

Genetics of Soybean-*Heterodera glycines* Interactions¹

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Abstract: The soybean cyst nematode, *Heterodera glycines*, is one of the most economically important pathogens of soybean. Effective management of the nematode is often dependent on the planting of resistant soybean cultivars. During the past 40 years, more than 60 soybean genotypes and plant introductions (PI) have been reported as resistant to *H. glycines*. About 130 modern soybean cultivars registered in the United States are resistant to certain races of *H. glycines*. Several resistance genes have been identified and genetically mapped; however, resistance levels in many soybean cultivars are not durable. Some older cultivars are no longer resistant to certain *H. glycines* populations in many production areas, especially if a soybean monoculture has been practiced. Past soybean registration reports show that all resistant cultivars developed in public institutions from the mid-1960s to the present have been derived from five PIs. This narrow genetic background is fragile. To further complicate the issue, soybean-*H. glycines* genetic interactions are complex and poorly understood. Studies to identify soybean resistance genes sometimes have overlapped, and the same genes may have been reported several times and designated by different names. Nevertheless, many potential resistance genes in existing germplasm resources have not yet been characterized. Clearly, it is necessary to identify new resistance genes, develop more precise selection methods, and integrate these resistance genes into new cultivars. Rational deployment of resistant cultivars is critical to future sustained soybean production.

Key words: genetics, *Glycine max*, *Heterodera glycines*, interaction, parasitism, resistance, review, soybean, soybean cyst nematode.

The soybean cyst nematode, *Heterodera glycines* Ichinohe, was first detected in North Carolina, in 1954 (Winstead et al., 1955) and now occurs throughout all major soybean-growing regions of the United States (Doupnik, 1993; Riggs, 1977). In 1979, economic damage caused by *H. glycines* was estimated at 1.52 million tons with a value of more than \$420 million (Brewer, 1981). Currently, these losses are estimated to be \$760 million in major soybean-production states in the United States (Noel, 1992; Sciombato, 1993). Planting of resistant soybean cultivars is the most widely used method for limiting yield losses caused by this nematode (Anand, 1991a; Hartwig, 1981). For example, it is estimated that the resistant cultivar Forrest prevented crop losses worth \$405 million between 1975 and 1980 (Bradley and Duffy, 1982). *Heterodera glycines* populations are dynamic with respect to their ability to parasitize resistant cultivars; thus, resistance-breaking *H. glycines* geno-

types may be selected over time in soybean-production fields, resulting in nondurable resistance (Young, 1994). Anand et al. (1994) concluded that 83% of *H. glycines* populations from the United States possessed genes to overcome resistance genes from 'Pickett', and most of the *H. glycines* populations collected from Arkansas, Florida, Georgia, Iowa, North Carolina, and South Carolina produced cysts on Pickett. Genes for parasitism on 'Bedford' proved to be common in the central United States (Hancock et al., 1985, 1987).

RACE CONCEPTS AND POPULATION STRUCTURE

Genetic variants among field populations of *H. glycines* were discovered within a few years of its first report in the United States. *Heterodera glycines* populations from North Carolina and Tennessee were compared for their ability to develop on PI88788 (Ross, 1962). Relatively sparse development of females of the Tennessee population was observed on PI88788 compared with that of the North Carolina population. This indicated that the two populations were genetically different. Furthermore, a population from Virginia was able to infect the resistant cultivar Pickett, which was developed in

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North Carolina (Miller and Duke, 1966; Miller, 1967). A "biotype" in Arkansas reproduced well on soybean cultivars that were resistant in the Mississippi valley (Riggs et al., 1968). Eleven populations from Virginia, North Carolina, Missouri, Arkansas, Tennessee, Illinois, Mississippi, and Kentucky were differentiated by their ability to develop egg-bearing females on 'Peking', 'Pine Dell Perfection', PI90763, PI88788, PI87631-1, PI79683, PI91684, and PI84611. The soybean genotypes were designated as either efficient or poor hosts to a given population (Miller, 1970).

As a result of a special *H. glycines* research workshop held in Beltsville, Maryland, in 1969, the term "race" was selected for designation of infraspecific forms of *H. glycines*. A set of soybean differentials was proposed for determining the race of a particular field population. The set of selected soybean cultivars and lines included Pickett, Peking, PI88788, PI90763, and the standard susceptible cultivar Lee 68. *Heterodera glycines* populations with production of 10% or more of the number of females (female index) on a resistant cultivar compared to Lee 68 would justify a positive ("+") rating, and less than 10% would justify a negative ("-") rating. Based on the soybean differentials, four races (races 1-4) were described (Golden et al., 1970). Although tail lengths of infective juvenile nematodes were included as supplemental data, the morphological information proved to be of little value and was abandoned as more populations were evaluated. Race 5 was later described from Japan, based on its ability to infect Pickett (Inagaki, 1979).

Because some *H. glycines* populations had different parasitic capabilities from those of the described races with respect to their ability to reproduce on the differentials, genetic structure among races and infraspecies variation within each field population were studied further (Riggs et al., 1981; Triantaphyllou, 1987), and the initial race scheme was expanded to include 16 possible races (Riggs and Schmitt, 1988). The use of statistics in race determination tests was suggested because parasitism tests on soybean

differentials were usually highly variable (Young, 1989). A new proposed rating index for *H. glycines* field population reproductive levels and rankings of soybean resistance was suggested to be a better method for describing *H. glycines*-soybean interactions in field settings (Schmitt and Shannon, 1992). In this scheme, the female index is compared to the susceptible host, and host response is classified separately from determination of *H. glycines* race. If the female index percentage is greater than 60%, the soybean is susceptible; 31-60%, the soybean is moderately susceptible; 10-30%, the soybean is moderately resistant; and 0-9%, the soybean is resistant.

Based on recent observations and published results of *H. glycines* distribution and tests of the parasitic ability of populations, it appears that at least eight races occur in the United States (Anand et al., 1994; Rao-Arelli et al., 1992b; Riggs et al., 1995). These races can be separated into two groups based on their ability to reproduce on PI88788. Races 3, 6, 9, and 14 do not reproduce on PI88788, whereas races 1, 2, 4, and 5 do. In addition, races 1 and 3 do not reproduce on Pickett, races 5 and 6 do not reproduce on Peking, and races 2 and 9 do not reproduce on PI90763. Races 4 and 14 reproduce on PI90763, but only race 4 overcomes all resistance in standard differentials (Table 1).

GENETIC ANALYSIS OF PARASITISM

A parasite must reproduce to successfully complete its life cycle. In this sense, the ability of a *H. glycines* individual to parasitize a soybean plant is measured by reproduction. In general, resistant hosts do not permit the female nematode to develop to reproductive maturity. Parasitism is a qualitative trait that the individual nematode either does or does not possess. In addition, nematode populations may be described quantitatively by their level of reproduction on a given host plant. Field populations of *H. glycines* are mixtures of many genotypes, some of which may confer the ability to overcome host resistance genes. Race designation of a field population is based upon the prevalent phe-

TABLE 1. *Heterodera glycines* races reported in the United States.

Race ^a	Differential host ^b				
	Pickett	Peking	PI90763	PI88788	Lee
Group I ^c					
3	R ^d	R	R	R	S
6	S	R	R	R	S
9	S	S	R	R	S
14	S	S	S	R	S
Group II					
1	R	R	R	S	S
2	S	S	R	S	S
4	S	S	S	S	S
5	S	R	R	S	S

^a Race designation according to Riggs and Schmitt (1988).^b Differential hosts based on Golden et al. (1970).^c Group I and Group II are separated based on parasitic ability on PI88788.^d R = Resistant or female index <10%; S = Susceptible or female index >10%.

notype in the population. Selection pressure from growing resistant cultivars can change this race designation by altering the frequency of alleles in the population for reproducing on a resistant host.

Research on the genetic basis of parasitism in *H. glycines* is difficult because measurement of the genetic capabilities of an individual nematode is nearly impossible. Furthermore, results from population measurements usually are biased by genetic variability among and within *H. glycines* populations, and the frequency of a certain gene for parasitism may affect phenotypic designation of either parasitism or the levels of reproduction (Dong and Opperman, 1997; Luedders, 1983; Opperman et al., 1995). Single-pair mating and F1 hybrid host range tests of *H. glycines* populations suggested that the parasitism genes in these populations of races 2 and 4 were partially dominant to the parasitism genes in races 1 and 3 (Price et al., 1978). Single cyst selection and inbreeding on a resistant host for many generations indicated that this nematode would tolerate concurrent selection and inbreeding (Dropkin and Halbrendt, 1986). Secondary selection of these inbred lines on a different resistant host resulted in suppressed cyst development on the previous selection host, suggesting that alleles of

parasitism genes exist for some hosts (Luedders, 1985; Leudders et al., 1983). However, other studies demonstrated that continuous selection of *H. glycines* on a resistant soybean increased frequency of parasitism genes in that group, but the frequencies of parasitism genes in other groups were not affected. This suggests that the parasitism genes in the PI88788 and PI90763 groups are not allelic but are independent loci (Triantaphyllou, 1975). Reciprocal crosses between field populations indicated that the parasitism genes were not sex-linked in the progeny (Triantaphyllou, 1975).

More recently, parasitism genes in *H. glycines* were analyzed by crossing two highly inbred lines (>29 generations) (Dong and Opperman, 1997). A nonparasitic *H. glycines* line, which produces zero females on PI88788 and PI90763, was used as the female and recurrent parent and was crossed to a parasitic line that reproduces on PI88788 and PI90763. The segregation ratio of the progeny lines developed by single female inoculation revealed that parasitism to these soybean lines was controlled by independent single genes in the nematode. We have defined these genes as *ror(s)* with the meaning of reproduction on a resistant host (Dong and Opperman, 1997). In these inbred lines, *Ror-1* (*kr1*) confers the ability to reproduce on PI88788 and is dominant. Reproduction on PI90763 is controlled by the recessive gene, *ror-2* (*kr2*).

SOURCES OF RESISTANCE

Genetic resources for *H. glycines* resistance were first evaluated in North Carolina field tests in 1957 (Ross and Brim, 1957), and 'Ilsoy', 'Peking', PI79693, PI90763, PI209332, and PI84751 were reported to be intermediate or highly resistant among ca. 2,800 selected soybean cultivars and lines (Table 2). Ross (1962) found that PI88788 was resistant to a Tennessee population. In Virginia, nine plant introductions were found to be resistant to *H. glycines* (Miller and Duke, 1966). Soybean resistance to a race 4 population was evaluated under greenhouse conditions (Epps and Hartwig, 1972). They recorded the number of fe-

TABLE 2. Soybean germplasm resistant to *Heterodera glycines*.

Germplasm	Race ^b								Citation
	1	2	3	4	5	6	9	14	
Cloud (PI16790)	— ^c	—	R	R	S	—	—	—	Epps and Hartwig (1972) Anand and Gallo (1984) Anand et al. (1988)
Columbia (PI22897)	—	—	R	—	—	—	—	—	Epps and Hartwig (1972) Anand and Gallo (1984)
Ilsoy (PI6384)	R	—	R	MR	S	—	—	—	Ross and Brim (1957) Anand et al. (1988)
Old Dominion	—	—	—	—	—	—	—	—	Miller and Duke (1966)
Peking (PI17852B)	R	S	R	S	R	R	S	S	Ross and Brim (1957) Miller and Duke (1966) Miller (1970) Epps and Hartwig (1972) Anand et al. (1985) Anand et al. (1988) Rao-Arelli et al. (1992a)
Pine Dell	—	—	—	—	—	—	—	—	Miller and Duke (1966) Miller (1970)
PI17852B	—	—	R	—	—	—	—	—	Anand and Gallo (1984)
PI54591	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI63468	—	—	—	—	—	—	—	—	Miller and Duke (1966)
P170218-2-19-3	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI79609	—	—	R	—	—	—	—	—	Anand and Gallo (1984)
PI79693	R	—	MR	—	—	—	—	—	Ross and Brim (1957) Miller (1970)
PI81042-1	—	—	—	—	—	—	—	—	Miller and Duke (1966)
PI84611	—	—	—	—	—	—	—	—	Miller and Duke (1966) Miller (1970)
PI84751	—	—	R	—	—	—	—	—	Ross and Brim (1957) Epps and Hartwig (1972)
PI85903	—	—	—	—	—	—	—	—	Miller and Duke (1966)
PI87631-1	—	R	R	R	S	—	—	—	Miller and Duke (1966) Miller (1970) Epps and Hartwig (1972) Anand and Gallo (1984) Anand et al. (1988)
PI88287	—	—	—	—	—	—	—	—	Miller and Duke (1966)
PI88788	S	S	R	S	S	R	R	R	Ross (1962) Miller and Duke (1966) Miller (1970) Epps and Hartwig (1972) Anand et al. (1985) Anand et al. (1988) Rao-Arelli et al. (1992a)
PI89008	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI89014	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI89772	R	R	R	S	R	R	R	S	Miller and Duke (1966) Epps and Hartwig (1972) Anand et al. (1988) Rao-Arelli et al. (1992a)
PI90763	R	R	R	S	R	R	R	S	Ross and Brim (1957) Miller and Duke (1966) Miller (1970) Epps and Hartwig (1972) Anand et al. (1985) Anand et al. (1988) Rao-Arelli et al. (1992a)
PI91138	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI91684	—	—	—	—	—	—	—	—	Miller (1970)
PI92720	—	—	R	—	—	—	—	—	Anand and Gallo (1984)

TABLE 2. Continued

Germplasm	Race ^b								Citation
	1	2	3	4	5	6	9	14	
PI92686	—	—	—	—	—	—	—	—	Miller and Duke (1966)
PI200495	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI206258	—	—	—	—	—	—	—	—	Miller and Duke (1966)
PI209331	—	—	—	—	—	—	—	—	Miller and Duke (1966)
PI209332	R	S	R	—	S	R	R	R	Ross and Brim (1957)
									Anand et al. (1988)
									Rao-Arelli et al. (1992a)
PI248511	—	—	—	—	—	—	—	—	Miller and Duke (1966)
PI303652	—	—	R	S	S	—	—	—	Anand and Gallo (1984)
									Anand et al. (1985)
PI339868B	—	—	R	S	MR	—	—	—	Anand and Gallo (1984)
									Anand et al. (1988)
PI398680	—	—	R	MR	S	—	—	—	Anand and Gallo (1984)
									Anand et al. (1988)
PI398682	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI399061	—	—	S	—	R	—	—	S	Young (1990)
PI404166	R	R	R	S	R	R	R	S	Anand and Gallo (1984)
									Anand et al. (1985)
									Anand et al. (1988)
									Rao-Arelli et al. (1992a)
PI404198A	—	—	R	S	R	—	—	—	Anand and Gallo (1984)
									Anand et al. (1985)
									Anand et al. (1988)
PI404198B	R	R	R	MR	MR	R	S	S	Anand and Gallo (1984)
									Anand et al. (1988)
									Rao-Arelli et al. (1992a)
PI407729	—	—	R	R	MS	—	—	—	Anand and Gallo (1984)
									Anand et al. (1988)
PI407944	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI408192-2	—	—	MR	S	S	—	—	—	Anand and Gallo (1984)
									Anand et al. (1985)
PI416762	—	—	R	R	S	—	—	—	Anand (1982)
									Anand et al. (1988)
PI417091	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI417094	—	—	MR	S	S	—	—	—	Anand and Gallo (1984)
									Anand et al. (1985)
PI424137B	—	—	MR	—	MR	—	—	MR	Young (1990)
PI424595	—	—	S	—	R	—	—	S	Young (1990)
PI437488	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI437654	R	R	R	R	R	R	R	R	Anand and Gallo (1984)
									Anand et al. (1985)
									Anand et al. (1988)
									Rao-Arelli et al. (1992a)
PI437655	—	—	R	R	S	—	—	—	Anand and Gallo (1984)
									Anand et al. (1985)
									Anand et al. (1988)
PI437679	—	—	R	S	MR	—	—	—	Anand and Gallo (1984)
									Anand et al. (1988)
PI437690	R	R	R	S	MR	R	S	R	Anand and Gallo (1984)
									Anand et al. (1988)
									Rao-Arelli et al. (1992a)
PI437725	—	—	R	—	—	—	—	—	Anand and Gallo (1984)
PI437770	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI438183	—	—	MR	—	—	—	—	—	Anand and Gallo (1984)
PI438342	—	—	S	—	R	—	—	S	Young (1990)
PI438489B	R	R	R	S	R	R	R	S	Anand and Gallo (1984)
									Anand et al. (1985)
									Anand et al. (1988)
									Rao-Arelli et al. (1992a)

TABLE 2. *Continued*

Germplasm	Race ^b								Citation
	1	2	3	4	5	6	9	14	
PI438496B	R	S	R	S	S	R	S	S	Anand and Gallo (1984) Anand et al. (1985) Rao-Arelli et al. (1992a)
PI438503A	S	S	R	MR	MS	R	R	S	Anand and Gallo (1984) Anand et al. (1985) Anand et al. (1988) Rao-Arelli et al. (1992a)

^a Soybean cultivars or plant introductions previously reported as being resistant or susceptible to *Heterodera glycines*.

^b Race designation according to Riggs and Schmitt (1988).

^c R = resistant or female index <10%; MR = moderately resistant; S = susceptible or female index >10%; — = no available information.

males collected as a measure of nematode reproduction (0 = none; 1 = 1–5; 2 = 6–10; 3 = 11–30; 4 = >30). Nine cultivars and plant introductions, out of 3,000 lines, exhibited some resistance (ratings of 0 to 2). Some of the resistant plant introductions had a mixture of genotypes, and the selected progeny of resistant plants were more uniformly resistant than the original stocks. Also, PI88788, PI89772, and PI87631-1 were recommended for use in breeding programs. They concluded that PI88788 was a superior germplasm line that also had a high degree of resistance to *Meloidogyne incognita* (Epps and Hartwig, 1972).

In 1982, Anand screened 2,153 plant introductions in the greenhouse against populations of races 3 and 4 (Table 2). He used a reproductive index similar to that used by Epps and Hartwig (1972): 0 = immune; 1–5 cysts = highly resistant, 6–10 cysts = resistant, 11–30 cysts = moderately susceptible and >30 cysts = highly susceptible. PI416762 was found to be highly resistant to both populations but susceptible to race 5 (Table 2). A total of 9,153 soybean germplasm lines were evaluated for their resistance to a race 3 population in 1984, and 19 highly resistant plant introductions were identified. In addition, 15 resistant lines also were reported (Table 2) (Anand and Gallo, 1984). Among these plant introductions, PI437654 and PI437655 were resistant to a race 4 population, and Peking, PI90763, PI404166, PI404198B, PI437654, and PI438489B were resistant to a race 5 population (Anand et

al., 1985). In 1988, eight soybean strains were added to the collections of genotypes with resistance or moderate resistance to race 4 populations, and three were added with resistance or moderate resistance to race 5 populations (Anand et al., 1988). Shortly thereafter, three other soybean plant introductions were identified as resistant to a race 5 population (Young, 1990; Young and Kilen, 1994).

Fifteen soybean cultivars and plant introductions were tested against populations of seven *H. glycines* races (race 1, 2, 3, 5, 6, 9, and 14) collected from the United States (Rao-Arelli et al., 1992b). All of them (Pickett, Peking, PI88788, PI90763, PI438489B, PI438496B, PI404166, 'Bedford', 'Custer', PI209332, PI404198B, PI437690, PI89772, PI438503A, and PI437654) had been reported previously to be resistant to various *H. glycines* populations. The results showed that all soybean lines tested were resistant to race 3 populations, 12 were resistant to race 1 populations, 5 were resistant to race 2 populations, 8 were resistant to the race 5 populations, 9 were resistant to race 6 populations, 9 were resistant to race 9 populations, and 6 were resistant to race 14 populations. Among these soybean cultivars and lines, PI437654 was resistant to most *H. glycines* populations tested from the United States (Table 2), and specifically to *H. glycines* race 3 (Anand and Gallo, 1984), to races 1, 2, 5, and 14 (Anand et al., 1985), and to races 6 and 9 (Rao-Arelli et al., 1992b).

Currently, more than 50 plant introduc-

tions are known to have moderate to high levels of resistance to *H. glycines* (Table 2). These plant introductions will provide genetic resources both for resistance breeding programs and for further characterization of *H. glycines* field populations.

GENETIC ANALYSIS OF RESISTANCE

The inheritance of resistance in soybean to *H. glycines* was first reported by Caldwell et al. (1960). Three recessive resistance genes, designated *rhg1*, *rhg2*, and *rhg3*, were identified as controlling resistance in Peking against several field populations of *H. glycines*. The same genes also were identified in PI90763 and PI84751 (Hartwig and Epps, 1970; Sugiyama and Katsumi, 1966). A fourth gene designated as *Rhg4* was identified in Peking in 1965 (Hartwig and Epps, 1970; Matson and William, 1965). However, the race concept had not been developed before those analyses were conducted.

Studies on host resistance to *H. glycines* have been expanded as more resources and information have become available, including quantitative estimates of genetic components and gene interactions (Mansur et al., 1993; Rao-Arelli et al., 1989). Different *ror* genes and gene frequencies within and among *H. glycines* field populations have made it more difficult for researchers to precisely determine the number of genes controlling resistance. Although numerous reports describe genetic analysis of *H. glycines* resistance genes in various soybean cultivars, it is currently not clear whether there are one, several, or many different alleles and loci. The following section summarizes genetic analyses from various workers for the populations so far examined. The list is not exhaustive. For example, little or no work has been performed on the genetics of resistance to race 1 populations.

Race 2: Resistance in PI90763 to the "Bedford biotype," actually a race 2 population according to standard differentials, was demonstrated to be controlled by a single recessive gene (Hancock et al., 1985, 1987).

Race 3: Peking has three resistance genes, *rhg1*, *rhg2*, and *Rhg4*, in common with PI90763, PI438489B, and PI437654 (Rao-

Arelli and Anand, 1986; Rao-Arelli and Anand, 1988; Rao-Arelli et al., 1988, 1990, 1992a). PI90763 has genes in common with PI404166, PI404198A, PI437654, and PI438489B. Resistance in PI88788 is controlled by two dominant genes, *Rhg4* and *Rhg5*, and one recessive gene. These genes were independently inherited and provided a nonallelic interaction. Segregation ratios from crosses between PI88788 and PI438496B also suggested two independent dominant genes. PI437654 has one dominant and two recessive genes in common with Peking and PI90763 (Myers and Anand, 1991; Anand and Sharma, 1996). Other data indicate that resistance in PI89772 and PI209332 is controlled by one dominant and one recessive gene, two recessive genes in PI438489, and two dominant genes and one recessive gene in PI404166 (Rao-Arelli, 1994). Resistance in 'Hartwig' is controlled by one dominant gene and one recessive gene (Faghihi et al., 1995).

Race 4: Thomas et al. (1975) suggested there were three alleles at a single locus that controlled host response to race 4. The resistance gene in PI88788 was recessive to PI90763, and the moderate resistance gene in PI90763 was recessive to the susceptible Peking. The same experiment also showed that resistance in PI90763 compared with 'Hill' and 'Mack' was controlled by one dominant gene and two recessive genes.

Race 5: Resistance to race 5 in Peking and PI90763 is each controlled by two recessive genes, and in PI438489B is controlled by one recessive gene. At least one gene in Peking, PI90763, and PI404166 is different. Other genes in Peking, PI84751, PI90763, PI404166, and PI438489B are controlled at the same loci (Anand and Rao-Arelli, 1987, 1989). Resistance in PI437654 is due to two dominant genes and two recessive genes, similar to the genes in PI90763 and Peking (Myers and Anand, 1991). Anand (1994b) further demonstrated that resistance in PI90763 is controlled by one dominant gene and in PI424595 is controlled by one recessive gene. PI90763 and PI424595 each share two other additional recessive genes (Anand, 1994b). Three or more genes were de-

scribed recently in resistant resources such as PI399061, PI424595, and PI438342 (Young and Kilen, 1994). Anand and Sharma (1996) reported that one dominant gene and one recessive gene in PI90763 controlled resistance to race 5. PI424595 may have an additional recessive gene for resistance to race 5, but this gene did not limit reproduction of a race 3 field population collected from Tennessee (Anand and Sharma, 1996).

Race 14: Data from PI437654 indicated that one dominant gene and two recessive genes control the host response to *H. glycines* race 14 populations. Among the three genes, the two recessive genes are the same as those in PI90763, and the dominant gene and one of the recessive genes are the same as those in Peking (Myers and Anand, 1991).

GENETIC MAPPING OF RESISTANCE AND PARASITISM GENES

The first report of *H. glycines* resistance gene linkage can be traced back to 1965 when the dominant gene *Rhg4* in Peking was found to be tightly linked to the black color seed coat gene *i* (Matson and William, 1965). Molecular markers such as RFLP (restriction fragment length polymorphism), RAPD (random amplified polymorphic DNA), and micro-satellites have been detected and placed on the soybean genetic map. By 1995, approximately 400 published RFLP and RAPD markers, a number of classical phenotypic morphological characters, and quantitative trait loci had been integrated into a 26-linkage-group soybean genetic map (Shoemaker and Specht, 1995). Some molecular markers are closely associated with *H. glycines* resistance genes. Weisemann et al. (1992) first identified molecular markers linked to the *Rhg4* gene. Concibido et al. (1994) mapped RFLP markers linked to the race 3 resistance genes on soybean linkage groups A, G, and K in PI209332. Webb et al. (1995) mapped the dominant gene *Rhg4* in PI437654 on soybean linkage group A within 1 centimorgan (cM) of the *i* gene, and their results confirmed those of Matson and Williams (1965)—that a domi-

inant gene for resistance is tightly linked to the *i* gene. In addition, Webb et al. (1995) found two other genes associated with *H. glycines* resistance that were located on groups G and M, respectively. These two genes possibly are the *rhg1* and *rhg2* genes described by Caldwell et al. (1960). Concibido et al. (1995, 1996a) further confirmed that the resistance locus on linkage group G is in common within several tested resistant resources. The locus accounted for 51.4% of total phenotypic variation in *H. glycines* race 3 response in PI209332, 52.7% in PI90763, 40.0% in PI88788, and 28.1% in Peking. In addition, this locus also explains the phenotypic variation to *H. glycines* races 1 and 6. There appears to be a resistance gene cluster on the G group (Concibido et al., 1995). Currently, the marker density at this region is about one RFLP for every 2.6 centimorgans (Concibido et al., 1995). Additional putative *H. glycines* resistance loci were identified on linkage groups D, J, L, and K (Concibido et al., 1995, 1996a,b).

Numerous RAPD markers have been detected among *H. glycines* field populations. Similarities in RAPD patterns are more dependent on geographical origin than on parasitism (Nevin Young, pers. comm.). A RAPD marker that can distinguish parasitic from nonparasitic populations in Indiana was characterized (Li et al., 1996). A modified bulk-segregant analysis was conducted to detect RAPD markers linked to a dominant parasitism gene of PI88788, *Ror-1*, in a recombinant inbred mapping population. Two markers detected are tightly linked to *Ror-1* (Dong and Opperman, unpubl.).

SUMMARY

At present, about 64 public cultivars with different levels of resistance to *H. glycines* have been released from public institutions in the United States (Table 3). The 16-race-scheme was proposed in 1988 (Riggs and Schmitt, 1988); however, some soybean breeders continue to use the old 5-race-scheme to designate the resistance in their cultivar registrations. Therefore, cultivars registered before 1988 may be resistant to more races than reported, and the resis-

TABLE 3. Modern public soybean cultivars resistant to *Heterodera glycines*, grouped by the original source of resistance.^a

Cultivar ^b	Year ^c	Parental line(s) ^d	Resistant to race(s) ^e	Literature
<u>Peking</u>				
Pickett	1966	Peking	3	Brim and Ross (1966a)
Custer	1968	Peking	3	Luedders et al. (1968)
Dyer	1968	Peking	3	Hartwig and Epps (1968)
Pickett 71	1971	Pickett	1, 3	Hartwig et al. (1971)
Mack	1972	Peking	3	Caviness et al. (1972)
Forrest	1972	Dyer	1, 3	Hartwig and Epps (1973)
Centennial	1977	Pickett	1, 3	Hartwig and Epps (1977b)
Franklin	1980	Custer	1, 3	Bernard and Shannon (1980)
Foster	1981	Centennial, Dyer, Forrest	1, 3	Hinson (1981)
McNair 770	1981	Pickett 71	3	Anand et al. (1981)
Narow	1985	Mack	3	Caviness et al. (1985)
Kirby	1983	Centennial, Dyer, Forrest	3	Hinson et al. (1983)
Gordon	1985	Forrest, Pickett 71	1, 3	Boerma et al. (1985)
TN 5-85	1986	Forrest	1, 3	Allen and Manuel (1986)
Gregg	1988	Pickett	3	Harville et al. (1988)
Twiggs	1988	Centennial, Forrest	1, 3	Boerma et al. (1988)
Sharkey	1988	Centennial	3	Hartwig et al. (1988)
CN210	1988	Custer	3	Bernard et al. (1988c)
CN290	1988	Custer	3	Bernard et al. (1988d)
Thomas	1989	Centennial	1, 3	Boerma et al. (1989)
Stonewall	1989	Centennial, Forrest	3	Weaver et al. (1989)
Lamar	1990	Centennial	3	Hartwig et al. (1990)
Newton	1991	CN210	3	Mansur et al. (1991)
Delsoy 4500	1991	Forrest	3	Anand (1991b)
Delsoy 4900	1991	Mack	3	Anand (1991c)
Walters	1991	Forrest	3	Caviness et al. (1991)
Hagood	1992	Centennial	3	Shipe et al. (1992)
Pharaoh	1993	Forrest	3	Schmidt et al. (1993)
TN 6-90	1993	unknown	3	Allen et al. (1993)
Doles	1994	Centennial, Forrest	3	Boerma et al. (1994)
Maxcy	1994	Centennial, Forrest	3	Shipe et al. (1995)
Nile	1995	Forrest	3	Schmidt et al. (1995)
Manokin	1996	Forrest	1, 3	Kenworthy et al. (1996)
<u>PI88788</u>				
Fayette	1988	PI88788	3, 4	Bernard et al. (1988a)
Cartter	1988	PI88788	3, 4	Bernard et al. (1988b)
Bell	1990	Fayette	3, 4	Nickell et al. (1990a)
Jack	1990	Fayette	3, 4	Nickell et al. (1990b)
Linford	1991	Fayette	3, 4	Bernard and Noel (1991)
Delsoy 4210	1992	PI88788	3, 4, 14	Anand (1992b)
Alpha	1994	Fayette	3	Orf and MacDonald (1994)
Saline	1994	Fayette	3, 14	Owen et al. (1994)
Yale	1995	Fayette	2, 3, 4, 14	Nickell et al. (1995)
<u>Peking and PI88788</u>				
Bedford	1977	Dyer, Forrest, PI88788	1, 3, 4	Hartwig and Epps (1977a)
Jeff	1982	Centennial, Dyer, Peking, PI88788	1, 3, 4	Caviness et al. (1982)
Nathan	1982	Dyer, Forrest, PI88788	3, 4	Hartwig and Epps (1982)
Bradley	1984	Dyer, Forrest, Pickett, PI88788	3, 4	Anand and Shannon (1984)
Epps	1984	Dyer, Forrest, Pickett, PI88788	1, 3, 4	Hartwig, (1984)
Leflore	1984	Centennial, Dyer, Forrest, PI88788	3, 4	Hartwig et al. (1984)
Egyptian	1987	Dyer, Forrest, Franklin, PI88788	3, 4	Myers and Schmidt (1987)
Pyramid	1988	Bedford, Franklin	3, 4	Myers and Schmidt (1988)
Avery	1988	Bedford	3, 4	Anand and Shannon (1988)
TN 4-86	1988	Bedford	3, 4	Allen et al. (1988)
A5474	1989	Bedford	3, 4	Shannon and Schillinger (1989a)
A5980	1989	Bedford	3, 4	Shannon and Schillinger (1989b)

TABLE 3. *Continued*

Cultivar ^b	Year ^c	Parental line(s) ^d	Resistant to race(s) ^e	Literature
Loyd	1990	Centennial, Forrest, PI88788	3, 4	Caviness et al. (1990)
Bryan	1991	Bedford, Centennial	1, 3	Boerma et al. (1991)
Rhodes	1994	Forrest, PI88788	3, 4, 14	Anand (1994a)
Lyon	1994	Bedford	3, 14	Hartwig et al. (1994)
Bronson	1995	Brandley, PI88788	3, 4, 14	Wilcox et al. (1995)
Carver	1995	Bedford, Centennial	3, 14	Weaver et al. (1995)
			Peking, PI88788, and PI90763	
Cordell	1990	Bedford, Dyer, PI90763	3, 4, 5	Hartwig and Young (1990)
			PI437654	
Hartwig	1992	Forrest, PI437654	1, 2, 3, 4, 5, 6, 9, 14	Anand (1992a)
			PI209332	
Delsoy 4710	1992	PI209332	3, 14	Anand (1992c)
Faribault	1995	PI309332	3	Org and MacDonald, (1995)

^a Public cultivars resistant to *Heterodera glycines* registered and published in *Crop Science* by August 1996.

^bBecause the "16-race-scheme" was proposed in 1988 (Riggs and Schmitt, 1988), cultivars registered before 1988 also could be resistant to other races, e.g. race 6, 9, or 14.

^c Year of registration.

^d Resistance gene(s) derived from PI or former cultivars.

^e Reported resistance to certain race(s) by breeder.

tance levels and resistant race designations in these cultivars need to be reconsidered.

Heterodera glycines field populations are usually heterogeneous, and parasitism test results of a given population on a certain resistant differential may show the presence or absence of *ror* alleles, but more likely will indicate the frequency of these alleles. Race designation is a population concept and a dynamic phenomenon. The high variability in host-range tests results in nematologists including both the mean and variability in related reports (Riggs et al., 1988; Riggs and Schmitt, 1991; Young, 1989). Nevertheless, the current race scheme is still useful to evaluate at least the pathogenic potential of a certain field population and resistance level of a given cultivar. Thus, it seems unlikely that the 10% female index (FI) will be abandoned in the near future. However, the use of either field populations or the 10% FI rule for theoretical genetic analysis of resistance gene and gene numbers is not advisable. A more precise system is needed to predict segregation ratios among soybean progeny lines and to estimate the related resistance gene numbers. This approach is especially important where several genes occur and the degrees of dominance of these genes are unknown. Inbred *H. glycines* lines also should be used in future genetic analy-

sis. For example, using an inbred line, Luedders (1987) demonstrated there was a single recessive resistance gene in PI88287, which was regarded as a susceptible host to heterogeneous *H. glycines* populations.

Many arguments focus on the current race schemes, and many researchers consider these schemes to be inadequate to characterize *H. glycines* field populations. Niblack (1992) concluded that the race classification system needs to be improved, in part because the genetic background of the differentials overlap. Pickett was derived from Peking, and theoretically Peking possesses all resistance genes in Pickett. Genetic analysis shows all reported resistance genes in Peking are present in PI90763, which also may have additional genes for resistance. Another shortcoming of the current differentials is that not all resistance genes in available soybean germplasm are included. By adding more resistant germplasm, the current races can be further separated, especially to newly identified resistance-breaking genotypes. For example, the so-called Race X (Hancock et al., 1985, 1987) actually was a race 2 population when evaluated on the standard differentials, but PI209332 further distinguished the population from race 2. Rao-Arelli et al. (1992b), using 15 resistant soybean genotypes in a

test with 32 *H. glycines* populations collected from 10 states in the United States, found that most of the standard designated races in their test could be further differentiated. Clearly, in order to genetically clarify *H. glycines* *ror* genes or gene numbers, and to enhance our understanding of *ror* gene frequencies among *H. glycines* populations, it will be necessary to develop a set of *H. glycines* differentials with a wider genetic background. One option is constructing a set of fully genetically characterized near-isogenic lines that carry all possible resistance genes from resistant germplasm. Simply including additional resistant PI into the current differential series is another choice. However, current host differentials and race schemes have been used by genetic researchers, extension personnel, and soybean breeders since 1970. In fact, most soybean cultivars with *H. glycines* resistance have been developed based on this race scheme. In the short term, one can only try to improve the current *H. glycines* race scheme rather than replace it entirely. As more *ror* genes are identified in *H. glycines*, the current race scheme can be replaced with a classification based on the *ror* genotype frequencies.

In practice, maintaining the same level of resistance in cultivars compared with the parent PI has been difficult. Breeders believe genes for resistance are lost during the backcrossing process (Anand and Shumway, 1984; Brim and Ross, 1966b). A precise method for detecting and tracking resistance genes is needed. Progress in modern molecular genetic research has resulted in the development of molecular markers that are tightly linked to resistance genes (Michelmore, 1995). Marker-assisted selection should greatly facilitate breeding for *H. glycines* resistance. In fact, map-based cloning and resistance gene transformation have enabled high-resolution mapping of the target genomic regions. Combined with genomic and cDNA physical maps, these techniques may enable researchers to ultimately clone and use these genes in transgenic soybean.

Properly deploying the genetic backgrounds for different resistance from avail-

able cultivars in a certain geographic area should minimize selection pressure on field populations and prevent the build-up of selected *ror* gene frequencies over a short time. However, rational deployment of these genes for resistance is difficult unless we can precisely identify them individually and clearly understand the genetic interactions between resistant soybean and *H. glycines* populations. Molecular linkage markers to these genes, especially in germplasm such as PI437654, may provide the necessary type of information. Finally, expansion of the soybean genetic base combined with a clear understanding of nematode parasitism will enhance the sustainability of *H. glycines* resistance in soybean.

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