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Plant Resistance

Response of Soybean Genotypes Challenged by a Stink Bug Complex (Hemiptera: Pentatomidae)

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Abstract

Pentatomids (stink bugs) are major pests of soybean, *Glycine max* (L.) Merril. These pests reach high levels of infestation, cause severe damage to seeds by feeding, are linked to leaf retention, and are difficult to control. Host plant resistance is considered to be a valuable tool in integrated pest management and can assist in reducing the damage caused by stink bugs. This research evaluated the resistance of soybean genotypes in Brazil to the stink bug complex, the Neotropical brown stink bug, *Euschistus heros* (F.), redbanded stink bug, *Piezodorus guildinii* (Westwood), southern green stink bug, *Nezara viridula* (L.), green belly stink bug, *Dichelops melacanthus* (Dallas), and *Edessa meditabunda* (F.), by assessing infestation assay, yield reduction, seed damage, and leaf retention. Certain genotypes expressed different categories of resistance: least infested, low yield reduction, low levels of damage in seeds, and low levels of leaf retention. PI lines and IAC 78-2318 showed antixenotic resistance, and 'IAC 100' showed tolerance for the stink bug complex. This is the first study to evaluate several parameters of yield and seed quality using different soybean maturity groups under relatively high infestation by the three stink bugs species. The promising genotypes might be used in regions with a high incidence of stink bugs to manage their populations in combination with other integrated pest management practices.

Key words: host plant resistance, tolerance, antixenosis

Soybean, *Glycine max* (L.) Merril, is one of the main agricultural crops worldwide; it has high yield potential and is an important source of protein and vegetable oil (Akond et al. 2014). The crop is attacked by pests, including members of Pentatomidae (stink bugs), which can cause serious injury to plants (Corrêa-Ferreira and Panizzi 1999). Salient species include the Neotropical brown stink bug, *Euschistus heros* (F.); the redbanded stink bug, *Piezodorus guildinii* (Westwood); and the southern green stink bug, *Nezara viridula* (L.). In addition, green belly stink bug, *Dichelops melacanthus* (Dallas); and *Edessa meditabunda* (F.) have increased in importance (Table 1; Panizzi et al. 2000, Depieri and Panizzi 2011).

Stink bugs damage soybeans by inserting their stylets through the pods into the seed, injecting salivary secretions that facilitate ingestion (Miner 1966, Depieri and Panizzi 2011). The injury can change the nutritional value of soybean seeds, and can create portals for plant pathogens (Panizzi and Slansky 1985). Damage caused by stink bugs, particulary *P. guildinii* (Sosa-Goméz and Moscardi 1995, Corrêa-Ferreira and Azevedo 2002), can also be related to leaf retention, a physiological condition that delays the maturation of soybean plants by maintaining the green leaves even after pod maturation.

Management of stink bugs is often hampered by the limited number of registered insecticides and rapid development of insecticide resistance, resulting in increased frequency of insecticide applications and the use of broad-spectrum products (Temple et al. 2009, Baur et al. 2010, Sosa-Goméz and Silva 2010). Host plant resistance can be efficient for protecting a crop, and it is easily assimilated into an integrated pest management strategy. Although host plant resistance can also exert resistance selection pressure on insects, this process typically involves more than one gene permitting greater stability relative to resistance selection pressure by insecticides (Painter 1951).

Host plant resistance to insects can be expressed in three ways: antibiosis, antixenosis, and tolerance (Akbar et al. 2013). In antibiosis, the plant is deleterious to the insect, whereas in antixenosis, a plant biochemical, physical, or biological factor deters pest colonization, oviposition, and feeding. Tolerant plants have the ability to withstand or recover from pest attack while remaining productive (Painter 1951).

Laboratory studies have demonstrated the antibiotic and antixenotic activities of certain soybean genotypes against *P. guildinii*

Table 1. Soybean lines assessed for resistance to the complex of stink bugs and other insects.

Maturity group	Lines	Pedigree and Origin	Resistance	Laboratory
Early (100–120 d)	'IAC 17'	D 72-9601-1 × 'IAC 8'	Antixenosis vs. *E. heros*; Antibiosis/Antixenosis vs. *B. tabaci*	Yes
	'IAC 23'	BR-6 × IAC 83-23		
	PI 171451	Japan	Antixenosis vs. *P. guildinii*; Antibiosis vs. *P. guildinii*; Resistance vs. Lepidopteran insects	Yes
	PI 229358	Tokyo, Japan	Antixenosis vs. *P. guildinii*; Antibiosis vs. *P. guildinii*; Resistance vs. Lepidopteran insects	Yes
	D 75-10169	'Govan' × (F4 'Bragg' × PI 229358)	Antixenosis vs. *P. guildinii*; Derived from PI 229358	Yes
	'Coodetec-208'	OC-4 × Williams 20		
Semiearly (120–130 d)	'IAC 18'	D 72-9601 × 'IAC 8'	Tolerance against stink bugs	No
	'IAC 24'	IAC80-1177 × IAC83-288	Antibiosis vs. *P. guildinii*; Antibiosis/ Antixenoses vs. *B. tabaci*	
	'IAC 100'	'IAC 12' × IAC 78-2318	Antixenosis vs. *E. heros*; Antixenosis vs. *P. guildinii*; Antibiosis vs. *P. guildinii*; Resistance vs. Lepidopteran defoliation; Resistance vs. *N. viridula*	Yes
	IAC 74-2832	'Hill' × PI 274454	Antibiosis vs. *P. guildinii*; Derived from PI 229687 and PI 274454	
	IAC 78-2318	D 72-96-1 × (Hill × PI 274454)	Antixenosis vs. *P. guildinii*; Antibiosis vs. *P. guildinii*; Derived from PI 229687 and PI 274454	Yes
	PI 227687	Okinawa, Japan	Antixenosis vs. *P. guildinii*; Antibiosis vs. *P. guildinii*; Resistance vs. Lepidopteran insects	Yes
Late (130–150 d)	'IAC 19'	D 72-9601-1 × 'IAC 8'	Antixenosis vs. *P. guildinii*; Antibiosis vs. *P. guildinii*; Antibiosis/Antixenosis vs. *B. tabaci*	Yes
	PI 274453	Okinawa, Japan	Antixenosis vs. *P. guildinii*; Resistance vs. Lepidopteran insects; Antibiosis vs. *P. guildinii*	Yes
	PI 274454	Okinawa, Japan	Antixenosis vs. *P. guildinii*; Resistance vs. Lepidopteran insects Antibiosis vs. *P. guildinii*	Yes
	L 1-1-01	BR-6 × 'IAC 100'	Antibiosis vs. *P. guildinii*	Yes
	'Conquista'	Lo76-4484^2 × Numbaíra	Antibiosis/ Antixenoses vs. *B. tabaci*	

Source: Miranda et al. 1979; Lourenção and Miranda 1987; Valle and Lourenção et al. 2002; Hulburt et al. 2004; McPherson and Buss, 2007; McPherson et al. 2007; Hesler and Dashiell, 2008; Lourenção et al. 2010; Silva et al. 2012; Silva et al. 2013; Silva et al. 2014; Souza et al. 2014.

(Silva et al. 2013, 2014), and some soybean genotypes have low attractiveness to *N viridula* under laboratory conditions (Souza et al. 2014). Field research has confirmed that soybean genotype 'IAC 100' expresses resistance against *N. viridula* (McPherson et al. 2007), but information on the mechanisms of resistance against pentatomids is limited. Moreover, host plant resistance involving the entire stink bug complex attacking soybean has not been reported, and such research might reveal multiple resistance (i.e., to >1 spp.) to stink bugs. The objective of this study was to evaluate soybean genotypes infested by a naturally occurring stink bug complex under field conditions in Brazil to identify potentially resistant genotypes.

Materials and Methods

Soybeans

Seventeen soybean genotypes belonging to three different maturation groups (early, semiearly, and late; Table 1) were evaluated. Lines PI 171451, PI 229358, PI 227687, PI 274453, and PI 274454 exhibit resistance to various pest insects (Hulburt et al. 2004). Lines IAC 78-2318, IAC 74-2832, and D 75-10169 are derived from PI 229358 and PI 274454, and have a history of resistance to herbivorous insects (Miranda et al. 1979, Lourenção and Miranda 1987, Hesler and Dashiell 2008). 'IAC 17', 'IAC 19', and 'IAC 24' were selected because they were resistant to *N. viridula* (Lourenção et al. 2000, Miranda et al. 2003); the silverleaf whitefly, *Bemisia tabaci* (Gennadius) biotype B; and defoliating caterpillars (Valle and Lourenção 2002, Silva et al. 2012). 'IAC 100' is resistant to *N. viridula* and other insects (McPherson et al. 2007, McPherson and Buss 2007), and L1-1-01 is derived from this genotype (Valle et al. 2012). 'Conquista' and 'Coodetec 208' are commercial genotypes widely cultivated in Brazil and have no known resistance to stink bugs.

Resistance Assay

Two field experiments were conducted, one in the 2011–2012 growing season and the second in the 2012–2013 growing season, under normal conditions in areas of the Fazenda de Ensino, Pesquisa e Extensão, College of Agronomic Science, São Paulo State University, Botucatu, São Paulo, Brazil (22° 82′48″ S and 48° 42′80″ W, 720 m elevation; and 22° 50′39″ S and 48° 25′28″ W, 780 m elevation).

Twenty days before sowing, the plot area was sprayed with glyphosate (Roundup WG, Monsanto, São José dos Campos, São Paulo, Brazil), at 1.5 kg [AI]/ha. The plots were planted 19 November 2011 and 28 October 2012 under no-tillage and fertilized at 200 kg/ha (4% nitrogen, 20% phosphorus, and 20% potassium, Minorgan, Mandaguari, Paraná, Brazil) at planting according to soil fertility analysis and recommendations for soybean (Raij et al. 1997).

In each of the experiments, an area of ≈8,000 m^2 was divided into three plots, each for a specific soybean maturity group (early, semiearly, and late). Four replicates of each genotype without stink bug control and four replicates of each genotype with chemical stink bug control were established. A total of 128 plots were established per experiment in a randomized complete block design.

The plots were composed of four 5-m-long adjacent rows with 0.45-m spacing (6.75 m^2). The "buffer" space around each plot was 1.5 m. To avoid possible drift effects, the plots sprayed with insecticide were located ≥10 m from the nonsprayed plots.

Before planting, the seeds of all genotypes were treated with the fungicides carboxin and thiram (Vitavax-Thiram 200 SC, Chemtura Corporation, Rio Claro, São Paulo, Brazil), at 60 g and 60 g, respectively, [AI]/100 kg of seed, and the insecticides imidacloprid and thiodicarb (Cropstar SC, Bayer CropScience, São Paulo, São Paulo, Brazil), at 75 g and 225 g, respectively, [AI]/100 kg of seed. The seeds were also inoculated with *Bradyrhizobium japonicum* Kirchner (Masterfix L, Stoller, Cosmópolis, São Paulo, Brazil), at 200 ml of commercial product per 50 kg of seeds, manually homogenized by shaking in plastic bags, and dried in a greenhouse for 12 h. The seeds were planted by hand, at 20/m, and 14 d after emergence the plants were manually thinned to a density of 16 plants/m.

Stink bug sampling was conducted using the beat cloth method between rows of soybean plants (Hoffman-Campo et al. 2012). In the insecticide-treated plots, which we designated as the controls, an action level of one stink bug/m was used for triggering applications of a combination of lambda-cyhalothrin and thiamethoxam (Engeo Pleno, Syngenta Protection of Crops, São Paulo, São Paulo, Brazil), 21.2 g and 28.2 g, respectively, [AI]/ha sprayed at a rate of 200 l/ha. Applications were conducted using an electric backpack sprayer (FT-16, Yamaho Incoprom Pulverizadores, Diadema, São Paulo, Brazil) with a tank capacity of 16 l, and an adjustable nozzle cone at a pressure of three bar. In the first growing season, three applications were necessary for early maturing genotypes and four applications were necessary for the other maturity groups from the R1 (beginning of flowering) stage (Fehr and Caviness 1977) to harvest. In the second growing season, three applications were needed for all genotypes.

Infestation of *E. heros*, *P. guildinii*, *N. viridula*, *E. meditabunda*, and *D. melacanthus* were assessed weekly from the R1 stage in the afternoon for eight consecutive weeks. For the evaluations, a 1- by 0.5-m (l by w) beat cloth on a wooden frame (Hoffmann-Campo et al. 2012) was carefully positioned between the rows, and the plants of both rows (≈30 plants) were gently bent and shaken over the cloth (Corrêa-Ferreira and Panizzi 1999). Two locations per plot were sampled, always in the central two rows, to obtain total numbers of stink bugs nymphs ≥0.5 cm long and adults. Nymphs smaller than 0.5 cm long were not counted because they do not inflict substantial injury on soybean (Hoffmann-Campo et al. 2012).

Two evaluators assessed the percentage of leaf retention and green stems by visual estimation in infested plots when the plants in the insecticide-treated plots reached the harvest stage (R8). It was established an average of leaf retention for the two growing seasons. Leaf retention was graded using the scale: 1, no leaf retention; 2, up to 10% leaf retention; 3, 11–25% leaf retention; 4, 26–50% leaf retention; and 5, >50% leaf retention (Lourenção et al. 2004).

The average kg fresh weight of soybeans/ha was obtained by extrapolating from weights obtained by manual harvest of 4 m of the central two rows in each plot and weighing the harvested seed. The data were subjected to factorial analysis (SAS Software 2011) of each of the three genotype maturity groups (6 × 2 for the early and semiearly genotypes and 5 × 2 for the late genotype, where 6 and 5 represent the number of genotypes and 2 represents the insecticide treated and infested plots), with four replicates of each treatment.

A sample of 50 seeds was randomly collected from each plot to assess damage which was classified as follows: 1, no visible damage; 2, punctured seeds; 3, partially deformed (wrinkled or undersized) seeds with punctures; and 4, seeds completely deformed (Jensen and Newson 1972). For comparison of genotypes with regard to the second class of damage, we used a model (Mantel 1963) for categorical data analysis of contingency tables in which the response variable class damage is ordinal. It was used as scores for each level of this variable the values of classification described above, i.e., scores in from 1 to 4. Thus, the statistical mean score is expressed as $Qs = (n-1)\sum_{i=1}^{s} n_{i+}(\overline{f}_i - \mu_a)^2/n\nu_a$, wherein $\overline{f}_i = \sum_{j=1}^{r} a_j n_{ij}/n_{i+}$, $\mu_a = \sum_{j=1}^{r} a_j n_{+j}/n$, and $\nu_a = \sum_{j=1}^{r} (a_j - \mu_a)^2 (n_{+j}/n)$. In this instance, Q_s has approximately chi-square distribution with (s − 1) degrees of freedom. If the null hypothesis that there are no differences between genotypes in relation to seeds to damage class was rejected, we used the same statistical mean score for comparisons of genotypes in pairs to differentiate the genotypes more resistant to stink bugs. In this case, the contingency table size was 2 × *r*, i.e., only two groups were compared. In all tests, Bonferroni correction was performed to control the Type I error rate ($P < 0.05$; Bonferroni 1935).

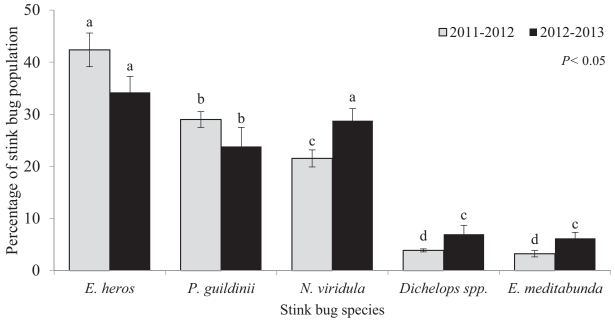

Fig. 1. Predominant species of stink bugs (% ± SE) (*Euschistus heros*, *Piezodorus guildinii*, *Nezara viridula*, *Dichelops melacanthus*, and *Edessa meditabunda*) in field trials with different soybean genotypes. Botucatu, São Paulo, 2011/2012 and 2012/2013. Means followed by the same letter per do not differ by Tukey's HSD ($P < 0.05$).

Results

Predominant Species and Population Fluctuation

Euschistus heros was the dominant species (first growing season, $F = 18.00$; df = 5; $P < 0.001$; second growing season, $F = 17.51$; df = 1, 5; $P < 0.018$), comprising 42 and 34% of the total number of stink bugs recorded in the respective growing seasons (Fig. 1). The incidence of *P. guildinii* was 29% in the first season and 24% in the second, and *Nezara viridula* represented 22 and 29% in the first and second growing seasons, respectively. *Dichelops melacanthus* and *E. meditabunda* were <10% in each growing season (Fig. 1).

During our study, the populations of stink bugs exceeded the economic injury level for soybean seed production, which is two stink bug adults or nymphs longer than 0.5 cm in 2 m of row (Hoffmann-Campo et al. 2012; Fig. 2). In the first growing season, the economic injury level was reached as early as 29 February in the early maturing genotypes and by 7 March in the other maturity groups. In the second growing season, the economic injury level was reached by 3 March in all maturity groups.

Early Maturing Genotypes

In the first growing season, there were no differences in stink bug numbers between early maturing genotypes in the nontreated plots (Table 2); however, in the second season, stink bug populations in D 75-10169, PI 171451, PI 229358, and 'IAC 17' were at least 27.5% lower than in 'Coodetec 208' ($F = 7.78$; df = 5, 18; $P < 0.0001$; Table 2).

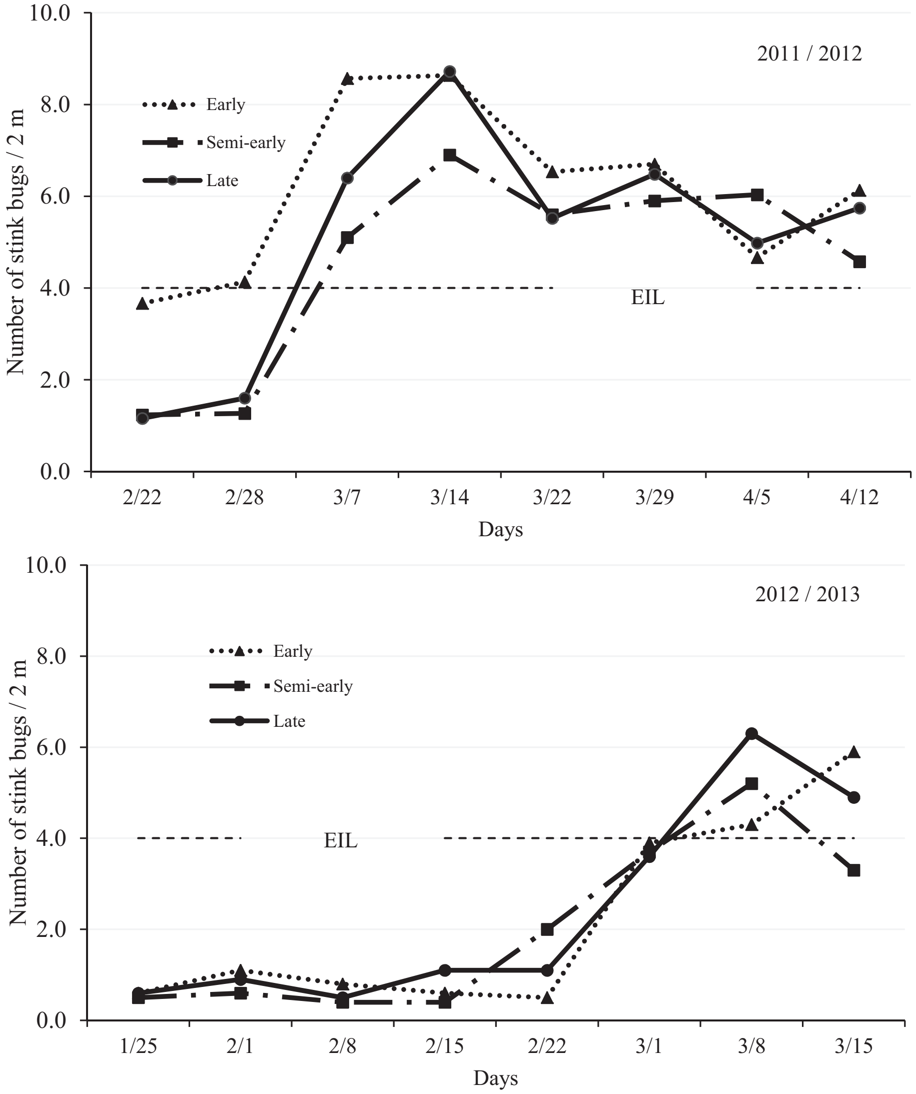

Fig. 2. Population fluctuation of stink bugs (*Euschistus heros*, *Piezodorus guildinii*, *Nezara viridula*, *Dichelops melacanthus*, and *Edessa meditabunda*) in field trials with early, semiearly, and late maturing soybean genotypes. Botucatu, São Paulo 2011/2012 and 2012/2013.

Table 2. Mean (±SE) numbers of stink bugs per 2-m row; yields of stink bug-infested and stink bug-controlled soybeans; and percent yield reduction in early maturing soybean during two crop seasons, Botucatu, São Paulo, 2011/2012 and 2012/2013

Lines	2011–2012				2012–2013			
	No. stink bugs[a]	Yield (kg ha^{-1}) and reduction (%)			No. stink bugs[a]	Yield (kg ha^{-1}) and reduction (%)		
		Insecticide treated[a]	Infested[a]	%		Insecticide treated[a]	Infested[a]	%
‘IAC 17’	7.3 ± 0.2	3,417 ± 138abA	1,808 ± 372aB	47	1.7 ± 0.3b	3,376 ± 103abA	1,711 ± 86 aB	49
‘IAC 23’	6.4 ± 0.6	3,609 ± 161aA	914 ± 134abB	75	2.9 ± 0.3ab	3,486 ± 67 aA	1,076 ± 161bB	69
PI 171451	4.4 ± 0.5	2,796 ± 165abA	1,708 ± 266aB	38	1.4 ± 0.3b	2,872 ± 173bcA	1,909 ± 186aB	33
PI 229358	5.6 ± 0.2	2,550 ± 163bA	896 ± 164abB	65	1.7 ± 0.2b	2,575 ± 171cA	1,014 ± 84bB	60
D 75-10169	6.3 ± 1.1	3,260 ± 357abA	297 ± 23bB	91	1.4 ± 0.2b	2,986 ± 225abcA	1,014 ± 41bB	66
‘Coodetec 208’	6.4 ± 0.8	3,708 ± 242aA	523 ± 25bB	86	4.0 ± 0.3a	3,522 ± 193aA	737 ± 74bB	79

[a] Means followed by the same lower case letter in each column and upper case letter in each row were not different, Tukey’s HSD ($P > 0.05$).

The yield of the insecticide-treated plots was 9–67% higher than yield of the plots infested by stink bugs in both respective growing seasons (Table 2). In the first growing season, ‘Coodetec 208’ and ‘IAC 23’ were more productive, ≥28.56%, than PI 229358 ($F = 3.76$; df = 5, 18; $P < 0.0001$; Table 2). The result was similar for the second growing season, with ‘Coodetec 208’ and ‘IAC 23’ having ≥ 17.43% greater yields in insecticide-treated plots than PI 229358 and PI 171451 ($F = 7.23$; df = 5, 18; $P < 0.0001$; Table 2).

Table 3. Means of leaf retention (± SE) caused by stink bug injury to early, semiearly, and late maturing soybean genotypes, Botucatu, São Paulo; data were pooled between the two growing seasons

Leaf retention (%)[a]					
Early		Semiearly		Late	
Lines	Retention (%)	Lines	Retention (%)	Lines	Retention (%)
'IAC 17'	60.50 ± 5.20a	'IAC 18'	78.75 ± 8.00a	'IAC 19'	88.75 ± 6.25a
'IAC 23'	75.00 ± 8.66a	'IAC 24'	17.50 ± 4.79de	PI 274453	60.00 ± 4.56b
PI 171451	13.75 ± 3.61b	'IAC 100'	47.50 ± 8.78bc	PI 274454	50.00 ± 5.40b
PI 229358	47.50 ± 16.52ab	IAC 74-2832	37.50 ± 6.61cd	L1-1-01	70.00 ± 7.07ab
D 75-10169	78.75 ± 4.27a	IAC 78-2318	70.00 ± 7.07ab	'Conquista'	88.75 ± 3.15a
'Coodetec 208'	70.00 ± 10.00a	PI 227687	5.00 ± 0.00e	–	–

[a] Means followed by the same letter per column do not differ by Tukey's HSD ($P > 0.05$).

Table 4. Mean seed stink bug damage score to early, semiearly, and late maturing soybean genotypes, Botucatu, São Paulo, 2011–2012 and 2012–2013

Maturity	Genotypes	Mean damage score[a]	
		2011–2012	2012–2013
Early	PI 171451	2.60c	2.08d
	'Coodetec 208'	3.37b	3.19a
	'IAC 23'	3.44ab	2.71b
	'IAC 17'	3.52ab	3.10a
	D 75-10169	3.58ab	2.70bc
	PI 229358	3.61a	2.40c
Semiearly	PI 227687	2.45d	1.90c
	IAC 78-2318	2.91c	2.70b
	'IAC 100'	2.95c	2.13c
	'IAC 18'	3.33b	2.75b
	IAC 74-2832	3.42b	2.95b
	'IAC 24'	3.88a	3.45a
Late	PI 274453	2.30d	1.68d
	PI 274454	2.83c	2.25c
	'IAC 19'	3.26b	3.19b
	'Conquista'	3.14b	3.51a
	L1-1-01	3.99a	3.26ab

[a] Means followed by the same letter in the column do not differ by chi-square test ($P > 0.05$). Transformed data on mean scores.

In the first growing season, 'IAC 17' and PI 171451 had greater yields, ≥ 65.54, than D 75-10169 and 'Coodetec 208', and low reductions in yield, $\leq 47\%$, in infested plots, while D 75-10169 and 'Coodetec 208' had lower yield and greater reductions, $\geq 86\%$. Similarly, in the second season, PI 171451 and 'IAC 17' had the highest yield with the least yield reductions, $\leq 49\%$, whereas 'Coodetec 208' showed the greatest yield reduction, $\geq 79\%$ (Table 2). PI 171451 expressed lower leaf retention between the early maturity genotypes, thereby differing $>45.5\%$ from D 75-10169, 'IAC 23', 'Coodetec 208', and 'IAC 17' ($F = 7.15$; df = 5, 18; $P < 0.0001$) (Table 3). Factorial analysis of early maturing genotype data did not detect an insecticide treatment × time interaction.

On the basis of the mean score of seed damage, PI 171451 had the lowest mean score for both harvests ($Qs = 272.49$; df = 5, 18; $P < 0.0001$, and $Qs = 155.62$; df = 5, 18; $P < 0.0001$, respectively; Table 4).

Semiearly Maturing Genotypes

Genotypes PI 227687 and IAC 74-2832 were $\leq 18\%$ less infested by stink bugs in the first growing season than the other semiearly maturing genotypes ($F = 9.73$; df = 5, 18; $P < 0.0001$; Table 5). In the second growing season, there were no differences among the genotypes for the infestation number of stink bugs.

Regarding yield reductions in 2011–2012 nontreated genotypes (Table 5), IAC 78-2318, 'IAC 100', and PI 227687 exhibited $\leq 18\%$ yield reductions ($F = 3.40$; df = 5, 18; $P = 0.012$), with no differences among the insecticide-treated plots, resulting in an insecticide treatment × genotype interaction ($F = 10.15$; df = 5, 15; $P < 0.0001$). On the other hand, 'IAC 18' and 'IAC 24' were more productive compared to PI 227687 in insecticide-treated plots. In the second growing season, all genotypes had lower yields, with reductions of $\geq 51\%$, in stink bug infested genotypes compared to insecticide-treated plots ($F = 30.69$; df = 5, 18; $P < 0.0001$). However, IAC 78-2318, PI 227687, and 'IAC 100' continued to exhibit smaller, $\leq 29\%$, yield reductions, 'IAC 100' being the most productive, followed by IAC 78-2318 and 'IAC 18'. 'IAC 24' and 'IAC 18' yields were reduced by $\geq 57\%$ (Table 5).

PI 227687 and 'IAC 24' showed the lowest leaf retention, $\leq 17.5\%$ ($F = 19.32$, df = 5, 18; $P < 0.001$), whereas 'IAC 18' and IAC 78-2318 had high levels of leaf retention, $\geq 70\%$ (Table 3). Differences in genotype relationship and damage class (Table 4; first growing season, $Qs = 405.55$; df = 5, 18; $P < 0.0001$; second growing season, $Qs = 282.46$; df = 5, 18; $P < 0.0001$) were observed, especially for PI 227687 and 'IAC 100', which were greater than 'IAC 24', 'IAC 18', and IAC 74-2832. 'IAC 24' had the most stink bug-induced seed damage.

Late Maturing Genotypes

PI 274453 and PI 274454 were least, $\leq 37.5\%$, infested by stink bugs in the first season ($F = 15.67$, df = 4, 12; $P < 0.0001$; Table 6) compared to 'IAC 19' and L1-1-01, which were more infested. In the second growing season, there were no differences between the genotypes.

Each of the stink bug-infested genotypes showed $\geq 90\%$ reductions in yield compared to their corresponding insecticide-treated genotypes, in the first growing season (Table 6). An insecticide treatment × genotype interaction was not detected in the late maturing genotype data. In the first growing season, the genotype L1-1-01 was more productive than PI 274454 by 25.1% in insecticide-treated plots ($F = 2.86$, df = 4, 12; $P = 0.040$), and 'IAC 19' by 52.6% in nontreated plots. In the second growing season, the most productive of the insecticide-treated genotypes was 'IAC 19' by 16.4% ($F = 6.0751$, df = 4, 12; $P < 0.0001$), followed by L1-1-01. Under insect infestation, L1-1-01 was more productive than PI 274454 and PI 274453, with $\leq 51\%$ yield loss.

Table 5. Mean (±SE) numbers of stink bugs per 2-m row; yields of stink bug-infested and stink bug-controlled soybeans; and percent yield reduction in semiearly maturing soybean during two crop seasons, Botucatu, São Paulo, 2011/2012 and 2012/2013

Lines	2011–2012				2012–2013			
	No. stink bugs[a]	Yield (kg ha^{-1}) and reduction (%)			No. stink bugs [a]	Yield (kg ha^{-1}) and reduction (%)		
		Insecticide treated[a]	Infested[a]	%		Insecticide treated[a]	Infested[a]	%
'IAC 18'	6.2 ± 0.8a	3,555 ± 92aA	2,208 ± 526aB	43	2.6 ± 0.9	4,206 ± 151aA	1,797 ± 201abB	57
'IAC 24'	6.4 ± 0.6a	2,900 ± 503aA	1,415 ± 291aB	51	1.9 ± 0.7	3,527 ± 58bA	1,216 ± 78cB	65
'IAC 100'	5.6 ± 0.3a	2,379 ± 167abA	2,247 ± 227aA	5	2.6 ± 0.9	2,962 ± 183cA	2,086 ± 134aB	29
IAC 74-2832	3.2 ± 0.4b	2,484 ± 210abA	1,167 ± 245aB	53	1.3 ± 0.5	3,720 ± 88abA	1,468 ± 167bcB	60
IAC 78-2318	4.2 ± 0.2ab	2,298 ± 281abA	2,239 ± 258aA	2	1.7 ± 0.6	2,597 ± 36cA	1,972 ± 58abB	24
PI 227687	2.3 ± 0.2b	1,264 ± 95bA	1,032 ± 47aA	18	1.8 ± 0.7	1,741 ± 51dA	1,292 ± 40cB	25

[a] Means followed by the same lower case letter in each column and upper case letter in each row were not different, Tukey's HSD ($P > 0.05$).

Table 6. Mean (±SE) numbers of stink bugs per 2-m row; yields of stink bug-infested and stink bug-controlled soybeans; and percent yield reduction in late maturing soybean during two crop seasons, Botucatu, São Paulo, 2011/2012 and 2012/2013

Lines	2011–2012				2012–2013			
	No. stink bugs[a]	Yield (kg ha^{-1}) and reduction (%)			No. stink bugs [a]	Yield (kg ha^{-1}) and reduction (%)		
		Insecticide treated[a]	Infested[a]	%		Insecticide treated[a]	Infested[a]	%
'IAC 19'	8.0 ± 0.7a	3,943 ± 301abA	146 ± 18bB	96	2.0 ± 0.7	3,839 ± 100aA	837 ± 202bcB	70
PI 274453	1.4 ± 0.2c	3,653 ± 97abA	367 ± 25aB	90	1.7 ± 0.6	3,212 ± 115bcA	1,331 ± 59abB	58
PI 274454	3.6 ± 0.3bc	3,040 ± 48bA	232 ± 40abB	92	2.0 ± 0.7	2,917 ± 52cA	1,157 ± 77abB	60
L1-1-01	6.6 ± 0.3a	4,057 ± 161aA	308 ± 23aB	92	3.0 ± 1.1	3,634 ± 193abA	1,762 ± 186aB	51
'Conquista'	5.6 ± 0.8ab	3,430 ± 348abA	214 ± 36abB	93	2.7 ± 1.0	3,204 ± 116bcA	484 ± 244cB	84

[a] Means followed by the same lower case letter in each column and upper case letter in each row were not different, Tukey's HSD ($P > 0.05$).

PI 274454 and PI 274453 showed ≤60% leaf retention ($F = 10$; df = 4, 12; $P < 0.0001$) compared to 'IAC 19' and 'Conquista' (Table 3). For each growing season, seeds of PI 274453 and PI 274454 were the least damaged (first growing season, $Qs = 305.1$; df = 4, 12; $P < 0.0001$; second growing season, $Qs = 412.24$; df = 4, 12; $P < 0.0001$; Table 4). Conversely, L1-1-01 and 'Conquista' showed high seed damage in the first and second growing seasons, respectively.

Discussion

Other studies have also reported the prevalence of *E. heros*, *P. guildinii*, and *N. viridula* compared to the other stink bug species in soybeans of neighboring regions (Lourenção et al. 2010, Sosa-Goméz and Silva 2010), and the three most abundant species inflict particularly heavy damage on soybeans (Panizzi and Machado-Neto 1992, Depieri and Panizzi 2011). *Dichelops melacanthus* and *E. meditabunda* occurred at lower levels in relation to the other stink bug species, hence, their status as a secondary pest of soybean in our study.

The larger stink bug infestation during the first growing season than during the second was probably because sampling began in February, whereas second growing season sampling began in January when stink bug populations had not yet built up. In the first growing season, stink bug populations began to increase in March, reaching the economic injury level during the same month. This is probably related to when the pods of early and semiearly genotypes were at R4/R6 (full pods to full seeds growth stages), which favor stink bug population growth (Oliveira and Panizii 2003). After the R6 soybean growth stage, stink bug populations tend to decline, mainly because of plant senescence and harvest-associated stink bug dispersion (Corrêa-Ferreira and Panizzi 1999). Similarly, early planted crops can support earlier pest population buildups than late planted crops of the same cultivar because the stage of the fruiting body that is preferred and provides nutritional quality for optimal egg production occurs earlier than in late plantings (Showler 2005, 2007, 2008; Showler et al. 2005). The April 2012 stink bug populations remained above the economic injury level suggests that stink bug numbers were relatively great at that time in the region.

The most severe seed damage caused by the stink bug complex occurred during the R5/R6 soybean stages and damage decreased as the seeds developed further (McPherson and McPherson 2000). In spite of the lower damage observed when the pods become more mature (McPherson and McPherson 2000, Molina and Trumper 2012), great infestations of stink bugs on soybean in stage R7 (beginning maturity) can still compromise the quality of the seed (Musser et al. 2011, Hush et al. 2014).

The early planting date in the second growing season may have been the main factor causing the delay in the stink bugs population buildup reaching the economic injury level in March.

The low incidence of stink bugs in PI 171451 (early), PI 227687 (semiearly), PI 274453 and PI 274454 (late), together with reduced leaf retention and low seed damage suggest antixenotic resistance. Although nontreated PI 229358 (early) exhibited intermediate yield, leaf retention, and seed damage, the low infestation by stink bugs also indicates resistance to some extent. Leaf retention is a physiological symptom linked to stink bug attack that delays senescence in soybean plants even after pod maturation (Daugherty et al. 1964).

The high yield of PI 171451 in infested plots can be related to the low incidence of stink bugs found on this genotype during the test, reinforcing the possibility of antixenotic resistance. Although PI 274453 and PI 274454 had greater yields compared to 'IAC 19' in the first growing season, and Conquista in the second growing season, the yield losses in the nontreated plots compared to the insecticide-treated plots might have occurred because the late maturing genotypes remain longer in the field, receiving immigrating of stink bugs from plots where early genotypes had already matured and have become less preferred than genotypes offering preferred stages of seed development (Jones and Sulivann 1979, McPherson 1996, McPherson et al. 2007).

The low incidence of stink bugs on the late-maturing genotypes PI 274453 and PI 274454, with low seed damage and low leaf retention, suggests the biosynthesis of secondary plant compounds that repel insects (Smith 2005). Soybean plants infested by *N. viridula* synthesize flavonoids, such as daidzin and genistin, which have deterrent effects against *N. viridula* and *P. guildinii* (Piubelli et al. 2003, 2005; Zavala et al. 2015). PI 227687, a semiearly maturing genotype (less attractive than 'IAC 18', 'IAC 24', and 'IAC 100' in this study), is known to produce relatively large amounts of such flavonoids (Piubelli et al. 2003, 2005; Zavala et al. 2015). Plants can also deter pests because of genotype differences in the plant's nutritional value (Tester 1977, Reay-Jones et al. 2007, Akbar et al. 2013). PI 227687 has less nitrogen and reduced sugars than commercial genotypes, which might explain the resistance of this genotype to insects (Van Duyn et al. 1971, Tester 1977), which corroborates what we observed.

The low levels of infestation on 'IAC 17' in the second season and the relatively low yield reductions in both seasons might indicate resistance against the stink bugs, but the genotype also showed sensitivity to stink bug injury. Moreover, this genotype tends to exhibit high leaf retention, which is commonly associated with stink bug injury (Daugherty et al. 1964), but also to high soil moisture during soybean maturation stages (Sosa-Goméz and Moscardi 1995) and potassium deficiency (Mascarenhas et al. 1988). During our study, precipitation during the maturation period was moderate, and fertilization was conducted on the basis of soil analysis (Raij et al. 1997); hence, we conclude that high leaf retention we observed in 'IAC 17' resulted from the sensitivity of this genotype to stink bug injury.

D75-10169 and IAC 74-2832 had low stink bug infestations in one of the growing seasons, but they also had low yields and moderate seed damage. Antixenosis resistance of D 75-10169 against *P. guildinii* has been reported (Silva et al. 2014), probably conferred by a parent, PI 229358, known to be resistant to *B. tabaci* biotype B (Valle et al. 2012) and the soybean aphid, *Aphis glycine* (Matsumura) (Hesler and Dashiell 2008). IAC 74-2832 expressed antibiosis against *P. guildinii* (Silva et al. 2013), and possibly conferred by PI 274454 which is resistant to some insects. Taking into account that the resistance is specific, and can vary for each species of stink bug (Smith 2005), and for combinations (complexes) of stink bugs, D 75-10169 and IAC 74-2832 appear not to be resistant against the stink bug complex.

'IAC 100' had high yield, despite being quite infested in the first growing season, with intermediate leaf retention and low seed damage. There was an expectation that 'IAC 100' would have low stink bug infestation because studies have demonstrated antixenosis against *N. viridula* (Campos et al. 2010) and *P. guildinii* (Silva et al. 2014). Moreover, 'IAC 100' and other genotypes with 'IAC 100' in their genealogy showed antixenotic resistance against herbivory by the velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner); soybean looper, *Chrysodeixis includens* (Walker); green cloverworm moth, *Hypena scabra* (F.) (McPherson and Buss 2007), and stink bugs (McPherson et al. 2007). Although the expression of antibiosis in 'IAC 100' cannot be ruled out, the yield results (yield reduction below 5% in the first growing season) suggest the expression of resistance based on tolerance (Smith 2005). Compensation for damage by soybean plants has been reported as a characteristic considered to be a form of resistance (Pinheiro et al. 2005). Resistance of 'IAC 100' can be ascribed to the parental lines (PI 229358, PI 274454, 'IAC 12', and IAC 78-2318) that feature resistance against more than one species of insect (Lourenção et al. 1987, Hoffmann-Campo et al. 1994, Carrão-Panizzi and Kitamura 1995, Rossetto et al. 1995). While genotypes resistant to soybean pests are available, their utility is mitigated by undesirable agronomic characteristics, such as reduced yield potential and late maturity (Boethel 1999).

IAC 78-2318 behaved similarly to 'IAC 100' for yield and infestation parameters, but this genotype also showed high and intermediate levels of leaf retention and seed damage. Although IAC 78-2318 did not express the relatively high levels of resistance expressed by 'IAC 100', some tolerance to the stink bug complex appeared to occur. Lourenção et al. (2010) suggested that 'IAC 18' is tolerant of stink bugs because it produces high yields while under high insect pressure, but those studies did not compare stink bug-infested plots to insecticide-treated plots. We found that 'IAC 18' had high yield in the insecticide-treated plots, but in the nontreated plots, high yield loss and high leaf retention indicated susceptibility.

PI lines, IAC 78-2318, and 'IAC 100' expressed limited degrees of resistance to the stink bug complex. This is the first study to assess different soybean maturity groups under high infestation pressure from the three main species of stink bug in the study area, and to consider several parameters for yield and seed quality. The commercial use of some of these genotypes, such as 'IAC 100', might fit well in an integrated pest management strategy for regions that are under pressure by the same, and possibly other, stink bug complex.

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