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Virulence and diversity of the *Blumeria graminis* f. sp. *tritici* populations in Lithuania and Southern Ukraine

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Abstract

For the present study, samples of cleistothecia were collected in Central Lithuania and Southern Ukraine. To characterize the virulence, complexity and diversity of powdery mildew (*Blumeria graminis* f. sp. *tritici*) populations, 80 isolates were derived from single ascospores, 40 isolates from each population. Pathotype analysis was conducted on 16 differentials with known *Pm* genes. According to the proposed nomenclature, 32 pathotypes were identified in the Lithuanian powdery mildew population and 30 – in the Ukrainian population. The most frequent phenotype in Lithuania was NGDE (7.5%), and in Ukraine it was NGKE (15%). The Ukrainian powdery mildew population was more complex and contained more virulence genes per isolate.

The virulence test was carried out by inoculation on detached leaves of 26 common wheat (*Triticum aestivum* L.) differentials with known *Pm* genes and 12 resistant winter wheat breeding lines and cultivars. The frequencies of virulence to these differentials ranged from 0% to 100%, and most of them had high level of virulence. No virulence was found to *Pm20* and *Pm25+3a* genes, cultivar 'Lastivka odeska' and breeding lines CN 89/16 and PI 170911 in both populations, whereas the frequencies of virulence were more than 50% to *Pm1a*, *Pm2*, *Pm3b*, *Pm3g*, *Pm4a*, *Pm5a*, *Pm6*, *Pm7*, *Pm8*, *Pm9*, *Pm10* and *Pm34* genes. The effectiveness of 25 *Pm* genes/alleles was estimated at the seedling and adult plant stages. Most of the genes were found to be ineffective. Genes *Pm20*, *Pm25+3a* and resistance of winter wheat cultivars 'Vykhovanka odeska', 'Kniahynia Olha' and 'Lastivka odeska' were highly effective both at the seedling and adult plant stages.

Key words: common wheat, genes of resistance, powdery mildew, race analysis.

Introduction

Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici*, is a common wheat (*Triticum aestivum* L.) disease with global importance. It is particularly economically significant in maritime and temperate climates with mild, rainy growing seasons. The severity of powdery mildew epidemics has decreased in the recent decades due to several reasons. The development of the strategy for race non-specific powdery mildew resistance in the breeding programs at the end of the 70s has improved cultivar resistance in further generations (Cowger et al., 2012; Li et al., 2014). This may also be partly attributed to the fact that powdery mildew has lost its relevance due to biological competition with other wheat diseases such as tan spot (*Pyrenophora tritici-repentis*) and Septoria leaf blotch (*Mycosphaerella graminicola*), which under conditions of modern agriculture appeared more plastic and aggressive, particularly tan spot. Compared with other wheat diseases, powdery mildew is more easily controlled by fungicides (Cowger et al., 2012; Babayants et al., 2015).

However, the disease causes economic losses in all the continents, where the wheat is grown. It can cause grain losses from 13% to 34% under low or moderate infestation and 50–100% under severe disease pressure (Singh, 2017). Normally, yield losses in Europe are below 10%, though powdery mildew causes losses of about 20% in a mild and wet climate of the United Kingdom. Moreover, powdery mildew is the most frequently occurring foliar disease, which is observed annually in most of the European countries; therefore, the losses are far from negligible for this area. In North America, it causes economic damage in the mild, humid mid-Atlantic states of the United States and in British Columbia of Canada. The losses of 30–35% were noticed in Russia and up to 62% in South America (Cowger et al. 2012; Singh et al., 2016; Singh, 2017). In China,

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powdery mildew is increasing its importance and for the last decade more than six million hectares of wheat cultivated area have been affected annually. Currently it is more dangerous than any other wheat diseases for this region (Zeng et al., 2014; Ma et al., 2015; Shen et al., 2015; Mwale et al., 2017). Some researchers predict powdery mildew to become more important in the future because of the climate change, which will provide more favourable conditions for the development of the disease (Tang et al., 2017). Because of the pathogen's ability to evolve and overcome host resistance and in order to prevent large-scale epidemics, continual research and monitoring of virulence is necessary.

The first studies on the powdery mildew population conducted in the 1930s revealed that it can be divided into different physiological races (synonyms: pathotype, phenotype) based on their virulence pattern – the ability to infect specific cultivars (Wolfe, Schwarzbach, 1978; Singh, 2017). Afterwards several nomenclatures were proposed: United States (Powers, 1957), Australian (Pugsley, Carter, 1953) and German (Nover, 1957) differential sets, which consisted of seven to eight cultivars. In the United States, Briggle (1969) developed near-isogenic lines of wheat on the basis of a susceptible wheat cultivar 'Chancellor', each of them carried one *Pm*-gene. A set of differentials used in Germany was modified by Wolfe and Schwarzbach (1978) and Frauenstein et al. (1979). The differential sets were developed to monitor the shifts and emergence of new virulence in the population, to timely adjust the breeding programs and replace the ineffective *Pm*-genes.

Nowadays, virulence and diversity of *Blumeria graminis* f. sp. *tritici* are being studied throughout the world: in the United States (Parks et al., 2008; Cowger et al., 2018), Europe (Carver, 2009; Cowger et al., 2012), Ukraine (Babayants et al., 2015), Iran (Elyasi-Gomari, Lesovaya, 2012), Egypt (El-Shamy et al., 2016; Abdelrhim et al., 2018) and China (Zeng et al., 2014). However, the last nomenclatures for race analysis were developed more than 40 years ago. The cultivars which have been proposed as differentials are becoming susceptible or moderately susceptible. Long-term race analysis on historical basis with old nomenclatures of Nover (1957), Wolfe and Schwarzbach (1978) and Frauenstein et al. (1979) has been retained in Hungary (Szunics et al., 2001) and in Ukraine (Babayants et al., 2015) on the nomenclature of Frauenstein et al. (1979) until now. In others countries, the virulence frequency to *Pm*-genes and/or pathotype analysis is being carried out on their own available differentials. However, if different genotypes and years are used for race identification, the results are not possible to compare.

In accordance with the gene-for-gene hypothesis, gene pyramiding of effective *Pm*-genes into single genotypes may provide more durable resistance, because the more genes that provide resistance, the more mutations of pathogen will be required to overcome such resistance. To use the strategy of gene pyramiding and combination of race-specific and race non-specific genes, one needs to pay special attention to the effectiveness of race-specific genes. Ideally, race-specific genes should be effective against all races. If this is not possible, the genes should be selected on the basis of virulence analysis. Monitoring of virulence frequency and complexity may provide useful information for combining of proper genes to develop and sustain durable resistance to powdery mildew (Babayants et al., 2015).

The objectives of this study were: (i) to examine the virulence and diversity of the Lithuanian and Ukrainian powdery mildew populations, (ii) to evaluate the effectiveness of *Pm*-genes and resistant cultivars and advanced breeding lines at seedling and adult plant stages, (iii) to update the nomenclature and the differential set for virulence and race analysis and (ix) to study the associations between virulence and avirulence, and determine what *Pm*-genes can be combined to enable durable resistance for a target region.

Materials and methods

Fungal material and inoculation. Samples of cleistothecia (synonym: chasmothecia) on common wheat (*Triticum aestivum* L.) leaves were collected from powdery-mildew susceptible, naturally-infected winter wheat cultivars in central region of Lithuania and southern region of Ukraine in 2016. The leaves with cleistothecia were treated alternately with low and high (4°C and 28°C) temperatures for 12 hours for 7 days to activate the cleistothecia. The powdery mildew (*Blumeria graminis* f. sp. *tritici*) population was multiplied according to Babayants method (Бабаянц, Бабаянц, 2014). Single isolates were separated from pustules by transferring conidium from a single pustule to a noninfected seedling in a tube using a sterile dissecting needle. A total of 80 isolates (40 from Lithuanian and 40 from Ukrainian powdery mildew populations) were obtained from cleistothecial samples.

Powdery mildew resistance at the seedling stage of plants was evaluated under controlled conditions of greenhouse and artificial inoculation. The plants were grown under 24-h photoperiod at a light intensity of 5000–6000 lx and with humidity of 60–80%. The inoculation was done with conidia of bulked isolates of *Blumeria graminis* f. sp. *tritici.* The powdery mildew resistance of differentials was scored 9 days after inoculation according to Babayants method (Бабаянц, Бабаянц, 2014). The pathotype analysis was done on isolated leaf pieces (2–3 cm) of the differentials at one to two-leaf stages of plants in two replications. The leaf fragments were placed in Petri dishes with a solution of 40 mg L^{-1} of benzimidazole and on the filter paper. They were inoculated by shaking the infected plants over the dishes according to Babayants method (Бабаянц, Бабаянц, 2014) at the Plant Breeding and Genetics Institute, Ukraine.

Plant material. A set of differentials for virulence analysis included a total of 38 genotypes. Nine near-isogenic lines of winter wheat cultivar 'Chancellor' with genes *Pm1a*, *Pm2*, *Pm3a*, *Pm3b*, *Pm3c*, *Pm4a*, *Pm5a*, *Pm6* and *Pm8*, and five winter wheat breeding lines with known genes KS93WGRC28 (*Pm20*), NC96BGTA5 (*Pm25+3a*), NC97BGTD7 (*Pm34*), NC96BGTD3 (*Pm35*) and NC99BGTAG11 (*Pm37*) were used. In addition, spring wheat cultivars: 'Khapli' (*Pm4a+*), 'Weihenstephaner M1' (*Pm4b*), 'Transec' (*Pm7*), 'Akabozu' (*Pm10+14+15*), and winter wheat cultivars: 'Aristide' (*Pm3g*), 'Normandie' (*Pm1+2+9*), 'Norin 4' (*Pm10+15*), 'Apollo' (*Pm2+4b+8*), 'Salmon' (*Pm8+11*), 'Amigo' (*Pm17*), 'Vykhovanka odeska' (*Pm17+38+39*) and 'Kniahynia Olha' (*Pm17+38+39*), with known *Pm* genes and gene combinations were included. Also, because of the excellent resistance to powdery mildew, three winter wheat lines with unknown *Pm* genes PI 170911, NC96BGTD2, NC97BGTD8 and cultivar 'Lastivka odeska' were added into the set of differentials. Another eight resistant advanced winter wheat breeding lines CN 9/16, CN 26/16, CN 84/16, CN

89/16, CN 19/16, CN 113/16, CN 117/16 and CN 169/16 which developed at the Plant Breeding and Genetics Institute, Ukraine were included. They derived from interspecific crosses with species of jointed goatgrass (*Aegilops cylindrica* Host), synthetic species *Triticum erebuni* Gandil. and *Aegilops peregrina* Hack. (syn. *Aegilops variabilis* Eig.).

The differentials with known genes were complemented and updated via USDA, Germplasm Resources Information Network (https://www.ars-grin.gov/).

Field experiments and meteorological conditions. Field experiments were set up in an eight-course crop rotation in Akademija (55°39′ N, 23°88′ E), Kėdainiai district, Lithuania during 2015–2016 and fallow-wheat rotation in Odesa (46°45′ N, 30°67′ E), Ukraine during 2016–2017. Weeds were controlled by herbicides in the autumn. Other pesticides during the plant growing season were not applied. Pesticide-untreated seeds of the differentials were sown in 1 m long rows with six replications in Ukraine and in 1.5 m^2 plots with two replications in Lithuania. The powdery mildew resistance of differentials under field conditions was evaluated at the end of April and in May in Ukraine and at the end of May and in June in Lithuania by visual scoring on a 1–9 score basis.

Average annual precipitation in Odesa (Ukraine) is about 459 mm, whereas in Akademija (Lithuania) it is 568 mm; also the average yearly temperature is colder in Lithuania than in Ukraine: 7.76°C and 10.23°C, respectively. The spring is much earlier and warmer in Ukraine (Fig. 1). Powdery mildew development and severity are determined by the weather conditions during the spring and autumn–winter period in Ukraine. In the 2015–2016 growing season, the autumn period was unfavourable with precipitation of 3.2 mm in September, whereas long-term average precipitation for this month is 37 mm. However, there was observed warm April and 107 mm of precipitation during spring in 2016 (Fig. 1). In the 2016–2017 growing season, the conditions of the autumn period were more favourable with precipitation of 206 mm during autumn months (long-term average precipitation is 104 mm) but colder April and drier March in 2017 (Fig. 1). As a result, the genotypes exhibited almost equal level of resistance during the two experimental years in Ukraine.

Development of powdery mildew is determined mostly by the weather conditions during the spring. Heavier precipitation during the spring in 2015 than in 2016 as well as warmer temperatures provided more favourable conditions for powdery mildew development in 2015 in Lithuania (Fig. 1).

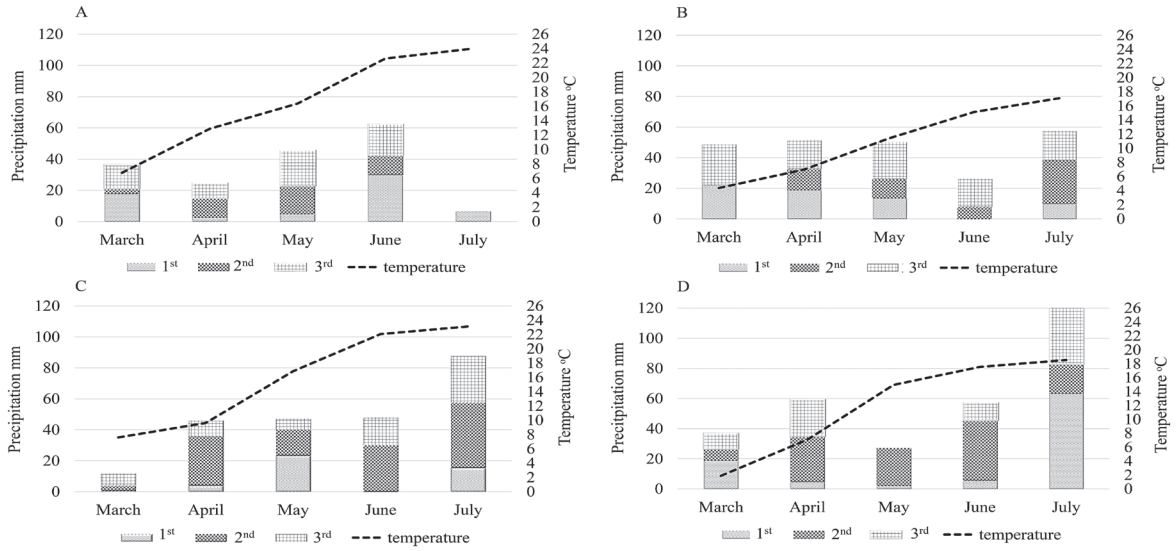

Figure 1. Monthly average precipitation by ten-day periods and average monthly temperatures during the field experiments in Ukraine 2016 (A), 2017 (C) and in Lithuania 2015 (B), 2016 (D)

Nomenclature. Pathotype analysis of powdery mildew population was done with a special code consisting of 16 differentials. The differentials were arranged and the name of race was designated by the main principle of North American system of nomenclature for leaf rust (Long, Kolmer, 1989). The differential hosts were arranged in four sets: set 1 – *Pm1a*, *Pm2*, *Pm3a*, *Pm4a*, set 2 – *Pm3c*, *Pm8*, *Pm17*, *Pm34*, set 3 – *Pm4b*, *Pm5a*, *Pm20*, *Pm35* and set 4 – *Pm7*, *Pm11*, *Pm25+3a*, *Pm37*. The code consists of 16 letters, which explain all possible variation of virulence and avirulence of 16 *Pm*-differentials. The number of letters is equal to the number of host sets. Accordingly, the code name of races consists of four letters; each letter is determined by virulence / avirulence pattern of corresponding host set (Table 1). The differential set can be easily expanded by adding new host sets.

Disease evaluation. The effectiveness of *Pm*-genes was studied at the seedling stage under controlled conditions in a greenhouse and at adult plant stage in the field. Resistance of seedlings was examined using artificial inoculation with a population of powdery mildew in the laboratory conditions at the Plant Breeding and Genetics Institute, Ukraine. Resistance in the field conditions was estimated under natural infection in Lithuania and Ukraine.

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. Resistance at adult plant stage in the field was scored according to a 9-point scale (Бабаянц, Бабаянц, 2014): 1 – very high resistance, 2 – high resistance, 3 – resistance, 4 – moderate resistance, 5 – moderate susceptibility, 6 – susceptibility, 7 – high susceptibility, 8–9 – very high susceptibility (Fig. 2).

Statistical analysis. Spearman correlation coefficients between the virulence and avirulence reactions of the differentials were reported at the

Table 1. Code of 16 differentials for identification of *Blumeria graminis* pathotypes

Code letter	Host set 1	*Pm1a*	*Pm2*	*Pm3a*	*Pm4a*
	Host set 2	*Pm3c*	*Pm8*	*Pm17*	*Pm34*
	Host set 3	*Pm4b*	*Pm5a*	*Pm20*	*Pm35*
	Host set 4	*Pm7*	*Pm11*	*Pm25*	*Pm37*
A		R	R	R	R
B		R	R	R	S
C		R	R	S	R
D		R	S	R	R
E		S	R	R	R
F		R	R	S	S
G		R	S	R	S
H		S	R	R	S
I		R	S	S	R
J		S	R	S	R
K		S	S	R	R
L		R	S	S	S
M		S	R	S	S
N		S	S	R	S
O		S	S	S	R
P		S	S	S	S

R – resistant, S – susceptible

0.05, 0.01 and 0.001 probability levels. All statistical procedures were performed by using software *SAS*, version 9.4 (SAS Inc., USA).

Results

Phenotype composition. The pathotype analysis was conducted using a set including 16 differentials. Thirty-two phenotypes were identified in the Lithuanian population, among which the phenotype NGDE predominated, its frequency of occurrence was 7.5%; the frequency of occurrence of GGDA, HGDD, KGKE, NGDA, NGDK and NGKK was 5% of each, while others were represented by single isolates. Thirty phenotypes were identified in the Ukrainian population, among which the phenotype NGKE predominated with a frequency of occurrence of 15%; the frequency of occurrence of the phenotypes NDDK, NGDN, PGDE, PGDK, PGKK was of 5% each, others were found only as single isolates (Table 2).

The most complex phenotypes were PLKN and NLNK with a frequency of occurrence of 5%, both

Figure 2. The scale for evaluation of wheat resistance to *Blumeria graminis* f. sp. *tritici*

Table 2. Virulence formula of the most frequent and virulent *Blumeria graminis* f. sp. *tritici* phenotypes identified in Ukraine and Lithuania on the set of 16 differentials

Phenotype	Avirulence / virulence formula	Frequency %	
		Ukraine	Lithuania
NGKE	*Pm3a*, *Pm3c*, *Pm17*, *Pm20*, *Pm35*, *Pm11*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm4b***, ***Pm5a***, ***Pm7***	15	2.5
NGKK	*Pm3a*, *Pm3c*, *Pm17*, *Pm20*, *Pm35*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm4b***, ***Pm5a***, ***Pm7***, ***Pm11***	5	2.5
NGDE	*Pm3a*, *Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm11*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***, ***Pm7***	–	7.5
NGDA	*Pm3a*, *Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm7*, *Pm11*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***	–	5
NGDK	*Pm3a*, *Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***, ***Pm7***, ***Pm11***	–	5
GGDA	*Pm1a*, *Pm3a*, *Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm7*, *Pm11*, *Pm25*, *Pm37* / ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***	–	5
HGDD	*Pm2*, *Pm3a*, *Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm7*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***, ***Pm11***	–	5
KGKE	*Pm3a*, *Pm4a*, *Pm3c*, *Pm17*, *Pm20*, *Pm35*, *Pm11*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm8***, ***Pm34***, ***Pm4b***, ***Pm5a***, ***Pm7***	–	5
NDDK	*Pm3a*, *Pm3c*, *Pm17*, *Pm34*, *Pm4b*, *Pm20*, *Pm35*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm5a***, ***Pm7***, ***Pm11***	5	–
NGDN	*Pm3a*, *Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm25* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***, ***Pm7***, ***Pm11***, ***Pm37***	5	–
PGDE	*Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm11*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm3a***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***, ***Pm7***	5	–
PGDK	*Pm3c*, *Pm17*, *Pm4b*, *Pm20*, *Pm35*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm3a***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm5a***, ***Pm7***, ***Pm11***	5	–
PGKK	*Pm3c*, *Pm17*, *Pm20*, *Pm35*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm3a***, ***Pm4a***, ***Pm8***, ***Pm34***, ***Pm4b***, ***Pm5a***, ***Pm7***, ***Pm11***	5	–
PLKN	*Pm3c*, *Pm20*, *Pm35*, *Pm25* / ***Pm1a***, ***Pm2***, ***Pm3a***, ***Pm4a***, ***Pm8***, ***Pm17***, ***Pm34***, ***Pm4b***, ***Pm5a***, ***Pm7***, ***Pm11***, ***Pm37***	2.5	–
NLNK	*Pm3a*, *Pm3c*, *Pm20*, *Pm25*, *Pm37* / ***Pm1a***, ***Pm2***, ***Pm4a***, ***Pm8***, ***Pm17***, ***Pm34***, ***Pm4b***, ***Pm5a***, ***Pm35***, ***Pm7***, ***Pm11***	2.5	–

were found in the Ukrainian population. The former on the differential set of 16 *Pm*-genes was avirulent to only four *Pm*-genes: *Pm3c*, *Pm20*, *Pm35* and *Pm25+3a*, the latter – to five *Pm*-genes: *Pm3a*, *Pm3c*, *Pm20*, *Pm25+3a* and *Pm37*. Virulence analysis of the Lithuanian and Ukrainian powdery mildew phenotypes demonstrated that phenotypes of the latter population were more complex than the former one. Each powdery mildew isolate was virulent to a minimum of 9 genes and a maximum of 18 genes in Ukraine, whereas in Lithuania to 2 and 15, respectively (Fig. 3).

Virulence analysis and associations between virulence of isolates. The obtained results demonstrate that frequencies of virulence to the most of studied differentials were higher in Ukraine than in Lithuania. No virulence was found for *Pm20*, *Pm35* and *Pm25+3a* genes, wheat breeding lines PI 170911, CN84/16, CN89/16 and CN113/16, and cultivars 'Khapli', 'Vykhovanka odeska', 'Kniahynia Olha' and 'Lastivka odeska' in Lithuania. Whereas, in Ukraine, no virulence was detected for *Pm20* and *Pm25+3a* genes, breeding lines PI 170911 and CN89/16, and cultivars 'Khapli' and 'Lastivka odeska' (Table 3). In the Lithuanian powdery mildew population, low frequencies (>20) of virulence were detected to genes *Pm3c* and *Pm17* (2.5%) as well as to breeding lines CN9/16, CN26/16, CN117/16 (2.5%), CN19/16 (5%) and CN19/16, genes *Pm3a* (7.5%) and *Pm37* (12.5%) and line NC97BGTD8 (20%). Virulence frequency to *Pm4b* gene was 27.5%, and to the gene combination *Pm8+11* it was 30% (Table 3).

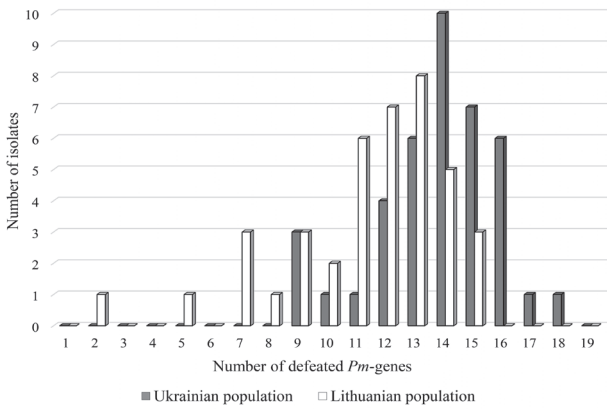

Figure 3. Complexity of Ukrainian and Lithuanian *Blumeria graminis* f. sp. *tritici* populations

Table 3. Evaluation of resistance of wheat differentials at the seedling and adult plant stages to *Blumeria graminis* f. sp. *tritici*

Pm-genes	Cultivar / line	Adult plant stage*				Virulence frequency %		Seedling stage
		Lithuania		Ukraine				
		2015	2016	2016	2017	Lithuania	Ukraine	
none	Carstens V	nd	nd	9	9	nd	nd	VS
Pm1a	Near isogenic line	7	6	7	7	62.5	87.5	S
Pm2	Near isogenic line	7	5	7	7	75	87.5	S
Pm3a	Near isogenic line	7	4	7	7	7.5	40	S
Pm3b	Near isogenic line	7	4	8	8	57.5	77.5	VS
Pm3c	Near isogenic line	4	4	2	2	2.5	5	R
Pm3g	Aristide	3	4.5	8	9	80	97.5	VS
Pm4a	Near isogenic line	7	5	7	7	80	80	S
Pm4a+	Khapli	nd	nd	2	2	0	0	R
Pm4b	Weihenstephaner M1	6	6	5	5	27.5	37.5	S
Pm5a	Near isogenic line	7	6	9	9	95	97.5	VS
Pm6	Near isogenic line	6	4	9	9	95	100	VS
Pm7	Transec	3	5	6	6	50	87.5	S
Pm8	Near isogenic line	6	6	8	8	90	97.5	VS
Pm2+4b+8	Apollo	nd	nd	6	6	62.5	80	S
Pm1a+2+9	Normandie	nd	nd	6	6	90	97.5	S
Pm10+15	Norin 4	nd	nd	6	6	90	97.5	S
Pm10+14+15	Akabozu	nd	nd	7	7	90	97.5	S
Pm8+11	Salmon	5	4	8	8	30	67.5	VS
Pm17	Amigo	4	4	2	2	2.5	10	R
Pm20	KS93WGRC28	1	1	2	2	0	0	R
Pm25+3a	NC96BGTA5	2	nd	2	2	0	0	VR
Pm34	NC97BGTD7	5	4	7	7	77.5	77.5	S
Pm35	NC96BGTD3	1	1	2	2	0	7.5	R
Pm37	NC99BGTAG11	nd	nd	7	7	12.5	22.5	S
Not known	PI 170911	nd	nd	2	2	0	0	R
Novel genes	NC96BGTD2	2	2	nd	nd	50	75	S
Novel genes	NC97BGTD8	5	4	nd	nd	20	45	S
Pm17+38+39	Vykhovanka odeska	1	1	2	2	0	17.5	R
Pm17+38+39	Kniahynia Olha	1	1	2	2	0	2.5	R
Not known	Lastivka odeska	1	1	2	2	0	0	R
Not known	CN9/16	nd	nd	nd	1	2.5	10	VR
Not known	CN26/16	nd	nd	nd	3	2.5	20	R, MR
Not known	CN84/16	nd	nd	nd	2	0	2.5	R
Not known	CN89/16	nd	nd	nd	2	0	0	R
Not known	CN19/16	nd	nd	nd	1	5	12.5	VR
Not known	CN113/16	nd	nd	nd	2	0	2.5	R
Not known	CN117/16	nd	nd	nd	2	2.5	10	R
Not known	CN169/16	nd	nd	nd	1	7.5	15	VR

* – 1 to 9 point scale, where 1 – very high resistance and 9 – very high susceptibility; VR – very resistant, R – resistant, MR – moderately resistant, S – susceptible, VS – very susceptible; nd – no data

In the Ukrainian powdery mildew population, low frequencies (>20) of virulence were detected to breeding lines CN19/16, CN169/16 and CN26/16 – 12.5, 15 and 20 %, respectively, to cultivar 'Vykhovanka odeska' – 17.5%. Virulence frequency to gene *Pm37* was 22.5%, to *Pm4b* – 37.5%, to *Pm3a* – 40% and to line NC97BGTD8 – 45%. Virulence to genes *Pm1a*, *Pm2*, *Pm3b*, *Pm3g*, *Pm4a*, *Pm5a*, *Pm6*, *Pm7*, *Pm8* and *Pm34* and gene combinations *Pm2+4b+8* ('Apollo'), *Pm1a+2+9* ('Normandie') and *Pm10+15* ('Norin 4') and line NC96BGTD2 occurred at frequencies of 50% to 100% for both powdery mildew populations (Table 3).

Coefficients of associations on the basis of virulence and avirulence pattern between *Pm*-genes (differentials or valuable breeding material) can provide additional information about their compatibility. The gene pairs were differentiated as negatively associated (disassociation, <0) or positively associated (>0). Some of them significantly associated; however, highly positive associations were detected more often for both populations in our experiment. Significantly negative associations were detected between CN26/16 and *Pm8* (−0.32, $P < 0.05$), and 'Vykhovanka odeska' and *Pm5a* (−0.35, $P < 0.05$) for Ukrainian powdery mildew population (Table 4). The differentials to which no virulence was detected did not associate (0.00) with any other differentials.

Table 4. Coefficients of association between virulence and avirulence pattern of the differentials in the Lithuanian and Ukrainian *Blumeria graminis* f. sp. *tritici* populations

Lithuanian / Ukrainian	*Pm1a*	*Pm2*	*Pm3a*	*Pm4a*	*Pm5a*	*Pm7*	*Pm8*	*Pm17*	*Pm34*	*Pm37*
Pm1a	1.00	0.27	0.02	0.26	0.06	0.36*	0.26	−0.21	0.20	0.14
Pm2	0.77***	1.00	0.16	0.14	0.13	0.58***	0.00	0.09	−0.03	0.22
Pm3a	−0.15	0.00	1.00	0.14	0.07	0.28	0.09	0.56***	−0.07	0.47**
Pm4a	0.57***	0.38*	−0.10	1.00	0.17	0.25	0.46**	0.08	0.03	0.19
Pm5a	0.42**	0.42**	−0.20	0.32*	1.00	0.00	−0.08	0.04	0.15	−0.26
Pm7	0.31*	0.09	0.15	0.19	−0.06	1.00	0.17	0.16	−0.06	0.38*
Pm8	−0.06	−0.06	0.13	−0.08	−0.03	−0.06	1.00	0.05	0.22	−0.13
Pm17	0.13	0.13	−0.10	0.17	0.05	−0.13	0.05	1.00	0.09	0.42**
Pm34	0.34*	0.16	0.07	0.33*	−0.09	0.34*	−0.09	0.18	1.00	−0.16
Pm37	0.02	−0.16	−0.07	0.27	0.09	0.20	0.09	0.22	0.15	1.00
CN26/16	0.00	0.00	0.10	0.25	0.08	0.19	−0.32*	0.04	0.12	0.48**
CN19/16	0.14	0.14	0.00	0.19	0.06	0.14	0.06	−0.13	0.02	0.16
Vykhovanka odeska	−0.02	−0.22	0.03	−0.1	−0.35*	0.17	0.07	0.07	0.09	0.22

Note. The values in the darkened part of table characterise the associations between differentials of the Ukrainian population, other values show the associations in the Lithuanian population; n = 40 (number of isolates); * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.0$.

Effectiveness of the Pm-genes in the seedling stage. Resistance to powdery mildew of the differentials was studied at the seedling stage. The disease symptoms were not observed for the differentials which carry *Pm25+3a* gene. Genes *Pm35*, *Pm20*, *Pm3c* and *Pm17*, cultivars 'Khapli' (*Pm4a*+), 'Vykhovanka odeska', 'Kniahynia Olha' and 'Lastivka odeska' and line PI 170911 belonged to the resistant group, whose plants exhibited either no symptoms or mild chlorotic spots. Other *Pm*-genes and differentials showed susceptibility and very high susceptibility. Cultivar 'Khapli' (*Pm4a*+) belonged to the resistant group, whereas the near isogenic line with a single *Pm4a* gene was susceptible to powdery mildew (Table 3). This indicates that resistance of the 'Khapli' was conferred not only by *Pm4a* but also by other *Pm*-genes. Evaluation of leaf segments under controlled conditions makes it possible to easily repeat examination each year and provide fast results. According to the obtained findings and on the basis of our long-term assessment (Babayants et al., 2015), in most cases such evaluation with natural populations of powdery mildew at seedling stage can predict the resistance of the studied material at an adult plant stage in the field (Table 3).

Field evaluation. The differentials were studies under field conditions in Lithuania and Ukraine. The genes *Pm20*, *Pm25+3a* and *Pm35* as well as resistance of winter wheat cultivars 'Vykhovanka odeska', 'Kniahynia Olha' and 'Lastivka odeska' were effective under natural powdery mildew infection at the adult plant stage during the two growing seasons. Cultivar 'Khapli' and line PI 170911, evaluated only in the environment of Ukraine, showed high resistance. *Pm17* as well as *Pm3c* genes were effective in Ukraine and moderately effective in Lithuania. Eight Ukrainian breeding lines were evaluated only under the environment of Ukraine and showed from high resistance to resistance. Other differentials showed from susceptibility to high susceptibility (Table 3).

Discussion

Annual survey of virulence and diversity of *Blumeria graminis* f. sp. *tritici* population in the target region is one of the most important measures in wheat breeding to sustain durability of resistance to the disease. In the present study, for race analysis we chose a set of 16 differentials and developed the nomenclature based on the principle of North American system (Long, Kolmer, 1989). According to this nomenclature, the Ukrainian and Lithuanian powdery mildew populations were separated into phenotypes, characterised by specific virulence frequency and complexity. For virulence analysis we used a differential set consisting of lines with single *Pm*-genes, lines and cultivars with gene combinations, modern resistant cultivars and promising advanced breeding lines.

Comparison of the obtained values of virulence frequencies of 21 studied *Pm*-genes with the values of the previous 10 years indicate that virulence frequencies

to genes *Pm3c* and *Pm17* decreased, whereas to *Pm4b* significantly increased. No other significant shifts in virulence of powdery mildew population were detected (Babayants et al., 2015). Virulence frequencies of the Lithuanian powdery mildew population were studied previously on the old differentials in 2000 and 2001. Virulence frequencies to *Pm3a*, *Pm3c* and *Pm17* genes decreased compared with those documented in the previous research (Liatukas, Ruzgas, 2005), probably because these *Pm*-genes more seldom occur in modern cultivars (Beschreibende Sortenliste, 2018). The lines KS93WGRC28 (*Pm20*) and NC96BGTD3 (*Pm35*) carry new *Pm*-genes for both areas, they show resistance at both plant stages and low virulence frequencies.

The field evaluation indicated that the Ukrainian winter wheat cultivars 'Vykhovanka odeska', 'Kniahynia Olha' and 'Lastivka odeska' were new for Lithuania and possessed very high resistance (score 1) at the adult plant stage in the environment of Lithuania. In Ukraine, these cultivars were also resistant to powdery mildew (score 2), but the virulence frequencies at the seedling stage were higher than in Lithuania. According to Galaev's research (unpublished), both cultivars 'Vykhovanka odeska' and 'Kniahynia Olha' carry one race-specific *Pm17* gene and two race non-specific genes *Pm38+Pm39*; the latter are known as race non-specific genes and confer partial adult plant resistance. However, the cultivars differ in resistance at the seedling stage; virulence frequency to 'Vykhovanka odeska' was higher than to 'Kniahynia Olha', and this may indicate that resistance of the latter is conferred by the additional *Pm*-genes. It is likely that such gene combination will protect plants against powdery mildew at the adult stage even if the efficiency of *Pm17* gene is defeated. The frequencies of virulence to advanced breeding lines and resistant cultivars, developed in Ukraine, in general were lower in Lithuania. This may indicate that cultivation of resistant plant material for several years even in small plots was sufficient to induce the emergence and shifts of virulence in the powdery mildew population. In general, the Ukrainian powdery mildew population is more virulent to the studied *Pm*-genes and its pathotypes are more complex. It is known that the more virulent the population is the more effective race-specific genes the cultivars should carry. Consequently, at the present time, it will be harder to attain durable resistance to powdery mildew in Ukraine than in Lithuania. In order to provide durability of resistance for this area, a focus should be placed on adult-plant resistance genes (quantitative trait loci (QTLs)) in addition to the effective race-specific genes.

The results of virulence analysis indicate that a combination of some *Pm*-genes provides decrease in resistance, for example, the virulence frequency to cultivar 'Apollo' (*Pm2+4b+8*) is higher than to single *Pm4b* gene in both populations. Virulence to cultivar 'Normandie' (*Pm1a+2+9*) was higher than to single *Pm1a* or *Pm2* genes (Table 3). Also, it was observed by other authors that in the case of combining several effective *Pm*-genes some *Pm*-genes were supressed by other *Pm*-genes, for example, *Pm8* gene was supressed by *Pm3* alleles (Hurni et al., 2014). A similar phenomenon was observed for leaf rust genes – after combining particular highly effective *Lr*-genes in one genotype the decrease of resistance was observed by Galaev (2016). Nonetheless, it is a known fact that some defeated race-specific *Pm*-genes provide residual resistance effect by limiting disease severity. Numerous researchers found that defeated major race-specific genes contribute to adult plant resistance. A residual effect was found for *Pm4a*, *Pm4b* and *Pm3c* (Nass et al., 1981; Tucker et al., 2007), *Pm5* (Keller et al., 1999) and *MlRE* (Chantret et al., 2001) genes. Paillard et al. (2000) demonstrated that wheat lines carrying defeated major race-specific (*Pm4b*, *Mlar* or *Pmx*) genes were more effective at adult stage than those without the postulated *Pm*-genes. So far, the mechanism of *Pm*-genes compatibility has not been fully understood. However, coefficients of associations based on virulence and avirulence patterns of pathogens isolates to the genes of resistance may provide additional information about nature of resistance for biotrophic pathogens (Parks et al., 2008; Wan et al., 2016). The highly positive associations of virulences between two genotypes probably may indicate their genetic similarity. In contrast, negative virulence associations probably demonstrate that their genetic patterns are different and consequently the combination of such resistances in one genotype possibly will provide durable resistance. Practical usefulness of combining genes with negative associations for development of durable resistance was proved for yellow rust (Chen, Kang, 2017). In our study, virulence associations were calculated by comparing reactions of 40 isolates to the differentials. In our opinion, such approach can provide additional valuable information for development of durable resistance to powdery mildew.

Research on race composition as well as the concept of race-specific resistance broadly applied in the practical breeding was very popular in the past, but short living of race-specific resistance, which was followed by devastating epidemics induced criticism of the concept (Vanderplank, 1982). There was a longstanding debate about what kind of resistance race non-specific / adult plant or race-specific, which is also known as seedling and all-stage resistance should be used for wheat breeding. Both of them have some advantages and disadvantages. Supporters of all-stage resistance claimed that mono genes are easier to use in breeding and they provide complete resistance. Race non-specific resistance as a rule is not complete, depends on the environments and plant growth stage, and plants with such resistance are vulnerable during seedling stage. For example, powdery mildew starts to infect plants at seedling stage and occasionally causes early epidemics under warm and wet conditions during the autumn in Ukraine. Afterwards, the fungus overwinters by forming sexual fruiting bodies cleistothecia. Sometimes, mild weather conditions and snow cover during sub-zero temperatures allow the conidia of powdery mildew to overwinter during the winter. If the plant resistance is based solely on adult-plant genes, such resistance cannot protect them during the seedling stage and a decrease of grain yield is observed (Babayants et al., 2015). Often, the differences between race-specific and race non-specific resistance are difficult to recognize. Defeated or half-defeated mono genes may confer residual effect and provide visual symptoms like adult-plant genes in the field. If the resistance is the result of numerous minor additive genes, it is difficult to include them in the breeding program. However, this is not an obstacle in the breeding schemes, where most of the genotypes possess a high quantitative resistance level (Cowger et al., 2012; Ren et al., 2017; Shah et al., 2018).

Followers of adult plant resistance maintain that resistance based on mono genes is race-specific and not durable, usually short-lived due to the pathogen's ability to overcome the host resistance (Lillemo et al., 2010). Miedaner and Flath (2007) proved that cultivars without major *Pm*-genes developed a few decades ago and currently widely grown showed durable and high powdery mildew resistance. For example, the resistance of barley cultivars based on race non-specific *Mlo* gene have proved its efficiency and durability against powdery mildew for several decades (Kusch, Panstruga, 2017).

Nowadays, the scientific community has reached consensus on the concept of using a combination of different types of all-stage resistance together with adult plant resistance. It is considered the best approach because a combination of all-stage resistance together with race non-specific resistance provides high-level of resistance and durability. Race-specific genes provide complete protection when they are effective, and race non-specific resistance will reduce severity when mono genes are ineffective. Such strategy has been used extensively in CIMMYT, United States and Europe for wheat breeding against wheat rusts and powdery mildew (Cowger et al., 2012; Li et al., 2014; Chen, Kang, 2017). For example, the resistance of winter wheat cultivars 'Stephens' and 'Madsen' to yellow rust is based on combination of mono genes and adult plant resistance genes. The former released in 1978, the latter – in 1982, and they are still showing high levels of adult plant resistance against yellow rust (Chen, Kang, 2017). The winter wheat line RE714 possess durable resistance to powdery mildew at all development stages, and its resistance is conferred by two major powdery mildew resistance (*MlRE* and *Pm4b*) genes and several QTLs (Chantret et al., 2001).

It is a well-known fact that "physiological races" are not a taxonomic term, they do not differentiate by morphology and it does not mean that all genotypes which belong to a certain race are genetically identical. They are differentiated only by phenotype – virulence or avirulence pattern on differential set. Nevertheless, such differentiation on special differential set of powdery mildew population may provide valuable information on virulence frequencies and race diversity that can be useful for wheat breeding programs. However, it is very important to choose proper genotypes as differentials for a race survey. The differentials should possess differentiability to provide diverse reactions (virulence / avirulence) to different isolates of population. It is important to include the *Pm*-genes, which are effective and broadly occur in modern cultivars. The differentials should not depend significantly on the range of climate conditions (temperature, light) and should provide useful prediction information for proper gene utilization and prevention of epidemics. When differentials carry several *Pm*-genes, this only demonstrates the effectiveness of gene combination, and phenotypic reaction will not indicate, which gene of the combination is effective. Also, from the practical viewpoint it is important to include advanced breeding lines, new resistant cultivars and the most popular cultivars into the differential set as supplemental differentials. Often, they are not fully suitable for race differentiation, but may provide valuable information for wheat breeding for resistance to powdery mildew.

Evaluation of breeding material and effectiveness of known *Pm*-genes is an important part of wheat breeding for resistance to powdery mildew. The large-scale surveys can determine the existing virulences, their frequencies and diversity of the powdery mildew population for specific areas and shifts over time and space.

Conclusions

1. The populations of powdery mildew (*Blumeria graminis* f. sp. *tritici*) consisted of different phenotypes, 32 and 30 phenotypes were identified by using a set of 16 differentials in Lithuanian and Ukrainian populations. Virulence analysis demonstrated that phenotypes of Ukrainian population are more virulent comparing to those of Lithuanian powdery mildew population.

2. Most of the studied *Pm*-genes did not provide sufficient resistance. No virulence was found for *Pm20* and *Pm25+3a* genes in both populations studied. They were highly effective against powdery mildew at seedling and adult plant stages. Little or no virulence was detected for breeding lines PI 170911, CN84/16, CN89/16 and CN113/16 and cultivars 'Khapli', 'Lastivka odeska', 'Vykhovanka odeska' and 'Kniahynia Olha'. They were highly resistant during all growth stages and can be used as sources of effective all-stage resistance for breeding for resistance against powdery mildew for the both regions (Central Lithuania and Southern Ukraine) studied.

3. The updated nomenclature is based on the main effective *Pm*-genes for target areas, the differentials exhibit good differentiability and could be used for race analysis.

4. Positive and negative associations between virulences to *Pm*-genes provide additional information for common wheat (*Triticum aestivum* L.) breeding to improve the powdery mildew resistance.

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Blumeria graminis f. sp. *tritici* populiacijų virulentiškumas ir įvairovė Lietuvoje ir Pietų Ukrainoje

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Santrauka

Kleistotecių pavyzdžiai tyrimui buvo surinkti Vidurio Lietuvoje ir Pietų Ukrainoje. Siekiant apibūdinti miltligės (*Blumeria graminis* f. sp. *tritici*) sukėlėjo virulentiškumą, kompleksiškumą ir įvairovę, 80 izoliatų buvo atrinkta iš atskirų askosporų, po 40 izoliatų kiekvienai populiacijai. Patotipų analizė atlikta naudojant 16 diferencijatorių su žinomais *Pm* genais. Atitinkamai pateiktam klasifikavimui, Lietuvos miltligės sukėlėjo populiacijoje buvo nustatyti 32 patotipai, Ukrainos populiacijoje – 30 patotipų. Lietuvos populiacijoje dažniausias patotipas buvo NGDE (7,5 %), Ukrainos – NGKE (15 %). Ukrainos miltligės sukėlėjo populiacija buvo kompleksiškesnė, o sukėlėjo izoliatai turėjo daugiau virulentiškumo genų.

Virulentiškumo tyrimas atliktas inokuliuojant 26 diferencijatoriaus su žinomais *Pm* genais ir 12 atsparių žieminio kviečio (*Triticum aestivum* L.) selekcinių linijų bei veislių daigų lapų segmentus. Virulentiškumo dažnis šių diferenciatorių *Pm* genams buvo nuo 0 iki 100 %, daugeliui iš jų virulentiškumo dažnis buvo aukštas. Virulentiškumas nenustatytas genams *Pm20*, *Pm25+3a*, veislei ‘Lastivka odeska’ ir selekcinėms linijoms CN 89/16 bei PI 170911 abiejų populiacijų atveju. *Pm1a*, *Pm2*, *Pm3b*, *Pm3g*, *Pm4a*, *Pm5a*, *Pm6*, *Pm7*, *Pm8*, *Pm9*, *Pm10* ir *Pm34* genams virulentiškumas buvo didesnis nei 50 %. 25 *Pm* genų efektyvumas buvo įvertintas daigų ir generatyviai besivystančių augalų tarpsniais. Daugelis *Pm* genų buvo neefektyvūs. Genų *Pm20*, *Pm25+3a* ir veislių ‘Vykhovanka odeska’, ‘Kniahynia Olha’, ‘Lastivka odeska’ atsparumas buvo efektyvus visą augalų vystymosi laikotarpį.

Reikšminiai žodžiai: atsparumo genai, miltligė, paprastasis kvietys, rasių analizė.