Inheritance of Powdery Mildew Resistance in Wheat Line IL72-2219-1

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ABSTRACT

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Experiments were conducted to study the inheritance of powdery mildew (Pm) (*Erysiphe graminis* f. sp. *tritici*) resistance in an experimental wheat (*Triticum aestivum*) line IL72-2219-1, which was crossed with the Pm-susceptible cultivars Hart and Blueboy to obtain F_2 and testcross progeny. When segregating generations were tested with a single powdery mildew isolate (144), a qualitative single dominant gene inheritance pattern was observed. Nonsegregating wheat host lines (including IL72-2219-1, Hart, Blueboy, Va66-54-10, and Arthur) were tested for reaction to six differential mildew isolates. The reactions of each line to the six isolates were then compared with reactions of near-isogenic wheat lines with known genes for resistance. Both IL72-2219-1 and its seed parent, Va66-54-10, appear to contain gene *Pm*3a.

Line IL72-2219-1 (line IL) is a soft red winter wheat (*Triticum aestivum* L. em Thell.) developed by C. M. Brown at the University of Illinois. During field trials in Pennsylvania from 1978 through 1980, line IL showed consistently high yields and excellent resistance to natural epidemics of powdery mildew (Pm) caused by *Erysiphe graminis* DC. Merat f. sp. *tritici* Marchal. These and other traits make line IL a useful source of germ plasm in a plant-breeding program. Knowledge of the genetics involved in resistance of line IL to powdery mildew will facilitate efforts to improve the line or use it as a source of powdery mildew resistance. This study was designed to determine the inheritance of resistance to powdery mildew carried by this line and which, if any, previously reported genes are involved in resistance of line IL to mildew.

Although most of the wheat lines tested in Pennsylvania showed varying degrees of susceptibility to powdery mildew, line IL was free of powdery mildew in the field. For this reason, we assume that the resistance of line IL is the "vertical" or race-specific type described by Vanderplank (10).

Vertical resistance to *E. graminis* f. sp. *tritici* appears to be due to a gene-for-gene relationship between the host and pathogen. This relationship, explained in detail by Ellingboe (4), is based on corresponding gene pairs; for every gene pair for reaction in the host, there is a corresponding pair for pathogenicity in the pathogen. Vertical resistance genes are usually inherited in a simple Mendelian fashion.

At least 10 genes for resistance to *E. graminis* f. sp. *tritici* in the host have been reported. These genes in the host are known as *Pm*1, *Pm*2, *Pm*3a, *Pm*3b, *Pm*3c, *Pm*4 (3), *Pm*5 (7), *Pm*6 (6), *Pm*7 (9), and *MA* (Michigan Amber) (8).

MATERIALS AND METHODS

Parental wheat lines were chosen on the basis of their resistance or susceptibility to powdery mildew in the field. The cultivars Hart and Blueboy were chosen as the susceptible parents and line IL was used as the resistant parent. Line IL is a selection from the cross Va66-54-10/Arthur.

E. graminis f. sp. *tritici* isolate 144, supplied by W. L. Pedersen, University of Illinois, Urbana, was used to evaluate the parents as well as the F_1, F_2, and testcross progenies for powdery mildew reaction. He indicated that powdery mildew isolate 144 was virulent on lines carrying genes *Pm*2, *Pm*3c, *Pm*4, *Pm*5, and *MA* (*personal communication*). Isolate 144 is virulent on Hart and Blueboy and avirulent on line IL.

Inoculum of isolate 144 was produced and maintained on Chancellor wheat seedlings. The F_1, F_2, and testcross seedlings were inoculated at the one- to three-leaf stage while in plastic flats containing 72 4-cm pots. The potting mixture used was made of two parts peat, one part sand, and one part soil. Twelve seedlings of the Pm-susceptible cultivar Hart were distributed throughout each flat as a check for uniform inoculation. At the time of inoculation, the flats were tilted about 30 degrees to expose more leaf surface area to the conidia of the pathogen. Infected Chancellor seedlings were held about 20 cm above the plants in flats and gently shaken, causing conidia to fall onto the exposed leaves of the seedlings. After 24 hr, this procedure was repeated with the flats tilted in the opposite direction. Inoculated seedlings were then placed in a small incubation room maintained at 20 C. Fluorescent lights placed about 60 cm above the seedlings supplied continuous light at 60 μEinsteins^{-2}sec^{-1}.

After 7 days in the incubation room, the lower leaf of each seedling was examined for macroscopically visible *E. graminis* f. sp. *tritici* colonies. Disease severity was rated on a 0–4 scale where 0 = highly resistant (no visible colonies or plant reaction), 1 = very resistant (no colonies visible but small chlorotic flecks visible on leaves), 2 = moderately resistant (small nonsporulating colonies visible on leaves), 3 = moderately susceptible (sporulating colonies visible on leaves but limited in size and number), and 4 = highly susceptible (numerous large sporulating colonies visible on leaves).

This rating system is a conservative version of the system used by Finkner et al (5). No plant was considered resistant to powdery mildew unless it was free of macroscopically observable conidiophores and conidia. Therefore, plants with ratings of 0, 1, or 2 were considered resistant to powdery mildew. Although

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such ratings are arbitrary, they are dependable if the environmental conditions are held near the optimum for the pathogen. Chi-square tests were used to analyze segregation ratios and homogeneity.

A second experiment was done to determine if any previously reported genes for powdery mildew resistance are present in line IL, Hart, Blueboy, Va66-54-10, and Arthur. The latter two lines are the parents of line IL and were studied to determine the source of powdery mildew resistance in line IL.

Identification of genes for powdery mildew resistance was accomplished by exposing each wheat line to six differential *E. graminis* f. sp. *tritici* isolates. Near-isogenic wheat lines (3) containing known genes for powdery mildew resistance were also exposed to the same isolates. One can determine which gene(s) for resistance to powdery mildew may be present in a given wheat line by comparing the powdery mildew reactions of the line with the reactions of the near-isogenic wheat lines (isolines).

Line IL, Hart, Blueboy, Va66-54-10, Arthur, and wheat isolines containing *Pm*1, *Pm*2, *Pm*3a, *Pm*3b, *Pm*3c, *Pm*4, *Pm*5, and *MA* were inoculated with each of six differential mildew isolates. These isolates, identified by the numbers 60, 135, 8, 272, 185, and 131, are a collection of powdery mildew isolates maintained by the Department of Plant Pathology at the Pennsylvania State University.

Several modifications of the previously described inoculation procedure were employed to prevent cross-contamination of these six isolates. About 10 seeds each of line IL, Hart, Blueboy, Va66-54-10, and Arthur were planted in separate short rows (10 seeds of one line per row) within a plastic tray (13 cm wide, 33 cm long, and 8 cm deep). Six trays were prepared and filled with the potting mixture described previously. A 30-cm wooden pot stake was taped vertically to each corner of each tray. Each tray was then placed in a large plastic bag so that the pot stakes supported the bag, creating a small moist chamber. Trays were then placed in the greenhouse (18–24 C) until the seedlings were about 8 cm tall. Each tray was then inoculated with a different isolate by opening the bag and shaking conidia from infected Chancellor plants over the seedlings. After the plants in each tray were inoculated, the surrounding bag was sealed with a wire tie. To prevent mixing inoculum, hands and arms of the investigator were washed and dried thoroughly before handling each isolate. Once all bags were sealed, the trays were placed in an incubation room at 20 C as described previously. After 7 days, the bags were opened and seedlings rated for their reactions to the various isolates according to the rating scale described previously. The near-isogenic wheat lines were also inoculated and rated in a similar manner.

Table 1. Reactions of wheat cultivars as parents and F_1s to powdery mildew isolate 144[a]

Cultivar or F_1	No. plants tested	Use in genetic study	Reaction to isolate 144	
			Rating[b]	Classification[c]
Line IL	32	Resistant parent	0–1	Resistant
Hart	2	Susceptible parent	4	Susceptible
Blueboy	2	Susceptible parent	3–4	Susceptible
Va66-54-10	16	Female parent of line IL	0–1	Resistant
Arthur	8	Male parent of line IL	3	Susceptible
Hart/line IL	5	F_1	0–1	Resistant
Line IL/Hart	6	F_1	0–1	Resistant
Blueboy/line IL	6	F_1	0–1	Resistant
Line IL/Blueboy	12	F_1	0–1	Resistant

[a] Line IL is wheat line IL72-2219-1. The powdery mildew isolate 144 is virulent on Hart, Blueboy, and Arthur and avirulent on line IL.
[b] Reaction based on rating scale of 0–4, where 0 = highly resistant (no visible colonies or plant reaction), 1 = very resistant (no colonies visible but small chlorotic flecks visible on leaves), 2 = moderately resistant (small nonsporulating colonies visible on leaves), 3 = moderately susceptible (sporulating colonies visible on leaves but limited in size and number), and 4 = highly susceptible (numerous large sporulating colonies visible on leaves).
[c] Ratings of 0, 1, or 2 were considered resistant; 3 and 4 were considered susceptible.

Table 2. Segregations of seven (Hart/line IL plus reciprocal) F_2 families for resistance to powdery mildew isolate 144 and tests of fit to a single-gene inheritance model[a]

F_2 family	F_1 parent	Observed segregation[b]		Chi-square for fit to 3:1	P[c]
		Resistant	Susceptible		
1	Line IL/Hart	13	5	0.0741	0.7–0.8
2	Line IL/Hart	40	14	0.0247	0.8–0.9
3	Line IL/Hart	7	2	0.0370	0.8–0.9
4	Hart/line IL	15	4	0.1579	0.5–0.7
5	Hart/line IL	26	15	2.9350	0.05–0.1
6	Hart/line IL	13	4	0.0196	0.8–0.9
7	Hart/line IL	14	1	2.6889	0.1–0.2
Pooled		128	45	0.0944	0.7–0.8

[a] Line IL is wheat line IL72-2219-1. The powdery mildew isolate 144 is virulent on Hart and avirulent on line IL.
[b] Reaction based on rating scale of 0–4, where 0 = highly resistant (no visible colonies or plant reaction), 1 = very resistant (no colonies visible but small chlorotic flecks visible on leaves), 2 = moderately resistant (small nonsporulating colonies visible on leaves), 3 = moderately susceptible (sporulating colonies visible on leaves but limited in size and number), and 4 = highly susceptible (numerous large sporulating colonies visible on leaves). Ratings of 0, 1, or 2 were considered resistant; 3 and 4 were considered susceptible.
[c] Not significant ($P > 0.05$).

RESULTS AND DISCUSSION

Reactions of lines, F_1s, and F_2s to isolate 144. Line IL and its female parent (Va66-54-10) showed resistance to the powdery mildew isolate 144, whereas Hart, Blueboy, and the male parent (Arthur) of line IL were susceptible to this isolate (Table 1). The resistance to powdery mildew is dominant because all 11 F_1s between Hart and line IL and all 18 F_1s between Blueboy and line IL were resistant to powdery mildew isolate 144.

Observed segregations in F_2 generations of both crosses showed a satisfactory fit to a 3:1 ratio (Tables 2 and 3) and both sets of F_2 families were homogeneous according to homogeneity chi-square tests ($0.2 < P < 0.3$ and $0.5 < P < 0.7$). Segregation for resistance to powdery mildew in the testcross Hart/line IL//Hart was 52 plants resistant and 47 plants susceptible to powdery mildew, whereas in the cross Blueboy/line IL//Blueboy, the segregation was 57 plants resistant and 49 plants susceptible to powdery mildew; both testcross segregations showed a satisfactory fit to a 1:1 ratio, $0.5 < P < 0.7$ and $0.3 < P < 0.5$, respectively. These ratios are characteristic of the inheritance model for a single dominant gene. The same type of inheritance was observed for many *Pm* genes (1,2,6).

Reactions of lines to differential powdery mildew isolates. Because any given powdery mildew isolate may contain a number of genes for virulence, the following possibilities exist: 1) Line IL may contain only one gene for resistance to powdery mildew; 2) line IL may contain one gene that controls compatibility with powdery mildew isolate 144 plus one or more genes for resistance that are ineffective against isolate 144; 3) Hart, Blueboy, or both may contain no genes for resistance to powdery mildew; and 4) Hart, Blueboy, or both may contain one or more genes for resistance that are ineffective against powdery mildew isolate 144, indicating that isolate 144 may possess one or more unidentified genes for virulence.

The second experiment was designed to eliminate some of the possibilities discussed. Reactions of line IL, Hart, Blueboy, Va66-54-10, Arthur, and the near-isogenic wheat lines to the six differential mildew isolates show that

Table 3. Segregations of eight (Blueboy/line IL[a] plus reciprocal) F_2 families for resistance to powdery mildew isolate 144 and tests of fit to a single-gene inheritance model

F_2 family	F_1 parent	Observed segregation[b]		Chi-square for fit to 3:1	P[c]
		Resistant	Susceptible		
8	Blueboy/line IL	14	4	0.0741	0.7–0.8
9	Blueboy/line IL	53	14	0.6020	0.3–0.5
10	Line IL/Blueboy	6	4	1.2000	0.2–0.3
11	Line IL/Blueboy	80	19	1.7811	0.1–0.2
12	Line IL/Blueboy	13	6	0.4386	0.5–0.7
13	Line IL/Blueboy	36	9	0.6000	0.3–0.5
14	Blueboy/line IL	11	7	1.8519	0.1–0.2
15	Blueboy/line IL	59	19	0.0171	0.8–0.9
Pooled		272	82	0.6365	0.3–0.5

[a] Line IL is wheat line IL72-2219-1. The powdery isolate 144 is virulent on Blueboy and avirulent on line IL.
[b] Reaction based on rating scale of 0–4, where 0 = highly resistant (no visible colonies or plant reaction), 1 = very resistant (no colonies visible but small chlorotic flecks visible on leaves), 2 = moderately resistant (small nonsporulating colonies visible on leaves), 3 = moderately susceptible (sporulating colonies visible on leaves but limited in size and number), and 4 = highly susceptible (numerous large sporulating colonies visible on leaves). Ratings of 0, 1, or 2 were considered resistant; 3 and 4 were considered susceptible.
[c] Not significant ($P > 0.05$).

Table 4. Reactions of wheat cultivars, lines, and isolines to six *Erysiphe graminis* f. sp. *tritici* isolates[a]

	Isolate					
	60	135	8	272	185	131
Wheat cultivar or line						
Line IL[b]	4	1–2	1–2	0–2	0–1	2
Va66-54-10	4	0	0	0	0	2
Arthur	4	4	4	2–3[c]	3	4
Hart	4	4	4	4	4	4
Blueboy	4	4	4	3[d]	4	4
Wheat isoline						
*Pm*1	0	0	4	4	0	0
*Pm*2	4	4	4	2	0	1
*Pm*3a	4	0	0	0	0	0
*Pm*3b	0	3	0	0	0	0
*Pm*3c	4	4	3	4	3	3
*Pm*4	3	4	3	0	0	0
*Pm*5	4	4	4	0	0	0
MA	4	4	3	4	1	4

[a] Reaction based on rating scale of 0–4, where 0 = highly resistant (no visible colonies or plant reaction), 1 = very resistant (no colonies visible but small chlorotic flecks visible on leaves), 2 = moderately resistant (small nonsporulating colonies visible on leaves), 3 = moderately susceptible (sporulating colonies visible on leaves but limited in size and number), and 4 = highly susceptible (numerous large sporulating colonies visible on leaves).
[b] Line IL is wheat line IL72-2219-1.
[c] Only a few conidial chains were observed macroscopically.
[d] Showed severe chlorosis in addition to limited sporulation of pathogen.

Hart, Blueboy, and Arthur were susceptible to all six mildew isolates (Table 4). Therefore, these cultivars do not contain any of the genes for resistance that were tested for, with the possible exception of the line carrying the gene *Pm*3c. Line IL and Va66-54-10 were resistant to the same powdery mildew isolates as the *Pm*3a wheat isoline. No other gene for resistance to powdery mildew gave the same differential reactions. The reactions of line IL to powdery mildew isolates 135, 8, 272, and 185 are not exactly like those of cultivar Va66-54-10 or *Pm*3a wheat isoline. Line IL showed chlorotic flecking of the leaves in the absence of powdery mildew and this phenomenon contributed to the disease severity rating (1 = very resistant) observed. Based on this evidence, it appears that line IL contains gene *Pm*3a or an undiscovered gene that reacts the same macroscopically as does *Pm*3a to these six isolates. Because gene *Pm*3a is known to be dominant (2), evidence from the first experiment supports the identification of this gene. It is also evident that line IL obtained its resistance to powdery mildew from Va66-54-10.

Both line IL and the *Pm*3a isoline are susceptible only to powdery mildew isolate 60. This isolate can also overcome *Pm*2, *Pm*3c, *Pm*4, *Pm*5, and *MA*; except for *Pm*3c, one cannot overlook the possibility that line IL contains one of these genes in addition to *Pm*3a. This possibility could be investigated if line IL were screened for resistance to powdery mildew with the proper isolates.

Unfortunately, wheat lines used as sources of resistance to many diseases are often poor sources of other agronomic traits. In addition to powdery mildew resistance, line IL shows such desirable agronomic traits as high yield, good standability, and winterhardiness. After hybridization of this line with other lines of proven performance, one might expect a relatively high frequency of useful agronomic wheat lines in the segregating generations.

Identification of specific genes for resistance to powdery mildew in breeding materials, such as line IL, is necessary to properly manage genetic resources in the host. Information about the distribution of genes for virulence within the pathogen population is also necessary. Once such information is obtained, plant breeders can determine which genes for resistance to powdery mildew will be effective in a particular geographic region.

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