Antixenosis to the Soybean Aphid in Soybean Lines

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Abstract: The soybean aphid, *Aphis glycines*, is a pest of soybean in Asia, and it has become a major pest of this crop in North America with large outbreaks that cause significant yield loss. Host-plant resistance is one management tactic being developed against soybean aphid in North America, and resistance may be manifested as antixenosis, antibiosis, or tolerance. In this study, choice tests were conducted to identify antixenosis to soybean aphids in several soybean lines. The soybean lines 'Dowling,' PI 230977, 'Jackson,' 'Cobb' and 'Palmetto' had strong antixenosis to soybean aphid, and lines PI 71506, G93-9223, 'Braxton,' 'Cook,' 'IAC-1,' 'Ripley,' and 'Tie feng 8' were moderately antixenotic. The intermediate level of antixenosis in PI 71506 contrasts with previous results, and suggests biotypic differences in the responses of soybean aphid to this line. Shoot length, shoot width, and seedling dry mass were also measured to test for any association between aphid host choice and plant size. Plant-size parameters varied by soybean line in all tests. However, the relation between aphid host choice and plant-size parameters was generally weak and not consistent across tests, suggesting that other undetermined plant characteristics were important in host selection. The identification of antixenosis in several soybean lines provides soybean breeders and pest management practitioners with additional options for managing soybean aphid through host-plant resistance. Antixenosis may be important on its own, and it may prove be complimentary to the antibiosis mode of resistance by reducing selection on resistance-breaking biotypes of soybean aphid, thereby prolonging the usefulness of plant resistance as a non-chemical means of managing soybean aphid.

Keywords: *Aphis glycines*, host-plant resistance, Cobb, PI 71506, PI 230977, Palmetto.

INTRODUCTION

The soybean aphid (*Aphis glycines* Matsumura) is a major invasive pest of soybean that was discovered in the U.S. in 2000 [1]. It has spread throughout much of the area where soybeans are grown in North America, but is problematic in the northern production region. In North America, soybean aphid overwinters on buckthorn (*Rhamnus* spp.), and summer forms are apparently monophagous on soybean [2]. Winged soybean aphids migrate from buckthorn in early summer, and populations gradually increase in soybean over several generations before sometimes reaching economically injurious levels [3-5]. Soybean aphid may also vector plant pathogenic viruses of soybean [6-8], and these viruses may cause further yield loss.

Recurring outbreaks of soybean aphid in North America are currently managed with insecticides pending the development of other management approaches such as host-plant resistance [9]. Host-plant resistance is often the hub of a sustainable pest-management system [10, 11], and the deployment and proper management of soybean lines with aphid resistance has potential to reduce insecticide use and the ensuing economic and environmental costs in soybean production systems [11].

Three modalities of host-plant resistance are conceptually recognized as tolerance, antibiosis, and antixenosis [12, 13]. Tolerance is a plant's ability to withstand or recover from arthropod damage. Antibiosis adversely affects arthropod development, reproduction, or survival, and antixenosis prevents arthropod colonization of a host plant. Two or more modalities may be evident within the same host plant, and in some cases it may be difficult to differentiate between antibiosis and antixenosis as they both adversely affect arthropod populations [13]. However, separate experiments may be conducted to detect antibiosis by no-choice tests and antixenosis via choice tests [12, 14, 15].

Choice tests may be designed to minimize the influence of extrinsic factors on host selection by aphids [14]. For instance, plant growth stage and positive phototaxis by aphids may confound host selection, and thus choice tests are typically run in the dark among plants of uniform growth stage [13, 15]. In addition, inherent differences in plant size among plants within the same growth stage might confound host selection by arthropods, and some studies have measured plant size (e.g. height and dry mass) in order to account for associations between aphid host choice and plant size [16-19]. However, the value of such measurements to soybean choice tests in general is unknown.

Several lines have been identified as resistant to soybean aphid, with antibiosis as a dominant mode of resistance [19-26]. Not all of the studies conducted choice tests, but some of them identified antixenosis in various lines [20, 23]. To date, soybean lines characterized with antixenosis include PI 71506, 'Dowling,' 'Jackson' and 'Palmetto' [19, 20, 23].

In other studies, responses by soybean aphid on resistant lines (e.g., reduced nymphiposition, plant abandonment) may have been due to antibiosis, antixenosis, or both [20, 24, 25]. These lines include PI 230977, 'Braxton,' 'Cobb,' and Tie

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feng 8.' Thus, we conducted follow-up experiments to test for antixenosis among these previously identified aphid-resistant soybean lines, and included measurements of plant size to test for any association with aphid host selection.

MATERIALS AND METHODS

Four choice tests were conducted within growth chambers at the North Central Agricultural Research Laboratory, Brookings, South Dakota, USA, in 2008 and 2009 to determine antixenosis resistance to soybean aphid among various soybean lines. Differential host selection was tested by introducing 90 apterous adult soybean aphids into the center of a circular arena comprising 6 plants of different soybean lines in four separate tests (designated I through IV) and counting adult aphids on each plant 48 h later [19]. Apterous soybean aphids are more practical to rear and handle than alates, and they have been successfully used to detect antixenosis in soybean lines [19, 20, 23], although it is winged aphids that choose host plants and colonize them in the field [13, 15]. A total of sixteen soybean lines was tested (Table **1**). The lines were grouped into four tests because of space limitations within the growth chamber, and because many of them had been grouped for other resistance tests in previous studies [19, 24, 25]. Dowling and PI 71506 (test I), Jackson (test II), and Palmetto and PI 71506 (test III) were used as resistant checks; '91B91' (tests I and II) and 'Williams 82' (tests II and IV) served as susceptible checks [3, 20, 25].

Test plants were prepared by sowing two seeds of a soybean line into a cup nearly full with soil mix. Seeds were covered with 2.5 cm of 40-mesh sand, gently watered, and thinned to one plant per cup 1 wk after emergence. Test plants were kept for 2 wk in a greenhouse (approximately 23°C, 25% RH; 16:8h L:D) until they had fully expanded unifoliolate leaves (VE stage) [27] for use in the test. One day before infesting, test plants of each soybean line were grouped with test plants of similar size, and a plant of each test line was placed randomly into one of six slots per replicate tray. Cups were placed so that their brims rested at the tray surface, and then the top of the cups and upper tray surface were covered with 3 cm of sand. Previous testing showed that soybean aphids move adequately across sand [19].

Each test arena was constructed from a covered cake-serving tray (29-cm diam) [19]. Six equally spaced, circular holes (7-cm diam) were cut into the tray, and each hole held a tapered plastic cup (7.5-cm diam top, 4.8-cm diam bottom, 9.5-cm ht, 2-cm diam hole in bottom) with a test plant of one soybean line. The tray was supported by thin metal strips and screws 3 cm above a plastic saucer (28-cm diam, 5-cm ht) that held water for test plants.

For each test, the arenas were covered with a vented, plastic top (15-cm ht, 30-cm diam) and secured by metal clips to the tray immediately after aphids were introduced. All eight arenas were then placed for 48 h in a single growth chamber without light that was set at approximately 30% RH and temperature to ramp up and down daily to 22°C midday and 18°C nighttime, respectively. Soybean aphids were counted on each plant at the end of the 48-h period. Eight replicate trays were infested initially, but replicates with less than 63 aphids on plants (70 percent of initial infestation) were excluded out of concern that arena integrity or aphid viability might have been compromised unwittingly and a relatively large proportion of aphids were unaccounted for. This resulted in seven (tests II and III) to eight replicate

Table 1. Soybean Lines Used in Antixenosis Tests with Soybean Aphids

Line	Other names, Pedigree, Resistance or Susceptibility to Soybean Aphid
91B91	Pioneer Hi-Bred International, Inc., Johnston, IA. Susceptible to soybean aphid [3,25].
Braxton	PI 548659. F59-1505 x ('Bragg' (3) x D60-7965) [35]. Mild resistance to soybean aphid [24].
Cobb	PI 548664. F57-735 (D49-772 x 'Improved Pelican') x D58-3358 [35]. Resistant to soybean aphid [24].
Cook	PI 553045. Selection from F5 plant from 'Braxton' x 'Young' [36]. Susceptible to soybean aphid [24]
Davis	PI 553039; D49-2573 × N45-1497 [37]. Susceptible to soybean aphid [19].
Dowling	PI 548663. 'Semmes' × PI 200492 [35]. Antibiosis [20] and antixenosis [23] to soybean aphid.
G93-9223	PI 595099. F_4-derived line from G83-559 x (G80-1515(2) x PI 230977) [35,38]. Mild resistance to soybean aphid [25].
IAC-1	PI 628842. 'Alianca Preta' / 'Palmetto' [35].
Jackson	PI 548657. ' Volstate'(2) x 'Palmetto' [35]. Antibiosis [20] and antixenosis [23] to soybean aphid.
Palmetto	PI 54840. Selected from PI 71587 [35]. Antibiosis [20] and antixenosis [23] to soybean aphid.
Pana	PI 597387. 'Jack' x Asgrow 'A3205' [39]. Susceptible to soybean aphid [20].
PI 71506	Undetermined pedigree. Resistant to soybean aphid, including antixenosis [20,25].
PI 230977	Undetermined pedigree. Resistant to soybean aphid [20,25].
Ripley	PI 536636. Pedigree: F_4-derived line from Hodgson × (York × PI 71506) [35,40].
Tie feng 8	PI 436684. 'Tong Zhou Xiao Huang Dou' × 'Jing Shan Pu' [41]. Moderate resistance soybean aphid [24].
Williams 82	PI 518671. 'Williams' (7) x 'Kingwa' [42]. Susceptible to soybean aphid [20].

blocks per test (tests I and IV). After aphids were counted, shoots were clipped at soil level, rinsed, and measured for width (i.e. distance between distal tips of unifolioles), length (soil base to apical tip of extended middle leaflet of uppermost trifoliole), and dry mass (45°C for 72 h) [19].

Each arena of six plants was considered a replicate block [15,19]. Counts were subjected to chi-square analyses to test for heterogeneity (i.e. line x replicate-block effect) and pooled across replicates to test for effects of soybean line (PROC FREQ) [28,29]. Each pooled count was converted to a proportion by dividing by the total number of adult aphids counted, and proportions were separated among soybean lines using a Tukey-type multiple comparison test for proportions [19, 29]. Data of plant measurements were subjected to separate analyses of variance (PROC ANOVA) [28] for a randomized complete block design. Analysis was also performed on the number of soybean aphids per plant versus shoot width, length, and dry mass to determine if preference for soybean lines by aphid was correlated with these plant growth parameters (PROC CORR) [28].

Soybean aphids used in the tests were obtained from a multiclonal stock colony maintained for multiple generations on plants of soybean variety 'Asgrow 0803' (Tests I, II and III; Monsanto Corp., St. Louis, MO) or 91B91 (Test IV) in growth chambers set with a 16:8 (L:D) photoregime and 22°C:18°C (L:D) temperature range at our laboratory. The colony aphids were collected from a soybean field in Brookings County, South Dakota, in summer 2007 and re-stocked with aphids in summer 2008. Soybean aphids newly collected from the field were caged and checked every few hours, with neonate offspring deposited within the first 30 h transferred to non-infested, two-week-old soybean plants to ensure that they were free of aphid-transmitted plant virus. Infested colony plants were maintained 3 to 4 wks, and then infested shoots were cut and transferred to non-infested, two-week-old soybean plants to perpetuate the colony.

RESULTS

Soybean aphid counts showed a line x replicate-block effect ($p < 0.001$) in each test (test I, $\chi^2 = 224.4$, $df = 35$; test II, $\chi^2 = 86.4$, $df = 30$; test III, $\chi^2 = 191.5$, $df = 30$; test IV, $\chi^2 = 211.0$, $df = 35$), and this justified analysis based on pooled counts across replicates. When pooled, the proportion of soybean aphids differed sharply among soybean lines in each test (Table **2**). In test I, PI 230977 and Dowling were strongly antixenotic, and 'Ripley,' G93-9223 and PI 71506 had intermediate levels of antixenosis compared to 91B91. In test II, Jackson and Cobb displayed strong antixenosis, and Braxton, 'Cook' and Tie feng 8 showed moderate antixenosis. In tests III and IV, Palmetto was strongly antixenotic, and 'IAC-1' and PI 71506 had intermediate levels of antixenosis. In test IV, 'Pana' showed moderate antixenosis compared to 'Williams 82.'

Soybean lines differed in shoot width, shoot length and dry mass in each test (Table **2**), which confirmed inherent differences in size among some lines. In test I, shoot length and dry mass were weakly and inversely correlated with the proportion of soybean aphids per line, indicating that aphids had a slight bias for smaller plants. Shoot length in test II was also inversely correlated with the proportion of soybean aphids per line. In contrast, results from test III showed shoot width and dry mass were positively correlated with the proportion of aphids per line, suggesting a bias of soybean aphids for larger plants. In test IV, the proportion of aphids per line was not correlated with shoot width, shoot length or dry mass. There were slight differences in plant size and aphid responses between tests III and IV. Plants of PI 71506 in test IV were somewhat larger in test III, but roughly the same proportion of soybean aphids chose this line in each test. The proportion of aphids choosing Pana in test III appeared modestly greater than in test IV, although the size of Pana plants was comparable between the two tests.

DISCUSSION

Various antixenotic and susceptible checks were used among the tests of this study. The use of different checks among tests precluded direct comparison of lines among tests, with the exception of PI 71506, which was included in three of four tests. Nonetheless, several antixenotic lines were found in each of the tests, and although not directly comparable, the relative strength of soybean lines was evident from each test. Dowling, PI 230977, Jackson, Cobb and Palmetto showed strong antixenosis to soybean aphid, and PI 71506, Ripley, G93-9223, Tie feng 8, Braxton, Cook, G93-9223, and IAC-1 had intermediate levels of antixenosis. Our results showing strong antixenosis in Dowling, Jackson and Palmetto agree with those of previous studies [19, 20, 22]. This is the first report definitively characterizing antixenosis in PI 230977 and Cobb, and moderate antixenosis in Ripley, G93-9223, Tie feng 8, Braxton, Cook, G93-9223, and IAC-1. PI 71506 was previously identified with strong antixenosis to soybean aphid [20], but in this study the level of antixenosis was greater in Dowling, PI 230977, Jackson, Cobb and Palmetto than in PI 71506. The *Rag1* and *Rag* genes have respectively been identified as responsible for resistance to soybean aphid in Dowling and Jackson [30, 31], but PI 71506 has a different genetic basis for resistance to soybean aphid [32]. The genetic basis for resistance in other lines tested in this study is not known.

It is unclear why PI 71506 was only moderately antixenotic in this study, whereas it had shown strong antixenosis in an earlier study [20]. The source of PI 71506 was the same as in previous studies, but soybean aphids were derived from geographically different areas (i.e., Illinois vs. South Dakota). The different levels of antixenosis in PI 71506 between the two studies may have been due to differences in host preferences and suggests the possibility that soybean aphid biotypes may be responsible [30, 32]. PI 71506 has also had low to intermediate infestation levels of soybean aphids in previous laboratory and field tests in South Dakota [25, 32], but it was undetermined whether antixenosis was responsible.

Theoretically, larger plants may be more conspicuous and thereby more readily colonized by aphids, but host selection of soybean lines by soybean aphids was neither strongly nor consistently related to plant size in the four tests of this study. Overall, the results suggest that soybean aphids chose soybean lines within the same growth stage based on undetermined factors other than plant size. Shoot length, shoot width, and seedling dry mass were not associated with

Table 2. Proportion of Adult Soybean Aphids among a Choice of Soybean Lines and Correlations between Proportions and Three Plant Measures. Asterisk indicates statistical significance ($p < 0.05$). Proportions not followed by the same letters differ significantly. Correlation coefficients calculated for proportions of aphids per line and individual plant measures for each test

Test	Line	Proportion of Aphids	Plant Measure (mean ± SE)		
			Shoot Width (mm)	Shoot Length (mm)	Dry Mass (mg)
I	PI 230977	9.2 a	11.5 ± 0.3 bc	9.6 ± 0.6 a	303.9 ± 14.2 a
	Dowling	10.9 ab	10.2 ± 0.2 d	8.8 ± 0.2 a	197.7 ± 6.8 b
	Ripley	15.1 bc	10.7 ± 0.3 cd	6.1 ± 0.1 bc	177.1 ± 5.0 b
	G93-9223	18.0 c	12.2 ± 0.2 a	7.1 ± 0.3b	205.5 ± 7.0 b
	PI 71506	19.0 c	11.7 ± 0.3 ab	5.3 ± 0.4 c	193.1 ± 10.0 b
	91B91	27.9 d	11.2 ± 0.3 bc	6.4 ± 0.2 bc	195.0 ± 9.3 b
	Statistics	$\chi^2 = 82.8$*	F = 12.14*	F = 22.70*	F = 35.67*
	df	5	5,35	5,35	5,35
	Correlation	r (df = 48)	0.15	-0.29*	-0.30*
II	Jackson	6.1 a	11.7 ± 0.2 ab	10.0 ± 0.4 a	264.7 ± 8.2 a
	Cobb	6.1 a	10.5 ± 0.2 bc	8.5 ± 0.2 ab	237.8 ± 13.5 ab
	Braxton	16.4 b	11.9 ± 0.2 ab	7.3 ± 0.5 bc	191.5 ± 8.3 b
	Cook	19.8 b	12.0 ± 0.3 ab	7.6 ± 0.3 bc	217.2 ± 32.7 ab
	Tie feng 8	21.1 b	9.2 ± 0.9 c	7.7 ± 0.8 bc	246.5 ± 19.8 ab
	91B91	30.3 c	12.3 ± 0.2 a	6.0 ± 0.2 c	225.9 ± 7.6 ab
	Statistics	$\chi^2 = 145.1$*	F = 9.14*	F = 9.51*	F = 2.56*
	df	5	5,30	5,30	5,30
	Correlation	r (df = 42)	0.17	-0.52*	-0.11
III	Palmetto	5.5 a	9.3 ± 0.2 a	4.5 ± 0.2 c	136.1 ± 6.3 a
	IAC-1	12.5 b	10.1 ± 0.2 ab	4.3 ± 0.3 c	166.7 ± 9.3 ab
	PI 71506	13.0 b	11.1 ± 0.4 c	4.2 ± 0.3 c	151.3 ± 8.3 ab
	Davis	20.8 c	10.9 ± 0.2 bc	5.8 ± 0.2 ab	190.8 ± 2.9 c
	Pana	21.6 c	9.7 ± 0.2 a	6.6 ± 0.4 a	179.8 ± 9.1 c
	Williams 82	26.7 c	11.3 ± 0.2 c	5.2 ± 0.2 bc	190.8 ± 5.1 c
	Statistics	$\chi^2 = 93.9$*	F = 15.69*	F = 14.89*	F = 14.79*
	df	5	5,30	5,30	5,30
	Correlation	r (df = 42)	0.35*	0.26	0.38*
IV	Palmetto	4.2 a	10.0 ± 0.5 a	4.6 ± 0.3 a	141.7 ± 8.1 a
	PI 71506	14.1 b	14.5 ± 0.3 d	5.8 ± 0.1 bc	278.8 ± 11.5 d
	IAC-1	15.5 b	11.4 ± 0.3 b	4.9 ± 0.2 ab	201.8 ± 9.3 b
	Pana	16.9 bc	10.5 ± 0.2 ab	6.4 ± 0.1 c	184.9 ± 8.8 b
	Davis	22.6 cd	11.1 ± 0.2 b	5.2 ± 0.2 ab	194.6 ± 8.2 b
	Williams 82	26.8 d	12.5 ± 0.2 c	6.1 ± 0.2 c	234.0 ± 9.5 c
	Statistics	$\chi^2 = 116.6$*	F = 50.23*	F = 10.60*	F = 45.52*
	df	5	5,35	5,35	5,35
	Correlation	r (df = 48)	0.10	0.28	0.15

choice of soybean lines by soybean aphid in a previous test [19]. Leaf pubescence, another physical-morphological trait, also does not affect levels of soybean aphids on soybean plants [19, 20]. Thus, future studies may need to focus on testing chemical and other morphological factors as a basis for antixenosis in soybean lines.

Antixenosis may be an important resistance modality in soybean against soybean aphid, as this modality can deter or delay aphid colonization and reduce the potential of infestations reaching economically injurious levels [33]. Deterrence may effectively manage aphid populations by reducing the number of initial colonizers and the proportion of successive generations that remain in the crop field [33]. Aphids that are deterred form settling on soybean plants may continue searching but become exhausted or be preyed upon before finding an acceptable host plant for nymphiposition. However, antixenosis that causes soybean aphids to move among plants in search of an acceptable host may be problematic in managing stylet-borne plant viruses, as greater plant-to-plant movement may increase the incidence of virus transmission [34].

Ideally, antixenosis and antibiosis may be mutually reinforcing modalities of resistance. That is, antixenosis may deter antibiosis-resistance-breaking biotypes from colonizing a plant, and antibiosis may reduce the fitness of those individuals that colonized. Many of the antixenotic lines in this study also have antibiosis resistance, and lines with strongest antixenosis also have strong antibiosis against soybean aphid [19-26]. Dual modalities of resistance may prove advantageous in developing lines against soybean aphid.

However, resistance in some lines with both antibiosis and antixenosis (e.g., Dowling) has been overcome by a biotype of soybean aphid [43]. It is unclear whether one gene such as *Rag1* confers both antibiosis and antixenosis in soybean lines such as Dowling. PI 71506 has a different genetic basis than *Rag1* for resistance to soybean aphid, and it was effective against an Ohio biotype of soybean aphid that has overcome *Rag1* resistance [32]. Thus, it may be advantageous to pair antibiosis derived from one source (e.g., Dowling) with antixenosis from a source with a different genetic basis for resistance (e.g., PI 71506) to mutually reinforce these modalities of resistance and thereby extend the stability of aphid resistance in soybean lines in the field. The deployment and proper management of soybean aphid-resistance genes has the potential to greatly reduce the frequency of aphicide applications and the ensuing economic and environmental costs in soybean production systems [9, 25].

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