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Interspecific Variation in Susceptibility to Insecticides by Lepidopteran Pests of Soybean, Cotton, and Maize Crops From Brazil

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Abstract

The interspecific variation in susceptibility to insecticides by lepidopteran species of soybean [*Glycine max* L. (Merr.)], cotton (*Gossypium hirsutum* L.), and maize (*Zea mays* L.) crops from Brazil were evaluated. Populations of *Anticarsia gemmatalis* (Hübner) (Lepidoptera: Erebidae), *Chrysodeixis includens* (Walker), *Helicoverpa armigera* (Hübner), *Spodoptera frugiperda* (Smith), *Spodoptera eridania* (Stoll), *Spodoptera cosmioides* (Walker), and *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae) were collected from 2019 to 2021. Early L3 larvae (F_2 generation) were exposed to the formulated insecticides methoxyfenozide, indoxacarb, spinetoram, flubendiamide, and chlorfenapyr in diet-overlay bioassays. The median lethal concentrations (LC_{50}) were used to calculate tolerance ratios (TR) of each species in relation to the most susceptible species to each insecticide. The lowest LC_{50} values were verified for *A. gemmatalis* to all insecticides tested. *Chrysodeixis includens* and most of the *Spodoptera* species were moderately tolerant to methoxyfenozide (TR < 8.0-fold) and indoxacarb (TR < 39.4-fold), whereas *H. armigera* was the most tolerant species to methoxyfenozide (TR = 21.5-fold), and indoxacarb (TR = 106.4-fold). *Spodoptera cosmioides*, *S. eridania*, and *S. albula* showed highest tolerance to spinetoram (TR > 1270-fold), *S. eridania*, *S. frugiperda*, and *S. albula* to flubendiamide (TR from 38- to 547-fold), and *S. albula* to indoxacarb (TR = 138.6-fold). A small variation in susceptibility to chlorfenapyr (TR < 4.4-fold) was found among the lepidopteran evaluated. Our findings indicate a large variation in susceptibility to indoxacarb, spinetoram, and flubendiamide and a relatively low variation in susceptibility to methoxyfenozide and chlorfenapyr by lepidopteran species of soybean, cotton, and maize from Brazil.

Key words: velvetbean caterpillar, soybean looper, old world bollworm, *Spodoptera* spp., IRM

Brazil is one of the largest soybean [*Glycine max* (L.) Merr.], cotton (*Gossypium hirsutum* L.), and maize (*Zea mays* L.) producers with a cultivated area of 38.5, 1.3, and 19.8 million ha, respectively, during the 2020/21 crop seasons (CONAB 2021). These crops can be attacked by numerous lepidopteran species, including *Anticarsia gemmatalis* (Hübner) (Lepidoptera: Erebidae), *Chrysodeixis includens* (Walker), *Helicoverpa armigera* (Hübner), and species of the genus *Spodoptera* such as *Spodoptera frugiperda* (Smith), *Spodoptera eridania* (Stoll), *Spodoptera cosmioides* (Walker), and *Spodoptera albula* (Walker) (Lepidoptera: Noctuidae) (Panizzi 2013, Bernardi et al. 2014, Specht et al. 2015, Dourado et al. 2021, Horikoshi et al. 2021). These species may cause significant economic losses due to defoliation and/or damage on reproductive structures (Santos et al. 2010, Bueno et al. 2011).

Historically, chemical control is one of the main tactics used for managing lepidopteran species on soybean, cotton, and maize in Brazil. Since the mid-2000s, the adoption of genetically modified plants expressing insecticidal proteins from *Bacillus thuringiensis*

(Bt) Berliner provided a new effective control strategy against key lepidopteran species of soybean, cotton, and maize (Bernardi et al. 2012; Blanco et al. 2016; Marques et al. 2016, 2021; Bacalhau et al. 2020). However, secondary pests such as *S. eridania*, *S. cosmioides*, and *S. albula* have natural low susceptibility to most Bt proteins expressed in Bt soybean and Bt cotton (Bernardi et al. 2014, Machado et al. 2020a, Horikoshi et al. 2021), whereas *S. frugiperda* evolved resistance to Bt proteins expressed in maize, affecting the performance of Bt soybean and Bt cotton technologies (Farias et al. 2014, Horikoshi et al. 2016, Omoto et al. 2016, Machado et al. 2020b).

The use of chemical insecticides against lepidopteran species has increased on Bt and non-Bt fields in Brazil due to outbreaks of secondary pests of Bt plants or resistance evolution. It is known that insecticides often have limited effectiveness against some pest species due to their natural variation in susceptibility or tolerance. Susceptible and tolerant species will be exposed to the same insecticide application, which may favor the survival and new outbreaks of more tolerant pest species, if the same insecticide is widely and repeatedly used (Tabashnik and Carrière 2017). On this basis, we conducted a series of laboratory bioassays to assess the variation in susceptibility to selected insecticides in lepidopteran species that attack soybean, cotton, and maize crops in Brazil.

Material and Methods

Insects

Field populations of lepidopteran species that attack soybean, cotton, or maize in Brazil (*A. gemmatalis*, *C. includens*, *H. armigera*, *S. frugiperda*, *S. cosmioides*, *S. eridania*, and *S. albula*) were collected from 2019 to 2021 in non-Bt growing areas (Table 1). Unfortunately, it was not possible to collect species in a same location or field as it is uncommon to find all species on specific crop at the same time. Furthermore, we collected a single population of *H. armigera* and *S. albula* due to the difficulty of finding a representative number of insects. Collected larvae were transported to the laboratory and reared on an artificial diet based on white beans, wheat germ, and yeast (Greene et al. 1976). Lepidopteran species were identified based on Gilligan and Passoa (2014) and Sosa-Gómez et al. (2014) protocols.

Insecticides

The susceptibility of lepidopteran species that infest soybean, cotton, and maize crops were evaluated for the following insecticides: methoxyfenozide (Intrepid 240 SC, 240 g active ingredient [a.i.]/liter, Corteva Agriscience, São Paulo, SP, Brazil), an ecdysone receptor agonist (IRAC group 18); indoxacarb (Avatar, 15 g a.i./liter, FMC Química do Brasil Ltda, Campinas, SP, Brazil), a voltage-dependent sodium channel blocker (IRAC subgroup 22A); spinetoram (Exalt, 120 g a.i./liter, Corteva Agriscience, São Paulo, SP, Brazil), a nicotinic acetylcholine receptor allosteric modulator (IRAC group 5); flubendiamide (Belt, 480 g a.i./liter, Bayer S.A., São Paulo, SP, Brazil), a ryanodine receptor modulator (IRAC group 28); and chlorfenapyr (Pirate, 240 g a.i./liter, Basf S.A., São Paulo, SP, Brazil), an inhibitor (uncoupler) of oxidative phosphorylation disrupting the proton gradient (IRAC group 13).

Bioassays

To perform bioassays, the artificial diet of Greene et al. (1976) was prepared and then poured in 24-well acrylic plates (Costar, São Paulo, SP, Brazil) at a volume of 1 ml/well and allowed to solidify inside a laminar air flow cabinet under ultraviolet light. Afterwards, 5–8 concentrations of each insecticide were prepared by dilution with distilled water. Triton X-100 (Sigma-Aldrich, São Paulo, SP, Brazil) was added to each concentration at 0.1% (v/v) for a uniform spread of the solution on the diet surface. After that, 30 µl/well were applied to the diet surface (area of 1.88 cm^2) using an automatic replication micropipette (Repetman, Gilson, São Paulo, SP, Brazil). The control treatment was distilled water and Triton X-100. After drying, a single early L3 larva from the F_2 generation was added to each well. Plates were closed and placed in a room at 25 ± 2°C, 60 ± 10% RH, and a photoperiod of 12:12 hr. The bioassay design was completely randomized with 2–5 replicates of 24 larvae/replicate, totaling 48–120 larvae tested/concentration/species. Larval mortality was assessed at 48 hr (indoxacarb, spinetoram, and chlorfenapyr), 96 hr (flubendiamide), and 120 hr (methoxyfenozide) after exposure as indicated by the Insecticide Resistance Action Committee (IRAC) protocols. Larvae without movement were considered dead when them did not respond after being touched with a fine brush.

Table 1. Location, date, and host plant sources of the field populations of lepidopteran species from Brazil

Field population	Location of collecting sites	Latitude (S) and longitude (W)	Date of collection	Host plant	Insect numbers
A. gemmatalis – 1	Missal, Paraná	25° 02′ 49″; 54° 12′ 50″	December 2019	Non-Bt soybean	550
A. gemmatalis – 2	Taquara Verde, Santa Catarina	26° 46′ 46″; 51° 12′ 47″	December 2019	Non-Bt soybean	620
C. includens – 1	Correntina, Bahia	12° 54′ 12″; 46° 12′ 41″	March 2019	Non-Bt soybean	500
C. includens – 2	Campo Verde, Mato Grosso	15° 22′ 59″; 55° 09′ 09″	January 2019	Non-Bt soybean	770
C. includens – 3	Casa Branca, São Paulo	21° 27′ 05″; 47° 06′ 14″	February 2019	Non-Bt soybean	954
H. armigera	Planaltina, Distrito Federal	15° 27′ 54″; 47° 34′ 29″	February 2021	Non-Bt soybean	405
S. cosmioides – 1	Santa Maria, Rio Grande do Sul	29° 42′ 57″; 53°44′ 03″	February 2019	Non-Bt soybean	280
S. cosmioides – 2	São Pedro do Sul, Rio Grande do Sul	29° 35′ 54″; 54°14′ 36″	February 2019	Non-Bt soybean	225
S. cosmioides – 3	São Sepé, Rio Grande do Sul	30° 04′ 18″; 53° 38′ 45″	February 2019	Non-Bt soybean	281
S. cosmioides – 4	Rio Verde, Goiás	17º 06′ 05″; 50° 46′ 57″	October 2020	Non-Bt soybean	390
S. eridania – 1	Santa Maria, Rio Grande do Sul	29° 43′ 20″; 53° 33′ 34″	March 2021	Non-Bt soybean	187
S. eridania – 2	Campo Verde, Mato Grosso	29° 43′ 20″; 53° 33′ 34″	January 2019	Non-Bt soybean	453
S. frugiperda – 1	Arroio do Meio, Rio Grande do Sul	15° 22′ 59″; 55° 09′ 09″	February 2019	Non-Bt maize	190
S. frugiperda – 2	Cascavel, PR	21°47′11‘; 49°36′52’	March 2020	Non-Bt maize	529
S. frugiperda – 3	Correntina, Bahia	13° 55′ 53″; 46° 10′ 29″	February 2021	Non-Bt soybean	182
S. frugiperda – 4	Casa Branca, SP	23° 37′ 09″; 48° 26′ 45″	May 2021	Non-Bt maize	1,261
S. albula	Sapezal, Mato Grosso	13° 29′ 29″; 58° 26′ 52″	February 2020	Non-Bt soybean	332

Statistical Analyses

To estimate the susceptibility to insecticides, concentration-mortality data were initially subjected to a goodness of fit test to measure how well data fit the assumptions of the probit model using a χ^2 test. In this test, values (response) predicted by the model are compared with those observed in the bioassays. If the values did not differ significantly ($P > 0.05$), the model is assumed fit to the data. Then, concentration-mortality data were used to estimate LC_{50} and LC_{90} lethal concentrations and respective 95% confidence intervals with the PROC PROBIT procedure in SAS software version 9.1 (SAS Institute 2002). A likelihood ratio test was also performed to test the hypothesis of parallelism and equality (same slopes and intercepts) of mortality lines of species exposed to each insecticide. If the hypothesis was rejected, the LC values were pairwise compared, and significance was declared if 95% confidence intervals did not overlap (Savin et al. 1977, Robertson et al. 2007). The tolerance ratios (TR) were also calculated by dividing the LC_{50} of a specific population by the LC_{50} of the most susceptible species or population to each insecticide.

Results

Susceptibility to Methoxyfenozide

There was a significant interspecific variation regarding susceptibility to methoxyfenozide in lepidopteran species of soybean, cotton and maize crops in Brazil as indicated by equality ($\chi^2 = 1040.0$; $df = 26$; $P < 0.001$) and parallelism ($\chi^2 = 119.0$; $df = 13$; $P < 0.001$) tests, which showed different lines of mortality. The nonoverlap of 95% confidence intervals of LC values also indicated variation in susceptibility to methoxyfenozide among the species studied (Table 2).

The LC_{50} and LC_{90} values of methoxyfenozide indicated that *A. gemmatalis* populations were the most susceptible, followed by *S. eridania*, *S. frugiperda*, *S. cosmioides*, *S. albula*, and *C. includens*, with a tolerance ratio up to 8-fold (Table 2). In contrast, the LC_{50} and LC_{90} values of methoxyfenozide for *H. armigera* were significantly higher compared to other lepidopteran species, with a tolerance ratio of 21.5-fold relative to the most susceptible species.

Susceptibility to Indoxacarb

The concentration-mortality lines of lepidopteran species that attack soybean, cotton, and maize crops from Brazil exposed to indoxacarb presented distinct angular and linear parameters as shown by equality ($\chi^2 = 1550.0$; $df = 26$; $P < 0.001$) and parallelism ($\chi^2 = 113.0$; $df = 13$; $P < 0.001$) tests. Significant differences were also verified for LC_{50} and LC_{90} values in which the 95% confidence intervals did not overlap (Table 3).

The LC_{50} and LC_{90} values of indoxacarb were significantly lower for *A. gemmatalis* and *S. cosmioides* populations than other lepidopteran species tested (Table 3). Moderate susceptibility was observed for *C. includens*, *S. eridania*, and *S. frugiperda*, indicating a tolerance ratio from 11.8- to 39.4-fold. In contrast, the LC_{50} and LC_{90} values were higher for *H. armigera* and *S. albula* populations. The tolerance ratio for these species was higher than 106-fold in relation to the most susceptible species.

Susceptibility to Spinetoram

The probit lines of lepidopteran species evaluated exposed to spinetoram was distinct as shown by equality ($\chi^2 = 2330.0$; $df = 30$; $P < 0.001$) and parallelism ($\chi^2 = 317.0$; $df = 15$; $P < 0.001$) tests. Significant differences were also verified for LC_{50} and LC_{90} values as indicated by the nonoverlap of 95% confidence intervals (Table 4).

A large interspecific variation regarding susceptibility to spinetoram was detected in lepidopteran species evaluated (Table 4). *Anticarsia gemmatalis* was the most susceptible species to spinetoram, followed by *C. includens* and *S. frugiperda* which also were highly susceptible, although presenting a tolerance ratio up to 90-fold relative to other species. However, the LC_{50} and LC_{90} values of spinetoram were significantly higher for *S. eridania*, *S. cosmioides*, and *S. albula*. The LC_{50} values of spinetoram against these species indicated a tolerance ratio >1,270-fold relative to the most susceptible species.

Susceptibility to Flubendiamide

Interspecific variation regarding susceptibility to flubendiamide were detected as verified by equality ($\chi^2 = 1910.0$; $df = 22$; $P < 0.001$) and

Table 2. Lethal concentration (LC; µg a.i./cm²) of methoxyfenozide to lepidopteran species of soybean, cotton, and maize crops in Brazil

		Fit of probit lines					
Species	*n*	Slope ± SE	χ^2 (*df*)	P[a]	LC_{50} (95% CI)[b]	LC_{90} (95% CI)[b]	Tolerance ratio[c]
A. gemmatalis – 1	768	2.00 ± 0.15	6.80 (5)	0.24	0.20 (0.18–0.24) a	0.89 (0.71–1.18) a	1.1
A. gemmatalis – 2	864	2.14 ± 0.14	5.37 (6)	0.50	0.18 (0.15–0.20) a	0.70 (0.59–0.88) a	–
C. includens – 1	505	1.50 ± 0.16	2.24 (5)	0.82	0.63 (0.46–0.80) bc	4.48 (3.30–6.87) cd	3.5
C. includens – 2	496	1.97 ± 0.21	2.92 (5)	0.71	1.19 (0.90–1.50) c	5.35 (4.12–7.59) d	6.6
H. armigera	432	1.80 ± 0.21	8.07 (6)	0.23	2.87 (228–3.65) e	14.80 (10.08–26.21) e	21.5
S. cosmioides – 1	576	1.81 ± 0.21	5.68 (6)	0.46	0.53 (0.36–0.70) b	2.72 (2.10–3.78) bc	2.9
S. cosmioides – 2	504	2.11 ± 0.22	7.32 (4)	0.12	0.98 (0.80–1.17) c	3.96 (3.10–5.53) cd	5.4
S. cosmioides – 4	552	1.60 ± 0.34	5.99 (4)	0.20	0.69 (0.39–0.96) bc	4.39 (2.85–9.16) cd	3.8
S. eridania – 1	384	2.42 ± 0.36	6.80 (5)	0.24	0.66 (0.50–1.80) bcd	2.23 (1.73–3.37) bc	3.7
S. eridania – 2	384	2.46 ± 0.30	2.58 (5)	0.76	0.61 (0.48–1.73) bcd	2.01 (1.58–2.84) b	3.4
S. frugiperda – 1	504	3.77 ± 0.40	3.90 (4)	0.42	0.94 (0.83–1.05) c	2.06 (1.77–2.54) b	5.2
S. frugiperda – 2	504	3.85 ± 0.43	4.01 (4)	0.40	0.98 (0.86–1.09) c	2.10 (1.80–2.60) b	5.4
S. frugiperda – 3	432	1.87 ± 0.28	3.96 (4)	0.41	0.49 (0.30–0.68) b	2.39 (1.82–3.54) bc	2.7
S. albula	504	3.15 ± 0.32	1.52 (4)	0.82	1.44 (1.24–1.64) d	3.68 (3.09–4.64) cd	8.0

[a] $P > 0.05$ in the goodness-of-fit test indicated good adjustment to the probit model.

[b] LC_{50} and LC_{90}: lethal concentration required to kill 50 and 90% of larvae, respectively, at 120 hr after exposure. LC_{50} and LC_{90} values followed by different letters within a column are significantly different from each other through nonoverlap of 95% confidence intervals.

[c] Tolerance ratio (TR_{50}) = (LC_{50} of a specific population)/(LC_{50} of the most susceptible species or population).

Table 3. Lethal concentration (LC; µg a.i./cm^2) of indoxacarb to lepidopteran species of soybean, cotton, and maize crops in Brazil

		Fit of probit lines					
Species	*n*	Slope ± SE	χ^2 (*df*)	P^a	LC_{50} (95% CI)^b	LC_{90} (95% CI)^b	Tolerance ratio^c
A. gemmatalis – 1	672	2.63 ± 0.23	6.83 (4)	0.15	0.05 (0.04–0.05) a	0.14 (0.10–0.20) a	–
A. gemmatalis – 2	768	2.27 ± 0.16	4.53 (5)	0.48	0.09 (0.08–0.10) a	0.33 (0.20–0.42) a	1.8
C. includens – 1	560	3.64 ± 0.43	7.48 (4)	0.11	1.84 (1.59–2.07) d	4.13 (3.51–5.21) bc	36.8
C. includens – 2	540	1.99 ± 0.18	7.66 (4)	0.11	1.01 (0.85–1.19) c	4.46 (3.47–6.24) bc	20.2
C. includens – 3	576	1.25 ± 0.18	4.87 (5)	0.43	0.59 (0.24–0.88) b	6.31 (3.99–12.83) bc	11.8
H. armigera	648	1.78 ± 0.22	6.30 (6)	0.39	5.32 (4.26–6.53) e	27.82 (19.56–48.05) e	106.4
S. cosmioides – 1	647	1.73 ± 0.21	4.87 (6)	0.56	0.59 (0.40–0.79) b	3.26 (2.53–4.57) b	11.8
S. cosmioides – 2	575	1.88 ± 0.24	7.17 (5)	0.21	0.67 (0.50–0.83) b	3.22 (2.43–4.90) b	13.4
S. cosmioides – 4	599	1.39 ± 0.17	6.71 (4)	0.15	0.30 (0.19–0.43) b	2.52 (1.71–4.28) b	6.0
S. eridania – 1	288	2.48 ± 0.42	0.07 (3)	0.99	1.89 (1.44–2.32) d	6.21 (4.66–10.42) c	37.8
S. eridania – 2	336	1.33 ± 0.24	2.79 (4)	0.59	1.97 (0.99–3.07) cd	18.02 (10.67–45.03) de	39.4
S. frugiperda – 3	648	1.70 ± 0.28	7.08 (4)	0.13	1.71 (1.00–2.32) c	9.73 (7.36–15.45) cd	34.2
S. frugiperda – 4	504	1.45 ± 0.14	1.48 (5)	0.91	0.68 (0.55–0.86) bc	5.11 (3.53–8.54) bc	13.6
S. albula	544	1.17 ± 0.10	2.80 (4)	0.59	6.93 (5.18–9.14) e	87.20 (56.52–156.19) f	138.6

[a] $P > 0.05$ in the goodness-of-fit test indicated good adjustment to the probit model.

[b] LC_{50} and LC_{90}: lethal concentration required to kill 50 and 90% of larvae, respectively, at 48 hr after exposure. LC_{50} and LC_{90} values followed by different letters within a column are significantly different from each other through nonoverlap of 95% confidence intervals.

[c] Tolerance ratio (TR_{50}) = (LC_{50} of a specific population)/(LC_{50} of the most susceptible species or population).

parallelism ($\chi^2 = 68.82$; $df = 22$; $P < 0.001$), which suggested that mortality curves had distinct slopes and intercepts. This was also confirmed by the differences in 95% confidence intervals of the LC values (Table 5).

The LC_{50} and LC_{90} values of flubendiamide were lower for *A. gemmatalis* populations, followed by *H. armigera*, *S. cosmioides*, and *C. includens*, indicating tolerance ratio ≤ 64-fold in relation to the most susceptible species (Table 5). In contrast, the LC values of flubendiamide were significantly higher for *S. eridania*, *S. frugiperda* – 4, and *S. albula*. For these species, the tolerance ratio ranged from 138- to 547-fold.

Susceptibility to Chlorfenapyr

The equality ($\chi^2 = 803.0$; $df = 30$; $P < 0.001$) and parallelism ($\chi^2 = 203.0$; $df = 15$; $P < 0.001$) tests indicated differences in probit lines of lepidopteran species exposed to chlorfenapyr (Table 6). The interspecific variation regarding susceptibility to chlorfenapyr was also confirmed by the nonoverlap of the 95% confidence intervals of lethal concentrations.

The LC_{50} and LC_{90} values of chlorfenapyr against the lepidopteran species studied indicated lower interspecific variation in susceptibility than previous insecticides (Table 6). The LC_{50} values of chlorfenapyr indicated tolerance ratio among lepidopteran species ≤4.4-fold. The most susceptible species to chlorfenapyr were *A. gematalis*, *C. includens*, *S. cosmioides*, and *S. frugiperda*, whereas *H. armigera*, *S. albula*, and *S. eridania* presented greater tolerance ratios.

Discussion

The knowledge of the interspecific variation regarding susceptibility to insecticides by polyphagous pests is important to improve integrated and resistance management strategies. Our findings indicated that two of the major soybean pests in Brazil, *A. gemmatalis* and *C. includens*, were susceptible to methoxyfenozide, indoxacarb, spinetoram, flubendiamide, and chlorfenapyr. Interestingly, both species also present high susceptibility to main Bt proteins (Cry1Ac, Cry1F, Cry2Ab2, and Vip3Aa) expressed in Bt soybean and Bt cotton (Bernardi et al. 2012, Sorgatto et al. 2015, Marques et al. 2016, Bacalhau et al. 2020, Horikoshi et al. 2021). A previous study also indicated that populations of *C. includens* from Brazil had high susceptibility to indoxacarb, spinetoram, flubendiamide, chlorantraniprole, and thiodicarb, but low susceptibility to lambda-cyhalothrin, methoxyfenozide, teflubenzuron, and novaluron (Stacke et al. 2019, Restelatto et al. 2021). However, the chemical control of *C. includens* is considered difficult for growers due to the larvae' behavior of staying on leaves of the middle part of the plant canopy, where they are protected from the insecticide application. Therefore, for the successful control of *C. includens* with insecticides, particular attention must be considered to the application technology and in the choice of the mode of action to be applied.

Unlike the previous species, *H. armigera* was the most tolerant to methoxyfenozide, indoxacarb, and spinetoram. The tolerance to insecticides in this polyphagous species can be explained, in part, by the enhanced activity of detoxification enzymes in response to plant allelochemicals (e.g., gossypol, sesquiterpene aldehydes, xanthotoxin, etc.), resulting in more rapid detoxification of the insecticide molecules (Tao et al. 2012, Dermauw et al. 2018, Chen et al. 2019). According to Pearce et al. (2017), the presence of several more detoxification genes of plant secondary metabolites in *H. armigera* compared to other species, probably is one of the reasons why this species quickly developed resistance to major chemical and biological insecticides. However, the low susceptibility of *H. armigera* to some insecticides detected in this study can further be influenced by the selection pressure before its introduction in Brazil, as reported for pyrethroids (Durigan et al. 2017). Therefore, the capacity of *H. armigera* to survive exposure to insecticides is also be linked with heritable genetic changes in the expression of detoxification enzymes and target-site insensitivity mutations (McCaffery 1998, Durigan et al. 2017, Wang et al. 2021). Despite these abilities, *H. armigera* showed high susceptibility to Bt proteins expressed in soybean and cotton plants (Dourado et al. 2016, Bacalhau et al. 2020, Marques et al. 2021, Horikoshi et al. 2021) and Brazilian populations of this species exhibited low variation in susceptibility to methoxyfenozide, indoxacarb, and diamides (Amado 2017, Durigan 2018, Pereira et al. 2020). Currently, *H. armigera* has been successfully controlled

Table 4. Lethal concentration (LC; µg a.i./cm^2) of spinetoram to lepidopteran species of soybean, cotton, and maize crops in Brazil

		Fit of probit lines					
Species	*n*	Slope ± SE	χ^2 (*df*)	*P*[a]	LC$_{50}$ (95% CI)[b]	LC$_{90}$ (95% CI)[b]	Tolerance ratio[c]
A. gemmatalis – 1	672	2.83 ± 0.23	5.23 (4)	0.26	0.003 (0.002–0.003) a	0.007 (0.006–0.009) a	–
A. gemmatalis – 2	672	2.08 ± 0.16	2.64 (4)	0.62	0.004 (0.003–0.005) a	0.013 (0.010–0.018) a	–
C. includens – 1	500	3.78 ± 0.41	1.57 (4)	0.81	0.15 (0.13–0.16) b	0.32 (0.27–0.39) b	50.0
C. includens – 2	504	2.80 ± 0.47	8.77 (4)	0.07	0.15 (0.10–0.21) b	0.44 (0.30–1.03) b	50.0
C. includens – 3	505	2.51 ± 0.29	1.27 (4)	0.87	0.21 (0.18–0.25) b	0.69 (0.53–1.01) b	70.0
H. armigera	504	2.41 ± 0.25	4.81 (4)	0.31	0.30 (0.26–0.35) b	1.02 (0.80–1.44) b	100.0
S. cosmioides – 1	576	1.23 ± 0.19	6.30 (5)	0.28	22.96 (14.84–31.37) d	250.65 (151.69–606.83) d	7,653.3
S. cosmioides – 2	719	1.10 ± 0.14	4.15 (7)	0.76	17.32 (10.48–24.95) d	255.63 (155.44–545.59) d	5,773.3
S. cosmioides – 3	647	1.37 ± 0.20	9.76 (6)	0.14	12.85 (8.34–17.50) d	111.00 (72.72–222.19) d	4,283.3
S. cosmioides – 4	840	1.61 ± 0.13	8.24 (6)	0.22	8.35 (6.63–10.25) d	52.16 (40.30–71.93) d	2,783.3
S. eridania – 1	432	1.40 ± 0.19	5.06 (6)	0.54	10.91 (6.84–15.69) d	89.64 (57.28–176.68) d	3,636.7
S. eridania – 2	336	2.03 ± 0.27	3.01 (4)	0.56	3.81 (2.67–5.04) c	16.29 (11.93–25.31) c	1,270.0
S. frugiperda – 1	574	2.11 ± 0.26	6.07 (5)	0.30	0.19 (0.15–0.22) b	0.77 (0.59–1.12) b	63.3
S. frugiperda – 2	503	1.95 ± 0.52	7.38 (4)	0.07	0.27 (0.03–0.44) b	1.21 (0.71–15.33) bc	90.0
S. albula	720	0.75 ± 0.11	8.35 (7)	0.30	5.65 (2.14–10.56) d	288.25 (154.96–752.83) d	1,883.3

[a] $P > 0.05$ in the goodness-of-fit test indicated good adjustment to the probit model.

[b] LC_{50} and LC_{90}: lethal concentration required to kill 50 and 90% of larvae, respectively, at 48 hr after exposure. LC_{50} and LC_{90} values followed by different letters within a column are significantly different from each other through nonoverlap of 95% confidence intervals.

[c] Tolerance ratio (TR_{50}) = (LC_{50} of a specific population)/(LC_{50} of the most susceptible species or population).

Table 5. Lethal concentration (LC; µg a.i./cm^2) of flubendiamide to lepidopteran species of soybean, cotton, and maize crops in Brazil

		Fit of probit lines					
Species	*n*	Slope ± SE	χ^2 (*df*)	*P*[a]	LC$_{50}$ (95% CI)[b]	LC$_{90}$ (95% CI)[b]	Tolerance ratio[c]
A. gemmatalis – 1	840	2.14 ± 0.15	4.94 (4)	0.29	0.01 (0.009–0.012) a	0.04 (0.03–0.05) a	–
A. gemmatalis – 2	1080	1.71 ± 0.10	5.48 (6)	0.48	0.02 (0.018–0.024) a	0.12 (0.10–0.15) a	2.0
C. includens – 2	504	1.98 ± 0.22	3.67 (4)	0.45	0.52 (0.34–0.71) c	2.29 (1.77–3.08) cd	52.0
C. includens – 3	672	1.74 ± 0.35	5.90 (3)	0.12	0.64 (0.50–0.77) c	3.51 (2.24–9.44) d	64.0
H. armigera	336	2.15 ± 0.25	1.54 (4)	0.81	0.05 (0.04–0.06) b	0.18 (0.13–0.28) b	5.0
S. cosmioides – 1	460	1.62 ± 0.28	7.55 (3)	0.06	0.32 (0.09–0.70) c	1.98 (0.88–4.18) cd	32.0
S. cosmioides – 4	648	1.44 ± 0.17	8.26 (5)	0.14	0.52 (0.28–0.81) c	4.09 (2.90–6.12) d	52.0
S. eridania – 1	336	1.59 ± 0.28	3.43 (4)	0.49	5.47 (2.58–8.51) e	31.09 (21.51–51.94) e	547.0
S. eridania – 2	398	1.55 ± 0.29	3.45 (5)	0.63	1.45 (0.95–1.93) d	9.69 (6.06–24.80) de	145.0
S. frugiperda – 3	576	2.14 ± 0.24	7.89 (5)	0.16	0.38 (0.30–0.46) c	1.51 (1.19–2.10) cd	38.0
S. frugiperda – 4	504	1.74 ± 0.20	0.96 (4)	0.92	1.38 (1.09–1.72) d	6.63 (4.07–12.69) d	138.0
S. albula	456	2.17 ± 0.25	2.78 (4)	0.59	4.93 (3.99–5.96) e	19.23 (14.62–28.64) e	493.0

[a] $P > 0.05$ in the goodness-of-fit test indicated good adjustment to the probit model.

[b] LC_{50} and LC_{90}: lethal concentration required to kill 50 and 90% of larvae, respectively, at 96 hr after exposure. LC_{50} and LC_{90} values followed by different letters within a column are significantly different from each other through nonoverlap of 95% confidence intervals.

[c] Tolerance ratio (TR_{50}) = (LC_{50} of a specific population)/(LC_{50} of the most susceptible species or population).

with Bt plants, chemical and biological insecticides, which reduce its population size in soybean and cotton fields in Brazil.

The species in the genus *Spodoptera* such as *S. cosmioides*, *S. eridania*, and *S. albula*—secondary pests of soybean and cotton in Brazil—exhibited high tolerance levels to spinetoram, and moderate tolerance to methoxyfenozide, indoxacarb, flubendiamide, and chlorfenapyr in relation to previous species. Interestingly, these species are also tolerant to major Bt proteins expressed in Bt soybean and Bt cotton, which did not provide stand-alone protection against its damage (Bernardi et al. 2014, Machado et al. 2020a, Horikoshi et al. 2021). In contrast, *S. frugiperda*—the most important *Spodoptera* species in Brazil—exhibited moderate tolerance to methoxyfenozide, indoxacarb, and flubendiamide. Previous studies reported low interpopulation variation regarding the susceptibility of *S. frugiperda* to flubendiamide (Ribeiro 2014), methoxyfenozide (Amado 2017), chlorfenapyr (Kanno et al. 2020), and indoxacarb (Kaiser et al. 2021). However, resistance of *S. frugiperda* to diamide insecticides has already been characterized in Brazil (Bolzan et al. 2019), which may contribute to the tolerance of this species to flubendiamide in this study. The abilities of *Spodoptera* species to tolerate insecticides and Bt proteins and to develop in several host plants contribute to frequent outbreaks under field conditions (Silva et al. 2017, Moraes et al. 2020).

The capacity of *Spodoptera* species to tolerate insecticides is influenced by its polyphagous habit (Dermauw et al. 2018). Studies with *Spodoptera litura* (F.) (Lepidoptera: Noctuidae) and *S. frugiperda* demonstrated the relationship among the production of enzymes to detoxify plant secondary compounds and lower susceptibility to insecticides (Karuppaiah et al. 2016, Gouin et al. 2017). We believe that similar metabolic processes can affect the susceptibility of

Table 6. Lethal concentration (LC; μg a.i./cm^2) of chlorfenapyr to lepidopteran species of soybean, cotton, and maize crops in Brazil

		Fit of probit lines					
Species	*n*	Slope ± SE	χ^2 (*df*)	*P*[a]	LC_{50} (95% CI)[b]	LC_{90} (95% CI)[b]	Tolerance ratio[c]
A. gemmatalis – 1	768	2.31 ± 0.16	4.16 (5)	0.53	0.16 (0.14–0.21) a	0.58 (0.48–0.72) b	–
A. gemmatalis – 2	672	1.80 ± 0.17	3.40 (4)	0.49	0.23 (0.20–0.28) a	1.20 (0.86–1.93) c	1.4
C. includens – 1	504	4.33 ± 0.50	3.34 (4)	0.50	0.19 (0.17–0.21) a	0.38 (0.33–0.48) a	1.2
C. includens – 2	432	3.64 ± 0.36	2.35 (3)	0.50	0.28 (0.21–0.31) a	0.63 (0.54–0.77) b	1.8
C. includens – 3	432	5.48 ± 0.74	2.46 (3)	0.48	0.21 (0.18–0.23) a	0.36 (0.31–0.43) a	1.3
H. armigera	432	2.02 ± 0.26	7.88 (6)	0.25	0.47 (0.34–0.59) c	2.03 (1.54–3.02) d	2.9
S. cosmioides – 1	503	3.21 ± 0.52	8.92 (4)	0.06	0.23 (0.15–0.31) a	0.59 (0.43–1.12) abc	1.4
S. cosmioides – 2	384	5.91 ± 076	0.70 (3)	0.70	0.22 (0.20–0.24) a	0.37 (0.33–0.44) a	1.4
S. cosmioides – 3	432	5.81 ± 0.73	3.96 (3)	0.27	0.21 (0.19–0.23) a	0.35 (0.32–0.43) a	1.3
S. cosmioides – 4	528	3.54 ± 0.43	1.78 (3)	0.62	0.24 (0.21–0.27) a	0.56 (0.47–0.72) b	1.5
S. eridania – 1	288	5.34 ± 0.72	2.40 (3)	0.49	0.59 (0.52–0.66) c	1.03 (0.89–1.27) c	3.7
S. eridania – 2	288	4.36 ± 0.72	4.90 (3)	0.18	0.70 (0.51–0.80) c	1.37 (1.15–1.85) c	4.4
S. frugiperda – 1	431	2.71 ± 0.38	1.56 (3)	0.67	0.25 (0.18–0.31) a	0.74 (0.60–0.97) bc	1.6
S. frugiperda – 2	431	3.31 ± 0.39	3.14 (3)	0.37	0.32 (0.27–0.37) b	0.78 (0.66–0.98) bc	2.0
S. frugiperda – 3	576	4.02 ± 0.42	4.87 (3)	0.18	0.28 (0.24–0.31) b	0.58 (0.51–0.68) b	1.7
S. albula	400	3.96 ± 0.61	1.33 (3)	0.51	0.46 (0.39–0.52) c	0.97 (0.83–1.25) c	2.9

[a] $P > 0.05$ in the goodness-of-fit test indicated good adjustment to the probit model.

[b] LC_{50} and LC_{90}: lethal concentration required to kill 50 and 90% of larvae, respectively, at 48 hr after exposure. LC_{50} and LC_{90} values followed by different letters within a column are significantly different from each other through nonoverlap of 95% confidence intervals.

[c] Tolerance ratio (TR_{50}) = (LC_{50} of a specific population)/(LC_{50} of the most susceptible species or population).

S. eridania, *S. cosmioides*, and *S. albula* to insecticides. Furthermore, the ability to resist the toxic effect of insecticides can be also associated with metabolic activity, such as multiple detoxification enzymes related with physiological and molecular mechanisms of detoxification (Boaventura et al. 2021, Hilliou et al. 2021). Similarly, its low susceptibility to certain Bt proteins is linked with reduced binding to specific midgut receptors, faster degradation by midgut proteases, enhanced detoxification, and target-site mutations (Aranda et al. 1996, Boaventura et al. 2021). Therefore, the development of highly efficacious insecticides and Bt plants with new modes of action may improve the control of *Spodoptera* complex.

The present study documents the interspecific variation in susceptibility to selected insecticides by lepidopteran species of soybean, cotton, and maize crops in Brazil and other South American countries. Our findings indicate a wide variation in susceptibility and tolerance to indoxacarb, spinetoram, and flubendiamide and a relatively low interspecific variation in susceptibility to methoxyfenozide and chlorfenapyr among the lepidopteran species studied. From a practical viewpoint, implementing a rotation scheme using the insecticides here evaluated for certain lepidopteran species can improve control and reduce the probability of selection of resistant insects, especially in intensive crop production systems, such as those in Brazil. Therefore, the ability to identify and monitor lepidopteran larvae under field conditions is essential to determine when they reach threatening levels and to help choose the most effective insecticide to prevent economic losses and the evolution of resistance.

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