

Characterization of resistance to *Aphis glycines* in soybean accessions

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Abstract The soybean aphid, *Aphis glycines* Matsumura, is a pest of soybean [*Glycine max* L. (Merrill)] in Asia, and its recent establishment in North America has led to large, recurring outbreaks that have challenged pest management practitioners there to seek environmentally responsible means for its control. Growth-chamber experiments were conducted to determine and characterize host-plant resistance among several soybean accessions. Soybean plants were first screened for resistance by rating the population growth of *A. glycines* in two tests. All plants of PI 230977 and 25% of PI 71506 plants were resistant (≤ 100 aphids per plant) in the first screening test. All ‘Dowling’, PI 71506 and PI 230977 were resistant (≤ 150 aphids per plant), and 50% of plants of line ‘G93-9223’ were resistant in the second test. Follow-up experiments showed that antixenosis was a modality of resistance based on reduced nymphiposition by *A. glycines* on Dowling, PI 230977 and PI 71506 in no-choice tests and on fewer numbers of *A. glycines* on Dowling, PI 230977, PI 71506 and G93-5223 in distribution tests. Antixenosis in Dowling and PI 230977 was stronger in the unifoliolate leaves

than in other shoot structures, whereas distribution of *A. glycines* within plants of PI 71506 and G93-5223 suggested comparable suitability between unifoliolate leaves and other shoot structures of these accessions. Antibiosis to *A. glycines* was evident as a lower proportion of aphids that reproduced on PI 230977 and from fewer progeny on PI 230977 and Dowling than on 91B91. The number of days from birth to reproduction by *A. glycines* did not differ among accessions. Results confirmed Dowling and PI 71506 as strong sources of resistance to *A. glycines*. The levels of antixenosis and antibiosis to *A. glycines* in PI 230977 and antixenosis to *A. glycines* in G93-9223 suggest that these accessions may also be valuable to soybean breeding programs as sources of resistance.

Keywords Antibiosis · Antixenosis · *Aphis glycines* · Host-plant resistance · PI 230977

Introduction

The soybean aphid, *Aphis glycines* Matsumura, is a soybean pest native to Asia (Wang et al. 1996). It was discovered infesting U.S. soybean fields in summer 2000 and has spread over a substantial portion of soybean-producing areas in North America (Venette and Ragsdale 2004). *A. glycines* has become a principal pest in infested

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areas, as large populations develop on plants and cause yield loss (Myers et al. 2005). In addition to causing direct physiological damage by feeding, *A. glycines* transmits soybean mosaic virus and other viruses to soybean plants (Clark and Perry 2002; Domier et al. 2003). Large, recurring outbreaks of soybean aphid in North America have challenged pest management practitioners to devise environmentally responsible means of protecting soybeans (Rutledge et al. 2004). Currently, insecticides are recommended as an immediate measure against soybean aphid until other management approaches, such as host-plant resistance, can be evaluated and developed (Rutledge et al. 2004).

Plant resistance is often the hub of an integrated pest management program for insect pests (Panda and Khush 1995; Wiseman 1998, 1999), and thus there is need to develop soybean varieties that are resistant to *A. glycines*. New sources of resistance should be categorized to understand the effect on the target insect and to optimize their development and use in cultivars (Panda and Khush 1995). The three basic categories of host-plant resistance are antixenosis, antibiosis, and tolerance (Kogan and Ortman 1978; Painter 1951; Smith 2005). Antixenosis and antibiosis are measured in terms of aphid responses to host plants, whereas tolerance is measured as differential responses among host plants to specific levels of aphid infestation. Antixenosis deters or reduces colonization by insects, whereas antibiosis causes adverse effects on insect life history. Tolerance is the ability of a plant to grow and reproduce despite supporting an infestation that would limit growth and reproduction of a susceptible host.

Sources resistant to *A. glycines* have recently been identified, with antibiosis and antixenosis as resistance modalities. Hill et al. (2004) reported resistance to *A. glycines* in several soybean accessions, including ‘Dowling’, ‘Jackson’, ‘Sugao Zarai’ and the plant introduction line (PI) 71506. Hill et al. (2004) and Li et al. (2004) showed that cultivars Dowling, Jackson, and Sugao Zarai possess antibiosis to *A. glycines*, and Hill et al. (2004) characterized PI 71506 as antixenotic. Hill et al. (2004) also noted that PI 230977 was resistant to *A. glycines* in a choice test, but did

not further characterize its resistance. Mensah et al. (2005) identified resistance PI 567541B and PI 567598B as antixenotic, and showed that PI 567543C and PI 567597C have antibiosis resistance to *A. glycines*.

Because of the limited information on *A. glycines*-resistance in PI 230977, additional testing with it and related lines is warranted. PI 71506 is a grandparent and PI 230977 is a great-grandparent of lines used in F₄-derivation, respectively, of the cultivar ‘Ripley’ (Cooper et al. 1990) and the advanced soybean line ‘G93-9223’ (Luzzi et al. 1997). We are unaware of any information about resistance to *A. glycines* in Ripley and G93-9223. However, adapted germplasm, such as Ripley and G93-9223, is generally more useful in breeding programs, and thus testing for *A. glycines*-resistance in these two lines is needed. The objectives of this study were to characterize the type of resistance to *A. glycines* in the progenitor lines PI 71506 and PI 230977 and two cultivars derived from them (G93-9223 and Ripley).

Materials and methods

We conducted experiments with the soybean accessions listed in Table 1. We performed four types of growth-chamber experiments to determine resistance to *A. glycines* among soybean accessions. The first experiment was used to screen accessions for resistance by rating population growth of *A. glycines* on plants. Three types of follow-up experiments were conducted to characterize resistance responsible for differences in population growth of *A. glycines* observed among accessions. In follow-up experiments, only six accessions were used, with Dowling as an *A. glycines*-resistant control, ‘91B91’ as the susceptible control, and PI 71506, PI 230977, G93-9223, and Ripley as other test entries. All experiments were conducted at the North Central Agricultural Research Laboratory, Brookings, SD, USA.

Plant accessions and aphids

Experimental plants were prepared by placing two seeds of an accession into an 8.5-cm square plastic pot filled with a 2:1:1 mixture of soil

Table 1 Soybean accessions used in host-plant-resistance experiments with *Aphis glycines*

Accession	Comments
Pioneer 91B91	Pioneer Hi-Bred International Inc., Johnston, IA, USA; favorable to substantial population growth of <i>A. glycines</i> (Beckendorf 2005)
Williams 82	Susceptible to <i>A. glycines</i> (Hill et al. 2004)
Dowling	Pedigree: Semmes × PI 200492 (adapted from NGRP 2006); antibiosis (Hill et al. 2004) and antixenosis (Li et al. 2004) to <i>A. glycines</i>
PI 71506	Antixenosis to <i>A. glycines</i> (Hill et al. 2004)
PI 230977	Resistant to <i>A. glycines</i> (Hill et al. 2004)
G93-9223 (PI 595099)	Pedigree: F ₄ -derived line from G83-559 × (G80-1515(2) × PI 230977) (NGRP 2006; Luzzi et al. 1997)
Ripley	Pedigree: F ₄ -derived line from Hodgson × (York × PI 71506) (NGRP 2006; Cooper et al. 1990)
Early Sunrise	Also known as 'FC 32141'; pureline adapted to South Dakota, USA (NGRP 2006)
Manchukota	Selection from 'Manchu' adapted to South Dakota, USA (NGRP 2006)
S19-V2RR	Syngenta Inc., Wilmington, DE, USA
S24-K4RR	Syngenta Inc., Wilmington, DE, USA

(fine-loamy, mixed Calcic Hapludolls), perlite, and coarsely ground coconut shells (Coir, J.R. Johnson Supply Inc., Roseville, MN, USA). One week after planting, pots were thinned to one seedling each based on uniform seedling growth. One plant of each accession was placed into a 26.5-cm × 51-cm plastic flat for a total of seven to nine accession plants per flat. Each flat was used as an experimental block, with experiments set up in a randomized complete block design with at least seven blocks (replications). Experiments commenced by placing *A. glycines* by artist's brush onto the abaxial surface of expanding unifoliolate leaves of 2-week-old plants (intermediate VC stage; Pedersen 2004), and they were run under a 16:8::L:D photoregime and 22°C:18°C::L:D temperature range.

All *A. glycines* used in the experiments were obtained from a virus-free, multiclinal stock colony maintained on soybean variety 'Asgrow 0801' (Monsanto Corp., St Louis, MO, USA) plants in growth chambers (16:8::L:D photoregime with 22°C:18°C::L:D temperature range) at our laboratory. The aphid colony was established by collecting aphids from a soybean field in Brookings County, SD, USA, in summer 2002 and re-stocked with aphids in summer 2005. Field-collected aphids were caged and checked every few hours, with neonate offspring deposited within the first 30 h transferred to non-infested plants to ensure that colony plants were free of

aphid-transmitted plant virus. Infested colony plants were maintained 3–4 weeks, and then infested shoots were cut and transferred to non-infested, 2-week-old soybean plants to maintain the colony.

Rating the population growth of *Aphis glycines*

Population-growth experiments were conducted with tested seven to nine accessions at a time, and commenced by placing five *A. glycines* on the underside of each unifoliolate leaf (ten aphids per individual accession plant). This was a choice test, as aphids were not caged on plants. After 14 days, *A. glycines* populations were evaluated on each plant. In the first test, individual plants were rated as resistant if they had ≤100 aphids (categories 1 and 2 of Hill et al. 2004). In that test, aphid response was generally bimodal, with individual plants either having about 100 aphids or having distinctly >>100 aphids. However, plants with slightly >100 aphids were not rated as resistant, and their potential for meaningful resistance to *A. glycines* could have been missed. Thus, the cutoff of the rating scale was raised to 150 *A. glycines* per plant in the second screening test to include accession plants with slightly >100 *A. glycines* as resistant. Data for population ratings were placed in a frequency table and analyzed for differences among accessions using a two-tailed, Fisher's

Exact Test (Zar 1998; PROC FREQ feature, SAS Institute 2002).

Distribution of aphids within and among plants

Based on observations of the distribution of *A. glycines* among test accessions in the population-growth tests, we hypothesized that aphids initially placed on unifoliolate leaves would differentially distribute themselves by remaining on or moving off of unifoliolate leaves and that patterns in their distribution on shoot structures would vary by accession and time. To test this, we placed five adult or third-instar *A. glycines* per each unifoliolate leaf (ten aphids per plant) without caging on the various accessions. The aphids were not caged, and thus were free to redistribute themselves on the test plants. Accessions were randomized and appeared once within each of ten replicate blocks. At 24 and 48 h after infesting, separate counts of adult aphids were made on the unifoliolate leaves and on the remaining shoot of each plant. A categorical log-linear model (Agresti 1990; PROC CATMOD feature, SAS Institute 2002) was used to analyze the effects of accession, shoot structure, and time and their interactions on the counts of *A. glycines* per plant.

No-choice nymphiposition

We hypothesized that differences in the population growth of *A. glycines* among accessions stemmed, at least in part, from differential nymphiposition by *A. glycines*. To test this, we performed two, no-choice nymphiposition tests in which *A. glycines* were confined by clip cages similar to those used by Hill et al. (2004) and Puterka and Peters (1988). The cages were made from plastic tubing (12 mm i.d., 12 mm long) and steel tension-clips (4.6 mm long; Hairart, Gardena, CA, USA). The tubing was glued to a perpendicularly bent clip prong. One end of the tube was covered with fine mesh screen (150- μ m openings; BioQuip, Rancho Dominguez, CA, USA), and the other was glued to a fiber washer (0.9 mm i.d., 19 mm o.d.). This washer had been glued to a similarly shaped piece of 1-mm thick

felt, and another washer was glued to the inner surface of the other clip prong to align with the felt and opposite washer. Aphids used in the test were selected arbitrarily from colony plants, and not necessarily uniform in age. They were transferred by small brush from colony plants to accession plants. Aphids were caged for 24 h (three adults) or 48 h (five adults), respectively, on an accession plant. At the end of each test period, the number of nymphs (alive and dead) per plant was counted and subjected to analysis of variance (PROC ANOVA feature; SAS Institute 2002).

Developmental time and number of progeny

This experiment was a continuation of the 24-h, no-choice nymphiposition test, and was used to test whether accessions affected (1) the number of days from birth to onset of reproduction and (2) the number of nymphs produced by individual *A. glycines* in the first 7 days of adulthood. After the number of nymphs per leaf was tallied for the initial 24-h nymphiposition period, aphids were thinned to one neonate per plant and re-caged. Beginning 5 days later, plants were checked daily for reproductive maturity of the remaining caged aphid. The number of *A. glycines* and the time (in days) to reach reproductive maturity was recorded. When reproduction began, second-generation neonates were counted and removed daily over a 7-day period. For some accessions, several nymphs did not survive to reproduce. Because of missing values for aphids that did not reach reproductive maturity, the number of days to reproduction was analyzed by a chi-square test of mean values for each accession (Zar 1998). If aphids failed to complete 7 days of reproduction, the number of second-generation nymphs was recorded as zero on days which the adult aphid was absent. Analysis of variance (PROC ANOVA) was used to test the effect of accession on the number of nymphs deposited over 7 days. Following a significant ANOVA ($\alpha = 0.05$), means for a response variable were separated by accession using Tukey's honest significant difference (Zar 1998). Because some accessions had a low proportion of aphids reach reproductive maturity, Fisher's Exact Test was used to

determine the probability of observing the distribution in survival of aphids among accessions. This was followed by a Tukey-type multiple comparison test ($\alpha = 0.05$; Zar 1998) to compare the proportion of plants in which aphids reached reproductive maturity among accessions.

Results

Rating the population growth of *Aphis glycines*

Frequencies in the ratings of aphid population growth differed among accessions in both tests (Table 2; $P < 0.001$, Fisher's Exact Test). In the first test, 100% of PI 230977 plants and 25% of PI 71506 plants were rated as resistant to aphid population growth (≤ 100 *A. glycines* per plant); other accessions had no plants rated as resistant. In the second test, three accessions (Dowling, PI 71506, PI 230977) had 100% of plants rated as resistant to population growth of *A. glycines* (≤ 150 aphids per plant), and 50% of G93-9223 plants were rated as resistant. Other soybean accessions had no plants rated as resistant, as numbers of *A. glycines* were much >150 per plant.

Table 2 Proportion of soybean accessions rated as resistant to *Aphis glycines* 2 weeks after initial infestation with ten aphids per plant

Accession	Proportion resistant ^a	
	Test 1	Test 2
91B91	0.00	0.00
PI 71506	0.25	1.00
PI 230977	1.00	1.00
Dowling	– ^b	1.00
G93-9223	0.00	0.50
Ripley	0.00	0.00
Early Sunrise	0.00	–
Manchukota	0.00	–
S19-V2RR	0.00	–
S24-K4RR	0.00	–
Williams 82	–	0.00

^aFrequencies of plants rated as aphid resistant were not equal among accessions in each test ($P < 0.001$, Fisher's Exact Test). Test 1—resistant if < 100 *A. glycines* per plant ($n = 8$); test 2— < 150 *A. glycines* per plant ($n = 8$)

^b Not included in test

Distribution within and among plants

The numbers of *A. glycines* on soybean plants differed by accession, shoot structure, and the accession \times shoot structure and shoot structure \times time interactions (Table 3). Across accessions, *A. glycines* were distributed more on unifoliolate leaves than other shoot structures (stems and trifoliolate leaf), but the difference decreased over time. At 24 h, there were 5.1 ± 2.8 aphids per unifoliolate pair vs 3.1 ± 2.8 aphids on other shoot structures, whereas 48 h after infestation, there were 4.3 ± 3.1 aphids per unifoliolate pair vs 3.2 ± 2.1 aphids on other shoot structures.

Figure 1 illustrates that the numbers of *A. glycines* differed markedly among accessions and between the two categories of shoot structures (unifoliolate leaves vs stems and trifoliolate leaf). The relatively low numbers of *A. glycines* on the shoots of PI 71506, G93-9223, Dowling and PI 230977 showed that plants of these accessions were antixenotic. *A. glycines* generally accepted placement on unifoliolate leaves of accessions 91B91 and Ripley, whereas distribution of aphids on other accessions showed that unifoliolate leaves were roughly equally (PI 71506 and G93-9223) or less acceptable (Dowling and PI 230977) to *A. glycines* compared to the stem and emerging trifoliolate leaf.

Table 3 Sources of variation in numbers of *Aphis glycines* per plant: distribution test

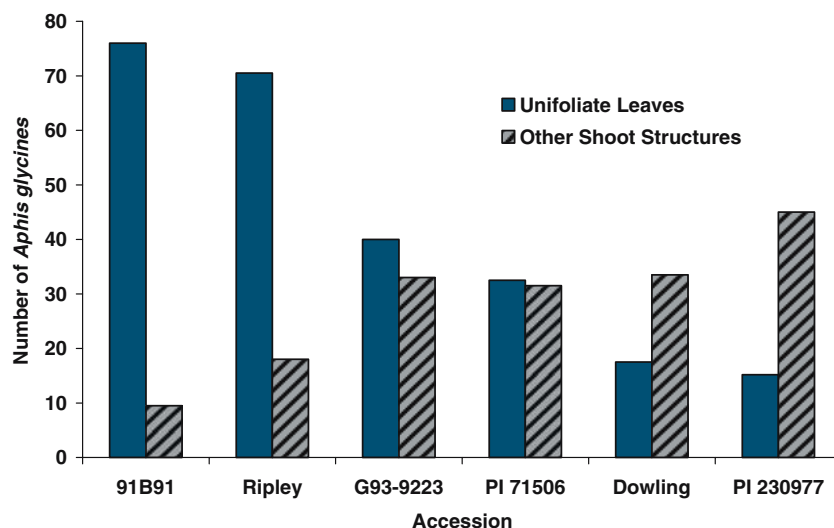
Source	df	χ^2	P value
Accession	5	16.63	0.005
Shoot structure ^a	1	14.70	0.001
Time ^b	1	1.64	0.201
Accession \times shoot structure	5	154.24	<0.001
Accession \times time	5	6.23	0.285
Shoot structure \times time	1	4.71	0.030
Three-way interaction	5	2.41	0.790

Results from analysis categorical log-linear model (adapted from Agresti 1990; PROC CATMOD feature, SAS Institute 2002)

^a Unifoliolate leaves vs stem and emerging trifoliolate leaf

^b At 24 and 48 h after infestation with ten *A. glycines* per unifoliolate leaves

Fig. 1 Number of *Aphis glycines* on unifoliolate leaves vs stems and trifoliolate leaf of various soybean accessions. Bars represent the mean number of aphids counted at 24 and 48 h after initial infestation with ten *A. glycines* per plant ($n = 9$). Sums for each pair of bars per accession may not equal 90 aphids due to abandonment of plants by *A. glycines*



No-choice nymphiposition

In the first test, the number of nymphs deposited over 48 h differed among accessions (Table 3; $F = 11.40$; $df = 5, 24$; $P < 0.001$). *A. glycines* deposited fewer nymphs on Dowling, PI 71506, and PI 230977 than on 91B91 and Ripley. The number of nymphs on G93-9223 did not differ from that on other accessions.

In the second test, the number of nymphs deposited over 24 h differed among accessions (Table 4; $F = 8.38$; $df = 5, 43$; $P < 0.001$). *A. glycines* deposited fewer nymphs on Dowling and PI 230977 than on 91B91, G93-9223, and Ripley. The number of nymphs on PI 71506 did not differ from that on other accessions.

Developmental time and number of progeny

The number of *A. glycines* reaching reproductive maturity differed among accessions (Fisher's

Table 4 Number of nymphs deposited over 48 h by five apterous *Aphis glycines* per plant caged on various soybean accessions

Accession	Mean \pm SE
91B91	13.0 \pm 1.5 a
Dowling	3.8 \pm 1.3 b
PI 71506	8.1 \pm 0.5 b
PI 230977	3.7 \pm 0.6 b
G93-9223	8.2 \pm 1.3 ab
Ripley	13.0 \pm 1.5 a

Exact Test, $P < 0.001$). A lower proportion of *A. glycines* reached reproductive maturity on PI 230977 than on 91B91, G93-9223, and PI 71506 (Table 5); a smaller proportion of aphids matured on Dowling than on PI 71506. The mean number of days to reproductive maturity for *A. glycines* did not differ among accessions ($\chi^2 = 4.06$; $df = 1$; $P = 0.54$). Accessions differed in the number of nymphs that *A. glycines* produced in the first 7 days of reproduction ($F = 15.03$; $df = 5, 43$; $P < 0.001$), with fewer *A. glycines* progeny on Dowling and PI 230977 than on 91B91, Ripley, and PI 71506 (Table 5). The number of nymphs produced on G93-9223 did not differ from that on other accessions.

Discussion

The results of our screening tests are consistent with a high level of resistance to *A. glycines* in soybean accessions Dowling and PI 230977 reported by Hill et al. (2004). We also found that PI 71506 was resistant to *A. glycines*, particularly when the resistance ratings included infestations up to 150 aphids per plant. In contrast, Hill et al. (2004) found that PI 71506 was highly resistant to *A. glycines*. The differences between our results and those of Hill et al. (2004) with regard to PI 71506 are unknown, but may have stemmed from different aphid test populations or perhaps their use of shorter test periods (<14 days). Our

Table 5 Performance of *Aphis glycines* caged on unifoliolate leaves of various soybean accessions

Accession	Nymphs deposited within 24 h of infestation (mean \pm SE) ^a	Proportion of aphids maturing to reproduction ^b	Days to reproduction (mean \pm SE) ^a	Second-generation nymphs produced (mean \pm SE) ^a
91B91	3.2 \pm 0.4 a	0.75 ab	6.3 \pm 0.2 a	19.8 \pm 3.7 a
Dowling	1.0 \pm 0.0 b	0.29 bc	8.0 \pm 1.0 a	2.4 \pm 2.1 b
PI 71506	2.4 \pm 0.4 ab	1.00 a	7.4 \pm 0.4 a	13.7 \pm 1.7 a
PI 230977	1.4 \pm 0.3 b	0.18 c	6.0 \pm 3.0 a	0.5 \pm 0.3 b
G93-9223	4.0 \pm 0.4 a	0.78 ab	6.6 \pm 0.2 a	9.4 \pm 2.1 ab
Ripley	3.7 \pm 0.5 a	0.67 abc	6.8 \pm 0.3 a	13.2 \pm 3.0 a

^a Means \pm SE within a column not followed by the same letter are significantly different. (Nymphs in 24 h: $F = 8.38$; $df = 5, 43$; $P < 0.001$, Tukey's HSD test; days to reproduction: $\chi^2 = 4.06$; $df = 5$; $P = 0.54$; second-generation nymphs: $F = 15.03$; $df = 5, 40$; $P < 0.001$, Tukey's HSD test.)

^b Proportions not followed by the same letter are significantly different ($P < 0.05$, Tukey-type multiple comparison test; adapted from Zar 1998)

screening also showed that 50% of accession G93-9223 plants were *A. glycines*-resistant when rated using an expanded resistance scale. PI 71506 and G93-9223 had some test plants that were characterized as resistant and others that were not. The lack of uniformity in resistance ratings may have arisen for two reasons. First, there is often rather large, general variability inherent in plant introductions such as PI 71506 and that variability is often preserved while such accessions are maintained in governmental and other institutional seed storage and preservation facilities (Smith 2005). Second, to our knowledge, neither PI 71506 nor G93-9223 had previously been selected for resistance to *A. glycines*, and thus susceptible plants of each accession could be expected.

The screening tests identified lines resistant to population growth of *A. glycines*, but further tests were conducted to determine whether the resistance was due to antixenosis, antibiosis, or both modalities. Antixenosis may be measured by choice or no-choice tests (Harris 1980). Choice tests determine the relative suitability of hosts as sites for feeding, shelter, progeny deposition, etc., whereas no-choice tests determine the inherent suitability of a resistant candidate as a host (Harris 1980). The no-choice nymphposition tests in our study revealed Dowling, PI 230977, and PI 71506 are less suitable hosts for nymphposition by *A. glycines*. In some cases, a decreased rate of nymphposition may be classified as antibiosis, largely because the host plant on which the mother aphid developed may have adversely

affected its fecundity (Adams and van Emden 1972; Smith 2005). However, the *A. glycines* used in our nymphposition tests had been reared on a suitable host (Asgrow 0801), and thus diminished nymphposition on particular accessions was a behavior indicating unsuitability (i.e., antixenosis) of the plant host.

Antixenosis was also evident from the fewer numbers of *A. glycines* on Dowling, PI 230977, PI 71506, and G93-5223 in the distribution test. The *A. glycines* in our tests may have been differentially distributed between unifoliolate leaves and other shoot tissue, in part, because of a preference for younger shoot tissue, but the overall decrease in aphid numbers on Dowling, PI 230977, PI 71506, and G93-5223 suggests that antixenosis was a factor in these accessions. Moreover, the expression of antixenosis in the shoot structures of Dowling and PI 230977 differed from that in PI 71506 and G93-5223. The distribution of *A. glycines* within plants of PI 71506 and G93-5223 suggested that the expression of antixenosis was comparable between unifoliolate leaves and other shoot structures of these two accessions. This contrasted with results for Dowling and PI 230977 in which antixenosis was stronger in the unifoliolate leaves than in other shoot structures based on the differences in aphid numbers. Hill et al. (2004) also demonstrated antixenosis to *A. glycines* in Dowling and PI 71506. Li et al. (2004) found that *A. glycines* departed from the trifoliolate leaves of Dowling 8–24 h after being placed on them, but comparisons between unifoliolate vs

trifoliolate leaves were not made in their study. In tests with the corn earworm, *Helicoverpa zea* (Boddie), Nault et al. (1992) found that third instars preferred older leaves of both resistant and susceptible soybean lines.

Antibiosis to *A. glycines* was apparent in Dowling and PI 230977 from the decreased number of progeny produced by adults that had matured on those plants, and in PI 230977 from the low number of aphids surviving to reproductive maturity. Our results agree with Hill et al. (2004) and Li et al. (2004), who found strong antibiosis in Dowling due to diminished rates of population growth, but they found high mortality of *A. glycines* on caged plants. Hill et al. (2004) found evidence for antixenosis, but not antibiosis, to *A. glycines* in PI 71506. Strong antibiosis, such as present in Dowling and PI 230977, may prevent aphids from reaching economic damage levels and is particularly useful to limit the secondary spread of plant viruses by aphids within crop fields (Gibson and Plumb 1977; Kennedy 1976).

Accessions G93-9223 and Ripley have pedigrees that include lines resistant to *A. glycines*. However, resistance to *A. glycines* was not apparent in our tests with Ripley, and resistance in G93-9223 was modest compared to its ancestor, PI 230977. Nonetheless, modest levels of resistance in G93-9223 may still effectively limit aphid infestations, particularly if complemented with other aphid management approaches such as biological control. Given this, and that G93-9223 is an improved breeding line, it may prove useful in programs to breed for *A. glycines* resistance.

Our study was restricted to evaluating antixenosis and antibiosis against *A. glycines*. Tolerance is an additional resistance modality that allows growth or yield of host plants when challenged with insect infestations that would significantly limit susceptible accessions (Panda and Khush 1995; Smith 2005). However, antixenosis and antibiosis are such dominant modalities in Dowling and PI 230977 that maintaining sufficient infestation levels of *A. glycines* to test for tolerance is impractical with these accessions. However, the lack of antibiosis resistance in PI 71506 and G93-9223 may allow sufficient numbers of *A.*

glycines to be caged on plants for tolerance testing. We suggest that future studies test for tolerance in PI 71506 and G93-9223.

There are now several sources of soybeans that have been identified with resistance to *A. glycines* (Hill et al. 2004; Li et al. 2004; Mensah et al. 2005; our data). The resistance to *A. glycines* is controlled by a single dominant gene (*Rag1*) in Dowling and Jackson (Hill et al. 2006a, b). The other *A. glycines*-resistant sources should be compared to understand the genetics and molecular biology of resistance in order to determine whether common genes for aphid resistance occur among accessions (Hill et al. 2004). This information is particularly important to develop effective strategies for the sustainable use of aphid-resistant lines because crop resistance to aphids from single genes has often been overcome by virulent biotypes within only a few years (Panda and Khush 1995; Smith 2005).

Nonetheless, the resistance found in PI 230977, Dowling, Jackson, and various other soybean accessions offers great potential for management of *A. glycines*. For instance, protection from *A. glycines* by the resistance manifested in Dowling was comparable to protection afforded by insecticide treatment of soybean plants in a field-cage experiment (Hill et al. 2004). PI 230977 showed a comparable level of resistance to Dowling (our data; Hill et al. 2004) and other highly resistant accessions (Hill et al. 2004). Thus, the deployment and proper management of cultivars with resistance to *A. glycines* has the potential to greatly reduce the frequency of aphicide application and the ensuing economic and environmental costs in soybean production systems.

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