Seedling and Adult Plant Resistance to Powdery Mildew in Chinese Bread Wheat Cultivars and Lines

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ABSTRACT

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Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is a widespread wheat disease in China. Identification of race-specific genes and adult plant resistance (APR) is of major importance in breeding for an efficient genetic control strategy. The objectives of this study were to (i) identify genes that confer seedling resistance to powdery mildew in Chinese bread wheat cultivars and introductions used by breeding programs in China and (ii) evaluate their APR in the field. The results showed that (i) 98 of 192 tested wheat cultivars and lines appear to have one or more resistance genes to powdery mildew; (ii) *Pm8* and *Pm4b* are the most common resistance genes in Chinese wheat cultivars, whereas *Pm8* and *Pm3d* are present most frequently in wheat cultivars introduced from CIMMYT, the United States, and European countries; (iii) genotypes carrying *Pm1*, *Pm3e*, *Pm5*, and *Pm7* were susceptible, whereas those carrying *Pm12*, *Pm16*, and *Pm20* were highly resistant to almost all isolates of *B. graminis* f. sp. *tritici* tested; and (iv) 22 genotypes expressed APR. Our data showed that the area under the disease progress curve, maximum disease severity on the penultimate leaf, and the disease index are good indicators of the degree of APR in the field. It may be a good choice to combine major resistance genes and APR genes in wheat breeding to obtain effective resistance to powdery mildew.

Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is an important disease of wheat (*Triticum aestivum*) worldwide, especially in highly productive areas with a maritime or semicontinental climate (1). Losses in grain yield from 12 to 45% have been reported in the United States (8,18,19,21). In China, powdery mildew on wheat occurred only occasionally in the southwestern plateau and coastal area of Shandong Province before the 1970s (23,31). However, its importance increased notably during the early 1980s, mainly due

to the high rates of nitrogenous fertilizer, production of semidwarf wheat cultivars, and expansion of irrigated areas. The area of wheat production affected by powdery mildew was 2.9 million ha in 1981. This increased to 12.0 million ha in 1990, with the disease causing an estimated grain yield losses of 14.4 million tons (33).

Utilization of resistant cultivars is the most economical and environmentally safe means of controlling powdery mildew (1). To date, 48 *Pm* genes or alleles at 32 loci are known to confer race-specific resistance in wheat (14,16). Selection pressure exerted by cultivars that carry single race-specific genes results in a rapid build-up of the pathogen population possessing matching virulence genes and contributes to reducing resistance durability (28). Therefore, knowledge of the presence and frequency of virulence genes in the pathogen population is useful for replacing ineffective genes with effective ones. Information on resistance genes present in important wheat cultivars and knowledge of avirulence or virulence in pathogen populations is valuable for planning crosses in wheat breeding

programs and for developing management strategies, including cultivar recommendations and deployment schemes (15,19,34). Such information is also valuable to predict the breakdown of resistance genes caused by shifting pathogen populations.

Resistance to powdery mildew that retards infection, growth, and reproduction of the pathogen in adult plants, but not in seedlings, has been defined as slow mildewing (28) or adult plant resistance (APR; 5). This type of resistance can be identified in cultivars with defeated race-specific genes or cultivars that lack race-specific resistance genes (1). APR to powdery mildew is more durable than race-specific resistance. For example, cv. Knox and its derivatives (e.g., cv. Massey) have remained resistant to powdery mildew infection for over 20 years, despite being grown commercially on large areas (9,28). Some wheat breeders are interested in using APR genes, and many genotypes with APR have been identified and used in wheat improvement (4,9,36).

China is the largest wheat producer in the world, with about 25 million ha sown annually. The Chinese Academy of Agricultural Sciences has divided the country's wheat area into 10 agro-ecological zones based on wheat types and the response to biotic and abiotic stresses. Winter, facultative, and spring wheat types sown in both autumn and spring are grown; therefore, Chinese wheat germ plasm is very diverse in many aspects. However, little attention has been paid to investigating APR to powdery mildew and achieving durable resistance to Chinese isolates of *B. graminis* f. sp. *tritici*. The objectives of our study were to (i) identify probable *Pm* genes that confer seedling resistance in Chinese wheat cultivars and various introductions frequently used by breeding programs in China and (ii) identify the presence of APR in these cultivars based on field trials.

MATERIALS AND METHODS

Isolates of *B. graminis* f. sp. *tritici*. Twenty isolates of *B. graminis* f. sp. *tritici*

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(Table 1) with different virulence patterns (7), collected from various regions of China, were used for identifying genes conferring resistance at the seedling stage. Isolate E20, with a broad spectrum of virulence, was used for evaluating APR to powdery mildew in field trials.

Wheat germplasm. Included in this study were 56 widely grown Chinese cultivars and 28 advanced breeding lines, as well as 108 cultivars and lines introduced from Europe, the United States, Brazil, and the International Maize and Wheat Improvement Center (CIMMYT) in Mexico (Tables 2 and 3). The cultivars and lines are available at the National Wheat Improvement Center of China upon request. Twenty differential cultivars and lines (Table 1) with known *Pm* genes (16,24) were included in each test, and the low and high infection types displayed by them toward *B. graminis* f. sp. *tritici* isolates were used for postulating resistance genes in the wheat cultivars tested.

Seedling studies. In all, 192 wheat cultivars and advanced lines were evaluated using 20 *B. graminis* f. sp. *tritici* isolates in the greenhouse at the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, in the spring of 1999 and 2003 according to the method described by Xiang et al. (35). Between five and seven plants of each cultivar and differential line were grown in flat plastic trays 70 by 45 by 18 cm in size. The highly susceptible check cv. Jingshuang 16 was planted randomly four times in each tray to evaluate uniformity of inoculum distribution. Inoculation with each of the 20 isolates was performed in separate trays, when the first

leaves were fully expanded. Host reactions were recorded 7 to 10 days after inoculation, when the susceptible checks were heavily infected. A 0-to-4 infection type scale (29) was used for recording the host response to infection, where 0 = no visible symptoms; 0; = hypersensitive necrotic flecks; 1 = minute colonies with few conidia produced; 2 = colonies with moderately developed hyphae, but few conidia; 3 = colonies with well-developed hyphae and abundant conidia, but colonies not joined together; and 4 = colonies with well-developed hyphae and abundant conidia, and colonies mostly joined together.

Field trials. During the 2000–01 and 2002–03 crop seasons, 52 and 76 winter wheat cultivars, respectively, were evaluated for APR to powdery mildew at the Institute of Crop Breeding and Cultivation, Chinese Academy of Agricultural Sciences. Thirty cultivars or lines were common to both experiments. Field trials were planted in a randomized complete block design with three replications; each plot consisted of two 2-m rows spaced 25 cm apart. Approximately 150 seed were sown in each plot. Spreader rows of the susceptible cv. Jingshuang 16 surrounded the test cultivars and lines and also were planted every 15 plots. The nursery was surrounded by triticale (*Triticosecale* Wittmack) to discourage contamination by other powdery mildew isolates. Inoculation was carried out with the isolate E20 of *B. graminis* f. sp. *tritici* prior to plants reaching stem elongation. The cultivar response to powdery mildew was scored for the first time 2 weeks after inoculation

and then at weekly intervals until leaves were physiologically mature. The infection severity on 10 arbitrarily selected plants from each plot was recorded based on the 0-to-9 scale described by Saari and Prescott (26). Powdery mildew severity on the penultimate leaf (= F-1 leaf) was rated 2 weeks after flowering, based on the actual percentage of leaf area covered by powdery mildew, and then every 6 to 8 days.

A disease index (I) was calculated using the formula $I = (0 \times n_0 + 1 \times n_1 + \dots + 9 \times n_9) / 9 \times (n_0 + n_1 + \dots + n_9)$, where n_i = numbers of plants at i th scale of infection severity (11). An area under the disease progress curve (AUDPC) was calculated based on the severity on penultimate leaf according to the formula described by Björk and Line (2). Six wheat cultivars (Alidos, Andros, FAP77517, Massey, Mercia, and Redcoat) with known APR to powdery mildew were used as checks.

Statistical analysis. Relative AUDPC was calculated by dividing the AUDPC of each cultivar or line by the AUDPC of susceptible check Jingshuang 16. The percentage of maximum disease severity (MDS) on penultimate leaf was transformed into inverse sine by the formula $x = \sin^{-1} \sqrt{\text{MDS}}$ for subsequent analysis of variance (ANOVA) and protected least significant difference (LSD) test. SAS software (SAS Institute, Inc., Cary, NC) was used to compute ANOVA as well as the LSD test of differences between the relative AUDPC and MDS of each cultivar or line and the mean value of six check cultivars with known APR.

Table 1. Reaction patterns of 20 differential wheat cultivars and lines with known resistance genes to 20 isolates of *Blumeria graminis* f. sp. *tritici* collected from various regions of China

Cultivar or line	Gene ^b	Infection types to <i>B. graminis</i> f. sp. <i>tritici</i> isolates ^a																	
		E01	E02	E03	E05	E06	E07	E10	E13	E15	E16	E17	E18	E20	E21	E23	E26	E30	E31
Chancellor	None	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Axminster/8*CC	<i>Pm1</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Ulka/8*CC	<i>Pm2</i>	0;	4	0;	4	0;	0;	0;	3	0;	0;	4	4	4	4	1	0;	0;	3
Maris Huntsman	<i>Pm2+6</i>	0;	0;	0;	0;	0;	0;	0;	4	0;	-	0;	4	4	3	0;	0;	0;	0;
Maris Dove	<i>Pm2+Mld</i>	0;	0;	0;	0;	0;	0;	0;	4	0;	0	0;	0;	3	4	0	0;	0;	0;
Brock	<i>Pm2+Ta</i>	0;	4	0;	4	0;	0;	0;	0;	2	2	4	0;	0;	4	0;	0;	0;	0;
Asosan/8*CC	<i>Pm3a</i>	0;	3	0;	4	3	4	4	4	4	3	0;	3	4	4	4	4	4	4
Kolibri	<i>Pm3d</i>	4	4	4	4	4	4	4	4	4	4	0;	3	4	4	4	2	4	4
W150	<i>Pm3e</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Michigan Amber/8*CC	<i>Pm3f</i>	4	4	3	0;	4	4	4	0;	4	3	4	4	4	4	0;	4	4	4
Khapli/8*CC	<i>Pm4a</i>	0;	4	0	0	1	0;	4	0	4	4	4	4	4	4	1	0;	1	0
Armada	<i>Pm4b</i>	0;	0;	0;	0;	0;	0;	2	1	0;	4	0;	4	4	4	0;	3	0;	0;
Baimian3	<i>Pm4+8</i>	0;	4	0;	0;	0;	0;	4	0;	0;	4	3	4	4	4	0;	0;	0;	0;
Hope	<i>Pm5</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Timgalen	<i>Pm6</i>	4	3	4	4	4	4	3	4	0;	3	3	4	4	3	4	4	3	3
CI 14189	<i>Pm7</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Kavkaz	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0;	4	4	0;
Wembley	<i>Pm12</i>	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;	0;
Brigrand	<i>Pm16</i>	0;	0;	0;	0;	1	0;	0;	0;	0;	0	0;	0;	2	0;	0;	0;	0	0;
Amigo	<i>Pm17</i>	4	4	4	4	3	4	3	4	0;	4	0;	4	4	4	0;	4	3	0;
Pm20	<i>Pm20</i>	0;	0;	0;	0;	0;	0;	0;	3	0;	0;	0;	0;	2	4	0;	2	0;	0;

^a Infection types are 0 = no visible symptoms; 0; = hypersensitive necrotic flecks; 1 = minute colonies with few conidia; 2 = colonies with moderately developed hyphae, but few conidia; 3 = colonies with well-developed hyphae and abundant conidia, but colonies not joined together; and 4 = colonies with well-developed hyphae and abundant conidia, and colonies mostly joined together.

^b Information obtained from Huang and Röder (16) and McIntosh et al. (24).

RESULTS

Identification of resistance genes effective at the seedling stage. Cultivars and lines with resistance genes *Pm1*, *Pm3e*, *Pm5*, and *Pm7* were susceptible to all isolates of *B. graminis* f. sp. *tritici* tested (Table 1). Genes *Pm12* and *Pm16* conferred resistance to all isolates, and *Pm20* gave a susceptible reaction to isolates E13 and E21 only. Genes *Pm2* and *Pm6* conferred resistance to 10 and 1 isolates, respectively. Maris Huntsman, which carries both the *Pm2* and *Pm6* genes, was resistant to 14 isolates of *B. graminis* f. sp. *tritici*.

Of the 192 wheat cultivars and lines tested, 94 were susceptible to all isolates (Table 2). Ninety-eight wheat cultivars and lines were found to carry one or more re-

sistance genes (Table 3). Of these, 11 cultivars and lines (Aiyuandong 3, CA8646, CA9632, Jinnong 8112, Lumai 13, Nongda 523, Zhoumai 13, Corydon, Jur/2*Tapar29/Pf83144, Kukuna, and Mv Optima) had the same reaction pattern as Kavkaz, which carries *Pm8*. Seven cultivars (BPM14, BPM28, CA9553, Lankao 906, Lu7you/C39, Nongdayoufan 5, and German 8661) showed the same reaction patterns as Armada, which carries *Pm4b*. Aizao 4110 and CA9550 displayed a combination of reaction patterns of Ulka/8*CC and Armada, which carry *Pm2* and *Pm4b*, respectively. Three cultivars (90-I89, Shan 229, and Milan/Ducula) showed the same reaction pattern as Kolibri which carries *Pm3d*, while seven cultivars or lines

(Zheng86115, 8030Versailles/Edch//Cd, Tnmu/Milan-2, Tx71A1039.V1*3/Ami//Trap#1, Vee/Koel//He1/3*CN079/3/Kauz, Soissons-2, and Soissons-3) showed evidence of unidentified *Pm* genes in addition to *Pm3d* (Table 3). Three cultivars (Nongda 280218, Nongda 883, and Rah122/94) showed the same resistance pattern as Khapli/8*CC, which carries *Pm4a*. BPM15 and Xingmai 883 displayed the same reaction patterns as Ulka/8*CC and Timgalen, respectively (Tables 2 and 3).

Twenty-one cultivars and lines (98301, Lumai 14, Shangdong200015537, Altar 84/Ae.squarrosa(219)//2*Seri, Br23/Emb40, Choix M95, Cty*3/Ta2450, Hahn/2*Weaver, Hussar, Irena/Weaver, Lfn/Ii58.57//Prl/3/Hahn/4/2*Mo88, Mon/Tmul/

Table 2. Origin, growth habit, and 1B/1R translocation status of 94 cultivars and lines that were susceptible to 20 *Blumeria graminis* f. sp. *tritici* isolates

Cultivar or line	Origin	Growth habit ^a	1B/1R status ^b	Cultivar or line	Origin	Growth habit ^a	1B/1R status ^b
Bainong 64	China	W	1B/1B	Bacanora T88	CIMMYT	S	1B/1R
Baofeng 7228	China	W	1B/1R	Batera	CIMMYT	W	...
CA 9532	China	W	1B/1R	Bow/Nkt//Ducula/3/Ducula	CIMMYT	S	1B/1B
Hongjuanmang	China	W	1B/1B	Emb27/Cep8825//Milan-1	CIMMYT	S	1B/1B
Hobbit/CA837	China	W	...	Emb27/Cep8825//Milan-2	CIMMYT	S	1B/1B
Ji 966185	China	W	...	F12.71/Bez//Tjb368.251/Buc/4/D6301/Heine VII//ERA/3/BUC	CIMMYT	W	1B/1B
Jimai 30	China	W	1B/1R	Filin	CIMMYT	S	1B/1R
Jimai 36	China	W	1B/1R	Filin/Milan-1	CIMMYT	S	1B/1B
Jimai 38	China	W	1B/1B	Filin/Milan-2	CIMMYT	S	1B/1B
Jin 411	China	W	1B/1B	Gen/Kauz	CIMMYT	S	1B/1R
Jinan 17	China	W	1B/1R	Hxl 8088/Ducula	CIMMYT	S	...
Jingdong 6	China	W	1B/1R	Inqalab 91	CIMMYT	S	1B/1B
Jingdong 8	China	W	1B/1R	Milan	CIMMYT	S	1B/1B
Jinmai 45	China	W	...	Milan/Pastor	CIMMYT	S	1B/1B
Jinmai 47	China	W	...	Saar	CIMMYT	S	1B/1B
Linfen 6010	China	W	1B/1B	Sha3/Seri//Sha4/Lira	CIMMYT	S	1B/1R
Lumai 21	China	W	1B/1B	Thb//Maya/Nac/3/Rabe/4/Milan	CIMMYT	S	1B/1B
Lumai 22	China	W	1B/1B	Ures/Kauz	CIMMYT	S	1B/1R
Lumai 23	China	W	1B/1R	Dulus	CIMMYT	S	1B/1B
Lunhui 201	China	W	1B/1B	Heilo	CIMMYT	S	1B/1B
Nongda123	China	W	1B/1B	Prointa Guazu	Argentina	S	1B/1R
Pm 20491	China	W	1B/1B	Prointa Cauquen	Argentina	S	1B/1B
Pm 499-1	China	W	...	110254-1.77W	France	W	...
Pm94081	China	W	...	Cp9106-1-2-1	France	W	...
Pm94082	China	W	1B/1R	Cp9111-3-2	France	W	...
Shan 213	China	W	1B/1R	Pistov-2	France	W	...
Shan 354	China	W	1B/1B	Alidos	Germany	W	...
Shangdong 935031	China	W	1B/1R	Andros	Germany	W	1B/1B
Shannong413863	China	W	1B/1B	Mv Emma	Hungary	W	1B/1R*
Tiegangmai	China	W	1B/1B	Mv Magdalena	Hungary	W	1B/1R
Wenmai 6	China	W	1B/1B	Mv Magvas	Hungary	W	1B/1B
Xiaoyan 6	China	W	1B/1R	Mv Palma	Hungary	W	1B/1R*
Xingmai 99	China	W	1B/1R	Mv Vilma	Hungary	W	...
Yumai 13	China	W	1B/1B	Dropia	Romania	W	...
Yumai 18	China	W	1B/1R	Arina	Switzerland	W	1B/1B
Yumai 21	China	W	1B/1B	Kariega	South Africa	S	1B/1B
Yumai 25	China	W	1B/1B	Manning/SDV1//DOGU88	Turkey	W	1B/1B
Yumai 47	China	W	...	Abn/Jun	United States	W	1B/1B
Yuzhan 9705	China	W	1B/1B	Ga841465-2-1-1-4	United States	W	...
Zhengmai 9405	China	W	1B/1B	Ga85164-3-2-4-2	United States	W	...
Zhongyou 9507	China	W	1B/1B	Houser	United States	W	1B/1B
Zhongyou 9701	China	W	1B/1B	Ks90175-1-2	United States	W	1B/1R
Zhongyou 9843	China	W	1B/1B	Redcoat	United States	W	1B/1B
Zhongyou 9844	China	W	1B/1R	Mercia	United Kingdom	W	1B/1B
Zhoumai 11	China	W	1B/1R	FAP74161	...	W	1B/1B
Zhoumai 16	China	W	1B/1R	FAP77517	...	W	1B/1R
Zhoumai 17	China	W	1B/1B				
24Ibwsn#278/Soissons	CIMMYT	W	1B/1B				

^a W = winter wheat; S = spring wheat.

^b Identified according to the method described by Gupta and Shepherd (12), except for those indicated by an asterisk, for which information obtained from Schlegel (27); ... = unknown.

Ald/Pvn, Mv Madrigal, Mv Magdalena, Nd610/Kauz//Tui, Prinia, Tinamou, Tnmu/Milan-1, Tnmu/Milan-3, Tnmu/Milan-4, and Vee/Koel//He1/3*Cn079/3/Kauz) showed evidence of unidentified resistance genes in addition to *Pm8*.

Thirty-six cultivars were resistant to one or several isolates; however, their reaction patterns did not match any of the known resistance genes or their combinations. Of these, Mv-17, Va91-51-26, Va91-52-65, and Pm93-625-4 were resistant to all isolates and showed the same reaction pattern as those of *Pm12* and *Pm16*.

APR to powdery mildew. Cultivars and lines differed significantly for relative AUDPC and MDS in the field trials (Table 4). Twenty-two cultivars and lines showed APR to powdery mildew (Table 5). The disease developed quickly on the susceptible check, Jingshuang 16, indicating a favorable environment for disease development (Fig. 1). Compared with susceptible cultivars, disease developed much more slowly on APR cultivars (Fig. 1).

Among the cultivars and lines, 11 (including 5 APR checks) were susceptible

to all isolates of *B. graminis* f. sp. *tritici* at the seedling stage, but showed slow disease progress at the adult stage in the field. In all, 17 cultivars (including 1 APR check) with resistance genes overcome by isolate E20 at the seedling stage showed moderate resistance in the field (Tables 3 and 5). In contrast, Aizao 4110, which carries *Pm2+4b*, was highly susceptible in the field, with a relative AUDPC and MDS of 0.73 and 42.7, respectively. A highly significant correlation was found between AUDPC and MDS on penultimate leaf ($r = 0.96$, $P < 0.001$).

Table 3. Reactions of 98 wheat cultivars or lines to 20 isolates of *Blumeria graminis* f. sp. *tritici* in seedling tests

Cultivar or line	Origin	GH ^b	Status ^c	Gene	Infection types to <i>B. graminis</i> f. sp. <i>tritici</i> isolates ^a																			
					E 01	E 02	E 03	E 05	E 06	E 07	E 10	E 13	E 15	E 16	E 17	E 18	E 20	E 21	E 23	E 26	E 30	E 31	E 32	E 42
98301	China	W	1B/1R	<i>Pm8+?</i>	4	4	4	4	4	4	4	4	4	4	4	4	3	1	4	0	4	0	4	
975297	China	W	1B/1R	?	4	4	4	4	4	4	4	4	4	4	4	4	4	3	4	4	4	0	4	
98Zhong 33	China	W	1B/1B	?	0	0	4	4	0	0	4	0	0	4	0	4	4	0	0	0	0	0	4	
Aiyuandong 3	China	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	3	4	0	4	
Aizao 4110	China	W	1B/1B	<i>Pm2+4b</i>	0	0	0	0	0	0	0	1	0	2	0	4	4	4	0	0	0	0	0	
BPM 14	China	W	1B/1B	<i>Pm4b</i>	0	0	0	0	2	0	0	0	0	4	0	4	3	4	0	4	2	0	0	
BPM 15	China	W	1B/1B	<i>Pm2</i>	0	4	0	4	0	0	1	3	0	0	4	4	4	4	0	0	0	3	4	
BPM 28	China	W	1B/1B	<i>Pm4b</i>	0	0	0	0	2	0	0	0	0	4	0	3	4	4	1	4	2	0	0	
CA 8646	China	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	3	4	4	
CA 9550	China	W	1B/1B	<i>Pm2+4b</i>	0	0	0	0	0	0	0	0	0	0	4	4	4	0	0	0	0	0	0	
CA 9553	China	W	1B/1B	<i>Pm4b</i>	0	0	0	0	0	0	1	1	0	3	0	4	3	4	0	4	0	0	0	
CA 9632	China	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	3	4	0	4	
CA 9641	China	W	1B/1B	<i>Pm3a+?</i>	0	0	0	0	4	0	0	4	0	0	0	4	4	4	0	1	0	0	4	
CA 8686	China	W	1B/1R	?	4	3	4	4	4	4	4	4	4	4	4	4	4	2	4	4	4	4	4	
CA 9722	China	W	1B/1B	?	0	4	0	0	3	0	4	4	4	4	4	4	4	4	3	2	0	0	0	
Jimai 3	China	W	1B/1B	?	4	4	4	4	4	0	4	4	4	4	4	4	4	4	4	0	4	0	4	
Jinnong 8112	China	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	3	4	0	4	
Lankao 906	China	W	1B/1B	<i>Pm4b</i>	0	0	0	0	2	0	0	0	0	4	0	4	4	4	0	4	2	0	0	
Lin 9303	China	W	1B/1R	?	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	2	4	0	4	
Lu7you/2/C39	China	W	1B/1B	<i>Pm4b</i>	0	0	0	0	2	0	0	0	0	3	0	4	4	4	0	3	0	0	0	
Lumai 13	China	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	3	4	0	4	
Lumai 14	China	W	1B/1R	<i>Pm8+?</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	0	4	0	4	
Neixiang 991	China	W	1B/1R	<i>Pm2+6+?</i>	-	0	0	0	0	0	0	0	0	4	0	0	4	4	0	0	0	0	0	
Neixiang 188	China	W	1B/1R	?	4	4	4	4	4	4	4	4	4	0	4	4	4	4	4	4	4	4	4	
Nongda 280218	China	W	1B/1B	<i>Pm4a</i>	0	4	0	0	1	0	3	0	4	4	3	3	4	4	0	0	1	1	0	
Nongda 523	China	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	3	4	0	
Nongda 883	China	W	...	<i>Pm4a</i>	0	4	0	0	2	0	3	0	4	4	4	3	4	0	0	1	2	0	0	
Nongdayoufan 5	China	W	...	<i>Pm4b</i>	0	0	0	0	2	0	0	2	0	3	0	4	4	4	0	3	0	0	0	
Qiantong 6	China	W	...	<i>Pm2+Ta</i>	2	4	0	4	0	0	2	0	0	2	4	0	0	4	0	0	2	0	4	
Pm93-625-4	China	W	1B/1B	<i>Pm30</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Shan 229	China	W	1B/1R	<i>Pm3d</i>	4	4	4	4	4	4	4	4	4	4	0	3	4	4	4	0	4	4	4	
Shangdong 20015537	China	W	1B/1R	<i>Pm8+?</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	0	4	0	4	
Shangdong 418	China	W	1B/1R	?	4	4	0	4	4	4	4	4	4	3	4	4	4	4	4	4	4	4	4	
Xingmai 883	China	W	...	<i>Pm6</i>	4	4	4	4	4	4	4	4	0	4	4	4	4	4	4	4	4	4	4	
YE-2416-7 ^a	China	W	1B/1B	?	4	0	4	4	4	3	4	4	0	4	0	4	4	0	3	1	0	0	0	
Zheng 86115	China	W	1B/1B	<i>Pm3d+?</i>	4	3	0	3	4	4	4	4	4	4	2	3	4	4	4	3	4	4	4	
Zhoumai 13	China	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	3	4	0	
Zhoumai 88	China	W	1B/1B	?	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	4	0	4	
494J6.11	CIMMYT	W	1B/1B	?	4	0	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	4	
8030 Versailles/Edch//Cd	CIMMYT	W	1B/1R	<i>Pm3d+?</i>	4	0	4	4	3	2	4	4	4	4	0	3	4	4	4	2	4	3	4	
Altar 84/Ae.squarrosa (219)//2*Seri	CIMMYT	S	1B/1R	<i>Pm8+?</i>	4	0	0	4	4	4	4	4	0	4	0	0	0	4	0	4	4	0	4	
Au/Up301//Gll/Sx/3/Pew/ 4/ Mai/Maya//Pew/5/Kea/6/2*R37/ Gh1121//Kal/Bb/3/Buc/Bul	CIMMYT	S	1B/1B	?	4	0	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
Catbird	CIMMYT	S	1B/1R	?	4	0	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	4	4	
Croc_1/Ae.squarrosa(205) //Kauz	CIMMYT	S	1B/1R	?	4	4	4	4	2	4	4	4	4	4	4	4	4	4	4	4	4	4	4	
Choix M95	CIMMYT	S	1B/1R	<i>Pm8+?</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	0	4	0	4	

(continued on next page)

^a Infection types are 0 = no visible symptom; 0; = hypersensitive necrotic flecks; 1 = minute colonies with few conidia; 2 = colonies with moderately developed hyphae, but few conidia; 3 = colonies with well-developed hyphae and abundant conidia, but colonies not joined together; and 4 = colonies with well-developed hyphae and abundant conidia, and colonies mostly joined together.

^b Growth habit: W = winter wheat and S = spring wheat.

^c Identified according to the method described by Gupta and Shepherd (12) except for those indicated by an asterisk, for which information was obtained from Kazman and Lein (17); ... and ? = unknown.

DISCUSSION

In the present study, known powdery mildew resistance genes were detected in 62 wheat cultivars and lines. Of these resistance genes, *Pm12* and *Pm16* were resistant to all isolates of *B. graminis* f. sp. *tritici* tested, indicating that they are effective resistance genes against powdery mildew in China. *Pm20* was resistant to most of the isolates and would confer effective resistance, at least in areas where virulence may be absent. Nevertheless, it is essential to monitor the virulence isolates of *B. graminis* f. sp. *tritici* to these resistance genes and diversify the

genes in wheat cultivars. Genes *Pm2* and *Pm6* conferred resistance to 10 and 1 isolates, respectively. However, Maris Huntsman, which carries both the *Pm2* and *Pm6* genes, was resistant to 14 isolates of *B. graminis* f. sp. *tritici*, indicating the presence of a previously unidentified resistance gene or genes in this cultivar. The resistance gene in the line Pm93-625-4 was derived from wild emmer (accession C20), which should be *Pm30* according to its origin.

Pm8 was the most frequently identified resistance gene, followed by *Pm4b* in Chinese wheat cultivars. *Pm8* in these culti-

vars is derived mainly from the 1B/1R cvs. Lovrin 13, Predgornaia 2, Kavkaz, Neuzucht, and their derivatives, which have been widely employed in wheat breeding programs in China since the early 1970s (13). At present, 46% of Chinese wheat cultivars possess the 1B/1R translocation (Z. L. Wang, unpublished). The high frequency of virulence to *Pm8* in Chinese *B. graminis* f. sp. *tritici* populations has remained stable at about 94% (6). This has led to increased losses in China due to powdery mildew.

All Chinese wheat cultivars and lines carrying the *Pm8* gene possess the 1B/1R

Table 3. (continued from preceding page)

Cultivar or line	Origin	GH ^b	Status ^c	Gene	Infection types to <i>B. graminis</i> f. sp. <i>tritici</i> isolates ^a																			
					E 01	E 02	E 03	E 05	E 06	E 07	E 10	E 13	E 15	E 16	E 17	E 18	E 20	E 21	E 23	E 26	E 30	E 31	E 32	E 42
Corydon	CIMMYT	S	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	3	4	0	4
Desconocido	CIMMYT	S	1B/1R	?	4	4	0	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Ducula	CIMMYT	S	1B/1B	?	4	4	4	4	4	4	4	4	4	4	4	0	4	4	4	4	4	4	4	4
Hahn/2*Weaver	CIMMYT	S	1B/1R	<i>Pm8</i> +	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	0	4	0	4	4
Irena/Weaver	CIMMYT	S	1B/1R	<i>Pm8</i> +	4	4	4	4	4	4	4	4	4	4	4	4	4	2	4	0	4	0	4	4
Ketupa	CIMMYT	S	1B/1R	?	4	0	0	4	4	4	4	4	0	4	0	4	4	3	4	4	4	0	4	4
Kukuna	CIMMYT	S	1B/1R	<i>Pm8</i>	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	3	4	0
Lfn/Ii58.57//Prl/3/Hahn/4/2*Mo88	CIMMYT	S	1B/1R	<i>Pm8</i> +	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	0	4	0	4
Milan/Ducula	CIMMYT	S	1B/1B	<i>Pm3d</i>	4	4	4	4	4	4	4	4	4	4	0	4	4	4	4	2	4	4	4	4
Mon/Tmu//Ald/Pvn	CIMMYT	S	1B/1R	<i>Pm8</i> +	4	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	0	4	0	4
Nadadores M63	CIMMYT	S	1B/1B	?	4	4	0	4	4	4	4	4	4	4	4	0	4	4	4	4	4	4	0	4
Otus	CIMMYT	S	1B/1R	?	4	3	4	4	4	4	4	4	4	4	4	4	4	0	4	4	4	4	4	4
Pastor	CIMMYT	S	1B/1B	?	4	0	2	4	4	4	4	4	4	4	4	4	4	4	4	3	3	4	4	4
Pbw343	CIMMYT	S	1B/1R	?	4	0	0	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	4	4
Prinia	CIMMYT	S	1B/1R	<i>Pm8</i> +6+	4	0	0	4	4	4	4	4	0	4	3	0	3	4	0	4	0	0	0	4
Seri/Attila	CIMMYT	S	1B/1R	?	4	0	0	4	4	4	4	4	4	4	4	4	4	4	4	4	3	4	4	4
Seri/Rayon	CIMMYT	S	1B/1B	<i>Pm3d</i> +	4	0	0	4	4	4	4	4	4	0	0	4	4	4	1	4	3	4	4	4
Tinamou	CIMMYT	S	1B/1R	<i>Pm8</i> +6+	4	0	0	4	4	4	4	0	4	4	4	4	0	4	0	4	0	0	0	4
Tnmu/Milan-1	CIMMYT	S	1B/1R	<i>Pm8</i> +	4	0	4	4	4	4	4	0	4	0	0	4	4	0	4	0	0	0	4	4
Tnmu/Milan-2	CIMMYT	S	1B/1R	<i>Pm3d</i> +	4	0	0	4	4	4	4	4	4	0	4	4	4	1	2	1	3	4	4	4
Tnmu/Milan-3	CIMMYT	S	1B/1R	<i>Pm8</i> +	4	3	0	4	4	4	4	4	4	4	4	4	4	0	4	0	3	0	4	4
Tnmu/Milan-4	CIMMYT	S	1B/1R	<i>Pm8</i> +	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	0	4	0	4
Tx71A1039.V1*3/Ami//Trap#1	CIMMYT	W	1B/1R	<i>Pm3d</i> +6+	4	0	0	4	4	4	4	4	0	4	0	3	3	3	0	2	4	0	4	4
Tx71A1039.V1*3/Ami//Turaco	CIMMYT	W	1B/1B	?	4	0	4	4	4	4	0	4	0	4	2	3	4	4	0	4	3	0	0	0
Vee/Koel//He1/3*Cno79/3/ Kauz	CIMMYT	S	1B/1R	<i>Pm8</i> +3d+	4	0	0	4	4	4	4	4	4	0	3	0	4	0	2	4	3	0	4	4
Yang87-158/Ducula	CIMMYT	S	1B/1B	?	4	0	4	4	4	4	4	4	4	4	4	0	4	4	4	4	3	4	4	4
Br23/Emb40	Brazil	S	1B/1R	<i>Pm8</i> +	4	0	0	4	4	4	4	4	4	4	4	0	3	4	0	4	0	0	0	4
Chat/Cep7780//Prl/Bow	Brazil	S	1B/1R	?	4	4	4	4	4	4	4	4	4	4	2	4	4	4	4	4	4	0	4	4
Embrapa 119	Brazil	S	...	?	4	4	0	4	4	4	4	4	0	4	3	4	4	4	4	4	3	4	4	4
Jur/2*Iapar29//Pfl83144	Brazil	S	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	0	4	3	4	0	4
Nd610/Kauz//Tui	Brazil	S	1B/1R	<i>Pm8</i> +	0	0	0	0	0	0	0	4	0	3	0	4	4	4	0	0	0	3	0	0
Stozher	Bulgaria	W	1B/1B	?	4	0	4	3	4	4	4	0	4	0	3	4	4	2	4	4	3	0	3	4
Soissons-1	France	W	1B/1B*	?	4	0	4	3	4	3	4	3	4	4	4	4	4	4	4	3	3	4	4	4
Soissons-2	France	W	1B/1B*	<i>Pm3d</i> +	4	0	4	4	3	0	4	3	4	0	4	4	3	4	2	4	3	4	4	4
Soissons-3	France	W	1B/1B*	<i>Pm3d</i> +	4	0	4	3	4	3	4	4	3	4	0	4	4	4	2	4	3	4	4	4
Contra	Germany	W	1B/1B*	<i>Pm4b</i> +	0	0	0	-	0	0	0	0	0	0	0	4	4	4	0	0	0	0	0	0
German 8661	Germany	W	...	<i>Pm4b</i>	1	0	0	2	0	0	0	0	0	1	3	0	4	4	0	3	0	0	0	0
Mv Madrigal	Hungary	W	1B/1R	<i>Pm8</i> +	4	4	4	4	4	4	4	4	4	4	4	4	4	2	4	1	4	0	4	4
Mv Magdalena	Hungary	W	1B/1R	<i>Pm8</i> +	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	1	4	0	4	4
Mv Optima	Hungary	W	1B/1R	<i>Pm8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	1	4	4	4	0	4	4
Mv-17	Hungary	W	...	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mv-23	Hungary	W	1B/1R	?	4	4	4	4	4	4	4	4	4	4	3	4	4	1	4	4	4	3	4	4
Campion	Romania	W	1B/1B	<i>Pm3a</i> +6+	0	0	0	0	4	4	3	4	0	3	0	0	0	3	2	4	4	0	3	4
Rah122/94	Romania	W	...	<i>Pm4a</i>	0	4	0	0	0	0	3	0	4	4	4	4	3	4	0	0	1	2	0	0
Lona	Switzerland	S	1B/1B*	?	4	4	4	4	0	4	4	4	3	4	4	4	4	0	4	4	4	4	4	4
Hussar	United Kingdom	S	1B/1R*	<i>Pm8</i> +	0	0	4	0	0	0	0	0	0	0	0	4	4	4	0	0	0	0	0	0
Cty*3/Ta2450	United States	W	1B/1R	<i>Pm8</i> +	4	0	3	3	4	4	0	4	0	4	2	3	3	3	0	1	2	0	0	0
Massey	United States	W	1B/1B	?	4	0	4	3	4	4	4	4	0	4	4	4	3	4	3	4	3	4	0	0
Va91-51-26	United States	W	...	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Va91-52-65	United States	W	...	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
90-I145	...	W	...	?	4	0	4	4	4	4	4	4	4	4	3	4	2	4	0	4	3	0	3	4
90-I89	...	W	...	<i>Pm3d</i>	4	4	4	4	4	4	4	4	4	4	0	4	4	4	4	0	4	4	4	4
Sxafa4-3	...	W	1B/1B	<i>Pm3f</i> +	4	4	0	0	0	0	4	0	4	4	3	4	4	4	0	0	0	0	4	0

Table 4. Analysis of variance of relative area under disease progress curve (AUDPC) for disease index and maximum disease severity (MDS) on penultimate leaf (F-1) in 52 and 76 wheat cultivars or lines tested in the 2000–01 and 2002–03 crop seasons, respectively

Season, parameter	Source of variation	df	Mean of squares	F value ^a
2000–01 AUDPC	Genotypes	51	0.2643	528.6**
	Replicates	2	0.0003	<1.0
	Error	102	0.0005	...
MDS	Genotypes	51	315.673	242.6**
	Replicates	2	0.427	<1.0
	Error	102	1.301	...
2002–03 AUDPC	Genotypes	75	0.1233	137.0**
	Replicates	2	0.0002	<1.0
	Error	150	0.0009	...
MDS	Genotypes	75	513.479	385.2**
	Replicates	2	0.311	<1.0
	Error	150	1.333	...

^a ** Indicates significant difference at $P = 0.01$.

Table 5. Twenty-two wheat cultivars and lines with adult plant resistance (APR) to powdery mildew identified in the 2000–01 and 2002–03 crop seasons^a

Cultivar or line	2000–01		2002–03		Reaction ^b
	AUDPC	MDS (%)	AUDPC	MDS (%)	
98301	...	...	0.04	2.2	4
8030 Versailles/Edch//Cd	...	...	0.04	2.5	4
Arina	...	...	0.02	1.0	4
Bainong 64	0.08	3.0	0.05	3.4	4
CA8686	...	...	0.02	1.4	4
CA9550	0.03	4.0	0.04	2.0	4
CA9641	0.03	4.0	0.02	1.0	4
Hussar	0.03	2.0	0.02	1.0	4
Lona	...	...	0.03	1.3	4
Mv Madrigal	...	...	0.03	1.7	4
Mv Magdalena	...	...	0.04	2.3	4
Mv-23	0.05	6.8	0.01	0.8	4
Shandong 418	...	...	0.02	1.4	4
Soissons-1	...	...	0.04	2.8	4
Soissons-2	...	...	0.03	1.7	4
Soissons-3	...	...	0.03	1.5	4
Sxafa4-3	0.04	4.0	0.00	0.0	4
Xingmai 99	0.03	3.0	0.02	1.5	4
YE-2416-7A	0.03	4.0	0.00	0.0	4
Yumai47	...	...	0.04	2.5	4
Yuzhan9705	...	...	0.03	1.7	4
Zhoumai 17	...	...	0.03	1.9	4
Alidos ^c	0.05	5.0	0.07	3.1	4
Andros ^c	0.06	6.0	0.05	3.0	4
FAP77517 ^c	0.06	5.0	0.04	2.0	4
Massey ^c	0.04	6.0	0.00	0.6	4
Mercia ^c	0.06	7.0	0.02	1.4	4
Redcoat ^c	0.06	5.0	0.02	1.0	4
Jingshuang 16 ^d	1.00	92.0	1.00	95.0	4

^a AUDPC = relative area under disease progress curve for disease index for cultivar or line divided by AUDPC for susceptible check Jingshuang 16; ... = not tested; MDS = maximum disease severity.

^b Seedling reaction to E20; 4 = colonies with well-developed hyphae and abundant conidia, and colonies mostly joined together.

^c Resistant check cultivar with known APR to powdery mildew.

^d Susceptible check cultivar.

translocation, as shown in Table 3. However, 71.5% of 1B/1R translocation lines did not show the reaction pattern expected for *Pm8* (Table 3), which might be due to the presence of suppressor genes for *Pm8* (25). This was consistent with the results of a previous study by Ren et al. (25), who found that, on average, only one-third of all CIMMYT wheats with 1B/1R tested actually expressed the *Pm8* gene.

We could not postulate resistance genes in 36 cultivars and lines due to the lack of *B. graminis* f. sp. *tritici* isolates or differential lines (Table 3). In addition, 94 genotypes were susceptible to all *B. graminis* f. sp. *tritici* isolates (Table 2), which indicates that they either carry no resistance genes or possess resistance genes that were overcome by matching virulence in all 20 *B. graminis* f. sp. *tritici* isolates used in this study.

There is an urgent need for a better genetic strategy for powdery mildew control. Several strategies have been proposed for developing durable resistance to powdery mildew, including the pyramiding of effective major resistance genes (32), the use of multilines with different resistance genes (3), and breeding cultivars with APR or slow mildewing resistance (28). The use of molecular markers to pyramid major genes seemed promising (22), but may cause the rapid formation of isolates with multiple matching virulence (10). Therefore, APR has been suggested as the most sustainable strategy for breeding wheat cultivars with durable powdery mildew resistance (1,28).

A series of studies on APR to powdery mildew were conducted during the last decade, and both qualitative and quantitative genes were detected in various wheat cultivars (4,5,9). Chae and Fischbeck (4) reported the effect of 14 chromosomes on APR to powdery mildew in cv. Diplomat; whereas, in cvs. Knox 62, Massey, Redcoat, and Houser, APR is governed by two to three genes with moderate to high heritability (5,9). CIMMYT has conducted several studies on slow rusting and found that combinations of four to five minor genes for APR to leaf rust and stripe rust give adequate protection in the field (30).

Bainong 64, a leading cultivar in China until 2000, was grown on about 700,000 ha annually for 8 years. Our study confirmed that it carries APR (Fig. 1). This cultivar was used widely as a parent, and we are testing several derived lines for possible release in the Huang-Huai winter wheat zone of China.

Description of APR can be carried out based on different parameters, such as a disease index, AUDPC, and MDS on penultimate leaf (11,36). In the present study, we used AUDPC, MDS, and a disease index to evaluate APR in the field. All cultivars or lines with APR showed lower values for AUDPC, MDS, and the disease index than susceptible cultivars (Table 5). In practical breeding, it is good to use a simple parameter to evaluate APR in the field. Investigations of AUDPC and the disease index are time-consuming and, because AUDPC and MDS are highly correlated ($r = 0.96$, $P < 0.001$), it is more practical to use the latter parameter for powdery mildew screening, with a single scoring at an appropriate time.

Generally, APR to powdery mildew is detected in cultivars that either have no identified major resistance genes or whose major-gene resistance has been overcome (1). As an example, most powdery mildew populations worldwide show high virulence frequencies for *Pm5* at the seedling stage (14), but the gene serves as a source of APR (14,20). In our study, 17 cultivars and lines whose race-specific resistance genes were overcome in the seedling stage by isolate E20 showed APR in the field, indicating that they might be carrying mi-

Fig. 1. Progress curve of powdery mildew development in wheat based on the index of disease at seven scoring dates (indicated as cumulative days; day 0 = 4 weeks after inoculation). Jingshuang 16 is a highly susceptible cultivar, Zhoumai 13 is a moderately susceptible cultivar, Bainong 64 is a Chinese cultivar with adult plant resistance (APR), Redcoat is a US cultivar with known APR, and Hussar is a UK cultivar with APR.

nor APR genes in addition to the major genes (Tables 3 and 5). Results indicate that it is possible to combine major resistance genes and APR genes to achieve durable resistance to powdery mildew in wheat cultivars.

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