core Team, 2017. R: the R project for statistical computing. Version 3.3.3. R Foundation for Statistical Computing, Vienna, Austria.

Ramalho, F.S., Azeredo, T.L., Nascimento, A.R.B., Fernandes, F.S., Nascimento Júnior, J.L., Malaquias, J.B., Silva, C.A.D., Zanuncio, J.C., 2011. Feeding of fall armyworm, *Spodoptera frugiperda*, on Bt transgenic cotton and its isoline. Entomol. Exp. Appl. 139, 207–214. https://doi.org/10.1111/j.1570-7458.2011.01121.x.

Rashid, A., Khan, J.A., Khan, F.F.J., Hamed, M., 2005. Resistance of different Basmati rice varieties to stem borers under different control tactics of IPM and evaluation of yield. Pak. J. Bot. 37, 319–324.

Scriber, J.M., Slansky Junior, J.R.F., 1981. The nutritional ecology of immature insects. Annu. Rev. Entomol. 26, 183–211.

Seifi, A., Visser, R.G.F., Bai, Y., 2013. How to effectively deploy plant resist- ances to pests and pathogens in crop breeding. Euphytica 190, 321–334. https://doi.org/10.1007/s10681-012-0823-9.

Silva, D.M., Bueno, A.F., Andrade, K., Stecca, C.S., Neves, P.M.O.J., Oliveira, M.C.N., 2017. Biology and nutrition of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) fed on different food sources. Sci. Agric. 74, 18–31. https://doi.org/10.1590/1678-992x-2015-0160.

Smith, C.M. 2005. Plant resistance to arthropods: molecular and conventional approaches. Springer, Berlin, pp. 423.

Smith, C.M., Clement, S.L., 2012. Molecular bases of plant resistance to arthropods. Annu. Rev. Entomol. 57, 309–328. https://doi.org/10.1146/annurev-ento-120710-100642.

Sousa, D.M.G., Lobato, E., 2004. Calagem e adubação para culturas anuais e semiperenes. In: Sousa, D.M.G., Lobato, E. (Eds), Cerrado: correção do solo e adubação. 2 ed. Embrapa Informação Tecnológica, Brasília, pp. 283–316.

Stout, M.J., Riggio, M.R., Yang, Y., 2009. Direct induced resistance in *Oryza sativa* to *Spodoptera frugiperda*. Environ. Entomol. 38, 1174–1181. https://doi.org/10.1603/022.038.0426.

Ta-Liao, C., Chen, C., 2017. Oviposition preference and larval performance of *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) on rice genotypes. J. Econ. Entomol. 110, 1291–1297. https://doi.org/10.1093/jee/tox071.

Viteri, D.M., Linares, A.M., Flores, L., 2018. Use of the entomopathogenic nematode *Steinernema carpocapsae* in combination with low-toxicity insecticides to control fall armyworm (Lepidoptera: Noctuidae) larvae. Fla. Entomol. 102, 327–329. https://doi.org/10.1653/024.101.0228.

Waldbauer, G.P., 1968. The consumption and utilization of food by insects. Adv. Insect Physiol. 5, 229–288. https://doi.org/10.1016/S0065-2806(08)60230-1.

Wang, R., Jiang, C., Guo, X., Chen, D., You, C., Zhang, Y., Wang, M., Li, Q., 2020. Potential distribution of *Spodoptera frugiperda* (J.E. Smith) in China and the major factors influencing distribution. Glob. Ecol. Conserv. 21, e00865.