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Plant Resistance

Resistance of Soybean Genotypes to *Anticarsia gemmatalis* (Lepidoptera: Erebidae): Antixenosis and Antibiosis Characterization

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Abstract

Injury by herbivores is a major biotic stress that limits soybean [*Glycine max* (L.) Merrill] crop production. Among the main soybean insect pests, *Anticarsia gemmatalis* Hübner is responsible for causing significant economic damage in soybean. The primary management strategy for this insect is chemical control and use of *Bt* transgenic soybean. Alternative strategies, such as host plant resistance, are considered an efficient and less-aggressive method, especially in association with other strategies as part of an integrated pest management (IPM) approach. In this study, we evaluated 30 soybean genotypes to verify antixenosis expression through oviposition, attractiveness, and food consumption tests. From this, we selected 13 promising genotypes to verify the possible presence of antibiosis. Our results suggest that antixenosis was found in genotypes 'TMG 133' RR, 'TMG 1179' RR, 'IAC 19', 'IAC 17', 'IAC 100', D75-10169, and IAC 78-2318. By influence on behavior and negative impact on larval viability, antixenosis and antibiosis were indicated for the genotypes IAC 74-2832, 'IAC 19', 'IAC 17', 'IAC 100', and PI 274454. 'TMG 7062' IPRO was found to provide antibiosis resistance by negatively affecting larval development and viability. Because of reduced food consumption by larvae, antixenosis was indicated for 'IAC 24'. These genotypes should be considered in soybean breeding programs focusing on soybean resistance to *A. gemmatalis*.

Key words: *Glycine max*, host plant resistance, velvetbean caterpillar

Soybean [*Glycine max* (L.) Merrill] is one of the most important agricultural crops, and it has been increasingly planted worldwide (SOYSTATS 2020). Soybean grain can be used as feed, or it can be processed to produce soybean byproducts, oil, and, more recently, biodiesel (USDA 2019). Soybean productivity can be severely reduced by insect pests that cause significant yield loss (Hoffmann-Campo et al. 2012, Oliveira et al. 2014, Wille et al. 2017). The velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner), is one of the main soybean insect pests. This species causes defoliation in different soybean-producing regions in the western hemisphere (Buschman et al. 1981, Sosa-Gómez et al. 2010, Bortolotto et al. 2015, Haase et al. 2015). Defoliation can be total, severely affecting yield when infestations are high (Bueno et al. 2011).

Traditionally, *A. gemmatalis* has been controlled with chemical insecticides. However, the extensive use of insecticide sprays can have significant negative effects to nontarget organisms, promote pest outbreaks, and select for insecticide-resistant insect populations (Vieira et al. 2011, Bel et al. 2019). In parallel, genetically modified soybean expressing a *Bacillus thuringiensis* (*Bt*) insecticidal protein has taken a prominent position in large-scale management of *A. gemmatalis* (Bernardi et al. 2012). Although *Bt* soybean varieties expressing Cry1Ac are high-dose events for this pest (Bernardi et al. 2012), their extensive use without appropriate resistance management plans can compromise their durability. In addition, this technology requires the presence of a refuge (i.e., soybean with no *Bt* plants), where the use of foliar insecticides should be minimized (Bortolotto et al. 2015). Thus, pest management in the refuge could be conducted by other

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methods, such as biological control (entomopathogenic virus, fungi, and bacteria), but not biological products based on *Bt* (IRAC 2021).

Despite the increase in the use of *Bt* technology, the size of the refuge, limitations of alternative control methods, high cost of seed, and other factors have resulted in many growers seeking alternative management strategies, such as the use of resistant soybean developed in classical breeding programs. Host plant resistance is considered an efficient and less-aggressive method, especially when integrated with other strategies, e.g., biological control. There is a need to identify and incorporate resistant soybean genotypes as pest management tools in integrated pest management (IPM) programs for soybean (Smith and Clement 2012, Canassa et al. 2017, Baldin et al. 2019).

Table 1. Soybean genotypes assessed for resistance to *A. gemmatalis*

Genotype	Source/origin
'IAC 17'	D72-9601× 'IAC-8'/IAC, Campinas, Brazil
'IAC 23'	BR-6 × IAC-83-23/IAC, Campinas, Brazil
'IAC 24'	IAC 80-1177 × IAC 83-288/IAC, Campinas, Brazil
IAC 74-2832	'Hill' × PI 274454/IAC, Campinas, Brazil
'IAC 100'	'IAC 12' × IAC 78-2318/IAC, Campinas, Brazil
IAC 78-2318	D 72-9601-1 × IAC 73-227/IAC, Campinas, Brazil
'IAC 19'	D 72-9601-1 × 'IAC 8'/IAC, Campinas, Brazil
D75-10169	'Govan' × (F4 'Bragg' × PI 229358)/IAC, Campinas, Brazil
PI 229358	Japan
PI 171451	Tóquio, Japan
PI 227687	Okinawa, Japan
PI 274453	Japan
PI 274454	Okinawa, Japan
'TMG 4182'	Tropical Melhoramento & Genética/Cambé, Brazil
'TMG 1179' RR	Tropical Melhoramento & Genética/Cambé, Brazil
'TMG 4185'	Tropical Melhoramento & Genética/Cambé, Brazil
'TMG 133' RR	Tropical Melhoramento & Genética/Cambé, Brazil
'TMG 132' RR	Tropical Melhoramento & Genética/Cambé, Brazil
'TMG 7062' IPRO	Tropical Melhoramento & Genética/Cambé, Brazil
'TMG 7262' RR	Tropical Melhoramento & Genética/Cambé, Brazil
'Anta 82'	Tropical Melhoramento & Genética/Cambé, Brazil
'KS-4202'	KS4694 × C1842/University of Nebraska, Lincoln, USA
UX-2569-159	U06-607094 × UX2324-34/University of Nebraska, Lincoln, USA
'Jackson' (PI 548657)	'Volstate' (2) × 'Palmetto' (USDA/USA)
'Dowling' (PI 548663)	'Semmes' × PI 200492 (USDA/USA)
L1-1-01	BR-6 × 'IAC-100'/ESALQ/USP, Piracicaba, Brazil
'Conquista'	Lo 76-4484 × 'Numbaíra'/EMBRAPA, Londrina, Brazil
'Coodetec 208'	OC-4 × Williams 20/Coodetec, Cascavel, Brazil
'BMX Potência' RR	Brasmax Genética/Cambé, Brazil
'FTS Campo Mourão' RR	FT Sementes, Ponta Grossa, Brazil

'Coodetec 208' and 'Conquista' were considered the susceptible checks.

Plant resistance can be divided into three categories: antibiosis, antixenosis, and tolerance (Panda and Khush 1995, Smith 2005, Baldin et al. 2019). Plants expressing antibiosis negatively affect colonizing insect biology by interfering with their development, reproduction, and survival. Negative impacts on various life-history traits of target pests are commonly caused by host plants expressing antibiosis. Antixenosis affects insect behavior and reduces host colonization by chemical, physical, and morphological factors. Tolerance is the ability of plants to resist or overcome from injury caused by a pest, without affecting the pest's biology or behavior (Painter 1951, Panda and Khush 1995, Smith 2005, Baldin et al. 2019). Plants exhibiting high levels of antixenosis can cause negative effects on insect development, like that of antibiosis. Thus, it is essential to differentiate antibiosis and antixenosis categories by using specific insect feeding studies (Beach and Todd 1988, Smith 2005, Baldin et al. 2015, Morando et al. 2017, Coelho et al. 2020).

Although some studies have evaluated soybean resistance to *A. gemmatalis* (Beach and Todd 1988; Hoffmann-Campo et al. 1994; Fugi et al. 2005; Piubelli et al. 2005; Franco et al. 2014, 2017), there are few studies characterizing resistance of a large number of soybean genotypes (with high genetic variability). Therefore, to identify new resistance sources, this study characterized the expression of antibiosis and antixenosis in 30 soybean genotypes under laboratory and greenhouse conditions.

Materials and Methods

The initial assays were performed with 30 soybean genotypes (Table 1) that were selected to represent wide genetic variability and include sources of resistance against other Lepidoptera species, other insect orders such as stinkbugs and whitefly, and commercial genotypes never previously tested. The plants were grown in a greenhouse and evaluated under greenhouse and laboratory conditions in 2018 and 2019 in Botucatu, São Paulo, Brazil. Polyethylene pots (2 liters) containing a mixture of soil, sand, manure, and substratum (1:1:1:1) were kept in a greenhouse free from insect infestation. All plants received recommended crop fertilization (Malavolta 2006) and other necessary cultural practices (e.g., irrigation, thinning, and cleaning). Leaves from plants at V4/V5 developmental stages (Fehr and Caviness 1977) were used in all experiments.

Rearing *A. gemmatalis*

A colony of *A. gemmatalis* was established from soybean field-collected larvae and pupae in the municipality of Botucatu, in the state of São Paulo. After emergence, the insects were identified and the colony was maintained under laboratory conditions (T: 25 ± 2°C, photoperiod of 12:12 h, RH: 60 ± 10%) at the Department of Crop Protection, São Paulo State University, Botucatu, São Paulo, Brazil. To reinvigorate the colony, insects were continually introduced until the colony population reached the level necessary to initiate the bioassays. The rearing methodology and bean-based artificial diet were adapted from the protocols of Greene et al (1976) and Parra (2001). Insects from this colony were used for the antixenosis bioassays. For the antibiosis bioassay, *A. gemmatalis* eggs were commercially acquired (Pragas.com, Piracicaba, Brazil).

Antixenosis Bioassays

Three different types of bioassays (oviposition preference, attractiveness, and food consumption) with 30 soybean genotypes were

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initially conducted. The objective was to verify the possible expression of antixenosis and select the most promising resistant genotypes for the subsequent phase of the study.

For the oviposition bioassay, five plants (five replicates) were arranged in a completely randomized design and infested with two females per plant. Egg number was counted 2 d after insect release by visual observation of the whole plant.

For attractiveness and free-choice food consumption bioassays, two fourth-instar larvae/genotype (Boiça Júnior et al. 2015) were released in arenas (23 cm of diameter), following a complete randomized block design. Each arena with 30 genotypes represented one block, totaling 10 blocks. To avoid contact among larvae and leaf tissues, discs (6.9 cm^2) were enclosed with a plastic micro arena (50 ml) partially covered with organdy fabric to allow volatile flow. Before the tests, larvae were starved for 2 h. The mean number of larvae on leaf discs was calculated 120 min after release.

For the no-choice food consumption, two larvae/genotype were isolated in Petri dishes (8 × 2 cm) with one leaf disc of each genotype, ten replicates per genotype, in a completely randomized design. In free- and no-choice tests, all replicates were visually observed until at least one of the leaf discs in any of the treatments had larval feeding reaching approximately 90%, at which time the study was concluded. The nonconsumed food (cm^2) was measured with a leaf area meter (LI-COR LI-3100, LI-COR, Lincoln, NE).

Life-History Traits of *A. gemmatalis* Feeding on Selected Genotypes

After initial bioassays, the 11 genotypes most resistant to *A. gemmatalis* were selected for further assessment. Genotype selection was based on higher resistance levels expressed in the previous bioassays, primarily selecting genotypes that were promising in two or more tests. Genotypes 'Conquista' and 'Coodetec 208' were included as susceptible commercial genotypes (Silva et al. 2012), totaling 13 genotypes. Based on other studies (Gómez et al. 2018, Bel et al. 2019, Coelho et al. 2020), first-instar larvae were used to initiate the experiment. However, to reduce stress caused by manipulating newly hatched neonates, 48-h-old larvae were transferred from the artificial diet and placed into individual Petri dishes (8 × 2 cm) lined with moist filter paper containing leaf disks (6.9 cm^2) from each genotype. Each Petri dish containing one larva, corresponding to one replicate (total of 50 replicates) in a completely randomized design.

The following biological parameters were evaluated daily: duration of each instar, total larval period, fifth-instar larval weight (24 h old), larval viability, prepupal and pupal duration, pupal weight (24 h old), pupal viability, development period (larvae–adult), preoviposition duration, oviposition period, and egg number. Fifth-instar larval and pupal weights were obtained with an analytical scale (AL-500, Marte Científica, São Paulo, SP, Brazil).

For further resistance evaluation and to discriminate antixenosis and antibiosis, each individual's food consumption (cm^2) was recorded. Leaf disks were replaced daily, and nonconsumed food was measured with the leaf area meter.

Statistical Analyses

Data were subjected to analysis of variance (ANOVA). Normality and homogeneity of the data were verified with Shapiro–Wilk and Levene tests (Winer et al. 1991). For the antixenosis study, data were compared using Scott–Knott test ($P < 0.05$; Scott and Knott 1974). For the antibiosis study, 'genotype' was considered a fixed effect and the pairwise *t*-test comparisons were conducted by least squares means (LS-means; $P < 0.05$), using the SAS 'Proc Glimmix' procedure (SAS Institute 2001).

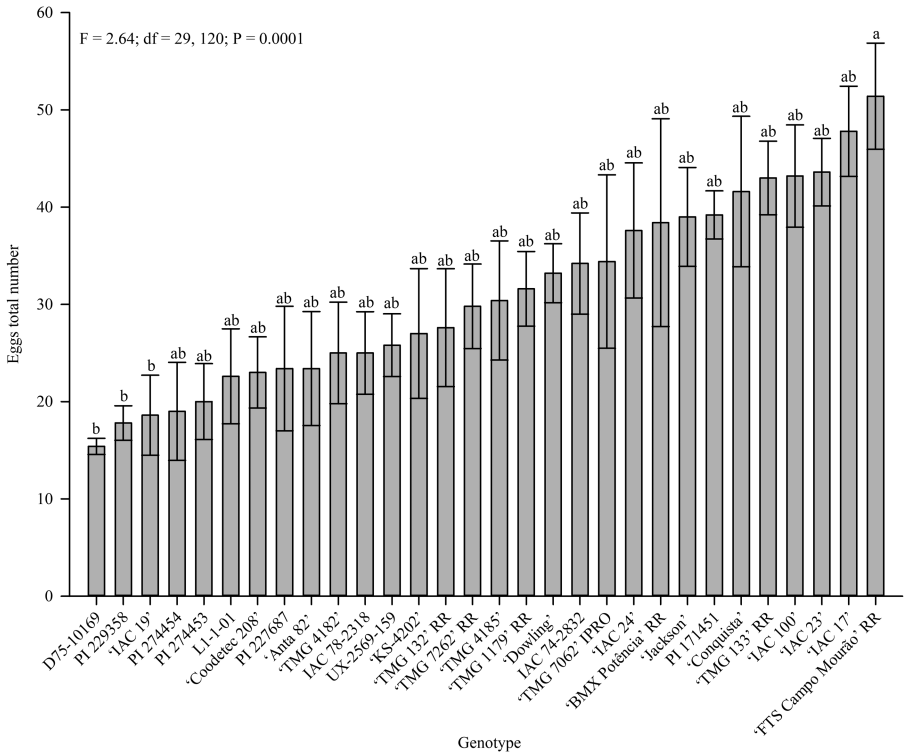


Fig. 1. Oviposition of *A. gemmatalis* on 30 soybean genotypes under greenhouse conditions. 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

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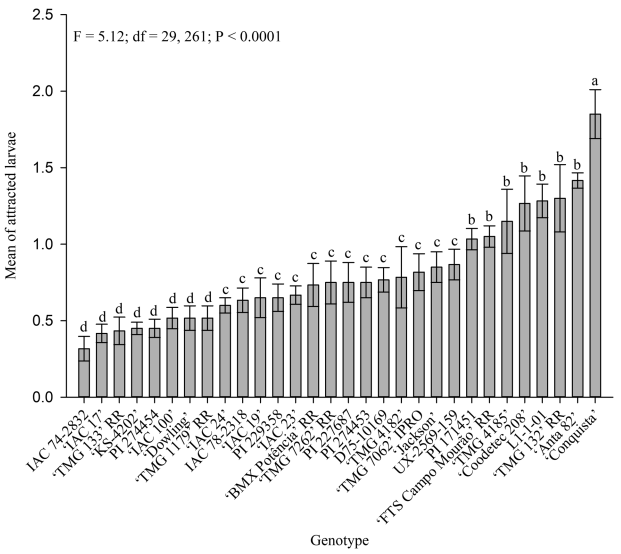


Fig. 2. Mean (±SE) of fourth-instar *A. gemmatalis* attracted to 30 genotypes after 120 min in the laboratory. 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

Results

Antixenosis Bioassays

In the oviposition test, D75-10169, PI 229358, and 'IAC 19' genotypes had the least number of eggs (15.40, 17.80, and 18.60 eggs, respectively), while 'FTS Campo Mourão' RR had the greatest number of eggs (51.40 eggs; $F = 2.64$; df = 29, 120; $P = 0.0001$; Fig. 1). Considering the attractiveness mean values after 120 min, IAC 74-2832, 'IAC 17', 'TMG 133' RR, 'KS-4202', PI 274454, 'IAC 100', 'Dowling', and 'TMG 1179' RR were the least infested (0.32–0.52 larvae), compared with 'Conquista' (1.85 larvae), 'Anta 82' (1.42 larvae), 'TMG 132' RR (1.30 larvae), L1-1-01 (1.28 larvae), 'Coodetec 208' (1.27 larvae), 'TMG 4185' (1.15 larvae), 'FTS Campo Mourão' RR (1.05 larvae), and PI 171451 (1.03 larvae; $F = 5.12$; df = 29, 261; $P < 0.0001$; Fig. 2).

In the free-choice food consumption in test, the genotypes 'TMG 1179' RR, 'IAC 100', D75-10169, 'IAC 17', 'IAC 23', IAC 78-2318, 'IAC 24', 'TMG 7062' IPRO, 'IAC 19', and IAC 74-2832 were the least consumed by fourth-instar *A. gemmatalis* larvae (<1.12 cm²; $F = 10.01$; df = 29, 261; $P < 0.0001$; Table 2). In the no-choice test, significant differences were observed among the genotypes ($F = 4.91$; df = 29, 270; $P < 0.0001$; Table 2); 'IAC 100', 'TMG 7062' IPRO, IAC 78-2318, 'IAC 23', and 'TMG 1179' RR being the least consumed (<1.50 cm²). In both tests, 'Conquista', 'Coodetec 208', and 'Anta 82' were the most consumed by *A. gemmatalis*.

Life-History Traits of *A. gemmatalis* Feeding on Selected Genotypes

The mean duration of first-instar developmental period was significantly longer when the insects were fed with leaves of 'IAC 19' (3.66 d) and 'IAC 17' (3.34 d) compared with 'Conquista' (2.74 d) and 'Coodetec 208' (2.94 d; $F = 4.09$; df = 12, 637; $P < 0.0001$; Table 3). Second-instar duration on genotypes 'IAC 19' (2.63 d), IAC 74-2832 (2.56 d), and 'IAC 17' (2.47 d) was prolonged compared with 'TMG 7062' IPRO (1.13 d) and PI 274454 (2.15 d; $F = 5.27$; df = 12, 517; $P < 0.0001$). Third-instar duration was longest for 'IAC 17' (3.24 d) and 'TMG 133' RR (2.88 d), while duration was shortest for 'IAC 19' and 'Coodetec 208' (<2.40 d; $F = 2.49$; df = 11, 462; $P = 0.0048$).

Table 2. Mean (±SE) food consumption (cm²) by fourth-instar *A. gemmatalis* on 30 genotypes in free- and no-choice antixenosis tests in the laboratory

Genotype	Food consumption (cm²)	
	Free-choice	No-choice
'TMG 1179' RR	0.67 ± 0.11d	1.47 ± 0.40c
'IAC 100'	0.88 ± 0.24d	1.34 ± 0.16c
D75-10169	0.89 ± 0.13d	1.66 ± 0.25c
'IAC 17'	0.97 ± 0.11d	1.51 ± 0.40c
'IAC 23'	0.99 ± 0.13d	1.46 ± 0.14c
IAC 78-2318	1.01 ± 0.15d	1.41 ± 0.11c
'IAC 24'	1.05 ± 0.11d	1.70 ± 0.43c
'TMG 7062' IPRO	1.05 ± 0.18d	1.39 ± 0.20c
'IAC 19'	1.08 ± 0.15d	1.89 ± 0.36c
IAC 74-2832	1.11 ± 0.17d	1.65 ± 0.35c
L1-1-01	1.26 ± 0.10c	1.57 ± 0.34c
'KS-4202'	1.33 ± 0.21c	2.05 ± 0.58c
PI 227687	1.40 ± 0.13c	2.25 ± 0.63c
'TMG 133' RR	1.46 ± 0.16c	1.93 ± 0.28c
'FTS Campo Mourão' RR	1.61 ± 0.18c	2.24 ± 0.28c
'TMG 4182'	1.73 ± 0.23b	2.27 ± 0.28c
PI 229358	1.79 ± 0.27b	2.10 ± 0.44c
'BMX Potência' RR	1.86 ± 0.18b	2.56 ± 0.24c
'Dowling'	1.87 ± 0.20b	2.29 ± 0.20c
PI 274453	1.98 ± 0.17b	2.40 ± 0.35c
PI 171451	2.02 ± 0.20b	2.45 ± 0.42c
'Jackson'	1.92 ± 0.15b	2.59 ± 0.26b
'TMG 7262' RR	1.94 ± 0.22b	2.74 ± 0.19b
PI 274454	2.03 ± 0.17b	2.59 ± 0.34b
'TMG 4185'	2.06 ± 0.25b	2.77 ± 0.42b
UX-2569-159	2.33 ± 0.23a	3.03 ± 0.35b
'TMG 132' RR	2.37 ± 0.30a	3.08 ± 0.22b
'Anta 82'	2.66 ± 0.26a	3.58 ± 0.24a
'Coodetec 208'	2.68 ± 0.16a	4.30 ± 0.59a
'Conquista'	2.95 ± 0.17a	4.00 ± 0.25a
P	<0.0001	<0.0001

Means followed by the same letter in the column are not significantly different by Scott–Knott test ($P > 0.05$). 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

The longest durations of fourth instars were observed for 'IAC 17', 'IAC 100', and 'IAC 19' (2.73–2.97 d) compared with D75-10169, L1-1-01, and 'TMG 1179' RR with the shortest durations (<2.30 d; $F = 3.48$; df = 11, 435; $P = 0.0001$). The longest duration of fifth instars was observed for 'Coodetec 208; 'Conquista', D75-10169, 'TMG 133' RR, and 'TMG 1179' RR (2.68–2.88 d), differing from most other genotypes with 'IAC 24' and PI 274454 presenting the shortest durations (2.05 and 2.09 d, respectively; $F = 2.02$; df = 11, 355; $P = 0.0256$). Sixth ($F = 1.59$; df = 11, 144; $P = 0.1081$) and seventh ($F = 2.00$; df = 5, 20; $P = 0.1222$) instar duration did not differ significantly among genotypes. The complete larval period was longest when larvae were confined to 'IAC 19', 'IAC 100', 'IAC 17', and 'IAC 24' (>18.90 d), while 'Conquista' resulted in the shortest larval period (<15.00 d; $F = 18.64$; df = 11, 269; $P < 0.0001$; Table 3).

Genotypes 'IAC 24', PI 274454, IAC 74-2832, and 'IAC 17' resulted in lower larval viability (≤36.00%; $F = 6.08$; df = 11, 588; $P < 0.0001$; Fig. 3). Larvae fed with leaves of 'TMG 7062' IPRO did not complete the larval phase. 'Conquista', 'TMG 1179' RR, D75-10169, and 'TMG 133' RR were the most suitable genotypes for larval development (56.00–72.00%).

Second-instar food consumption was lowest for 'IAC 24' (1.14 cm²), followed by 'IAC 19' (1.22 cm²), 'IAC 100' (1.26 cm²),

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and 'IAC 17' (1.31 cm^2; $F = 3.18$; df = 11, 501; $P = 0.0003$; Table 4). Second-instar food consumption observed for 'TMG 7062' IPRO was negligible and could not be measured with the leaf area meter. Third-instar food consumption was lowest for 'TMG 1179' RR (6.18 cm^2), 'IAC 19' (6.26 cm^2), D75-10169 (6.40 cm^2), and 'IAC 100' (6.49 cm^2; $F = 35.63$; df = 11, 462; $P < 0.0001$). Fourth-instar food consumption was lowest for 'IAC 100' (9.80 cm^2; $F = 25.14$; df = 11, 435; $P < 0.0001$). Fifth-instar food consumption was lowest for 'IAC 19' (12.01 cm^2), 'IAC 100' (12.44 cm^2), 'IAC 24' (12.78 cm^2), 'IAC 17' (13.59 cm^2), D75-10169 (14.06 cm^2), L1-1-01 (14.35 cm^2), 'TMG 1179' RR (15.14 cm^2), and 'TMG 133' RR (15.83 cm^2; $F = 66.78$; df = 11, 356; $P < 0.0001$). Sixth-instar food consumption was lowest for D75-10169 (11.57 cm^2; $F = 4.21$; df = 11, 144; $P < 0.0001$). We did not find significant differences among genotypes in seventh-instar food consumption ($F = 1.93$; df = 5, 20; $P = 0.1341$). 'Conquista' was the most preferred genotype by *A. gemmatalis* in second, third, fifth, and sixth instars, with consumption of 2.09, 14.99, 28.35, 62.97, and 24.99 cm^2, respectively.

Fifth-instar mean weight was lowest for 'IAC 19' (0.09 g), 'IAC 24', 'IAC 100', and 'IAC 17' (0.10 g; $F = 13.94$; df = 11, 304; $P < 0.0001$; Table 5). Fifth-instar weight was highest for 'Conquista' (0.18 g) and 'Coodetec 208' (0.16 g) and lowest for 'IAC 19' and 'IAC 100'. Pupal weight was lowest for 'IAC 17' (0.12 g) and 'IAC 24' (0.13 g), and highest for 'Conquista' (0.21 g) and 'Coodetec 208' (0.19 g; $F = 16.75$; df = 11, 255; $P < 0.0001$; Fig. 4; Table 5). Larvae feeding on 'TMG 7062' IPRO did not transition to fifth-instar larvae and, consequently, pupae.

Prepupal duration was longest for 'IAC 17', 'IAC 100', 'IAC 19', and 'IAC 24' (>2.00 d), differing from other genotypes, and was shortest for 'Conquista' (1.08 d), L1-1-01 (1.25 d), and 'TMG 1179' RR (1.28 d; $F = 13.00$; df = 11, 268; $P < 0.0001$; Table 6). Pupal duration was longest for 'IAC 74-2832' and the same genotypes as for prepupal duration (>11.20 d), differing from most of the other genotypes, and shortest for 'Conquista' (9.31 d; $F = 25.20$; df = 11, 231; $P < 0.0001$; Table 6). Pupal viability did not differ significantly among genotypes ($F = 1.33$; df = 11, 268; $P = 0.2087$; Fig. 5). Larvae confined to 'TMG 7062' IPRO did not reach the pupal stage. The larvae–adult duration was significantly longer when the insects were fed with 'IAC 17', 'IAC 100', 'IAC 19', and 'IAC 24' (>32.00 d; $F = 18.24$; df = 11, 231; $P < 0.0001$; Table 6). The shortest larvae–adult duration was observed for 'Conquista' (27.82 d).

Preoviposition period was significantly affected by genotype ($F = 8.12$; df = 11, 59; $P < 0.0001$; Table 7). The longest duration was observed for 'IAC 100', 'IAC 17', 'IAC 19', and 'IAC 24' (≥5.00 d), differing from 'Conquista' and 'Coodetec 208' (1.85 and 2.80 d, respectively), with the shortest durations. Oviposition period was significantly affected by genotype ($F = 3.53$; df = 11, 59; $P = 0.0008$; Table 7). The longest duration was observed for 'Conquista' (13.54 d) and L1-1-01 (11.60 d) and shortest for 'IAC 100', 'IAC 24', 'IAC 17', and 'IAC 19' (4.75–5.89 d). Egg number per female was significantly affected by the genotype ($F = 5.44$; df = 11, 59; $P < 0.0001$; Table 7), being lowest for 'IAC 24', 'IAC 17', 'IAC 100', 'IAC 19', and 'TMG 1179' RR (110.50–240.43 eggs). The highest number of eggs was recovered for 'Conquista', D75-10169, L1-1-01, 'TMG 133' RR, and PI 274454 (>400 eggs).

Table 3. Mean (±SE) duration of each larval instar and larval period of *A. gemmatalis* on 13 soybean genotypes in the laboratory

	Days							
Genotype	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Seventh instar	Larval period
'IAC 19'	3.66 ± 0.15a (*n* = 50)	2.63 ± 0.21a (*n* = 38)	2.39 ± 0.24cd (*n* = 31)	2.73 ± 0.29abc (*n* = 30)	2.19 ± 0.23bcd (*n* = 27)	2.61 ± 0.29a (*n* = 23)	2.20 ± 0.33a (*n* = 5)	19.86 ± 2.13a (*n* = 21)
'IAC 100'	3.08 ± 0.10bc (*n* = 50)	2.42 ± 0.17abcd (*n* = 43)	2.51 ± 0.19bcd (*n* = 41)	2.85 ± 0.24ab (*n* = 39)	2.48 ± 0.24abcd (*n* = 31)	2.26 ± 0.25a (*n* = 23)	2.11 ± 0.27a (*n* = 9)	19.24 ± 2.08a (*n* = 21)
'IAC 17'	3.34 ± 0.14ab (*n* = 50)	2.47 ± 0.16abc (*n* = 43)	3.24 ± 0.30a (*n* = 41)	2.97 ± 0.27a (*n* = 35)	2.64 ± 0.29abc (*n* = 25)	2.30 ± 0.26a (*n* = 20)	2.00 ± 0.27a (*n* = 4)	19.22 ± 2.18a (*n* = 18)
'IAC 24'	3.28 ± 0.13b (*n* = 50)	2.43 ± 0.19abcd (*n* = 40)	2.76 ± 0.26bcd (*n* = 33)	2.72 ± 0.29abcd (*n* = 29)	2.05 ± 0.26d (*n* = 22)	2.56 ± 0.34a (*n* = 9)	2.00 ± 0.27a (*n* = 3)	18.91 ± 2.50ab (*n* = 10)
PI 274454	3.20 ± 0.12bc (*n* = 50)	2.15 ± 0.14d (*n* = 41)	2.62 ± 0.22bcd (*n* = 39)	2.53 ± 0.27bcd (*n* = 34)	2.09 ± 0.24cd (*n* = 22)	2.60 ± 0.34a (*n* = 10)	3.00 ± 0.42a (*n* = 2)	17.50 ± 2.13bc (*n* = 14)
IAC 74-2832	3.04 ± 0.12bcd (*n* = 50)	2.56 ± 0.28ab (*n* = 39)	2.63 ± 0.24bcd (*n* = 35)	2.38 ± 0.22cde (*n* = 34)	2.65 ± 0.30abc (*n* = 23)	2.93 ± 0.37a (*n* = 15)	3.33 ± 0.49a (*n* = 3)	17.35 ± 1.98c (*n* = 17)
D75-10169	2.92 ± 0.12cd (*n* = 50)	2.44 ± 0.14abcd (*n* = 45)	2.80 ± 0.22bc (*n* = 44)	2.29 ± 0.18de (*n* = 42)	2.69 ± 0.25a (*n* = 35)	2.60 ± 0.38a (*n* = 10)	—	17.34 ± 1.49c (*n* = 32)
'TMG 1179' RR	2.92 ± 0.13cd (*n* = 50)	2.29 ± 0.12bcd (*n* = 45)	2.45 ± 0.18bcd (*n* = 42)	2.07 ± 0.13e (*n* = 42)	2.68 ± 0.20ab (*n* = 40)	2.11 ± 0.27a (*n* = 9)	—	17.25 ± 1.30c (*n* = 36)
'TMG 133' RR	3.04 ± 0.14bcd (*n* = 50)	2.31 ± 0.14bcd (*n* = 45)	2.88 ± 0.22ab (*n* = 42)	2.45 ± 0.19bcde (*n* = 40)	2.68 ± 0.26ab (*n* = 34)	2.28 ± 0.27a (*n* = 18)	—	17.21 ± 1.63c (*n* = 28)
L1-1-01	2.92 ± 0.11cd (*n* = 50)	2.20 ± 0.15cd (*n* = 41)	2.58 ± 0.21bcd (*n* = 38)	2.08 ± 0.18e (*n* = 36)	2.55 ± 0.26abcd (*n* = 31)	2.20 ± 0.28a (*n* = 10)	—	17.04 ± 1.77c (*n* = 24)
'Coodetec 208'	2.94 ± 0.11cd (*n* = 50)	2.16 ± 0.13cd (*n* = 43)	2.33 ± 0.17d (*n* = 40)	2.63 ± 0.22abcd (*n* = 40)	2.88 ± 0.32a (*n* = 33)	2.35 ± 0.33a (*n* = 7)	—	15.52 ± 1.61d (*n* = 23)
'Conquista'	2.74 ± 0.08d (*n* = 50)	2.27 ± 0.10bcd (*n* = 48)	2.56 ± 0.15bcd (*n* = 48)	2.63 ± 0.16abcd (*n* = 46)	2.73 ± 0.19a (*n* = 44)	2.00 ± 0.28a (*n* = 2)	—	14.53 ± 1.11e (*n* = 36)
'TMG 7062' IPRO	3.32 ± 0.10b (*n* = 50)	1.13 ± 0.15e (*n* = 16)	—	—	—	—	—	—
P	<0.0001	<0.0001	0.0048	0.0001	0.0256	0.1081	0.1222	< 0.0001

(—) = insects did not turn into the instar. LS-means with the same letter in the column are not significantly different ($P > 0.05$). 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

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Discussion

Some of the soybean genotypes evaluated in this study significantly affected *A. gemmatalis* behavior and biological parameters, characterizing expression of two resistance categories, antixenosis and antibiosis (Smith 2005). Even though a previous study indicated a few promising soybean genotypes with resistance to *A. gemmatalis* (Fugi et al. 2005), in this study, for the first time, we assessed the behavior and development of *A. gemmatalis* immature and adult stages across a wide selection of soybean germplasm with high genetic variability.

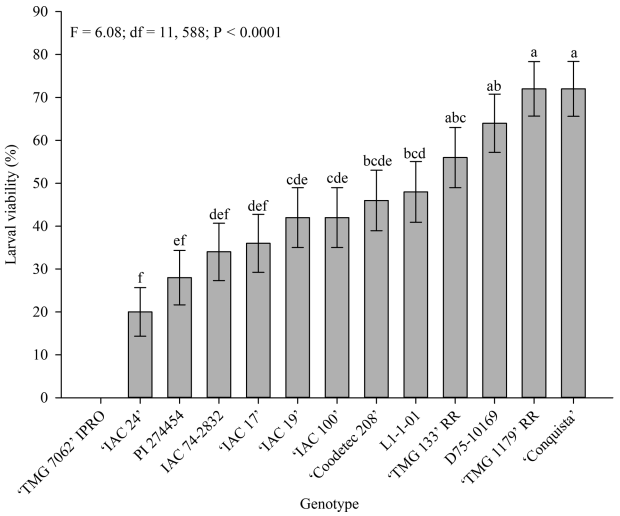


Fig. 3. Mean (±SE) larval viability of *A. gemmatalis* on 13 soybean genotypes in the laboratory. LS-means bars with the same letter are not significantly different. 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

In practical terms, the number of eggs laid in a field is particularly important because eggs will initiate a pest infestation. Results from the initial antixenosis bioassays in the greenhouse revealed differences among the soybean genotypes for the number of eggs laid by *A. gemmatalis*. Other studies have also indicated differences in the number of eggs laid among soybean genotypes by other insect species. In a no-choice test, PI 274453 and L1-1-01 had the fewest eggs laid by *Chrysodeixis includens* (Walker) (Lepidoptera: Noctuidae) (Schlick-Souza et al. 2018). In a multiple-choice oviposition test with 15 soybean genotypes, 'IAC 19' and UX-2569-159 had the lowest number of eggs laid by *Bemisia tabaci* (Gennadius) biotype B (Hemiptera: Aleyrodidae), indicating antixenosis. In the same study, PI 229358 was the least attractive and least used for oviposition. The antixenosis expressed by these genotypes to whitefly was related to characteristics of their trichomes (lower density and inclined; Valle et al. 2012, Baldin et al. 2017), which could also explain the low number of eggs laid on these genotypes in our study.

In this study, micro arenas were used to avoid contact among larvae and leaf disks, so larvae were attracted exclusively by volatile compounds released by each genotype. In this context, regarding the total mean of larvae attracted over the time, IAC 74-2832, 'IAC 17', 'TMG 133' RR, 'KS-4202', PI 274454, 'IAC

Table 4. Mean (±SE) food consumption per instar by *A. gemmatalis* on 13 soybean genotypes in the laboratory

	Food consumption (cm^2)					
Genotype	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar	Seventh instar
'IAC 24'	1.14 ± 0.16c (n = 40)	6.58 ± 0.71cd (n = 33)	10.50 ± 1.03cd (n = 29)	12.78 ± 1.44d (n = 22)	15.24 ± 2.00abcd (n = 9)	13.58 ± 1.86a (n = 3)
'IAC 19'	1.22 ± 0.17bc (n = 38)	6.26 ± 0.70d (n = 31)	10.46 ± 1.02cd (n = 30)	12.01 ± 1.24d (n = 27)	14.36 ± 1.60bcd (n = 23)	12.96 ± 1.75a (n = 5)
'IAC 100'	1.26 ± 0.17bc (n = 43)	6.49 ± 0.55d (n = 41)	9.80 ± 0.73d (n = 39)	12.44 ± 1.20d (n = 31)	14.28 ± 1.58bcd (n = 23)	12.18 ± 1.57a (n = 9)
'IAC 17'	1.31 ± 0.18bc (n = 43)	6.77 ± 0.57cd (n = 41)	11.41 ± 1.05cd (n = 35)	13.59 ± 1.47d (n = 25)	16.04 ± 1.85abcd (n = 20)	10.32 ± 1.43a (n = 4)
IAC 74-2832	1.39 ± 0.18abc (n = 39)	9.38 ± 0.91b (n = 35)	14.18 ± 1.39 bcd (n = 34)	21.12 ± 2.46cd (n = 23)	17.83 ± 2.20ab (n = 15)	12.24 ± 1.72a (n = 3)
'TMG 1179' RR	1.42 ± 0.14abc (n = 45)	6.18 ± 0.49d (n = 42)	11.59 ± 0.76cd (n = 42)	15.14 ± 1.19d (n = 40)	11.92 ± 1.58cd (n = 9)	—
'TMG 133' RR	1.42 ± 0.18abc (n = 45)	7.44 ± 0.63bcd (n = 42)	14.89 ± 1.17bc (n = 40)	15.83 ± 1.38d (n = 34)	14.49 ± 1.75bcd (n = 18)	—
D75-10169	1.48 ± 0.18abc (n = 45)	6.40 ± 0.38d (n = 44)	11.37 ± 0.76cd (n = 42)	14.06 ± 1.25d (n = 35)	11.57 ± 1.52d (n = 10)	—
PI 274454	1.56 ± 0.16abc (n = 41)	8.86 ± 0.79bc (n = 39)	14.46 ± 1.39bcd (n = 34)	29.57 ± 3.85c (n = 22)	17.64 ± 2.31ab (n = 10)	15.54 ± 2.19a (n = 2)
L1-1-01	1.57 ± 0.15abc (n = 41)	9.50 ± 0.88b (n = 38)	14.59 ± 1.28bcd (n = 36)	14.35 ± 1.37d (n = 31)	16.64 ± 2.17abcd (n = 10)	—
'Coodetec 208'	1.96 ± 0.18ab (n = 43)	12.38 ± 0.95a (n = 40)	17.23 ± 1.37b (n = 40)	50.20 ± 4.83b (n = 33)	18.66 ± 2.47ab (n = 7)	—
'Conquista'	2.09 ± 0.14a (n = 48)	14.99 ± 0.55a (n = 48)	28.35 ± 2.53a (n = 46)	62.97 ± 5.03a (n = 44)	24.99 ± 3.46a (n = 2)	—
'TMG 7062' IPRO	—* (n = 16)	—	—	—	—	—
P	0.0003	<0.0001	<0.0001	<0.0001	<0.0001	0.1341

(—) = insects did not turn into the instar. (—*) = Consumption was low, and the leaf area meter did not register the value. LS-means with the same letter in the column are not significantly different ($P > 0.05$). 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

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100', 'Dowling', and 'TMG 1179' RR had the least number of larvae (i.e., most repellant), indicating antixenosis, which could be governed by a chemical factor present in the genotypes. In a similar study testing the influence of different genotypes, 'IAC 19', 'IAC 18', 'IAC 23', L1-1-01, PI 274453, PI 229358, PI 171451, 'IAC 100', 'IAC 24', 'IAC 17', and IAC 74-2832 were classified as repellents for *C. includens* (Schlick-Souza et al. 2018). The lower attractiveness or level of colonization of an insect to a genotype suggests the presence of factors that inhibit the acceptance by the specific material, and consequently feeding and/or oviposition, which usually occurs in plants exhibiting antixenosis (Smith 2005, Baldin et al. 2019).

Table 5. Mean (±SE) *A. gemmatalis* weight of fifth instar and pupae on 13 soybean genotypes in the laboratory

	Weight (g)	
Genotype	Fifth instar	Pupae
'IAC 19'	0.09 ± 0.02f (n = 23)	0.12 ± 0.01d (n = 20)
'IAC 24'	0.10 ± 0.01ef (n = 13)	0.13 ± 0.02cd (n = 8)
'IAC 100'	0.10 ± 0.02ef (n = 25)	0.12 ± 0.02d (n = 15)
'IAC 17'	0.10 ± 0.02ef (n = 23)	0.12 ± 0.02d (n = 15)
IAC 74-2832	0.12 ± 0.02de (n = 22)	0.16 ± 0.02b (n = 15)
PI 274454	0.13 ± 0.02cd (n = 18)	0.16 ± 0.02bc (n = 14)
'TMG 133' RR	0.14 ± 0.01bcd (n = 30)	0.16 ± 0.02b (n = 22)
D75-10169	0.15 ± 0.02bc (n = 33)	0.16 ± 0.02bc (n = 27)
'TMG 1179' RR	0.15 ± 0.02bc (n = 38)	0.16 ± 0.01b (n = 31)
L1-1-01	0.15 ± 0.02bc (n = 27)	0.16 ± 0.02b (n = 22)
'Coodetec 208'	0.16 ± 0.02b (n = 25)	0.19 ± 0.02a (n = 19)
'Conquista'	0.18 ± 0.02a (n = 39)	0.21 ± 0.02a (n = 35)
'TMG 7062' IPRO	—	—
P	<0.0001	<0.0001

(—) = insects did not turn into fifth-instar larvae and pupae. LS-means with the same letter in the column are not significantly different ($P > 0.05$). 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

Volatile compounds expressed by resistant plants are common defenses; however, in crops, their potential has not been fully realized for the biological control of pests. In addition to their effect on pests, certain volatiles attract natural enemies (predators and parasitoids), so both types of effects should be considered when devising strategies to improve biological control in refuge areas (Stenberg et al. 2015).

Food consumption was low for 'TMG 1179' RR, D75-10169, 'TMG 7062' IPRO, and the 'IAC' genotypes in the free- and no-choice tests, indicating antixenosis. Similar results were observed in another study where 'IAC 100' and IAC 74-2832 were rejected by *A. gemmatalis* larvae based on a consumption index (Hoffmann-Campo et al. 1994). Genotypes D75-10169, 'IAC 100', IAC 78-2318, and 'IAC 19' were also less attractive and less consumed by *Piezodorus guildinii* (Westwood) (Hemiptera: Pentatomidae) (Silva et al. 2014). Low consumption may indicate the presence of deterrents, the lack of a feeding stimulant, or leaf hardness, which are all known to decrease feeding (Reynolds et al. 1984). However, antixenosis and antibiosis commonly overlap in resistance bioassays, making it difficult to interpret the two resistance categories in isolation (Panda and Khush 1995, Smith 2005). Thus, it is important to evaluate other parameters through larval development, with the purpose to exclude or to confirm the additional presence of antibiosis.

The capacity of resistant plants to reduce larval consumption also has implications in conjunction with insecticide use. *Chrysodeixis includens* reared on resistant soybean leaves (PI 227687) were significantly more susceptible to acephate (two times) than when they were reared on susceptible leaves (Rose et al. 1988). This enhanced efficacy could also reduce insecticide use and be particularly important and directly affect resistance management in a crop system.

Larvae that fed on 'TMG 7062' IPRO were unable to transform into third instar because the insecticidal protein (Cry1Ac) was present in these *Bt* plants. In general, the 'IAC' genotypes showed a similar response. Most larvae fed 'IAC' genotypes had relatively short instar duration, but required more time (days) to complete the larval phase because of an additional instar extending the cycle. The total larval period (14.53–19.86 d) had a difference of 5.33 d between low and high mean, indicating a high degree of antibiosis and/or antixenosis. A previous study conducted with *P. guildinii* testing 17 soybean genotypes also indicated antibiosis resistance in some genotypes, especially 'IAC 100' and 'IAC 19', where 'IAC 100' significantly prolonged nymphal development (Silva et al. 2013).

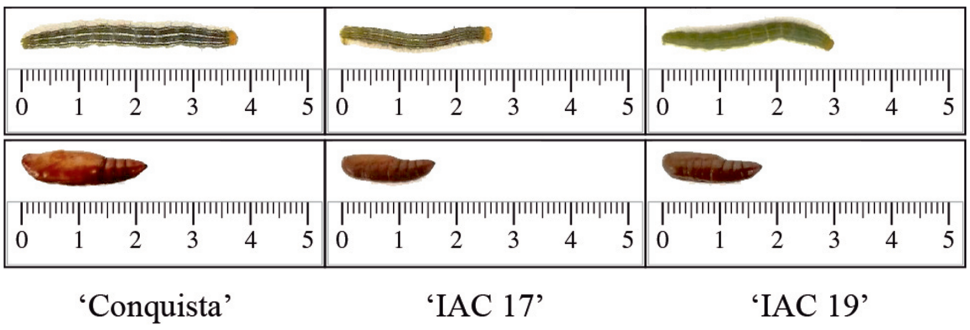


Fig. 4. Comparative development of *A. gemmatalis* fifth-instar larvae and pupae on susceptible ('Conquista) and resistant ('IAC 17' and 'IAC 19') soybean genotypes. 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

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Table 6. Mean (±SE) duration of prepupal, pupal, and larvae–adult periods of *A. gemmatalis* on 13 soybean genotypes in the laboratory

Genotype	Days		
	Prepupal	Pupal	Larvae–adult
'IAC 19'	2.00 ± 0.22a (n = 21)	11.65 ± 1.28a (n = 20)	32.47 ± 3.54a (n = 20)
'IAC 24'	2.00 ± 0.25ab (n = 10)	11.25 ± 1.46abc (n = 8)	32.25 ± 4.22a (n = 8)
'IAC 100'	2.10 ± 0.24a (n = 21)	11.73 ± 1.39a (n = 15)	32.13 ± 3.83a (n = 15)
'IAC 17'	2.11 ± 0.26a (n = 18)	11.20 ± 1.33bc (n = 15)	32.00 ± 3.75a (n = 15)
PI 274454	1.79 ± 0.22abc (n = 14)	10.86 ± 1.31cde (n = 14)	29.29 ± 3.55b (n = 14)
IAC 74-2832	1.65 ± 0.20bcd (n = 17)	11.40 ± 1.35ab (n = 15)	29.14 ± 3.40b (n = 15)
'TMG 133' RR	1.43 ± 0.16de (n = 28)	10.55 ± 1.12def (n = 22)	28.68 ± 3.05bc (n = 22)
'TMG 1179' RR	1.28 ± 0.11ef (n = 36)	10.65 ± 0.93de (n = 31)	28.65 ± 2.50bc (n = 31)
D75-10169	1.47 ± 0.14de (n = 32)	10.26 ± 0.99f (n = 27)	28.62 ± 2.76bc (n = 27)
'Coodetec 208'	1.57 ± 0.18cd (n = 23)	10.95 ± 1.22bcd (n = 19)	28.53 ± 3.20bc (n = 19)
L1-1-01	1.25 ± 0.14ef (n = 24)	10.50 ± 1.11ef (n = 22)	28.52 ± 3.02bc (n = 22)
'Conquista'	1.08 ± 0.09f (n = 36)	9.31 ± 0.73g (n = 35)	27.82 ± 2.18c (n = 35)
'TMG 7062' IPRO	—	—	—
P	<0.0001	<0.0001	<0.0001

(—) = insects did not turn into pre-pupae, pupae, and adult. LS-means with the same letter in the column are not significantly different ($P > 0.05$). 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

Table 7. Mean (±SE) preoviposition and oviposition periods, and number of eggs *A. gemmatalis* on 13 soybean genotypes in the laboratory

Genotype	Preoviposition (days)	Oviposition (days)	Number of eggs
'IAC 24'	5.00 ± 1.28abc (n = 2)	5.00 ± 1.31cd (n = 2)	110.50 ± 28.56c (n = 2)
'IAC 17'	5.00 ± 1.15ab (n = 4)	5.25 ± 1.25cd (n = 4)	131.00 ± 38.68c (n = 4)
'IAC 100'	5.50 ± 1.29a (n = 4)	4.75 ± 1.10d (n = 4)	158.75 ± 40.92c (n = 4)
'IAC 19'	5.00 ± 0.88abc (n = 9)	5.89 ± 1.03cd (n = 9)	178.78 ± 37.28c (n = 9)
'TMG 1179' RR	3.57 ± 0.70cd (n = 7)	9.43 ± 2.16bcd (n = 7)	240.43 ± 47.93c (n = 7)
IAC 74-2832	4.00 ± 0.89bcd (n = 5)	9.00 ± 2.16bcd (n = 5)	277.20 ± 76.68bc (n = 5)
'Coodetec 208'	2.80 ± 0.64de (n = 5)	9.00 ± 2.62bcd (n = 5)	292.20 ± 65.88bc (n = 5)
PI 274454	3.67 ± 0.87cd (n = 6)	8.67 ± 1.96bcd (n = 6)	419.00 ± 100.69ab (n = 6)
'TMG 133' RR	3.50 ± 0.73cd (n = 6)	10.83 ± 2.43abc (n = 6)	426.17 ± 108.50ab (n = 6)
L1-1-01	3.80 ± 0.85bcd (n = 5)	11.60 ± 2.61ab (n = 5)	451.00 ± 11.16ab (n = 5)
D75-10169	3.60 ± 0.79 cd (n = 5)	8.60 ± 1.96bcd (n = 5)	462.60 ± 115.69ab (n = 5)
'Conquista'	1.85 ± 0.15e (n = 13)	13.54 ± 1.22a (n = 13)	696.69 ± 74.34a (n = 13)
'TMG 7062' IPRO	—	—	—
P	<0.0001	0.0008	<0.0001

(—) = insects did not turn into adult. LS-means with the same letter in the column are not significantly different ($P > 0.05$). 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

Prolongation of the immature phase may result from intake of deleterious compounds typically present in antibiotic genotypes that inhibit insect development. However, genotypes with high levels of antixenosis can also cause this effect, either by hampering insect feeding, nutritional improprieties, or poor nutritional quality of host (Painter 1951). In practical terms, the prolongation of the larval cycle increases the exposure of an insect to natural enemies or other mortality factors.

All larvae died on genotype 'TMG 7062' IPRO during initial larval development, confirming its antibiotic effect. Low larval viability was observed for 'IAC 24', PI 274454, IAC 74-2832, and 'IAC 17', which suggests antibiosis, reinforcing the probable presence of toxic compounds that inhibit larvae development. For 'IAC 17' and 'IAC 24', the results confirm Fugi et al. (2005), where in addition to inducing lower larval viability, adult deformation levels of 12.50 and 23.60% were observed for 'IAC 17' and 'IAC 24', respectively. Low larval viability was also observed when larvae of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) were fed leaves of PI 274454 and 'IAC 17' (Coelho et al. 2020).

Genotype 'IAC 100' has significant levels of the flavonoids rutin and genistin, which suggests these compounds may be involved in resistance observed for *A. gemmatalis*, similar to that documented for *P. guildinii* (Bentivenha et al. 2018). These compounds were also related to resistance against *A. gemmatalis* in another study where leaf extracts of 'IAC 100' were offered to larvae (Piubelli et al. 2005). However, chemical and morphological analysis of the other genotypes is needed to fully understand the role of various resistance factors.

Fifth-instar larvae fed 'IAC 19', 'IAC 24', 'IAC 100', and 'IAC 17' leaves weighed less, which indicates resistance. The values observed in these genotypes (0.09 and 0.10 g) were half that observed in the susceptible genotype 'Conquista' (0.18 g). Similarly, *Spodoptera cosmioides* (Walker) (Lepidoptera: Noctuidae) larvae had reduced weight when fed 'IAC 100' (Boiça Júnior et al. 2015), and fifth-instar *H. armigera* had reduced weight when fed 'IAC 19' (Coelho et al. 2020).

Pupal weight was also significantly affected by the 'IAC 19', 'IAC 24', 'IAC 100', and 'IAC 17'. Larvae fed 'IAC 19', 'IAC 100', or 'IAC 17' weighed 0.12 g, and 0.13 g for those fed 'IAC 24', while pupae from the susceptible genotypes 'Coodetec 208' and 'Conquista' weighed 0.19 and 0.21 g, respectively. *Anticarsia gemmatalis* fed PI 229358, 'IAC 17', 'IAC 24', and 'IAC PL-1' in a biological development study did not show significant differences in pupal weight (Fugi et al. 2005); however, in another study, *A. gemmatalis* pupal weight was significantly reduced when larvae were fed 'IAC 17' (Gazzoni and Tutida 1996). The reduction in larval and pupal weights may be associated with low reserves acquired during the larval period because of a reduction in the food's nutritional value. Together, these effects might compromise the performance of the insect in the reproductive stage by reducing the number of copulations, oviposition, and fertility (Smith and

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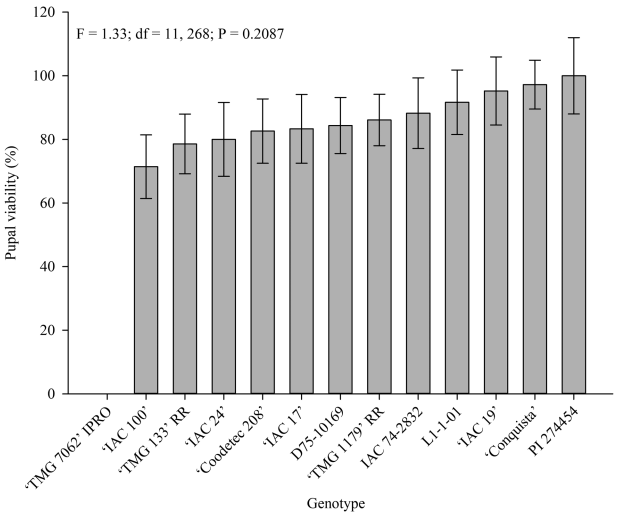


Fig. 5. Mean (±SE) pupal viability of *A. gemmatalis* on 13 soybean genotypes in the laboratory. 'Coodetec 208' and 'Conquista' were considered the susceptible checks.

Clement 2012, Smith and Chuang 2014), which are generally associated with the expression of resistance.

In our study, the 'IAC' genotypes caused significant changes in *A. gemmatalis* life cycle (i.e., larval through pupal developmental time). Similarly, 'IAC 100' was found to provide resistance by extending the life cycle of *Spodoptera eridania* (Cramer) (Lepidoptera: Noctuidae) (Souza et al. 2014), and *H. armigera* larvae fed 'IAC 17' had a higher numerical mean life cycle duration (Coelho et al. 2020). Genotypes that result in the longest life cycle durations usually have low nutritional quality, which can influence insect development (Pereyra and Sánchez 2006). The increase in life cycle duration affects directly on population dynamics and may determine the success of the species on the host plant. Another consequence is fewer insect generations per year (Green et al. 2002, Rajapakse and Walter 2007).

As expected, the adult parameters were severely affected by the genotypes. Differences were observed in the preoviposition period (1.85–5.50 d) and oviposition period (4.75–13.54 d). These results could be a consequence of reduced nutrition of resistant plants during the larval period that translates into deficiencies, quantitative, or qualitative nutrient imbalances in the adult phase (Souza et al. 2014). Significant effects of the genotypes were also observed by the low number of eggs laid by *A. gemmatalis* fed 'IAC 24', 'IAC 17', 'IAC 100', and 'IAC 19' (110.50–178.78 eggs). Egg production can be affected by physical or chemical differences in the food, by the amount of food ingested during insect development, and by the nutritional value that each host can offer to the insect (Umbanhowar and Hastings 2002). Negative effects on fecundity, as well as in the number of progeny, are common for insects feeding on genotypes expressing antibiosis (Panda and Khush 1995, Smith 2005).

Based on the bioassays performed, high levels of antixenosis were found in genotypes 'TMG 133' RR, 'TMG 1179' RR, 'IAC 19', 'IAC 17', 'IAC 100', D75-10169, IAC 78-2318, and IAC 74-2832, as evidenced by lower rates of attractiveness, larval food consumption, and oviposition. By influencing behavior and impacting larval viability, genotypes IAC 74-2832 and PI 274454 were shown to express antixenosis and/or antibiosis. Genotype 'TMG 7062' IPRO was found to provide antibiosis by affecting larval development and larval viability. Genotypes 'IAC 19', 'IAC 24, 'IAC 17', and 'IAC 100' were shown to express antibiosis by compromising several biological parameters, mainly larval development and viability, and reducing pupal weight. Because of low food consumption by larvae on 'IAC 24', antixenosis was also expressed by the genotype.

Planting resistant materials in a refuge area, e.g., could be a good strategy to reduce the number of foliar insecticide sprays, since insects in the refuge would feed less, have lower viability, and cause reduced or no economic impact. Thus, resistant cultivars would be agronomically desirable and compatible with other IPM strategies (Stenberg 2017).

The resistance found in some of the evaluated genotypes increases their importance as sources of resistance to *A. gemmatalis*, and possibly other insect pests. Our study provides baseline information which can be useful for developing management strategies for this species in soybean, especially in South America. In the future, further trials must be carried out under field conditions to validate whether the genotypes are effective in suppressing *A. gemmatalis* populations.

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