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Race Composition of *Blumeria graminis* (DC) Speer f. sp. *tritici* in the South of Ukraine and Effectiveness of *Pm*-genes in 2004–2013

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The virulence frequency of 750 wheat powdery mildew isolates of wheat genotypes, carrying 23 *Pm*-genes and gene combinations, was studied over ten consecutive years from 2004 to 2013. Seventy-eight previously known and 39 new pathotypes were identified during this period. The results indicate that the majority of *Pm*-genes have high level of virulence. Sixty to ninety percent of the isolates were virulent to *Pm6*, *Pm8*, *Pm8+11*, *Pm2+4b+8*, *Pm3g*, *Pm10+15*, *Pm10+14+15*. The virulence frequency was variable for *Pm1a*, *Pm2*, *Pm3a*, *Pm3b*, *Pm3c*, *Pm5*, *Pm7* genes and reached high level in certain years. The virulence frequency to genes *Pm20*, *Pm37*, *Pm4a+* and to gene combination with *Pm3c+5a+35* and breeding lines CN240/06, CN98/06 and CN158/06 ranged from 1 to 8%. Bread wheat lines CN240/06, CN98/06 and CN158/06, derived from interspecific crosses, proved to be highly resistant to powdery mildew.

Keywords: powdery mildew, winter wheat, genes of resistance, race analysis

Introduction

Powdery mildew (*Blumeria graminis* (DC) Speer f. sp. *tritici*) is one of the main diseases of bread wheat in the south of Ukraine. In the last years, it has slightly lost its relevance because of the advent and competition from the new wheat diseases such as *Pyrenophora tritici-repentis, Scolecotrichum graminis* and others. However, the pathogen has high biology-ecological adaptation and survives on plants of winter wheat in early spring, late autumn and even partially in winter. In 2006 and 2008, we observed epiphytotic development of powdery mildew in later autumn, which, due to the warm weather, continued in the winter. Under such conditions, the pathogen causes a grain yield decrease of up to 20% (Babayants 2011).

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The pathogen is able to rapidly evolve new virulent pathotypes, and because it is airborne this induces migration of the genes of virulence. Resistance of cultivars and breeding material is overcome by the pathogen in short time (Limpert 1999; Bogdanovich 2002). Therefore several breeding strategies have been proposed to enhance the durability of resistance to powdery mildew. The pyramiding strategy is based on incorporation of several effective race-specific genes into one genotype. Another breeding strategy is race-nonspecific resistance or partial resistance, known also as slow-mildewing resistance. It does not confer full immunity but provides durable long-term resistance. This resistance is polygenic or oligogenic and is controlled by minor genes. A sufficient level of this type of resistance is attained by accumulation of minor polygenes. The third strategy is combining race-specific genes with slow-mildewing resistance. It can be implemented successfully when breeding material selected for crosses possesses high partial resistance and completely effective major genes (Wang et al. 2005; Hysing et al. 2007; Liatukas and Ruzgas 2008; Bai et. al. 2012).

The information about 68 genes and their alleles of resistance against pathogen of powdery mildew is presented in the Catalogue of Gene Symbols for Wheat (McIntosh et al. 2013). Most of them are not efficient, the new sources of effective genes of resistance may be found in wild relative species of bread wheat. Wheat breeding lines were developed from interspecific crossings with *Aegilops tauschii* Coss., *Aegilops variabilis* Eig and *Aegilops cylindrica* Host. at the Plant Breeding and Genetics Institute – National Centre of Seed and Cultivar Investigation (PBGI-NC SCI), Ukraine. They possess resistance against 5–7 diseases of wheat, including powdery mildew (Babayants et al. 2010; Babayants 2011).

For successful wheat breeding for powdery mildew resistance, continuous virulence monitoring of pathogen population is necessary. Knowledge of virulence dynamics and shifts is important for the choice of effective race-specific *Pm* genes and timely replacement of the ineffective ones, as well as for adjustment of the breeding programs and prediction of large scale epiphytoties. Such investigations have been conducted at the PBGI-NC SCI since 1975 (Babayants 1999; Babayants et al. 2004).

The current paper presents the findings of research into pathotype composition of powdery mildew population, effectiveness of known *Pm*-genes and breeding lines CN240/06, CN98/06, CN158/06, derived from interspecific crosses, against powdery mildew in the south of Ukraine.

Materials and Methods

The infection material for studying pathotype composition of the pathogen was collected in the fields of bread wheat in the south of Ukraine. Monospore isolates were selected from the infected samples and pathotype analysis was conducted using differential set of Krivchenko. A set of differentials for pathotype analysis consists of the following 9 differentials: Carstens V, Neuzucht-14-44 (syn. Salzmunder-Bartweizen) (*Pm8*), Ulka/*8CC (*Pm2*), Axminster/*8CC (*Pm1a*), Halle Stamm 13471 (*Pm2+Mld*), Weihenstephaner M1 (*Pm4b*), Hope/8*Chancellor (*Pm5a*), Chul/*8CC (*Pm3b*), Asosan/*8CC (*Pm3a*) (Krivchenko et al. 1980).

During 2004–2012, eighteen differentials were used for virulence analysis, and in 2013 another thirteen differentials were added. Nine near-isogenic lines of cv. Chancellor with genes Pm1a, Pm2, Pm3a, Pm3b, Pm3c, Pm4a, Pm5a, Pm6 and Pm8 were used. Also, ten cultivars/lines with additional genes and combinations – Khapli (Pm4a+), Weihenstephaner M1 (Pm4b), Transec (Pm7), Neuzucht-14-44 (Pm8), Normandie (Pm1+2+9), Halle Stamm 13471 (Pm2+Mld), Tp114/65A (Pm2+6), Apollo (Pm2+4b+8), Sorbas (Pm4b+6), Kronjuwel (Pm4b+8) were used. In 2013, Aristide (Pm3g), Arkas (Pm4b), Dauntless (Pm8), Amigo (Pm17), KS93WGRC28 (Pm20), NC99BGTAG11 (Pm37), Norin 4 (Pm10+15), Salmon (Pm8+11), Akabozu (Pm10+14+15), NC96B-GTD3 (Pm3c+5a+35) and NC97BGTD7 (Pm3a+5a+34) were additionally used.

The resistant breeding lines CN240/06, CN98/06, CN158/06, developed in the PBGI-NC SCI, were added to the set of differentials. They were derived from interspecific crosses with species *Aegilops cylindria* Host., *Triticum erebuni* Gandil., *Aegilops variabilis* Eig.

The set of differentials was updated and carriers of genes of resistance, new for us, were obtained via USDA, Germplasm Resources Information Network – (GRIN) (2014).

Analyses of pathotypes were done on isolated pieces of wheat leaves placed in a solution of 40 mg/l of benzimidazol according to Babayants method (1988).

Effectiveness of powdery mildew resistance genes was studied at the seedling stage in the greenhouse and on adult plants in the field. Resistance of seedlings was examined using artificial inoculation with a population of powdery mildew in the laboratory conditions. Resistance in the field conditions was estimated on the natural infection background.

Resistance at the seedling stage was scored according to the scale: VR – very resistant, R – resistant, MR – moderately resistant, MS – moderately susceptible, S – susceptible, VS – very susceptible. Adult resistance in the field was scored according to a 9-point scale: 1-2 – very high susceptibility, 3 – high susceptibility, 4 – susceptibility, 5 – moderate susceptibility, 6 – moderate resistance, 7 – resistance, 8 – high resistance, 9 – immunity. Type of resistance and disease severity were scored using scales of Babayants (Babayants 1988; Babayants 2011).

Results

During 10 years, with the aid of 9 differentials, in the population of pathogen, there were found 78 known pathotypes and 39 new pathotypes that had not been described earlier. One of them was detected between 2011–2013. It is a new race, which we designated as Mr39 (Table S1*).

By the frequency of occurrence during 2004–2013, the pathotypes of powdery mildew were differentiated as dominating (1, 2, 4, 15, 27, 35, 44, 46, 51, 58, 59, Mr39), accom-

^{*} Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

panying (0, 9, 21, 22, 28, 32, 43, 45, 53, 55, 60, 61, 63, 66, 64, 67, Mr8, Mr18, Mr20, Mr22, Mr23, Mr26, Mr30, Mr33) and seldom occurring (7, 10, 14, 29, 33, 34, 50, 52, 59, 65, 71, 73, Mr1, Mr3, Mr5, Mr6, Mr9, Mr11, Mr12, Mr16, Mr25). Pathotypes which were virulent against the range of cultivars and the breeding lines with the more effective *Pm*-genes from 2004 to 2013 are presented in Table 1. The pathotypes differ in specificity and spectrum of virulence to the breeding lines and the cultivars with the different *Pm*-genes. A broad spectrum of virulence was determined for pathotypes 51, 53, 59, 69 and 75, a narrow spectrum was established for pathotypes 27, 44, 58, 66 and 74 (Table 1).

Monoisolates of pathotypes 35, 53, 46, 44 were found to be virulent against cv. Khapli but their frequency of occurrence during the experimental years was very low in the population of the pathogen. In 2013, single monoisolates of pathotypes 9, 60 and 23 were virulent against the wheat lines KS93WGRC28 (*Pm20*), NC96BGTD3 (*Pm3c*+5*a*+35), NC99BGTAG11 (*Pm37*) (Table 1). The above-mentioned pathotypes of the pathogen can be dangerous to all of these cultivars and lines if their virulence frequency and/or aggressiveness will increase. In this case, their effectiveness as donors of resistance will decrease. As a result, regular monitoring of powdery mildew population is necessary.

The research indicates that most of the pathotypes of powdery mildew are virulent to the carriers of *Pm6*, *Pm8* genes (Table 2). Gene *Pm3g* and combinations of genes Pm10+15, Pm8+11, Pm10+14+15 were similar in virulence level to *Pm6*, *Pm8* genes in the population of powdery mildew in the south of Ukraine. These genes are not effective against powdery mildew. The frequency of virulence to genes *Pm1*, *Pm2*, *Pm3a*, *Pm3b*,

Cultivar	Pathotypes
Weihenstephaner M1	61, 69, 51, 60, 59, 74, 45, 72, 55, 71, 54, 62, 63, 68, 49, 75, 90, Mr14, Mr3, Mr26, Mr36, Mr8
Halle Stamm 13471	51, 71, 49, 54, 76, 85, 29, 37, Mr2, Mr12, Mr15, Mr16, Mr21, Mr22, Mr23, Mr25, Mr30, Mr34, Mr36
Sorbas	61, 69, 51, 74, 49, 71, 90, 66
Apollo	61, 69, 51, 60, 59, 49, 68, 75, Mr14, Mr36
Tp114/65A	69, 51, 53, 46, 66, 71, 72, 75, Mr34, Mr14
Century	69, 51, 53, 54, 59, 60, Mr3
Khapli	35, 53, 46, 44, 61, Mr3, Mr36
Normandie	69, 51, 53, 46, 66, 71, 72, 75
CN 240/06	69, 51, 53
CN 98/06	69, 51, 53, 60, 59
CN 158/06	69, 51, 53, 54, 59, 60
KS93WGRC28	9
NC96BGTD3	60
NC99BGTAG11	23

Table 1. Pathotypes of Blumeria graminis (DC) Speer f. sp. tritici virulent to wheat lines and cultivars with different Pm-genes during 2004–2013

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$T_{\mathcal{G}}$	uble 2. The frequency of vi	irulence to Pm-gene	s (%) (Blumeria graminis (DC) Speer f. sp. tritici) in the south o	of Ukraine dur	ing 2004–201	3
			с;г-п	2004-	-2012	C10C
Pm-genes	Cultivar, line	Accession number	reagree-	min	max	5102
I	Carstens V	PI 191311	Carstens III / Dickkopf // Dickkopf / Criewener 104	98	100	100
Pmla	Near Isogenic	Cltr 14114	Axminster /8 * Chancellor	45	71	80
Pm2	Near Isogenic	Cltr 14118	Ulka /8 * Chancellor	22	58	31
Pm3a	Near Isogenic	Cltr 14120	Asosan /8 * Chancellor	26	52	54
Pm3b	Near Isogenic	Cltr 14121	Chul /8 * Chancellor	30	61	17
Pm3c	Near Isogenic	Cltr 14122	Sonora /8 * Chancellor	40	58	I
Pm3g	Aristide	PI 512253	Boulmiche // Mexique 50 / B21	I	I	94
Pm4a	Near Isogenic	Cltr 14123	Khapli /8 * Chancellor	I	I	60
Pm4a+	Khapli	Cltr 4013	Triticum turgidum subsp. dicoccon (Schrank) Thell.	1	7	I
Pm4b	Weihenstephaner M1	Ι	Koga / 3 / Lichti-Fruh // Lichti-Fruh / (Tr.ca) Schwarzen- Persischer	11	29	66
Pm4b	Arkas	PI 428502	Lichti Fruh-Merlin – Opal / Firlbeck I-CA – Mehltau Halle	I	I	74
Pm5a	Near Isogenic	Cltr 14125	Hope /8 * Chancellor	59	95	37
Pm6	Near Isogenic	Cltr 15888	Michigan Amber /8 * Chancellor	92	98	89
Pm7	Transec	Cltr 14189	Chinese Spring / irradiated Cornell Sel. 82a1-2-4-7	14	62	20
Pm8	Neuzucht-14-44	PI-340749	Criewener-104 / (Se.ce) Petkus	63	94	86
Pm8	Near Isogenic	Ι	Kavkaz /8 * Chancellor	78	100	06
Pm8	Dauntless	PI 592142	MMG 435-46-3 / Hobbit	I	I	91
Pm17	Amigo	PI 578213	Teewon sib, OK66C3190 / 6 / Gaucho / 4 / Tascosa / 3 / Wichita // Wichita / Teewon / 5 / 2 * Teewon	I	I	43
Pm20	KS93WGRC28	PI 583795	$BC_{1}F_{4}$ – derived line from MS6RL (6D) / TAM 104	I	I	3
Pm37	NC99BGTAG11	PI 615588	Saluda * 3 / PI 427315	I	I	3
¹ Accession nu ² Pedigree in a	umbers in accordance with Re. accordance with Genetic Resou	search Service Germpla arces Information Syste	asm Resource Information Network – (GRIN). em for Wheat and Triticale – (GRIS).			

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Table 3. The frequency of virulence against cultivars/lines with different combinations of Pm-genes (%) (Blumeria graminis (DC) Speer f. sp. tritici) in the south of Ukraine, during 2004-2013

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D	Cultiment line	Accession	<u>رik</u> t	2004-	2012	0100
rm-genes		number ¹	Louigice	min	тах	CT07
PmI+2+9	Normandie	PI 172312	Vilmorin 27 / Hybride 40	20	24	Ι
Pm2+Mld	Halle Stamm 13471	PI 340753	1	8	28	9
<i>Pm2+6</i>	Tp114/65A	PI 352240	CI-12633 / Cappelle-Desprez // Chinese-166 / 3 / 2 * Cappelle-Desprez	42	49	58
Pm2+4b+8	Apollo	PI 191755	Maris-Beacon / Clement // Kronjuwel	29	54	66
Pm4b+6	Sorbas	PI 636367	Maris-Huntsman / W-641-65	22	34	37
Pm4b+8	Kronjuwel	I	Tenor / (T4A.5R) Triticale-Derivative // 2 * Caribo	24	47	52
PmI0+I5	Norin 4	PI 235228	Yushoki 347 / Hiroshima Shipree 3	Ι	Ι	67
Pm8+II	Salmon	PI 542976	1	Ι	Ι	91
PmI0 + I4 + I5	Akabozu	Cltr 8427	Landrace	I	I	77
Pm3c+5a+35	NC96BGTD3	PI 597350	Saluda * 3 / TA 2377	I	I	3
Pm3a+5a+34	NC97BGTD7	PI 604033	Saluda * 3 / TA 2492	I	I	43
PmAc1, PmAc2	CN240/06	I	Odesskaya polukarlikovaya / <i>Aegilops cylindrica</i> / Odesskaya polukarlikovaya / Lutescens 23397	6	٢	I
PmTel, PmTe2	CN98/06	I	<i>Triticum erebuni /</i> Obriy / Odesskaya 162 / 2 / Ukrainka odesskaya	4	∞	I
PmAv1, PmAv2	CN158/06	1	Donskaya polukarlikovaya / <i>Aegilops variabilis /</i> Ukrainka odesskaya / Nikonia	1	4	I
¹ Accession numl ² Pedigree in acco	oers in accordance with Reservation of the second of the s	arch Service Germp ces Information Sys	blasm Resource Information Network – (GRIN). stem for Wheat and Triticale – (GRIS).			

Pm3c, Pm5 and Pm7 varied and reached relatively high enough level in different years (Tables 2 and 3). Thus, these genes are insufficiently effective and unreliable against powdery mildew.

The frequency of virulence against cvs. Weihenstephaner M1 with gene Pm4b, Sorbas with Pm4b+6, Kronjuwel with Pm4b+8 and Apollo with Pm2+4b+8 was from 11 to 66% (Tables 2 and 3). The investigation of virulence dynamics since 1984 till now has revealed breakdown of the resistance. Thus, from 1984 to 1999, virulence frequency to cv. Weihenstephaner M1 varied from 0 to 10% and in 2001 the virulence reached 56%. Similar variation and breakdown of resistance was noticed for cvs. Sorbas, Kronjuwel and Apollo. The virulence frequency to Sorbas from 1984 till 1999 was from 0 to 10% and in 2002 reached 27%. The virulence frequency to Kronjuwel from 1984 to 1999 varied from 0 to 10% and in 2000 it increased to 21%, in 2001 to 50%, and in 2002 to 66%. The virulence frequency to Apollo from 1984 to 2003 varied from 0 to 9% and in 2004–2012 increased to 54%, in 2013 to 66% (Table 3) (Babayants 1999; Babayants et al. 2004). This suggests that these combinations and gene Pm4b are not effective in the south of Ukraine.

About half of isolates were virulent to combination of genes Pm2+6 of cv. Tp114/65A in the research years (Table 3). In the previous years (1984–2003), the virulence varied from 0 to 42%. The virulence frequency to the combination of genes Pm1+2+9 (Normandie) was 20–24% and Pm2+Mld (Halle Stamm 13471) 8–28% (Table 3). The same level was observed in the previous thirty years (Babayants 1999; Babayants et al. 2004). The virulence to gene Pm17 (Amigo) reached high level in 2013 (Table 2). The low frequency of virulence (not higher than 3%) continues to remain against the cultivar Khapli (Pm4a+). Moseman et al. (1980) have reported that apart from Pm4a Khapli carries at least another two Pm-genes. The frequency of virulence to isogenic line (Pm4a) in the background of cv. Chancellor (Khapli/8* Chancellor) was 60%.

The frequency of virulence was minimal against genes Pm20 of line KS93WGRC28, Pm37 of line NC99BGTAG11 which were investigated for the first time in the local population (Table 2). The low frequency of virulence was to breeding lines CN240/06 (3–7%), CN98/06 (4–8%) and CN158/06 (1–4%) (Table 3).

Among the studied material, 14 lines/cultivars carry combinations of *Pm*-genes. The minimal frequency of virulence was against the following combination of genes: Pm3c+5a+35 (line NC96BGTD3). The frequency of virulence was relatively high against other combinations of genes (Table 3).

In the field test carried out from 2004 to 2013, high resistance at the adult plant stages to the pathogen of powdery mildew was shown by the cvs. Khapli, Century and breeding lines CN240/06, CN98/06 and CN158/06. Cultivar Sorbas was resistant to highly resistant. Cultivars Kronjuwel and Apollo were moderately resistant to resistant. Cultivar Weihenstephaner M1 was moderately susceptible to resistant. Line Ulka/8*Chancellor and cvs. Halle Stamm 13471 and Tp114/65A possess from moderate susceptibility to moderate resistance. All the rest of the cultivars/lines shared different degree of susceptibility (Table S2).

Discussion

Since 1975, the population of powdery mildew in the south of Ukraine has been monitored annually in the PBGI-NC SCI. The frequency of virulence and the effectiveness of known *Pm*-genes have been studied annually. Moreover, new donors of resistance were developed for wheat breeding for powdery mildew resistance. Using interspecific crossing and further saturation crossing with recurrent wheat cultivars and multiple selection in the artificially infected nurseries with separate and combined diseases, a series of bread wheat lines, including powdery mildew resistant ones, were developed. Besides the high resistance to powdery mildew and other wheat diseases, these lines have high values of agronomically important traits and are valuable plant breeding material. Wild cereals were used as a source of disease resistance for wheat (Babayants et al. 2010; Babayants 2011).

The results of investigation of powdery mildew population on the set of differentials indicate that the population of southern Ukraine consists of 78 known pathotypes, annually 1–5 new pathotypes are found, a total of 39 new pathotypes have been identified over the last 10 years. The broad composition of *Blumeria graminis* pathotypes is the result of a high variability of the pathogen and absence of bread wheat cultivars highly resistant to powdery mildew among the ones currently grown in the south of Ukraine.

Among the studied genes of resistance, Pm4a+ and Pm17 showed sufficient level of resistance in the field conditions. The breeding lines CN240/06, CN98/06, CN158/06 also possess high resistance against powdery mildew. The breeding lines were derived from interspecific crosses between susceptible bread wheat cultivars and wild cereal species: *Triticum erebuni* Gandil., *Aegilops cylindrica* Host, *Aegilops variabilis* Eig. The previous study indicates that lines carry dominant complementary genes that are designated by provisional symbols *PmTe1*, *PmTe2*, *PmAc1*, *PmAc2*, *PmAv1* and *PmAv2*. These genes are new and derived from above-mentioned species (Babayants et. al. 2010; Babayants 2011). Thus the species *Aegilops cylindrica* Host. was used as a source of genes of resistance against powdery mildew for the first time. The breeding lines listed above can be used as donors of resistance for breeding for resistance against powdery mildew.

KS93WGRC28 is a breeding line homozygous for wheat-rye translocation *T6BS.6RL* and carries gene Pm20 (Friebe et al. 1994). The breeding line NC99BGTAG11 was obtained after three backcrosses of line PI 427315 (derived from *T. timopheevii* subsp. *armeniacum*) with the cultivar Saluda. The resistance against powdery mildew is conferred by gene Pm37 transferred from *T. timopheevii* subsp. *armeniacum* (McIntosh et al. 2013). The investigation of virulence frequency at the seedling stage suggests that genes Pm20 and Pm37 are highly effective (frequency of virulence up to 3%). These genes are new for our region and their effectiveness has been studied for the first time.

The lines NC96BGTD3 and NC97BGTD7 obtained after three backcrosses of lines from *Aegilops tauschii* Coss. with the cultivar Saluda carry different combinations of *Pm*-genes (Maxwell 2008; Jarrett 2011; Genetic Resources Information System for Wheat and Triticale – (GRIS) 2014) (Table 3). Among these lines, NC96BGTD3 was highly effective in the south of Ukraine. We suppose that it high level of resistance is conferred by gene *Pm35*.

The research on the major powdery mildew resistance genes showed that Pm4a+, Pm20, Pm37 and combination of genes Pm3c+5a+35 provide sufficient level of resistance. In spite of the high level of virulence at the seedling stage, Pm17 (T1AL.1RS) still confers resistance at the adult plant stage. To our knowledge, Pm4a+ is not present in commercial cultivars. Since Pm20, Pm35, Pm37 are new for our area, there are no grown cultivars containing these genes or only few percent may carry them, which may explain low frequency level of virulent pathotypes in the powdery mildew population in the south of Ukraine. The research into virulence indicates that virulent pathotypes against all these race-specific genes are already present in the population. Changes in the population and increased virulence frequency and/or aggressiveness of these pathotypes will enable the pathogen to overcome these race-specific powdery mildew resistant genes. A lot of researchers established that resistance based on Quantitative Trait Loci (QTL) or the combination of minor genes with effective race-specific genes provides long-term resistance to Blumeria graminis (DC) Speer f. sp. tritici (Miedaner and Flath 2007; Mikulová et al. 2008; Bai et al. 2012). According to the results of Chen et al. (2009) the QTL QPm.osu. 1A associated with the race-specific Pm3a allele. Thus, NC97BGTD7 besides several racespecific genes incorporate quantitative trait loci that may be used as a solid base for wheat breeding for powdery mildew resistance. Some major genes or gene combinations and breeding lines CN240/06, CN98/06, CN158/06 with low level of virulence in the present study could be useful in pyramiding effective major Pm-genes or in combining them with non-specific genes for achieving more durable powdery mildew resistance.

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at http://www.akademiai.com/content/120427/

Electronic Supplementary *Table S1*. The virulence formula for known and new races detected during 2004–2013

Electronic Supplementary *Table S2*. Evaluation of wheat lines and cultivars to *Blumeria graminis* (DC) Speer f. sp. *tritici* during 2004–2013