

Discovery of Soybean Aphid Biotypes

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ABSTRACT

The soybean aphid [*Aphis glycines* Matsumura (Hemiptera: Aphididae)] is an invasive insect pest of soybean [*Glycine max* (L.) Merr.] that was first reported in North America in 2000. There are currently no reports of soybean aphid biotype diversity and this information is needed before aphid resistance genes are deployed. The objective of this research was to test for aphid biotype variation. The response of two *A. glycines* isolates, one collected in Ohio and the other in Illinois, were compared by infesting eight soybean genotypes in nonchoice tests. The same genotypes also were tested with the Ohio isolate using a choice test. In the nonchoice test, there was a significant ($P < 0.0001$) effect of aphid isolate, genotype, and a significant aphid isolate by soybean genotype interaction for the number of aphids per plant 10 and 15 d after infestation. The responses of the eight genotypes to the Ohio isolate in the choice test were similar to their responses in nonchoice tests. PI 200538 and PI 567597C were resistant to both the Ohio and Illinois isolates and will be useful sources of resistance to both isolates. These tests confirm that there are at least two distinct biotypes of *A. glycines* in North America.

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Abbreviations: MG, maturity group; PDI, plant damage index; QTL, quantitative trait loci.

THE SOYBEAN APHID, *Aphis glycines* Matsumura, is an invasive insect pest that is new to North America. The aphid is native to eastern Asia including China, Eastern Russia, Japan, Korea, Thailand, the Philippines, and Vietnam and is new to Australia (Krupke et al., 2005). The soybean aphid was not reported in North America before July 2000 (Hartman et al., 2001) and has rapidly spread throughout the midwestern United States and southern Canada since its first report (Venette and Ragsdale, 2004).

High soybean aphid populations reduce soybean [*Glycine max* (L.) Merr.] yield directly when their feeding causes stunting, leaf distortion, and reduced pod set (Sun et al., 1990; Hill et al., 2004a). Yield losses of greater than 50% were attributed to the aphid in fields in Minnesota during 2001 (Ostlie, 2002) and yield losses of 58% were reported in China (Wang et al., 1996). A severe soybean aphid outbreak occurred in 2003 which damaged 1.6 million ha of soybean in Minnesota and 0.5 million ha in Illinois (Associated Press, 2003; Steffey, 2004). Losses were estimated at \$80 million in Minnesota and \$45 million in Illinois. Nearly 3 million ha of soybean in the United States were sprayed to control the soybean aphid during that year (Landis et al., 2003) includ-

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ing \$9 to 12 million spent on insecticide applications in Illinois (Steffey, 2004).

An additional threat posed by the soybean aphid is its ability to transmit plant viruses to soybean such as *Alfalfa mosaic virus*, *Soybean dwarf virus*, and *Soybean mosaic virus* (Sama et al., 1974; Iwaki et al., 1980; Hartman et al., 2001). Honeydew excreted by soybean aphids onto leaves leads to the development of sooty mold, which results in further yield losses (Krupke et al., 2005).

Plant resistance can provide an effective, economical, and environmentally sound method of insect control. Because the soybean aphid has only recently been identified as an insect pest in the United States, relatively little research on the genetic basis of resistance to this pest has been conducted. One of the prerequisites for developing soybean aphid resistant cultivars is the identification and characterization of sources of resistance. There are three kinds of plant insect resistance that have been described (Painter, 1951; Kogan and Ortman, 1978), and two of them, antibiosis and antixenosis, have been found to occur in soybean responses to soybean aphid (Hill et al., 2004a). Antibiosis is the ability of a plant to reduce the survival, growth, or reproduction of insects that feed on it and can be measured by comparing the survival, size, fecundity, or rate of development of insects that have fed on different test plants. Antibiosis is often caused by the production of toxic chemicals or the secondary metabolites by the plant while antixenosis or nonpreference is the ability of a plant to repel insects, causing a reduction in oviposition or feeding. The third kind of resistance described by Painter (1951) is tolerance. This may not actually be a form of resistance because it allows plants to be colonized by insects; however, tolerant genotypes have the ability to withstand equal levels of colonization that occur on susceptible genotypes without significant loss in yield.

Hill et al. (2004a) reported resistance to soybean aphid in nine soybean germplasm accessions. Among the resistant genotypes, Dowling and Jackson were characterized as having resistance that is primarily antibiosis in action based on choice and nonchoice greenhouse experiments (Li et al., 2004). Hill et al. (2006a, 2006b) studied the genetic basis of resistance in these two sources and found that resistance was controlled by a single dominant gene named *Rag1* in Dowling and *Rag* in Jackson. These genes were recently mapped to the same position on soybean linkage group M (Li et al., 2007), which suggests that the resistance genes in both cultivars may be allelic.

Mensah et al. (2005) identified four sources of aphid resistance by screening 2147 soybean accessions. Two sources were shown to carry antibiosis resistance and the remaining showed antixenosis resistance. Preliminary reports from genetic studies revealed that resistance in PI 567541B is controlled by quantitative trait loci (QTL) and resistance in PI 567598B is controlled by two recessive genes (Chen et

al., 2006; Mensah et al., 2006). Mian et al. (2008) identified three maturity group (MG) IV accessions from China that are highly resistant to a soybean aphid isolate collected in Ohio and two of these plant introductions also are resistant to a second aphid isolate from Illinois.

The broad use of cultivars that have a single aphid resistance gene may encourage the selection and rapid spread of aphid biotypes adapted to this resistance. For example, biotypes for both Russian wheat aphid [*Diuraphis noxia* (Mordvilko)] and greenbug [*Schizaphis graminum* (Rondani)] were found capable of overcoming deployed resistance genes (Burd and Porter, 2006; Haley et al., 2004).

There are no published reports of the occurrence of *A. glycines* biotypes. However, there have been anecdotal reports of the occurrence of aphid populations in the northeastern United States and eastern Canada that are able to colonize breeding lines with *Rag1*. The objective of this study was to determine if there is *A. glycines* biotype variation in North America.

MATERIALS AND METHODS

Aphid Culture

The Illinois aphid isolate was collected in Urbana, IL, in 2000 (Hill et al., 2004a). The Ohio isolate was established at the Ohio Agricultural Research and Development Center, Wooster, OH, during the summer of 2005 by collecting aphids from nearby soybean fields. Both isolates were maintained on a continuous supply of plants of the aphid susceptible cultivar Williams 82 in growth chambers as described previously (Hill et al., 2004a, 2004b). The Ohio isolate was selected because it had been observed to defeat soybean lines with *Rag1* in field cage experiments in Ohio (data not shown). A number of aphid-infested soybean seedlings from the growth chamber were shipped to Dr. G.L. Hartman during the fall of 2006 (APHIS permit no. P526-061106-004). The Ohio and Illinois aphid isolates have been maintained in plant growth chambers located in different buildings at the University of Illinois to avoid mixing.

Aphid Age Synchronization

The age of the aphids used for infesting plants in the nonchoice tests was synchronized before inoculation by placing several viviparous apterae on detached leaves of Williams 82 in petri dishes containing moist filter paper for 24 h. All of the viviparous apterae were removed after 24 h leaving only 1-d-old nymphs. For easier handling and improved survivability of soybean aphids, third instar nymphs were collected from the dishes to infest plants.

Plant Material and Culture

Eight soybean genotypes with known reactions to the Illinois isolate were used in the tests (Table 1). These included Dowling, LD05-16611, PI 200538, Jackson, PI 567597C, and PI 567541B, which were previously shown to be resistant to the Illinois isolate. Hill et al. (2004a) identified Dowling, Jackson, and PI 200538 as resistant using the Illinois isolate. Mensah et

Table 1. Soybean genotypes tested in the choice and nonchoice tests and background information for these genotypes.

Soybean genotype	PI no.	Collection region or pedigree	Previously known reaction to soybean aphid and resistance gene if known	Reference
Dowling	548663	Semmes × PI 200492	Resistant/ <i>Rag1</i>	Hill et al. (2004a, 2006a)
Dwight	597386	Jack × A86-303014	Susceptible	
Jackson	548657	Volstate(2) × Palmetto	Resistant/ <i>Rag</i>	Hill et al. (2004a, 2006b)
Sugao Zairai	200538	Japan	Resistant	Hill et al. (2004a)
Williams 82	518671	Williams(7) × Kingwa	Susceptible	Hill et al. (2004a)
Gun li huang	567541 B	Shandong, China	Resistant	Mensah et al. (2005)
Xiao huang dou	567597C	Shandong, China	Resistant	Mensah et al. (2005)
LD05-16611	None available	Dwight (3) × (Loda × Dowling)	Resistant/ <i>Rag1</i>	

al. (2005) found PI 567597C and PI 567541B were resistant to aphids collected in Michigan and were later tested with the Illinois isolate. All six resistant genotypes with the exception of PI 567597C and LD05-16611 were found to have antibiosis type resistance in nonchoice tests. PI 567597C was reported to have antixenosis resistance (Mensah et al., 2005) and LD05-16611 carries *Rag1* and is therefore assumed to have antibiosis resistance, but had not been previously evaluated in a nonchoice test. LD05-16611 was developed by the University of Illinois through backcrossing the *Rag1* resistance gene from Dowling into the MG II cultivar Dwight. The pedigree of LD05-16611 is Dwight (3) × (Loda × Dowling). The cultivars Williams 82 and Dwight were included as susceptible controls. Seed of resistant soybean genotypes Jackson, PI 567541B, PI 567597C, and PI 200538 was obtained from the USDA Soybean Germplasm Collection in Urbana, IL.

Nonchoice Tests

Two nonchoice tests with the same treatments but separated by time were conducted. Each test was a factorial experiment arranged in a randomized complete block design with three replications. The two factors in each experiment were the eight soybean genotypes and the two aphid isolates. The experimental unit was an individual plant grown in an 11-cm-diameter pot. The tests were conducted in a growth chamber with the temperature set at 22°C and 14 h daily illumination at 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation irradiation. At the V1 growth stage (Fehr et al., 1971), three third instar nymphs were placed on the upper side of a unifoliolate leaf of each plant with a moist camel's hair brush. After infestation, the plants were isolated with cages to restrict aphid movement among plants. The cages were 100- by 300-mm clear plastic cylinders with 80- by 180-mm side windows and tops covered with a plastic mesh with 100- μm opening (Hill et al., 2004a). Ten and 15 days after nymphs were placed on plants, the number of aphids on each plant was counted.

Choice Test

A choice test was conducted in a growth chamber with environmental conditions as described above for the nonchoice test. In the choice test, the eight soybean genotypes were grown in 60 by 60 by 60 mm plastic multi-pot inserts (Hummert Intl., Earth City, MO) contained inside plastic trays without holes (Hummert Intl., no. F1020) (Hill et al., 2004a). The plants were arranged in a randomized complete block design with six rep-

licates. The experimental unit was an individual plant in a pot. To avoid disrupting the aphids, plants were bottom watered by flooding the trays containing the plants as needed (Hill et al., 2004a). Leaves of Williams 82 that were each infested with 50 to 200 aphids of the Ohio isolate at all growth stages were placed on top of V_E-stage seedlings (Fehr et al., 1971). Resistance was evaluated 10 and 15 d after infestation by counting the total number of aphids on each plant and by scoring plants with a plant damage index (PDI). The PDI ranged between 1, for no stunting and leaf distortion, and 5, for severe plant damage. A PDI of 1 or 2 was classified as resistant, whereas a PDI of 3, 4, or 5 was classified as susceptible.

Statistical Analysis

Analysis of variance (ANOVA) for choice and nonchoice tests was conducted by using PROC GLM of SAS (SAS Institute, 2000). Means were separated using the least significant difference (LSD) at $P = 0.05$ if their effects were found to be significant in the ANOVA. The results from the nonchoice test were transformed with a logarithm (\log_{10}) transformation to normalize the data.

RESULTS

Nonchoice Tests

There was a significant ($P = 0.05$) effect of test, but no interaction term including the test effect was significant, therefore, only results across the two tests are presented. With the combined data, there was a significant ($P < 0.0001$) effect of soybean genotype, aphid isolate, and a significant soybean genotype by aphid isolate interaction for the number of aphids per plant 10 and 15 d after infestation. All genotypes previously identified as resistant (Hill et al., 2004a; Mensah et al., 2005) showed strong antibiosis to the Illinois isolate (Table 2) at both 10 and 15 d after infestation. In contrast, there were significant differences in the numbers of Ohio aphids on the genotypes previously found to be resistant to the Illinois isolate at both 10 and 15 d after infestation. Both PI 200538 and PI 567597C had low numbers; PI 567541B had moderate numbers; and Dowling, Jackson, LD05-16611, Dwight, and Williams 82 had high numbers of Ohio aphids. These results indicate that the Ohio isolate can overcome the resistance gene or genes *Rag1* and *Rag*. There were high

Table 2. The average number of aphids per plant 10 and 15 d after infestation by the Ohio and Illinois aphid isolates across the two nonchoice tests.

Soybean genotype	10 d after infestation		15 d after infestation	
	Illinois isolate	Ohio isolate	Illinois isolate	Ohio isolate
	No. of aphids plant ⁻¹			
Dowling	7de [†]	168ab	9cd	604a
Dwight	156ab	184a	420a	355a
Jackson	5e	158ab	8cd	353a
PI 200538	5e	8de	6cd	6cd
Williams 82	210a	204a	668a	510a
PI 567541B	13cd	80b	10cd	93b
PI 567597C	21c	9de	11cd	4d
LD05-16611	10cde	198a	20c	605a

[†]Means followed by the same letters in the 10 d after infestation columns or the 15 d after infestation columns are not significantly different by the least significant different test ($P = 0.05$).

aphid numbers of both aphid isolates on the susceptible genotypes Dwight and Williams 82.

Choice Tests

Plants were infested only with the Ohio isolate in the choice test to determine if the pattern of resistance response was similar between the choice and nonchoice tests for this isolate. With the choice test, there were significant differences in aphid numbers among the soybean genotypes 10 d after infestation and the resistance responses were generally similar to the results for the Ohio isolate in the nonchoice test (Table 3). PI 200538, PI 567597C, and PI 567541B had low numbers, Jackson had moderate numbers, and the remaining genotypes had high numbers of Ohio aphids. Plant damage due to aphid infestation was not observed 10 d after infestation and therefore PDI ratings were not taken at this time.

The aphid counts 15 d after infestation showed lower aphid numbers and less clear differentiation among genotypes than observed 10 d after infestation. Aphid numbers

Table 3. The average number of aphids per plant 10 d after infestation and the plant damage index (PDI) 15 d after infestation with the Ohio isolate in the choice test.

Soybean genotype	No. of aphids plant ⁻¹ 10 d after infestation	Average PDI 15 d after infestation [†]
Dowling	157a [†]	4.2a
Dwight	180a	4.0a
Jackson	110b	4.3a
PI 200538	24c	1.2d
Williams 82	166a	4.5a
PI 567541B	38c	2.2c
PI 567597C	32c	2.2c
LD05-16611	172a	3.0b

[†]The plant damage index (PDI) ranges from 1 (no stunting and leaf distortion) to 5 (severe plant damage).

[†]Means followed by the same letters in a column are not significantly different by the least significant different test ($P = 0.05$).

may have been reduced by the significant plant damage that occurred on susceptible genotypes that reduced the capacity of plants to support aphid colonies. Therefore, only the numbers counted 10 d after infestation are reported. The greater plant damage observed in this test 15 d after infestation compared to the nonchoice test is at least partially the result of the early V_E inoculation of plants in the choice test compared to plant inoculations at V_1 in the nonchoice tests. This early infestation of aphids allowed for high populations to develop on seedlings of susceptible genotypes inhibiting growth and thus limiting the number of aphids the plants could support. PI 200538, PI 567597C, and PI 567541B had PDI of 1 or 2, both of which are classified as resistant reactions, and continued their growth into V_1 or V_2 growth stages (Table 3). Dowling, Dwight, Jackson, Williams 82 and LD05-16611 had a PDI of 3 to 5 and their growth was stopped at V_C growth stage.

DISCUSSION

An understanding of the genetic diversity present in soybean aphid populations is critically important to soybean breeders developing cultivars with resistance to this pest. Researchers need to know whether aphid biotypes are present that can defeat resistance genes that are deployed or potentially will be deployed in the future. There were anecdotal reports from the northeastern United States and eastern Canada of aphid populations defeating the resistance gene *Rag1*, and this study demonstrates that the Ohio isolate can colonize plants carrying this gene. Our results clearly indicate that the Illinois and Ohio isolates are different biotypes based on their unique virulence patterns on soybean genotypes. To our knowledge, this is the first published report of the occurrence of distinct biotypes of *A. glycines*.

We selected the Ohio isolate for this test because there was evidence that it could overcome the *Rag1* resistance gene. F_1 plants carrying the *Rag1* gene were all susceptible to the Ohio aphid isolate in both greenhouse and field-cage evaluations in the spring and summer of 2006 in Wooster, OH. Later during fall of 2006, both Dowling and Jackson were observed to be susceptible to this Ohio isolate under greenhouse conditions (Mian et al., 2008).

Multiple biotypes occur in other aphid species such as Russian wheat aphid and greenbug. Burd and Porter (2006) recently collected greenbug populations in the United States and found many unique biotypes. Biotype variation for Russian wheat aphid has been known to exist worldwide since the early 1990s (Puterka et al., 1992). However, no biotype diversity was observed in the United States from when the aphid was first discovered in the country in 1986 until 2003, when a biotype was identified that could overcome *Dn4*, the major resistance gene used to protect wheat (*Triticum aestivum* L.) from this aphid

(Haley et al., 2004). There is a need to systematically collect and test soybean aphid isolates in North America and other parts of the world to improve our understanding of biotype variation in soybean aphid.

All current North American cultivars tested for aphid resistance by Hill et al. (2004a) were found to be susceptible. In addition, no cultivars carrying *Rag1* were released in the northern United States or Canada and very limited field testing of experimental lines carrying this gene has occurred. Therefore, the emergence of a biotype that overcomes *Rag1* is not likely the result of selection of aphids on plants carrying this gene in North America. Although the *Rag1* resistance gene is not effective against the Ohio isolate, soybean researchers in other Midwest states such as Illinois, Iowa, Minnesota, South Dakota, and Wisconsin have found *Rag1* to be effective against soybean aphids present in their states. Research is needed to determine the distribution and frequency of biotypes that can overcome *Rag1* and other sources of aphid resistance.

Our results suggest that *Rag1* from Dowling is different from the resistance gene *Rag* found in Jackson. Both resistance genes map to the same chromosomal location (Li et al., 2007), suggesting that they may reside at the same locus. However, in the choice test with the Ohio isolate, the number of aphids on Jackson 10 d after infestation was significantly lower than on Dowling. This suggests that Jackson may have a different allele at the same resistance locus as Dowling, a resistance allele at a different locus in the same region as *Rag1*, or the intermediate resistance observed in Jackson is the result of background genes modifying the expression of *Rag1* in Jackson. Further experiments are needed to determine which of these possibilities is the cause of the different resistant reaction observed for these two genotypes.

PI 200538 and PI 567597C are resistant and PI 567541C is moderately resistant to both aphid biotypes, indicating that they possess resistance alleles different from *Rag1*. Deploying resistance from these sources should be beneficial and the development of cultivars with resistance from PI 200538 is underway.

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