

A Single Dominant Gene for Resistance to the Soybean Aphid in the Soybean Cultivar Dowling

Curtis B. Hill,* Yan Li, and Glen L. Hartman

ABSTRACT

The soybean aphid (*Aphis glycines* Matsumura), a new pest of soybean [*Glycine max* (L.) Merr.], rapidly spread throughout North America after its arrival in 2000 and caused millions of dollars in economic losses. At present, the application of insecticides is the only means to control the soybean aphid. However, genetic resistance to the aphid was recently discovered in soybean germplasm and the soybean cultivar Dowling was identified as having strong antibiosis-type aphid resistance. The objective of this study was to determine the inheritance of resistance to the soybean aphid in Dowling. Resistance in F₁, F₂, and F₂-derived F₃ (F_{2,3}) families from crosses between Dowling and the two susceptible soybean cultivars Loda and Williams 82 was analyzed. All F₁ plants were resistant to the aphid. Heterogeneity of segregation of F₂ plants in 14 Dowling × Loda F₂ families was nonsignificant ($P = 0.16$), and pooled F₂ data, with 132 resistant to 45 susceptible plants, fit a 3:1 ratio ($P = 0.90$). F₂ plants from Dowling × Williams 82 segregated 135 resistant to 44 susceptible, also fitting a 3:1 ratio ($P = 0.89$). Segregation among the F_{2,3} families fit a 1:2:1 monogenic inheritance pattern. These results indicated that a single dominant gene named *Rag1* controlled resistance in Dowling. The monogenic dominant nature of resistance will enable breeders to rapidly convert existing susceptible cultivars to resistant cultivars using backcrossing procedures.

SINCE ITS ARRIVAL FROM ASIA in 2000 (Hartman et al., 2001), the soybean aphid has spread throughout soybean production areas in North America (Ragsdale et al., 2004). High aphid populations reduce soybean production directly by causing severe plant damage during feeding, including leaf distortion, stunting, and desiccation. Soybean plants are indirectly affected by the growth of black sooty mold fungus on aphid honeydew that inhibits plant photosynthesis and through the vectoring of serious soybean viruses such as *Soybean mosaic virus* (Hartman et al., 2001). In 2003, extensive economic losses caused by the soybean aphid occurred in soybean in several midwestern states. An estimated 1.6 million ha damaged was reported in Minnesota resulting in a loss of US\$80 million (Associated Press, 2003). In Illinois, about 0.5 million ha were damaged with an estimated loss of US\$45 million (Steffey, 2004).

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Presently, the only means that soybean growers have to control the soybean aphid is with the application of registered insecticides. During the 2003 soybean aphid outbreak, nearly 3 million hectares of soybeans in the USA were sprayed to control the soybean aphid (Landis et al., 2003). From \$9 to 12 million was spent on insecticide applications in Illinois alone in 2003 (Steffey, 2004).

Plant insect resistance is an important component of an integrated pest management program that utilizes several types of control methods to control insects, including insecticide application and cultural management practices (Auclair, 1989; Harrewijn and Minks, 1989). Plant insect resistance is also the most cost effective and environmentally safe way to control insects such as the soybean aphid (Luginbill, 1969).

Plant resistance to the soybean aphid was recently discovered in soybean germplasm (Hill et al., 2004). Resistance in the cultivar Dowling had strong antibiosis that limited aphid colonization on plants in non-choice tests. In field experiments, Dowling performed as well without treatment with the systemic insecticide imidacloprid [(EZ)-1-(6-chloro-3-pyridylmethyl)-N-nitroimidazolidin-2-ylideneamine] (Marathon, Olympic Horticultural Products, Mainland, PA) as it did with the treatment, and effectively controlled aphid population development during all soybean growth stages. Detailed analysis of the effects of antibiosis on aphid biology indicated that the resistance in Dowling significantly reduced aphid survival, longevity, fecundity, and development (Li et al., 2004).

Resistance to insects is governed by genetic mechanisms like other plant traits (Auclair, 1989). Knowledge of the inheritance of insect resistance, as with any other economic plant trait, facilitates the design of appropriate breeding procedures to develop resistant cultivars and is useful for the identification of biotypes of insects that may already exist or develop over time (Smith, 1989). Qualitative, or simply inherited, traits require different breeding methods than quantitative traits controlled by many genes.

The objective of this study was to determine the inheritance of the aphid resistance in Dowling soybean.

MATERIALS AND METHODS

Crosses were made between the soybean aphid resistant cultivar Dowling and two susceptible soybean cultivars, Loda and Williams 82, inside a plant growth chamber (Conviron, model no. CMP4030, Winnipeg, MB, Canada) at 27°C, 70% relative humidity, under a 12-h photoperiod provided by a mixture of incandescent and fluorescent lighting giving 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR irradiation. All crosses were made in one direction; pollen from Loda and Williams 82 flowers was transferred onto stigmata of Dowling flowers. Seed produced from individual crosses was harvested and planted separately for F₂ seed production in a greenhouse maintained at 28°C

with supplemental lighting provided by a mixture of 1000-W high intensity discharge and high pressure sodium vapor lamps set to give a 14-h photoperiod. F₁ hybrid plants were distinguished from selfs by the expression of morphological markers for flower and pubescence color that were polymorphic among the parents. Loda had purple flowers, whereas Dowling and Williams 82 had white flowers. Purple flower color is dominant over white (Takahashi and Fukuyama, 1919). Williams 82 had tawny and Loda and Dowling had gray pubescence. Tawny pubescence is dominant over gray (Piper and Morse, 1910). Seed from individual F₁ hybrid plants was harvested separately.

The parents, F₁, and F₂ plants were tested for soybean aphid resistance in choice tests in the greenhouse. Separate tests for each cross, Dowling × Loda and Dowling × Williams 82, were conducted. Both tests were planted in soilless media (Sunshine Mix, LC1, Sun Gro Horticulture Inc., Bellevue, WA) in 48-pot plastic inserts, with 12 rows of four pots (Hummert International, Earth City, MO, no. 1204) contained in flats without drainage holes (Hummert International, Earth City, MO, no. F1020). Depending on seed availability, 8 to 20 seeds of 14 Dowling × Loda F₂ families (seed from different F₁ plants) and 200 seeds from a single Dowling × Williams 82 F₂ family were planted along with three Dowling × Williams 82, 22 Dowling × Loda F₁ seeds, 20 Williams 82, 32 Dowling, and 32 Loda seeds. Genotypes were planted into four-pot rows that were randomized and interspersed within each test. In one test, 48 rows of Dowling × Loda F₂ plants, six rows of Dowling × Loda F₁ hybrid plants, eight rows of Dowling, and eight rows of Loda plants were planted, and in another test, 50 rows of Dowling × Williams 82 F₂ plants, one row (three seeds) of Dowling × Williams 82 F₁ hybrid plants, five rows of Dowling, and five rows of Williams 82 were planted. The planting rate was one seed per pot.

Plant culture and aphid infestation with a soybean aphid clone collected in Illinois were conducted using previously described methods (Hill et al., 2004). The level of aphid colonization on each individual plant was estimated 3 wk after aphid infestation by visually examining aphid density, aphid mortality, and plant damage on leaves and stems. Dense aphid colonies typically develop on the upper part of the stem, but can occur on the undersides of the leaves as well.

Levels of aphid colonization on resistant Dowling and susceptible Loda and Williams 82 are distinctly different (Hill et al., 2004; Li et al., 2004). Dense, established colonies of aphids develop on Loda and Williams 82, often accompanied with visible plant damage, such as leaf distortion and stunting. Both cultivars are equally susceptible, with numbers of aphids not significantly different in choice and non-choice tests. Dowling expresses strong antibiosis toward soybean aphids that prevents aphid colonization (Li et al., 2004).

It is rare to find plants without aphids in choice tests because the aphids are free to roam to find suitable plant hosts. Aphids that appear to be transient, possibly probing for feeding sites, are often observed on resistant plants in choice tests, along with dead aphids. Sometimes several viviparous aptera, surrounded by a few nymphs, may be observed on resistant plants without the development of established colonies. Based on these observations, the following rating scale was developed and used to estimate aphid colonization: 0 = no aphids present, 1 = few solitary live or dead aphids (dead aphid bodies) present, 2 = several transient aphids present with some viviparous aptera surrounded by a few nymphs, 3 = dense colonies, and 4 = dense colonies accompanied by plant damage. Dowling plants had ratings of 0, 1, or 2 with a rating of 1 most frequent and 0 and 2 rare. Loda and Williams 82 plants typically had ratings of 3 or 4. Progeny from crosses between Dowling and the susceptible

parents were considered to be resistant with ratings of 0 to 2 and susceptible with ratings of 3 or 4.

F₂ plants were transplanted into soilless potting medium (Sunshine Mix, LC1, Sun Gro Horticulture Inc., Bellevue, WA), in 12.5-cm diameter plastic azalea pots (Hummert Intl., Earth City, MO), and placed in a greenhouse maintained at 28°C with supplemental lighting provided by a mixture of 1000-W high intensity discharge and high pressure sodium vapor lamps set to give a 14-h photoperiod, to produce F_{2,3} seed (F₂-derived F₃ lines) for progeny testing. A total of 12 seeds from F₂ plants that produced at least 12 seeds was planted with the parents and tested for aphid resistance in randomized four-pot rows as described above.

χ^2 Tests were performed to test the goodness of fit of observed segregations among F₂ plants and among F_{2,3} families with different genetic ratios. Homogeneity of segregation among the Dowling × Loda F₂ families was analyzed. Segregation among F_{2,3} families with a minimum of 11 plants was analyzed after classifying each family as homozygous resistant, if all plants were resistant (rating 0 to 2), homozygous susceptible, if all plants were susceptible (rating 3 to 4), and heterozygous, if both resistant and susceptible plants were identified. *P* values for goodness of fit were calculated with the aid of JMP version 5.1 (SAS Institute, 2004).

RESULTS

Reactions of F₂ and F_{2,3} plants to aphid infestation appeared to be qualitative in expression. Only the parental phenotypes were observed in the segregating populations. The overall frequency distribution of aphid colonization ratings in both Dowling × Loda and Dowling × Williams 82 F₂ populations was non-normal and skewed toward rating 1 (data not shown).

Aphid colonization ratings for Dowling plants were 0, 1, or 2 (Tables 1 and 2). Ratings for Loda and Williams

Table 1. Observed and expected aphid colonization ratings of soybean Dowling × Loda F₂ plants and parents 21 d after infestation by the soybean aphid.

Genotype	Number of plants	Observed†		Expected (3:1)		χ^2	<i>P</i>	
		R	S	R	S			
F ₂ family	4021	19	14	5	14.25	4.75	0.02	0.89
	4281	14	11	3	10.5	3.5	0.09	0.76
	4301	16	13	3	12	4	0.33	0.56
	4302	11	11	0	8.25	2.75	3.67	0.06
	4303	11	9	2	8.25	2.75	0.27	0.60
	4304	12	8	4	9	3	0.44	0.50
	4306	15	8	7	11.25	3.75	3.76	0.05
	4307	8	5	3	6	2	0.67	0.41
	4308	6	2	4	4.5	1.5	5.56	0.02
	4309	13	9	4	9.75	3.25	0.23	0.63
	4310	10	8	2	7.5	2.5	0.13	0.72
	4343	8	8	0	6	2	2.67	0.10
	4344	15	11	4	11.25	3.75	0.02	0.88
4531	19	15	4	14.25	4.75	0.16	0.69	
Total Pooled		177	132	45	132.75	44.25	0.02	0.90
Heterogeneity							18.01	0.16
Dowling	32	32	0					
Loda	32	1‡	31					
Dowling × Loda (F₁)	22	22	0					

† R (resistant) = 0, 1, 2 aphid colonization rating and S (susceptible) = 3, 4 rating, where 0 = no aphids present, 1 = few solitary live or dead aphids present, 2 = several transient aphids present with some viviparous aptera surrounded by a few nymphs, 3 = dense colonies, and 4 = dense colonies with plant damage, including leaf distortion and stunting.

‡ One Loda plant had an aphid colonization rating of 2.

Table 2. Observed and expected aphid colonization ratings of soybean Dowling × Williams 82 F₂ plants and parents 21 d after infestation by the soybean aphid.

Genotype	Number of plants	Observed†		Expected (3:1)		χ^2	P
		R	S	R	S		
4041 (F ₂ family)	179	135	44	134.25	44.75	0.00	0.89
Dowling	19	19	0				
Williams 82	20	0	20				
Dowling × Williams 82 (F ₁)	3	3	0				

† R (resistant) = 0, 1, 2 aphid colonization rating and S (susceptible) = 3, 4 rating, where 0 = no aphids present, 1 = few solitary live or dead aphids present, 2 = several transient aphids present with some viviparous aptera surrounded by a few nymphs, and 4 = dense colonies with plant damage, including leaf distortion and stunting.

82 plants were 3 or 4 with one exception for Loda. All F₁ plants tested from Dowling × Loda and Dowling × Williams 82 crosses, confirmed to be true hybrids and not Dowling selfs after examining flower and pubescence color, were given either 0 or 1, with a few plants given a 2, indicating that they were resistant to the soybean aphid and that resistance was dominant over susceptibility.

Twelve of the 14 Dowling × Loda F₂ families segregated in a 3:1 resistant/susceptible ratio. Plants in two of the families were all resistant but segregated for flower color, indicating that they were the progeny of true hybrids between Dowling and Loda and were not selfs from Dowling. Heterogeneity of segregation among the F₂ families was nonsignificant ($P = 0.16$). Pooled F₂ data totals were 132 resistant to 45 susceptible plants (Table 1). This segregation pattern fit a ratio of 3:1, expected for monogenic dominant gene inheritance ($P = 0.90$). Dowling × Williams 82 F₂ plants from a single F₂ family segregated 135 resistant to 44 susceptible plants (Table 2), also fitting a 3:1 ratio ($P = 0.89$). Segregation among Dowling × Loda (Table 3) and Dowling × Williams 82 (Table 4) F_{2,3} families for aphid resistance fit

Table 3. Observed and expected aphid colonization ratings of soybean Dowling × Loda F_{2,3} families 21 d after infestation by the soybean aphid.

F ₂ family†	Number of F _{2,3} families‡	Observed§			Expected (1:2:1)			χ^2	P
		R	H	S	R	H	S		
4021	16	4	8	4	4	8	4	0.0	1.00
4281	12	3	5	4	3	6	3	0.5	0.78
4301	12	0	9	3	3	6	3	4.5	0.11
4303	10	2	6	2	2.5	5	2.5	0.4	0.82
4306	14	4	3	7	3.5	7	3.5	5.9	0.05
4309	10	2	5	3	2.5	5	2.5	0.2	0.90
4344	11	2	6	3	2.75	5.5	2.75	0.3	0.87
4531	17	2	8	7	4.25	8.5	4.25	3.0	0.22
Total								14.7	
Pooled	102	19	50	33	25.5	51	25.5	3.9	0.14
Heterogeneity								10.8	0.09

† F₂ families are listed that had data from a minimum of 10 F_{2,3} families.

‡ 12 seeds from each F₂ plant were sown.

§ R (resistant) = all plants in an F_{2,3} family were resistant (aphid colonization rating 0–2, where 0 = no aphids present, 1 = few solitary live or dead aphids present, 2 = several transient aphids present with some viviparous aptera surrounded by a few nymphs); H (heterozygote) = plants in a family segregated for resistance; S (susceptible) = all plants in a family were susceptible (aphid colonization rating 3 or 4, where 3 = dense colonies, and 4 = dense colonies with plant damage, including leaf distortion and stunting).

Table 4. Reactions of soybean Dowling × Williams 82 F_{2,3} families 21 d after infestation by the soybean aphid.

F ₂ family	Number of F _{2,3} families†	Observed‡			Expected (1:2:1)			χ^2	P
		R	H	S	R	H	S		
4041	128	35	63	30	32	64	32	0.42	0.81

† 12 seeds from each F₂ plant were sown.

‡ R (resistant) = all plants in an F_{2,3} family were resistant (0, 1, or 2 aphid colonization rating, where 0 = no aphids present, 1 = few solitary live or dead aphids present, 2 = several transient aphids present with some viviparous aptera surrounded by a few nymphs); H (heterozygote) = plants in a family segregated for resistance; S (susceptible) = all plants in a family were susceptible (3 or 4 aphid colonization rating, where 3 = dense colonies, and 4 = dense colonies with plant damage, including leaf distortion and stunting).

a 1:2:1 resistant/segregating/susceptible ratio, $P = 0.14$ and $P = 0.81$, respectively, confirming the monogenic inheritance found in the F₂ phenotype analyses.

These results indicated that a single dominant gene controls resistance in Dowling. Using the convention specified by the Soybean Genetics Committee, the gene symbol for the gene identified in Dowling is named *Rag1*, with 'ag' standing for *Aphis glycines*, and the number 1 indicating that it is the first gene identified for resistance to the soybean aphid in soybean.

DISCUSSION

Segregation of F₂ plants and F_{2,3} families derived from crosses between the aphid resistant soybean cultivar Dowling and the susceptible cultivars Loda and Williams 82 clearly fit a monogenic dominant inheritance pattern for resistance to the soybean aphid in Dowling. The gene, named *Rag1*, is the first gene identified in soybean that controls resistance to the soybean aphid.

Dominant genes are usually involved in aphid resistance (Auclair, 1989) and there are many examples of monogenic dominant resistance to aphids. Resistance to the Russian wheat aphid (*Diuraphis noxia* Mordvilko) in wheat (*Triticum aestivum* L.) is controlled by at least nine dominant genes (*Dn1–9*) (Liu et al., 2001). Three of the *Dn* genes are tightly linked. Two dominant genes, *Rsg1a* and *Rsg2b*, confer resistance to several biotypes of the greenbug [*Schizaphis graminum* (Rondani)] in barley (*Hordeum vulgare* L.) (Porter and Mornhinweg, 2004; Puterka et al., 1988; Webster and Starks, 1984). Other examples of monogenic dominant aphid resistance include resistance in apple (*Malus* spp.) to the rosy leaf-curling aphid, *Dysaphis devectora* Wlk. (Alston and Briggs, 1977), resistance in peach (*Prunus persicae* L.) to the green peach aphid, *Myzus persicae* (Sulzer) (Pascal et al., 2002), resistance in *Medicago truncatula* Gaert. to the blue alfalfa aphid, *Acyrtosiphon kondoi* Shinji (Klingler et al., 2005), and resistance in cowpea, *Vigna unguiculata* (L.) Walp., to the cowpea aphid, *Aphis craccivora* Koch (Bata et al., 1987; Pathak, 1988). The gene *Mi-1.2* (Goggin et al., 2004) controls resistance in tomato (*Lycopersicon esculentum* Mill) to the potato aphid, *Macrosiphum euphorbiae* Thomas (Kaloshian et al., 1995), and two other pests: root-knot nematodes, *Meloidogyne* spp. (Rossi et al., 1998), and tobacco white flies, *Bemisia tabaci* (Gennadius) (Nombela et al., 2003).

Resistance to aphids may be quantitative rather than qualitative in expression. For instance, expression of resistance to the cabbage aphid, *Brevicoryne brassicae* (L.), in the wild species *Brassica fruticulosa* Cirillo is quantitative (Pink et al., 2003). A quantitative trait locus involved in adult plant cereal aphid resistance has also been detected and mapped in barley (Moharrampour et al., 1997).

Resistance to other insects in soybean is quantitative in expression and inheritance (Kilen and Lambert, 1998; Narvel et al., 2001; Rowan et al., 1991), including resistance to the Mexican bean beetle, *Epilachna varivestis* (Mulsant) (Rufener et al., 1989; Sisson et al., 1976), resistance to the corn earworm, *Helicoverpa zea* Boddie, (Rector et al., 1998, 1999, 2000), and other insects (Ojo and Ariyo, 1999; Souza et al., 1995). A number of quantitative trait loci for resistance to soybean insects have been identified and mapped (Narvel et al., 2001; Rector et al., 1998, 1999, 2000; Terry et al., 2000).

A simple rating scale with two classes, resistant and susceptible, could have been used to evaluate the plants in this study because only the two distinctive parental resistance phenotypes were observed in the segregating populations. The discontinuous bimodal frequency distribution of F₂ ratings indicated the qualitative or simple inheritance of the resistance trait. Zhu et al. (2004) initially planned to use a 1-to-6 scale, based on plant damage with incremental increases in plant chlorosis with each step in the scale, to evaluate segregating wheat populations in the greenhouse for resistance to greenbug. Because no intermediate levels of chlorosis were expressed in the segregating populations, plants were scored as resistant or susceptible. Genetic analysis of the data helped to identify and map the dominant *Gbz* gene for greenbug resistance in wheat. A 0-to-3 rating scale, based on leaf folding, leaf rolling, and chlorosis or streaking in response to aphid feeding, was used in a greenhouse test to determine the inheritance of resistance and map genes for resistance to the Russian wheat aphid in wheat (Liu et al., 2001). Plants with a rating of 0 to 1 were considered resistant in the genetic analysis and plants with a rating of 2 or 3 were considered susceptible. In a field study of the inheritance of soybean aphid resistance in crosses between soybean aphid resistant wild soybean (*G. soja* L.) and susceptible soybean lines (Zhiqiang et al., 1990), a continuous 0-to-5 rating system, based on numbers of aphids in increasing increments up the scale, was used to measure aphid colonization. As found in this study, the resistant wild soybean and susceptible soybean parents had distinctive resistance phenotypes. However, it was not clear if the trait was simple or quantitative in inheritance. There may be more variability in aphid colonization on resistant and susceptible plants in the field compared with tests conducted in the greenhouse.

Introgression of *Rag1* into adapted, elite soybean germplasm in soybean aphid resistance breeding programs will be relatively straightforward because of its simple inheritance and because soybean plants carrying it are easily distinguished from susceptible plants in aphid resistance bioassays. Backcross breeding would be an effective procedure to rapidly convert existing soy-

bean cultivars into aphid resistant cultivars. The identification of DNA markers tightly linked with *Rag1* would facilitate and increase the efficiency of selection for resistant plants in segregating populations through marker-assisted selection procedures.

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