Identification of Powdery Mildew Resistance Genes in Cultivars of Soft Red Winter Wheat

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ABSTRACT

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Twenty-two soft red winter wheat (*Triticum aestivum*) cultivars were inoculated with isolates of *Erysiphe graminis* f. sp. *tritici* to determine genes for resistance. Cultivars were tested with a total of 27 isolates that had been characterized from reactions on differential host lines. Gene determinations were completed separately in two laboratories with different isolates and the results were combined. Intact 10-day-old seedlings or detached primary leaves on benzimidazole-amended agar were inoculated, and evaluations based on pustule number and type were made 10–14 days later. Resistance genes were postulated based on application of the gene-for-gene concept and pedigree analysis. One cultivar was not fully characterized, while results indicated some cultivars carried no known powdery mildew resistance genes (*Pm*). The genes *Pm*3a, *Pm*5, and *Pm*6 were present in some of the cultivars tested.

Powdery mildew of wheat (*Triticum aestivum* L.) caused by *Erysiphe graminis* DC. ex Merat f. sp. *tritici* (Em. Marchal) is a prevalent disease in the soft red winter wheat region of the United States. This disease was shown to cause yield losses of approximately 12%, 27%, and 34% in the Midwest, East and Southeast, respectively, on recently developed cultivars, some of which possess single genes for powdery mildew resistance (9,15,20). Similar losses can be anticipated in commercial production because fungicide usage on soft red winter wheat is currently limited to a small percentage of the hectarage.

Control of powdery mildew has relied heavily on the use of single gene resistance, and the common management strategy has been to replace cultivars when their resistance is no longer effective (33). Information on the presence and frequency of virulence genes in the pathogen population is necessary in order to replace ineffective resistance genes with genes that are currently useful. Similarly, a knowledge of availability and usage of host genes is a major consideration for development and recommendation of new cultivars. Five virulence surveys have recently been completed in the United States and Canada that provide important information on the pathogen (2,17,23,25,27). A number of host genes for powdery mildew resistance have also been identified (22). Pedigree relationships have been used to suggest possible genes for mildew resistance that have been incorporated into U.S. soft red winter wheat cultivars (4,27); however, direct evidence of which genes are located in specific cultivars actually being used is unavailable.

Information on powdery mildew resistance for most of the German spring and winter wheat cultivars has been published (11,12). Determinations were completed both through inoculations with isolates of *E. g.* f. sp. *tritici* selected to differentiate powdery mildew resistance genes *Pm*1–*Pm*9 and *Mlk* phenotypically and through the examination of pedigree relationships. Combined with virulence data (10,19), this information has been valuable for European wheat breeders planning crosses and is essential for developing management strategies involving cultivar recommendations, deployment schemes, multilines, and cultivar mixtures. Information on host resistance can also be combined with virulence data to forecast the collapse of resistance caused by shifting pathogen populations. Lack of this specific genetic information on U.S.-grown cultivars has hindered breeding and management efforts.

The objective of this study was to use cultures of *E. g.* f. sp. *tritici* with known virulence genes, through the application of Flor's gene-for-gene hypothesis (8) and pedigree relationships, to postulate which genes for powdery mildew resistance occur in selected soft red winter wheat cultivars. A preliminary report has been published (16).

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Table 1. Cultivars, accession numbers and seed sources of 22 soft red winter wheat cultivars characterized for powdery mildew resistance

Cultivar	Accession number	Seed source
Abe	CI 15375	H. W. Ohm, Purdue University
Arthur	CI 14425	G. E. Shaner, Purdue University
Arthur 71	CI 15282	G. E. Shaner, Purdue University
Blueboy	CI 14031	J. P. Murphy, North Carolina State University
Caldwell	CI 17897	H. W. Ohm, Purdue University
Coker 747	None	H. F. Harrison, Coker's Pedigreed Seed Co.
Coker 762	None	H. F. Harrison, Coker's Pedigreed Seed Co.
Coker 797	None	H. F. Harrison, Coker's Pedigreed Seed Co.
Coker 983	None	H. F. Harrison, Coker's Pedigreed Seed Co.
Double Crop	CI 17349	R. K. Bacon, University of Arkansas
Florida 301	CI 17769	R. D. Barnett, University of Florida
Florida 302	PVP 8500054	R. D. Barnett, University of Florida
Ga 1123	CI 13292	J. P. Murphy, North Carolina State University
Hardired	CI 12411	J. P. Murphy, North Carolina State University
Knox 62	CI 13701	H. W. Ohm, Purdue University
McNair 701	CI 15288	H. F. Harrison, Coker's Pedigreed Seed Co.
McNair 1003	None	H. F. Harrison, Coker's Pedigreed Seed Co.
Oasis	CI 15929	H. W. Ohm, Purdue University
Pioneer S-76	None	J. P. Murphy, North Carolina State University
Redcoat	CI 13170	J. P. Murphy, North Carolina State University
Redhart	CI 8898	J. P. Murphy, North Carolina State University
Saluda	PI 480474	J. P. Murphy, North Carolina State University

Table 2. Reactions of 22 cultivars or lines with known genes for powdery mildew resistance after inoculation with 11 isolates of *Erysiphe graminis* f. sp. *tritici* in Raleigh, North Carolina

Cultivar or line	Resistance gene(s)	Isolates of *Erysiphe graminis* f. sp. *tritici*										
		ABK	Yuma	140	7-12	Asosan	Quincy	Pm4a	129	144	Mo10	Pm4
Axminster/8*CC[a]	*Pm1*	S[b]	R	R	R	R	R	R	R	R	R	R
Ulka/8*CC	*Pm2*	S	S	S	R	S	S,I	S	R,I	S	R	S
Galahad	*Pm2*	...	...	...	...	...	...	...	...	...	...	...
Avalon	*Pm2*	...	...	...	...	...	...	...	...	...	...	...
Asosan/8*CC	*Pm3a*	R	S	I,R	S	S	I	S	...	R	R,I	I
Chul/8*CC	*Pm3b*	R	R	R,I	S	R	S,I	R	S	R	R,I	R
Sonora/8*CC	*Pm3c*	R	S	R,I	S	R	S,I	S	S	R,I	S	I
Khapli/8*CC	*Pm4a*	R	R,I	R	R	R,I	R	S	S	I,R	R	R
Yuma/8*CC	*Pm4a*	R	R	R	R	R,I	R	S	R	I,R	R	R
Orbis	*Pm4b*	...	...	...	...	...	...	...	...	...	...	...
Rektor	*Pm5*	...	...	...	...	...	...	...	...	...	...	...
Wattines	*Pm5*	...	...	...	...	...	...	...	...	...	...	...
TP114	*Pm2* + *Pm6*	R	S	R	S	S	R	S	R	S	R	I
Transec	*Pm7*	R	S,I	R	R	R	R	R	R	R	R	R
Kavkaz	*Pm8*	R	R,I	R	R	R	R	R	S	R	R	...
Disponent	*Pm8*	...	...	...	...	...	...	...	...	...	...	...
Goetz	*Pm8*	...	...	...	...	...	...	...	...	...	...	...
Ralle	*M1k*	...	...	...	...	...	...	...	...	...	...	...
Hustler	*Pm2* + *Pm6*	...	...	...	...	...	...	...	...	...	...	...
Bert	*Pm5* + *Pm6*	...	...	...	...	...	...	...	...	...	...	...
Granada	*Pm5* + *Pm8*	...	...	...	...	...	...	...	...	...	...	...
Mephisto	*Pm1* + *Pm2* + *Pm9*	...	...	...	...	...	...	...	...	...	...	...

[a] "8*CC" indicates that the line to the left of the slash was crossed to Chancellor, and seven subsequent backcrosses to Chancellor were then completed.

[b] Reaction types are summarized into three primary categories: R = resistant, I = intermediate, and S = susceptible. The comma indicates that in these cases, the three categories were sufficient for explaining observed variations. R,I indicates that although clear resistant reactions were primarily observed, intermediate reactions were also observed.

MATERIALS AND METHODS

Seed of near-isogenic lines of the Chancellor series with known genes for powdery mildew resistance was originally obtained from J. G. Moseman, USDA-ARS, Beltsville, MD; these lines have previously been described (5–7,21). Seed of lines TP114, Transec, and Kavkaz carrying *Pm6*, *Pm7*, and *Pm8*, respectively (14,21), was also obtained from J. G. Moseman. Seed of Avalon and Galahad, both carrying *Pm2* (4,31), and Hustler, carrying *Pm2* and *Pm6* (22), was provided by the National Institute of Agricultural Botany, Cambridge, UK. The remaining cultivars possessing known powdery mildew resistance genes (11,12) were provided by German plant breeders via the "Bundessortenamt," Hannover, FRG. Seed of the U.S. cultivars characterized in this study was obtained from numerous sources (Table 1).

Greenhouse Evaluation—Raleigh, North Carolina. Plants were grown in the spring of 1988 and 1989 in the greenhouse under natural light at North Carolina State University in Raleigh. Four

Table 3. Reactions of 22 cultivars or lines with known genes for powdery mildew resistance after inoculation with 16 isolates of *Erysiphe graminis* f. sp. *tritici* in Weihenstephan, West Germany

Cultivar or line	Resistance gene(s)	Isolates of *Erysiphe graminis* f. sp. *tritici*										
		4a	9a	10	$E_2$15	$E_3$25	$E_3$37	85135	6	$E_3$14	$E_3$20	W72/27
Axminster/8*CC[a]	*Pm1*	I,S[b]	R	R,I	R	S	R	S	S	R,I	R	S
Ulka/8*CC	*Pm2*	...	...	...	...	...	...	...	...	...	...	...
Galahad	*Pm2*	R	S	R	R	R	R	S	S	R	R	S
Avalon	*Pm2*	R	S	R	R	R	R	S	S	R	R	S
Asosan/8*CC	*Pm3a*	R	S	R	R	R	R	R	R	R	S	R
Chul/8*CC	*Pm3b*	R	R	R	R	R	R	R	R	R	R	R
Sonora/8*CC	*Pm3c*	S	S	...	S	S	S	R	S	R	S	...
Khapli/8*CC	*Pm4a*	S	S	I	R	S	S	S	S	S	S	R
Yuma/8*CC	*Pm4a*	S	S	I	R	S	S	S	S	S	S	R
Orbis	*Pm4b*	R	S	R	R	S	S	S	S	S	S	R
Rektor	*Pm5*	S	S	S	S	S	R,I	I	I	S	S	I
Wattines	*Pm5*	S	S	S	S	S	R,I	I,R	I	S	S	I
TP114	*Pm2* + *Pm6*	...	...	...	...	...	...	...	...	...	...	...
Transec	*Pm7*	...	...	...	...	...	...	...	...	...	...	...
Kavkaz	*Pm8*	...	...	...	...	...	...	...	...	...	...	...
Disponent	*Pm8*	S	S	S	S	S	S	I,R	I,R	S	S	R,I
Goetz	*Pm8*	S	S	S	S	S	S	R,I	R,I	S	S	R,I
Ralle	*M1k*	S	I,R	S	R	R	R	R	S	R	R	R
Hustler	*Pm2* + *Pm6*	R	S	R	R	R	R	S	S	R	R	I
Bert	*Pm5* + *Pm6*	S	S	I	I	S	R	I	I	I	I,R	I,R
Granada	*Pm5* + *Pm8*	S	S	S	S	S	R,I	R	R	S	S	R
Mephisto	*Pm1* + *Pm2* + *Pm9*	R	R	R	R	R	R	S	R,I	R	R	S

[a] "8*CC" indicates that the line to the left of the slash was crossed to Chancellor, and seven subsequent backcrosses to Chancellor were then completed.

[b] Reaction types are summarized into three primary categories: R = resistant, I = intermediate, and S = susceptible. The comma indicates that in these cases, the three categories were sufficient for explaining observed variations. R,I indicates that although clear resistant reactions were primarily observed, intermediate reactions were also observed.

Table 4. Reactions of 21 soft red winter wheat cultivars after inoculation with 11 previously characterized isolates of *Erysiphe graminis* f. sp. *tritici* in Raleigh, North Carolina

Cultivar or line	Putative resistance gene(s)	Isolates of *Erysiphe graminis* f. sp. *tritici*										
		ABK	Yuma	140	7-12	Asosan	Quincy	Pm4a	127	144	Mo10	Pm4
Arthur 71	None	S[a]	S	S	S	S	S	S	S	S	S	S
Blueboy	None	S	S	S	S	S	S	S	S	S	S	S
McNair 701	None	S	S	S	S	S	S	S	S	S	S	S
McNair 1003	None	S	S	S	S	S	S	S	S	S+R	S	S
Pioneer S-76	None	S	S	S	S	S	S	S	S	I	S	S
Knox 62	None	R+S	S	S	S	S	...	...	S	S	...	...
Redcoat	None	S	S	S	S	S	S	S	S	S	S	S
Redhart	None	...	S	S	S+R	S	...	...	...	S	...	S
Coker 797	*Pm*3a	R	S	R	S	S	R,I	S	R	R	R	S
Florida 301	*Pm*3a	R	S	R	S	S	I	S	R	R	R	S
Florida 302	*Pm*3a + ?	R	S	R	I	I	R	R,I	R	R	R	S,I
Saluda	*Pm*3a	R	S	R	S	S	I	S	R	R	R	S
Caldwell	*Pm*5	R	S	S	S	S	S	S	R,I	S,I	R,I	S
Ga 1123	*Pm*5	R	...	...	S	...	S	S	R	R,I	S+R	S
Hardired	*Pm*5	R	S	...	S	...	S	S	...	S+R	S+R	S
Abe	*Pm*6	R	S	R	S	S	R	S	R	S	R	S
Coker 747	*Pm*6	R	S	R	S	S	R,I	S	R+I	S	...	S
Oasis	*Pm*6	R	S	R	S	S	...	S	R	S	...	S
Arthur	*Pm*5 + *Pm*6[b]	R,I	S	I,S	S	S	R	S	R	S+R	R,I	S
Coker 983	*Pm*5 + *Pm*6	R	S	R	I	S	R	I	R	S+R	R	S
Double Crop	*Pm*5 + *Pm*6	R	S	I,R	S	S	R	S	R	S	R	S

[a] Reaction types are summarized into three primary categories: R = resistant, I = intermediate, and S = susceptible. The comma and the "+" indicate that in these cases the three categories were insufficient for explaining observed variations; therefore, combined classifications were used. R,I indicates that clear resistant reactions were primarily observed, but intermediate reactions were also observed. The "+" indicates that both reaction types were observed, with the predominant reaction listed first.

[b] It is likely that Arthur is not homogenous based on observation of *Pm*5 reactions.

seeds of the differentials and test cultivars were planted in 7.5-cm-diameter clay pots in a commercial potting mix (Metro-Mix, W. R. Grace & Co., Cambridge, MA) and thinned shortly after emergence to leave two plants. Two pots of each cultivar were included for each isolate, and pots were arranged randomly in 60 × 60 × 30 cm or 60 × 30 × 30 cm (L × W × H) glass chambers to eliminate contamination among isolates. Susceptible controls were included to ensure the uniformity of deposition of inoculum.

2	3	5	8	85072
S	S	R	S	S
...	...	...	...	...
R	R	R	S	R
R	R	R	S	R
R	R	R	R	R
R	R	R	R	...
...	...	...	...	...
S	S	I	S	R
S	S	I	S	R
S	S	R	S	R
S	I	S	S	I
S	I	S	S	I
...	...	...	...	...
...	...	...	...	...
...	...	...	...	...
S	S	S	S	S
S	S	S	S	S
R	I	R	R	R
R	R	R	R,I	R
...	R,I	R	R,I	R
S	I	S	S	R,I
...	...	...	...	...

Inoculum was maintained by growing plants of the susceptible cv. Chancellor for 10 days in 7.5-cm-diameter pots in an enclosed chamber on a greenhouse bench. Pots were then removed and fitted with 25-cm-tall lamp chimneys plugged with cotton. Conidia from a few pustules of an isolate were deposited at the top of the chimney to initiate new cultures. Just before inoculation, pots were drenched with 50 ml of a 50 ppm solution of chlormequat chloride (Cycocel, American Cyanamid Co., Ft. Wayne, NJ) to retard plant growth. Cultures were maintained at 8 C and transferred every 6 wk over the course of the study. Cultures ABK, Yuma, Quincy, Asosan, 129, 140, 144, Mo10, Pm4, and Pm4a, were obtained from J. G. Moseman, USDA-ARS, Beltsville, MD. Origin of some of these cultures has been reported elsewhere (24). Culture 7-12 was originally recovered in a virulence survey in 1986 in a field of Saluda wheat in Stanly County, North Carolina (17). It was also transferred repeatedly from single pustules to ensure purity before inclusion in our collection. Inoculations of the test cultivars were performed by gently shaking conidia from 2-wk-old cultures at the top of the glass chambers. Plants were at the three- to four-leaf stage at inoculation and remained in the greenhouse an additional 10–12 days until evaluation.

Laboratory evaluation—Weihenstephan, West Germany. Thirty-five seeds of each of the wheat genotypes were sown in 7.5-cm-diameter styrofoam pots covered with cellophane bags to prevent contamination and were grown at 19 C. After 10 days, 3-cm long pieces taken from the middle portion of the primary leaves were placed on 0.5% water agar amended with 50 ppm benzimidazole in 19 × 10 × 1.5 cm plastic dishes. Three leaf pieces of each genotype were positioned at defined places in one plastic dish, with two dishes representing one replication of the experiment. Dishes were stored overnight to equalize leaf turgor; inoculations were completed in a settling tower by uniformly dispersing conidia formed on detached leaves of the highly susceptible cv. Kanzler (11). Direct counts of conidia ensured inoculation densities of 200–400 spores per square centimeter. Following inoculation, leaves were placed at 17 ± 1 C under low light intensity for 10–14 days until evaluation. Additional details of these methods have been published elsewhere (1,11).

Spores for inoculation were produced on detached leaves on Kanzler, similar to procedures described above. Single pustule-derived isolates 2, 3, 4a, 5, 6a, 8, 9a, 10, $E_3$14, $E_2$15, $E_3$20, $E_3$25, and $E_3$37 were collected in West Germany from 1984 to 1986 (11). Isolate W72/27 was provided by W. Summers, Cambridge, UK; isolates 85072 and 85135 were provided by P. M. Fried, Zürich, Switzerland. All isolates of *E. g.* f. sp. *tritici* have been maintained in the collection at Weihenstephan, West Germany. These cultures have been described previously, but because the wheat/powdery mildew-host/pathogen system may be influenced by environ-

Table 5. Reactions of 21 soft red winter wheat cultivars after inoculation with 16 previously characterized isolates of *Erysiphe graminis* f. sp. *tritici* in Weihenstephan, West Germany.

Cultivar or line	Putative resistance gene(s)	Isolates of *Erysiphe graminis* f. sp. *tritici*										
		4a	9a	10	$E_2$15	$E_3$25	$E_3$37	85135	6	$E_3$14	$E_3$20	W72/27
Arthur 71	None	S[a]	S	S	S	S	S	S	S	S	S	S
Blueboy	None	S	S	S	S	S	S	S	S	S	S	S
McNair 701	None	S	S	S	S	S	S	S	S	S	S	S
McNair 1003	None	S	S	S	S	S	S	S	S	S	S	S
Pioneer S-76	None	S	S	S	S	S	S	S	S	S	S	S
Knox 62	None	S	S	S	S	S	S,I	S,I	S	S	S	S
Redcoat	None	S	S	S	S	S	S	S,I+R	S	S	S	S
Redhart	None	S	S	S+R	S	S	S,I+R	S,I	S	S	S,I	S
Coker 797	*Pm*3a	R	S	R	R	R	R	R,I	R	R	S	R
Florida 301	*Pm*3a	I,R	S	R	R	R	R	R	R	R	S	R
Florida 302	*Pm*3a + ?	R	S	R	R	R	R	R	R	R	I	R
Saluda	*Pm*3a	I,R	S	R	R	R	R	R	R	R	S	R
Caldwell	*Pm*5	S	S	S	S	S	R,I	I,R	I	S	S	R,I
Ga 1123	*Pm*5	S	S	S,I	S	S	I+R	I,S	S	R	S	I,R+S
Hardired	*Pm*5	S	S	S	S	S	I	I,S	S,I	S	S	I
Abe	*Pm*6	S	S+R	I,S	S,I+R	S	I	S	S	S	S	I
Coker 747	*Pm*6	S	S	I,S	I,S	S	I	S	S	S	S	I
Oasis	*Pm*6	S	S	S,I	I,S	S	I	S	S+R	S	S+R	I
Arthur	*Pm*5 + *Pm*6[b]	S	S	I,S	R+S	S+R	I,R	S	S	S	I,S	I+R
Coker 983	*Pm*5 + *Pm*6	S	S	I,S	I,S	S+R	R,I	I	I	S	I,S+R	R
Double Crop	*Pm*5 + *Pm*6	S	S	I,S	I,R	S	R	R	R	S	I,S	R

[a] Reaction types are summarized into three primary categories: R = resistant, I = intermediate, and S = susceptible. The comma and the "+" indicate that in these cases the three categories were insufficient for explaining observed variation; therefore, combined classifications were used. R,I indicates that clear resistant reactions were primarily observed, but nearly intermediate reactions were also observed. The "+" indicates that both reaction types were observed, with the predominent reaction listed first.

[b] It is likely that Arthur is not homogenous based on observation of *Pm*5 reactions.

mental conditions, test cultivars possessing known powdery mildew resistance genes were inoculated simultaneously with cultivars to be characterized in each experiment.

Evaluation. Greenhouse evaluations were completed according to an evaluation scale modified from Moseman (24). The scale is based on infection types (IT) where 0 = immune, no visible sign of infection; 1–3 = resistant, increasing from 1) flecks with no necrosis to 2) necrosis, to 3) chlorosis, while the amount of mycelium went from none to a detectable amount; 4–6 = intermediate, chlorotic areas decreasing in amount while mycelium and conidia production increased from slight to moderate; 7–9 = susceptible, increasing amount, size, and density of mycelium and conidia to a fully compatible reaction. The reactions were summarized by combining IT into three groups with resistant (R) = 0–3, intermediate (I) = 4–6, and susceptible (S) = 7–9. Assessment of detached leaves in laboratory evaluation was based upon 1) infection severity from 0 to 9, where 0 = no visible symptoms and 9 = 50–100% of the leaf area covered with pustules, and 2) infection type from 0 to 4, where 0 = no pustules visible and 4 = large pustules without a hypersensitive host response. From these two evaluation scales, three major classes (resistant, intermediate, and susceptible) of host response again were formed. However, in some cases in both greenhouse and laboratory studies, these three classes of host response were insufficient in explaining the observed reaction. Therefore, a combined classification was introduced. R,I indicates that although resistant responses were primarily observed, some intermediate reactions were also observed.

All experiments were repeated at least twice, and infection data were summarized across replications and experiments from one location. Gene postulations were based on comparisons of phenotypes expressed by test cultivars to previously characterized host lines when inoculated with the same isolates. Pedigree information was also used to determine if known gene donors were in the pedigree of a test cultivar.

RESULTS

Susceptible checks placed in the glass chambers indicated that inoculations were uniform in greenhouse studies. The isolated control plants remained free of symptoms in all greenhouse studies, indicating that contamination did not affect results. In laboratory studies, conidia counts on glass microscope slides indicated that inoculum was uniformly distributed and nearly equal across replications.

The reactions of seven near-isogenic lines and 15 wheat cultivars with previously identified genes for powdery mildew resistance to 11 isolates of *E. g.* f. sp. *tritici* from the U.S. and to 16 isolates from the collection at Weihenstephan are presented. The U.S. cultures allowed separation of lines with resistance genes *Pm*1–*Pm*4a and *Pm*6–*Pm*8, including three alleles at the *Pm*3 locus (Table 2). Virulence to a gene reported to be from cv. Michigan Amber was also evaluated by comparing reactions of test cultivars to reaction on CI 14033, a Chancellor backcross line (7,18). However, the cultures were not tested against *Pm*4b or *Pm*5. Isolates of *E. g.* f. sp. *tritici* from the Weihenstephan collection were effective in distinguishing host genotypes with *Pm*1–*Pm*9, including the multiple alleles at the *Pm*3 and the *Pm*4 loci, and a recently identified gene designated as Mlk (11,13) (Table 3). These cultures were not used to detect *Pm*7 or the gene reported from Michigan Amber. However, the resistance conditioned by both *Pm*5 and *Pm*6 is not expressed in the clear patterns associated with the other *Pm* genes. This was seen with isolates $E_3$37 and 85135 on Rektor and Wattines. The background into which these genes are incorporated appears to be influencing the degree to which they are expressed (Tables 2 and 3).

The reaction of 21 soft red winter wheat cultivars against 27 characterized isolates of *E. g.* f. sp. *tritici* were evaluated (Tables 4 and 5). The reaction of Coker 762 to four isolates of *E. g.* f. sp. *tritici* is not shown, because tests were completed separately. Reactions concerning Michigan Amber are not shown in the interest of brevity and because there was no evidence that the gene from that cultivar was present in any of the cultivars evaluated. Five cultivars, Arthur 71, Blueboy, McNair 701, McNair 1003, and Pioneer S-76, were highly susceptible to all the isolates of *E. g.* f. sp. *tritici* used in this study, indicating that none of the abovementioned *Pm* genes are within these cultivars. Cultivars Knox 62, Redcoat, and Redhart also reacted as highly

2	3	5	8	85072
S	S	S	S	S
S	S	S	S	S
S	I	...	...	S,I
S	S	S	S	S
S	S	S	S	S
S+R	S+R	S	S	S
S	S+R	S	S+R	S+R
S+R	S+R	...	...	I,S
R	R	R	R	R
R	R	R	R	R
R	R	R	R	R
R	R	R	R	R
S	I,R	S	I,S	I
S	I,R	S	I,S	I,S
S	I,R	S	S+I	S,I
I+S	I	I	I	I,R
S	I	S,I	I	I,S
I,R	I+R	R	I,R	R
R,I	R,I	R,I	R,I	R
I	R	I	R,I	R
I	R,I	R,I	R,I	R

susceptible to most of these isolates, and some intermediate reactions were observed with two European isolates (Table 5), but this could not be clearly attributed to any of the above-mentioned resistance genes.

Four cultivars, Coker 797, Florida 301, Florida 302, and Saluda, showed a resistance pattern characteristic of *Pm*3a. Florida 302 must possess some additional resistance as indicated by its intermediate-to-resistant reactions to six cultures virulent to *Pm*3a (Tables 4 and 5). Coker 762 also reacted resistant to eight isolates with *Pm*3a virulence (*data not shown*). From the virulence pattern of these isolates, it can be inferred that either *Pm*3a or *Pm*3b is in Coker 762.

Caldwell, Ga1123, and Hardired showed a resistance pattern (Table 5) indicative of the presence of *Pm*5 when compared to the patterns of characterized cultivars (Table 3). The resistance gene *Pm*6 appears to account for the reaction patterns of Abe, Coker 747, and Oasis. It is logical that both *Pm*5 and *Pm*6 are incorporated in Arthur, Coker 983, and Double Crop based on resistance patterns (Tables 4 and 5), however, the reaction pattern for Arthur is not as characteristic of these genes as the other two lines.

DISCUSSION

The isolates of *E. g.* f. sp. *tritici* used in this study were selected for their capacity to distinguish among lines possessing different powdery mildew resistance genes. However, in order to fully characterize these cultivars, crosses between lines with known genes for resistance are necessary, as is the subsequent testing with isolates done here. Phenotypic analysis, as done in this study, can provide much of this information, and many more lines can be tested than if crosses are completed for genotypic analysis. The use of isolates from both collections has enhanced our ability to postulate these resistance genes based on expression of infection types. For example, most of the European isolates are virulent to *Pm*8, making it difficult to distinguish between *Pm*5 and *Pm*8. However, with one exception, the Raleigh isolates are avirulent to *Pm*8. In a combined analysis, the clear separation of *Pm*5 and *Pm*8 effects becomes possible.

Cultivars Arthur 71, Blueboy, McNair 701, McNair 1003, and Pioneer S-76 are highly susceptible to all of the 27 isolates of *E. g.* f. sp. *tritici* used in these studies. Therefore, it is concluded that these cultivars carry none of the powdery mildew resistance genes analyzed, specifically *Pm*1–*Pm*9 and *Mlk*. Similar conclusions have been formed concerning Knox 62, Redcoat, and Redhart, but in these cases some intermediate reactions were observed. These intermediate reactions occurred with the same isolates, $E_3$37 and 85135, that resulted in intermediate reactions on cultivars with *Pm*5, such as Caldwell, Ga1123, and Hardired. Both Redcoat and Knox 62 have cultivar Hope, the original *Pm*5 source, in their pedigrees (18,34), and Wolfe has considered the resistance in Redcoat to be identical to that in Hope (32). These discrepancies may have arisen because of the difficulty in detecting *Pm*5, which conditions an adult plant resistance that does not give a clear reaction in seedling tests (11). However, an important point in reaching our conclusions was that these cultivars do not express the intermediate reaction that 16 cultivars carrying *Pm*5 showed to isolate W72/27 in another study (11). Further, Knox 62 and Redcoat do not differ from Redhart in these tests, and Redhart shows no apparent source of *Pm*5 in its pedigree (34). It seems that the documented slow-mildewing characteristics of Knox (29) and, presumably, those of Knox 62, are not caused by any known monogenic adult plant resistance. This serves to point out that cultivars with the same or without previously identified genes for mildew resistance do not always express identical levels of resistance. This is attributed either to differences conditioned by genes with smaller effects or to uncharacterized genes with larger effects.

The gene *Pm*5 was found in Caldwell, Ga1123, and Hardired, where reactions to isolates $E_3$37, 85135, and 6a were consistent with the check cultivars. Pedigree analysis shows Hope as a parent of both Ga1123 and Hardired but does not explain the existence of *Pm*5 in Caldwell other than to say the line is from the breeding program at Purdue, which we now show to have produced other lines containing *Pm*5 (26,34). The three cultivars containing *Pm*6 (Abe, Coker 747, and Oasis) exhibited intermediate reactions to isolate W72/27, as did Hustler, which also has *Pm*2. The resistance was attributed to *Pm*6 because this isolate also carries virulence to *Pm*2 as shown by the susceptibility of Avalon and Galahad. Similarly, these cultivars reacted resistant (as did TP114, known to have *Pm*2 and *Pm*6) when inoculated with isolates ABK and 140 at Raleigh, while Ulka/8CC with *Pm*2 was susceptible. All three of these cultivars can be traced to Arthur, which carries *Pm*6 (33).

The common lack of clear reaction types (susceptible or resistant) with lines carrying *Pm*5 or *Pm*6 may be attributable to variable expression of these genes in different genetic backgrounds (11).

In addition to *Pm*6, Arthur has also been reported to carry *Pm*2 (4), presumably from CI 12633. We disagree with the previous report (4) that *Pm*2 is present in Arthur. This is shown clearly with isolates 7-12 and 4a. Sebastian et al (28) also concluded that *Pm*2 was not in Arthur and that the powdery mildew resistance in Arthur did not rely on *Pm*1–*Pm*5. Our results conflict with both of these reports. Although we agree with Bennett (4) that Arthur carries *Pm*6, we did not detect *Pm*2. This was in agreement with Sebastian et al (28), but conversely we also found that the cultivar carries *Pm*5. The fact that Sebastian et al (28) did not detect this gene could be attributed to two factors. It is likely that Arthur is segregating at the *Pm*5 locus based on reactions with seven of our cultures, and this could make inheritance studies difficult to interpret. Further, Sebastian et al (28) used CI 14125 as a source for *Pm*5, and our observations indicate that the gene evaluated here is not the same gene found in Hope. The fact that Hope is present in the pedigree of Arthur also makes our conclusion reasonable. These comments concerning Arthur are applicable to Double Crop, which is a direct selection from Arthur (34), but it appears that Double Crop is stable for both *Pm*5 and *Pm*6. The donor of these two genes in Coker 983 is not clear from pedigree analysis, but the genes may have come from the Purdue-derived germ plasm in the pedigree of Coker 983.

The four lines that clearly show *Pm*3a resistance are all from the Southeast and may explain the high frequency of virulence to this gene in North Carolina (17). The pedigrees of Saluda, Fl302, and Coker 797 show Hadden as a parent for each, and this cultivar is considered the common donor for *Pm*3a in hexaploid wheat (4,30). Fl301 has Holley as a parent (partially derived from Suwon 92) which also carries a gene at the *Pm*3 locus (3,5). Reactions from Coker 762 indicated the presence of either *Pm*3a or *Pm*3b; however, pedigree analysis did not reveal potential sources of either of these genes and, therefore, a decision

between the two could not be reached.

Currently, 17 genes for powdery mildew resistance have been described (22), yet only three are represented in the 22 cultivars we tested. This implies an opportunity and a need to gain greater genetic diversity for mildew resistance in soft red winter wheat. This could be done simply by utilizing previously described sources of resistance. In the future, more sources will be described, and their resistances, as well as those in other cultivars, should also be characterized. This is essential to enable breeders to plan their crosses to obtain high levels of resistance. This information will also give wheat breeders the opportunity to maximize diversity for mildew resistance among breeding programs in a geographical area.

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