Inheritance of Resistance to Powdery Mildew in Soybeans

D. G. LOHNES and R. L. BERNARD, Agronomy Department, University of Illinois, 1102 S. Goodwin Avenue, Urbana 61801

ABSTRACT

Lohnes, D. G., and Bernard, R. L. 1992. Inheritance of resistance to powdery mildew in soybeans. Plant Dis. 76:964-965.

Reaction of soybeans (*Glycine max*) to powdery mildew (*Microsphaera diffusa*) has been reported to be regulated by a single gene pair *Rmd rmd*, with the dominant allele *Rmd* activating adult-plant resistance and *rmd* causing susceptibility. Resistance from the seedling stage on was observed in the greenhouse in several soybean cultivars, and these cultivars were resistant in the field with natural and artificial inoculation. F_2 and F_3 segregation ratios in the greenhouse and field show that this resistance, derived from the cultivar CNS, is controlled by a single allele, symbolized *Rmd-c*, which is allelic to *Rmd rmd*.

Powdery mildew of soybeans (*Glycine max* (L.) Merr.), caused by the fungus *Microsphaera diffusa* Cooke & Peck, was first reported in North Carolina in 1947 (8). Yield losses up to 35% have been reported on susceptible cultivars (10). Powdery mildew is sometimes a serious disease on greenhouse-grown soybeans, and *M. diffusa* is perhaps the only soybean leaf pathogen that can be disseminated and infect plants under greenhouse conditions. Other soybean leaf pathogens require free water for infection.

Grau and Laurence (7) used cultivar Chippewa 64 as a source of resistance and cv. Corsoy as a source of susceptibility and found powdery mildew resistance to be inherited as a single dominant trait. They also reported that there were two types of resistant cultivars and referred to them as resistant (e.g., Chippewa 64) and highly resistant (e.g., Wilkin). In field and greenhouse studies, Dunleavy (5) observed the reactions of 50 soybean cultivars to powdery mildew and found that some cultivars that were susceptible in the greenhouse were resistant in the field, whereas others were susceptible in both places. All cultivars that were resistant in the greenhouse also were resistant in the field. Buzzell and Haas (4) observed the segregation in crosses of the adult-plant resistant cultivar Blackhawk with susceptible cultivars Harosoy 63 and PI 65.388 and proposed the gene symbols *Rmd* (adult-plant resistant) and *rmd* (susceptible). Buss et al (3) observed the segregation of powdery mildew reaction in crosses of York with Kwanggyo and Kwanggyo and Ogden with Marshall. They concluded that York and Marshall carry single dominant genes for resistance to powdery mildew. The adult-plant resistance of Clark, Mukden, and other cultivars has been described in depth by Mignucci and Lim (9). No reports on the inheritance of powdery mildew resistance throughout the entire life cycle of the soybean plant have been found.

Accepted for publication 13 April 1992.

MATERIALS AND METHODS

In addition to the three commercial cultivars, Harosoy (susceptible), Blackhawk (adult resistant), and Williams (adult resistant), two Williams BC_5 isolines were used as parents (Table 1). These were a susceptible isoline, L82-2024, with Jefferson as the donor parent (1), and a resistant isoline, L76-1988, with D54-2437 as the donor parent (2). The source of the resistance is the cultivar CNS, which we have found to be resistant to powdery mildew throughout its entire life cycle. Other parents of the resistant donor line D54-2437 are Ogden, which is susceptible, and Lincoln, Richland, and Roanoke, which were seedling susceptible and adult-plant resistant in our greenhouse tests. L76-1988 had been selected for the gene *Rps2* (resistance to the root rot caused by *Phytophthora sojae* M. J. Kaufmann & J. W. Gerdemann), but the powdery mildew resistance also was transferred, apparently because of genetic linkage. We have suspected powdery mildew resistance to be linked to *Rps2* in L76-1988 and several other backcross-developed isolines.

Crosses were made between the resistant and susceptible isolines, and six F_1 plants were grown. In the summer of 1989, 237 F_2 plants were grown in the field at Urbana, inoculated with *M. diffusa*, and classified for powdery mildew reaction at the R6 growth stage (6). F_3 progenies were inoculated with *M. diffusa* and classified in 1990 in both the greenhouse and the field for powdery mildew reaction. In addition, seeds from F_1 plants of Williams × Harosoy and Williams × Blackhawk were obtained, and F_2 classification for powdery mildew reaction was conducted in the greenhouse from 1990 through 1992 and in the field during 1990.

To inoculate seedlings grown in the greenhouse in sand benches with *M. diffusa*, seedlings were brushed with infected leaf tissue from Harosoy when the unifoliolate leaves were fully expanded, about 1 wk after planting. Powdery mildew readings were taken about 2 wk later. Greenhouse temperatures ranged from 20 to 30 C. Lighting was supplemented with incandescent and fluorescent lamps set on a 14-hr photoperiod. Field inoculations were performed the same as in the greenhouse at the seedling stage and repeated twice during the growing season. Powdery mildew reactions observed were taken approximately 3 mo after planting at the R4 growth stage (6).

RESULTS AND DISCUSSION

In the greenhouse, the susceptible cultivar Harosoy and the susceptible Williams isoline L82-2024 had symptoms of powdery mildew on the unifoliolate leaves and on the upper leaves as the plants grew. Williams exhibited similar symptoms on the unifoliolate leaflets and on the first one or two trifoliolate leaves, but then powdery mildew development was arrested and did not proceed to younger leaves. The resistant Williams isoline L76-1988, when inoculated

Table 1. Cultivars used and their powdery mildew reaction and parentage

Cultivar	Powdery mildew reaction	Parentage[a]
Harosoy	Susceptible	Mandarin (Ottawa) × A.K. (Harrow)
Williams	Adult-plant resistant	Wayne × (Clark × Adams)
Blackhawk	Adult-plant resistant	Mukden × Richland
L76-1988	Resistant	Williams × (Harosoy × D54-2437)[b]
L82-2024	Susceptible	Williams × Jefferson

[a] Mandarin (Ottawa) was crossed twice, Williams was crossed six times, and Harosoy was crossed five times.

[b] D54-2437 parentage is CNS, Lincoln, Odgen, Richland, and Roanoke. In our greenhouse tests, Ogden was susceptible; Lincoln, Richland, and Roanoke were seedling susceptible, adult-plant resistant; and CNS was resistant.

Table 2. Segregation for powdery mildew reaction in progeny of a cross between L76-1988 (resistant) and L82-2024 (susceptible)

Population	Number of plants			χ^2 probability[a]
	All resistant	Segregating	All susceptible	
Observed in F_2	183		54	0.43
Expected (3:1)	177.75		59.25	
F_2 based on observed F_3 in the field[b]	47	72	37	0.33
Expected (1:2:1)	39	78	39	
F_2 based on observed F_3 in the greenhouse[b]	37	62	34	0.69
Expected (1:2:1)	33.25	66.5	33.25	
Observed F_3 plants in segregating progenies in the field	843		265	0.41
Expected (3:1)	831		277	
Observed F_3 plants in segregating progenies in the greenhouse	1,074		382	0.28
Expected (3:1)	1,092		364	

[a] Probability of a greater chi-square value due to chance.
[b] Number of F_2 plant progenies based on 16 F_3 plants per F_2 plant. Resistant F_2 plants either bred true or segregated and all susceptible F_2 plants bred true.

similarly, had no symptoms of powdery mildew. In the field, inoculation with *M. diffusa* did not produce symptoms until the plants had reached the R4 growth stage (6), about 3 mo after planting. Both Williams and its resistant isoline had no powdery mildew symptoms in the field.

The reaction of Williams coincided with the observations by Dunleavy (5) that some cultivars are susceptible to powdery mildew in the greenhouse and resistant in the field and also with the description by Mignucci and Lim (9) for the development and remission of powdery mildew on adult-plant resistant cultivars. The Williams reaction also was similar to Chippewa 64 (7), Blackhawk (4), York, and Marshall (3). The reaction of the resistant Williams isoline coincides with that reported for certain cultivars (Ada, Altona, Bavender Special, Beeson, Burwell, Cayuga, Grant, Jogun, Mandell, and Wilkin) tested by Grau and Laurence (7) and Dunleavy (5).

A small F_2 population from Williams × Harosoy segregated 40 adult resistant plants to 14 susceptible plants (chi-square probability = 0.87 for 3:1 ratio), indicating that the adult resistance of Williams has the same type of inheritance (gene *Rmd*) as that previously reported (3,4,7). An F_2 population consisting of 70 plants from Williams × Blackhawk did not segregate for powdery mildew reaction with all of the plants exhibiting adult-plant resistance. This confirms that Williams contains the *Rmd* gene. In the cross between the susceptible and resistant Williams isolines, F_2 and F_3 data (Table 2) indicate that the powdery mildew reaction is controlled by a single gene pair and that resistance is dominant. Because none of the 1,456 plants classified in the greenhouse in the F_3 had the Williams phenotype (adult resistance), it is clear that the gene for resistance is at the same locus as *Rmd* and that the substituted gene in each isoline had replaced the *Rmd* gene of Williams. The symbol *Rmd-c* was chosen to represent this allele for resistance from CNS. The genotype *Rmd Rmd-c* has not yet been tested in the greenhouse, therefore, its seedling phenotype is unknown.

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