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Virulence Structure of *Blumeria graminis* f. sp. *avenae* Populations in Poland across 2014-2015

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The purpose of this study was to determine the virulence structure of oat powdery mildew (*Blumeria graminis* f. sp. *avenae*, *Bga*) populations in Poland collected in 2014 and 2015. Powdery mildew isolates were collected from 18 locations in Poland. In total, nine lines and cultivars of oat, with different mildew resistance genes, were used to assess virulence of 180 isolates. The results showed that a significant proportion of the *Bga* isolates found in Poland were virulent to differentials with *Pm1*, *Pm3*, *Pm6*, and *Pm3 + Pm8* genes. In contrast *Pm4*, *Pm5*, *Pm2*, and *Pm7* genes were classified as resistant to all pathogen isolates used in the experiment. Based on obtained results we can state that there are differences in virulence pattern and diversity parameters between sites and years, but clear trends are not deducible.

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Common oat (*Avena sativa* L.) is one of the six most popular cereal species in the world. According to the Food and Agriculture Organization of the United Nations, the largest oat producers, are the Russian Federation, Canada, Poland, Finland, Australia, United Kingdom, Brazil, Spain, and the United States of America (Food and Agriculture Organization of the United Nations, 2020). Oat is widely used as animal feed, but due to its nutritional value it is also used in the human diet, e.g., for the production of flakes, groats, and bran. Oat is also used in the cosmetics and pharmaceutical industries (Rasane et al., 2015; Sterna et al., 2016).

Powdery mildew, caused by the biotrophic parasite fungus *Blumeria graminis* f. sp. *avenae* (*Bga*), is one of the most important fungal diseases that occur in oats. Its occurrence is influenced by weather conditions; therefore, oat plants growing in cool and humid regions of northwestern and eastern Europe are mainly exposed to this pathogen infections (Aung et al., 1977; Sebesta et al., 1991). Survival and efficient reproduction of the parasite depend on living host tissues due to the obligate biotrophic character. The presence of infection can be observed as a white coating, subsequently changed into a dense mat with black bodies producing sexual spores (Braun et al., 2002; Troch et al., 2012). The pathogen is able to cover leaf surface that negatively affects plant metabolism (Carver and Griffiths, 1981) and reduces the number of fertile panicle, thousand-grain weight, and total biomass production. Ultimately, all these factors result in the deterioration of grain quality and quantity (Roderick and Jones, 1988; Roderick et al., 2000). Annual crop losses from mildew infections are estimated to range from 5-10% up to 39% (Jones, 1977; Lawes and Hayes, 1965; Roderick and Clifford, 1995).

The pathogen is equipped with an effective method of spreading anamorphic conidia over long distances and it is able to survive unfavorable conditions, particularly low temperatures and drought, using the telomorphic stage (Braun et al., 2002). Currently, fungicides and resistant cultivars are used to control powdery mildew. Reduction of

losses in cereal production caused by powdery mildew can be achieved by applying appropriate agricultural treatments (Czembor and Czembor, 2005; Gacek, 2000). The introduction of crop cultivars that contain effective resistance genes is the most effective and environmentally friendly method of infection control (Okoń et al., 2016). To date, 11 powdery mildew resistance genes have been identified and characterized in oat (Herrmann and Mohler, 2018; Hsam et al., 2014; Ociepa et al., 2020). The relationship between the host and powdery mildew is closely related to the "gene-for-gene" hypothesis, which says that a virulence gene (*Avr*) in the pathogen's genome is directed against a resistance (*R*) gene in the plant (Flor, 1971; Heath, 2000; Okoń and Ociepa, 2017). However, due to the sexual life cycle and overcoming the oat resistance barrier, genes responsible for virulence may have different evolutionary potential (Okoń 2012; Wolfe and Schwarzbach, 1978).

The aim of this study was to investigate the virulence of powdery mildew populations occurring in oat in several regions of Poland during the years 2014 and 2015, as well as to postulate the structure and dynamics of pathogen population changes.

Materials and Methods

Pathogen samples were collected in 2014 and 2015 from different geographical and climatic locations in Poland. Leaves of oat cultivars (*Avena sativa* L.) infected with *Bga* were originally collected randomly from fields belonging to both private farms and plant breeding companies. The pathogen population from 2014 was represented by samples collected at nine different locations; similarly, the population from 2015 was represented by samples collected also at nine different locations. These locations depended on the occurrence of powdery mildew symptoms in oats in a given year. In three locations (Czesławice, Polanowice, and Strzelce), symptoms of the disease were observed both in 2014 and 2015, therefore samples from these locations are found in both populations. The localization and year of sampling are marked in Fig. 1.

Under laboratory conditions single-spore isolates were obtained from leaves collected from each location in accordance with the methodology previously described Hsam et al. (1997, 1998). Ten single-spore isolates were obtained
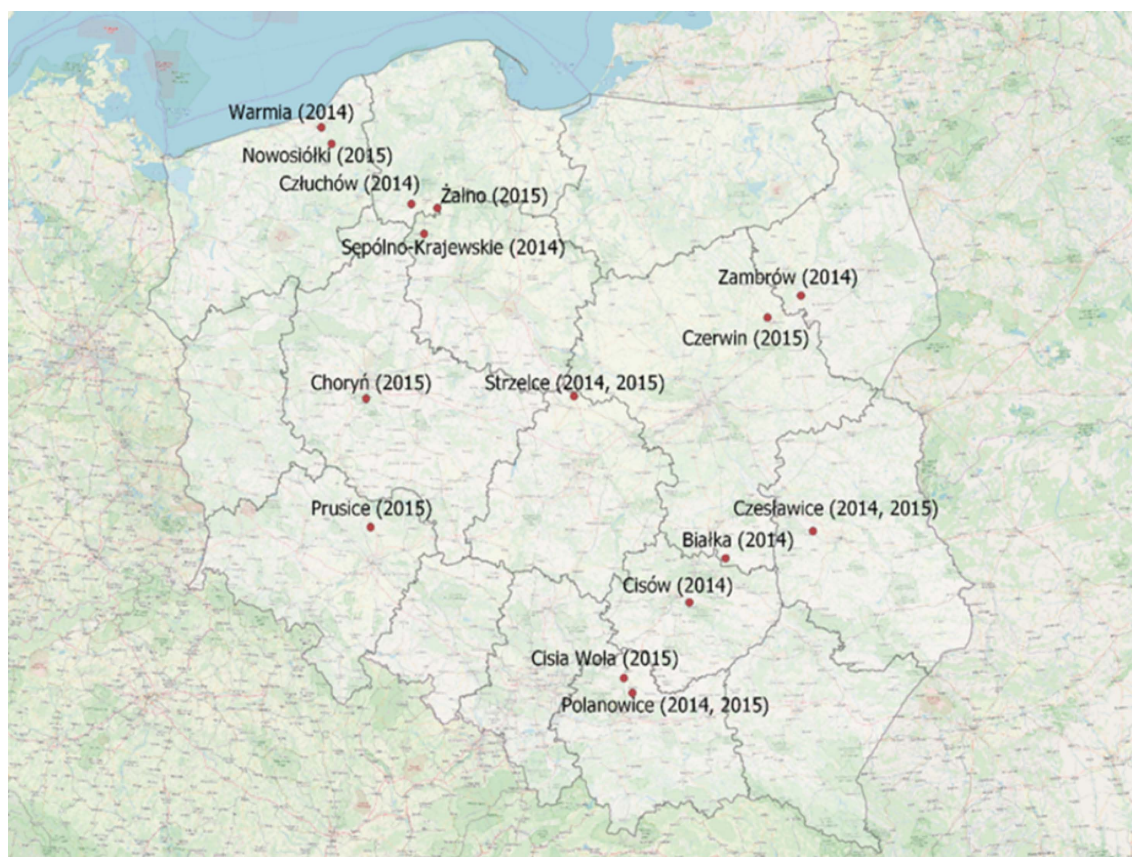

Fig. 1. The geographical distribution of *Blumeria graminis* f. sp. *avenae* isolates used in the host-pathogen tests.

Table 1. Standard differential set of oat line and cultivars with known resistant genes used to characterize virulence structure of the *Blumeria graminis* f. sp. *avenae* populations on oat in Poland across 2014-2015 (Hsam et al., 1997, 1998, 2014)

Cultivar/Line	Gene symbol	Pedigree
Jumbo	*Pm1*	Flämingsstern/AJ20–61/Faggot
CC3678	*Pm2*	*Avena hirtula*
Mostyn	*Pm3*	05443/Condor
Av1860	*Pm4*	*A. sativa*/*A. barbata*
Am27	*Pm5*	*A. sativa*/*A. macrostachya* derivative
Bruno	*Pm6*	Halla/Gambo
APR122	*Pm7*	*A. sativa*/*A. eriantha* derivative
Canyon	*Pm7*	*A. sativa*/*A. barbata*
Rollo	*Pm3 + Pm8*	LP75-512/W17286
Fuchs	-	-

from each location, and each of the two analyzed populations was finally represented by 90 single-spore isolates.

In order to analyze the virulence of the pathogen population, host-pathogen tests were carried out using nine oat genotypes, with known powdery mildew resistance genes. The cultivar Fuchs, without any powdery mildew resistance genes was used as a susceptible control. The characteristics of control genotypes are presented in Table 1.

Host-pathogen tests were carried out on the first leaves of 10-day-old seedlings. Leaf segments were placed in 12-well culture plates with 6 g/l agar and 35 mg/l benzimidazole. The plates with the leaf segments were inoculated in a settling tower by spreading 500-700 powdery mildew spores per 1 cm^2. The plates were then incubated in a growing chamber at 17°C and an illuminance of approximately 4 kLx. All tests were performed twice, to confirm the response of the tested accessions to *Bga* isolates.

Infection level were determined 10 days after inoculation and scored according to a 0-4 modified scale (Mains, 1934); where 0 = no infection, no visible symptoms; 1 = highly resistant, fungal development limited, no sporulation; 2 = moderately resistant, moderate mycelium with some sporulation; 3 = moderately susceptible, extensive mycelium, more sporulation; 4 = highly susceptible, large colonies, and abundant sporulation. If disease symptoms were scored as 0, 1, or 2, the isolates were classified as avirulent to known genes against oat powdery mildew. If disease symptoms were scored as 3 or 4, the isolates were classified as virulent.

Parameters for comparing *Bga* populations collected in 2014 and 2015 were calculated on the basis of isolate virulence patterns on the set of differential genotypes (Table 1).

Virulence frequency (*p*) as $p = x/n$ (where *x* is the number of times a virulent reaction type was detected and *n* is the total number of samples tested in a particular year) was calculated for each year. The total number of virulent reaction types for each isolate was calculated and reported as the virulence complexity. The frequency of the virulence complexity was determined for each year. The compiled reaction type data for each isolate to differential genotypes were coded as individual pathotypes using the Gilmour code (Gilmour, 1973).

Diversity within populations was assessed using different types of parameters: genetic diversity like Simpson (*Si*) and Shannon (*Sh*) and genetic distance (Rogers index; *R*) based on the pathotype structure of populations; gene diversity like Nei index (*Hs*) which is equivalent to a measure of the average dissimilarity within a population (ADW_m) regarding the simple mismatch coefficient *m*, and the Nei gene distance (*N*) based on the population virulence, and genetic diversity (KW_m) and distance (KB_m) measured by the Kosman indices, based the population pathotype and virulence structure (Dreiseitl and Kosman, 2013; Kosman, 1996; Kosman and Leonard, 2007).

The infection profile of single-spore *Bga* isolates was also used to infer the presence of different subgroups in the analyzed populations of oat powdery mildew and to determine the pathogen population structure of the in STRUCTURE 2.3.4 software (Porras-Hurtado et al., 2013).

The main coordinate analysis (principal coordinate analysis, PCoA), using Dice distance, was performed to represent the distances between the group of isolates from the same locations in GeneAIEx v.6.4 (Peakall and Smouse, 2012).
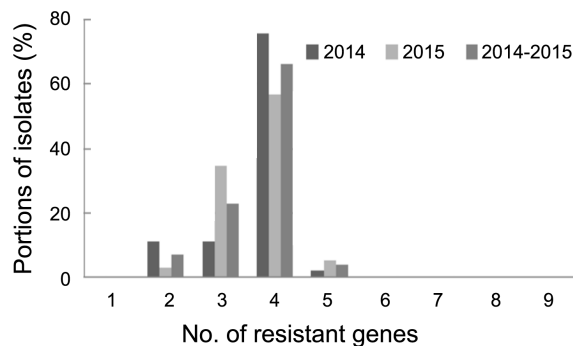
Results

The tested *Bga* isolates from two populations collected in 2014 and 2015 showed a high level of virulence against the *Pm1*, *Pm3*, *Pm6* genes, and the cultivar Rollo that contained the *Pm3 + Pm8* genes. The frequency of virulence in the population collected in 2014 ranged from 88.9 to 100%, while it decreased and reached 65.6-100% in population collected in 2015. A low virulence (2.2% in 2014 and 8.9% in 2015) was observed for the source of resistance identified in the cultivar Canyon. None of the tested isolates from both populations were classified as avirulent against genotypes carrying the *Pm2*, *Pm4*, *Pm5*, and *Pm7* genes (Table 2). However, isolates that infected the APR122 line with the *Pm7* gene were identified in both 2014 and 2015, but the level of infection was classified as 1 or 2 (data not shown).

Table 2. Virulence frequencies of *Blumeria graminis* f. sp. *avenae* isolates sampled from oat in 2014-2015

Cultivar	Gen	Frequency (%)		
		2014	2015	2014-2015
Jumbo	*Pm1*	88.9	90	89.4
CC3678	*Pm2*	0	0	0
Mostyn	*Pm3*	100	100	100
Av1860	*Pm4*	0	0	0
Am27	*Pm5*	0	0	0
Bruno	*Pm6*	88.9	65.6	77.2
APR122	*Pm7*	0	0	0
Canyon	*Pm7*	2.2	8.9	5.6
Rollo	*Pm3 + Pm8*	88.9	100	94.4

Fig. 2. Virulence complexity of Polish *Blumeria graminis* f. sp. *avenae* population in 2014-2015.

Bga isolates, collected in 2014 and 2015, most often overcame the resistance of four out of nine genes analyzed (Fig. 2). In 2014 it was 76% of the isolates and 57% in 2015. Many tested isolates overcame the resistance of 3 (11% in 2014 and 34% in 2015) and 2 (11% in 2014 and 3% in 2015) out of nine genes. Several isolates overcame the resistance of five genes (2% in 2014 and 6% in 2015). None of the *Bga* isolates was able to overcome the resistance of 1, 6, 7, 8, and 9 genes.

Pathotypes of the analyzed isolates were determined us-

ing a three-digit code developed by Gilmour (Gilmour, 1973) based on an infection model of individual control lines by the tested *Bga* isolates. In total, 180 *Bga* isolates collected in 2014 and 2015 were grouped into nine pathotypes (Table 3). The population collected in 2014 was represented by four pathotypes, while the population collected in 2015 was more diverse and represented by eight pathotypes. Pathotype 544 was the most common, represented by 65% of the analyzed isolates. This pathotype occurred with the highest frequency in both 2014 (75.6%) and 2015 (54.4%), and was virulent against the *Pm1*, *Pm3*, *Pm6*, and

Table 3. Virulence spectra of nine pathotypes of *Blumeria graminis* f. sp. *avenae*

Pathotype	*Pm1*	*Pm2*	*Pm3*	*Pm4*	*Pm5*	*Pm6*	*Pm7* (*Apr122*)	*Pm7* (*Canyon*)	*Pm3 + Pm8*	Frequency (%)		
										2014	2015	2014-2015
404	-	-	+	-	-	-	-	-	+	0	3.3	1.7
406		-	+	-	-	+	-	+	+	0	1.1	0.6
440	-	-	+	-	-	+	-	-		11.1	0	5.6
444	-	-	+	-	-	+	-	-	+	0	4.4	2,2
446	−	-	+	-	-	+	-	+	+	0	1.1	0.6
504	+	-	+	-	-	-	-	-	+	11.1	28.9	20
506	+	-	+	-	-		-	+	+	0	1.1	0.6
544	+	-	+	-	-	+	-	-	+	75.6	54.4	65
546	+	-	+	-	-	+	-	+	+	2.2	5.6	3.9

Table 4. Diversity analysis of all powdery mildew isolates

Parameter	2014	2015
No. of isolates	90	90
No. of different pathotypes	4	8
No. of different pathotypes with count > 1	4	5
Gene diversity (Nei index H_s) equivalent to ADW_m diversity	0.071	0.083
Genetic diversity (Simpson index *Si*)	0.404	0.610
Genetic diversity (Shannon normalized index *Sh*)	0.174	0.276
Genetic diversity (Kosman index KW_m)	0.079	0.117

Pm3 + Pm8 genes. Pathotype 504 was also widely represented and grouped 20% of the isolates. The remaining pathotypes represented less than 10% of the isolates.

Different types of diversity parameters within the *Bga* populations collected in Poland in 2014 and 2015 are presented in Table 4. All parameters clearly showed that the *Bga* population collected in 2015 was more diverse than the population collected in 2014. However, the low distance values between the populations ($R = 0.322$, $N = 0.009$, $KB_m = 0.047$) suggested that changes in the following years were very slow.

The studied isolates were subjected to the PCoA implemented in Genalex 6.5. PCoA analyses were based on virulence patterns and showed differences between localization of the *Bga* isolates (Fig. 3). The first group consisted of the isolates from Białka collected in 2014, which was avirulent towards the *Pm1*, *Pm2*, *Pm4*, *Pm5*, *Pm7*, and *Pm3 + 8* genes. The second cluster consisted of isolates collected in 2014 in Polanowice, and izolates from 2015 collected in Prusice, and Nowosiółki which were avirulent against the *Pm2*, *Pm4*, *Pm5*, *Pm6*, and *Pm7* genes. The remaining isolates formed the third largest group. The grouping

PCoA reflected the clusteing of isolates into pathotypes and the similarity of pathotypes to each other. The isolates collected in 2014 at the Białka location, due to the unique pattern of infestation of the control lines, formed a separate pathotype 440. This grouping confirmed that this pathotype differed the most from the others. The isolates clustered in the second group represented pathotype 504, which also showed little similarity to other pathotypes. The third group included the remaining pathotypes (406, 444, 446, 504, 506, 544, and 546) which reflected a high similarity these pathotypes to each other.

STRUCTURE ($K = 3$) shows differences in the distribution of different virulence variants in populations using a Bayesian iterative algorithm by grouping samples based on similar variation patterns. The analyzed *Bga* isolates from two populations collected in 2014 and 2015 from different locations were divided into three subgroups sharing a similar virulence pattern, which confirmed a slight variation between *Bga* isolates in Poland. The first cluster (red) grouped isolates from the populations collected in 2014 in Białka and Cisia Wola and was dominant among isolates obtained from Czerwin. It was also represented
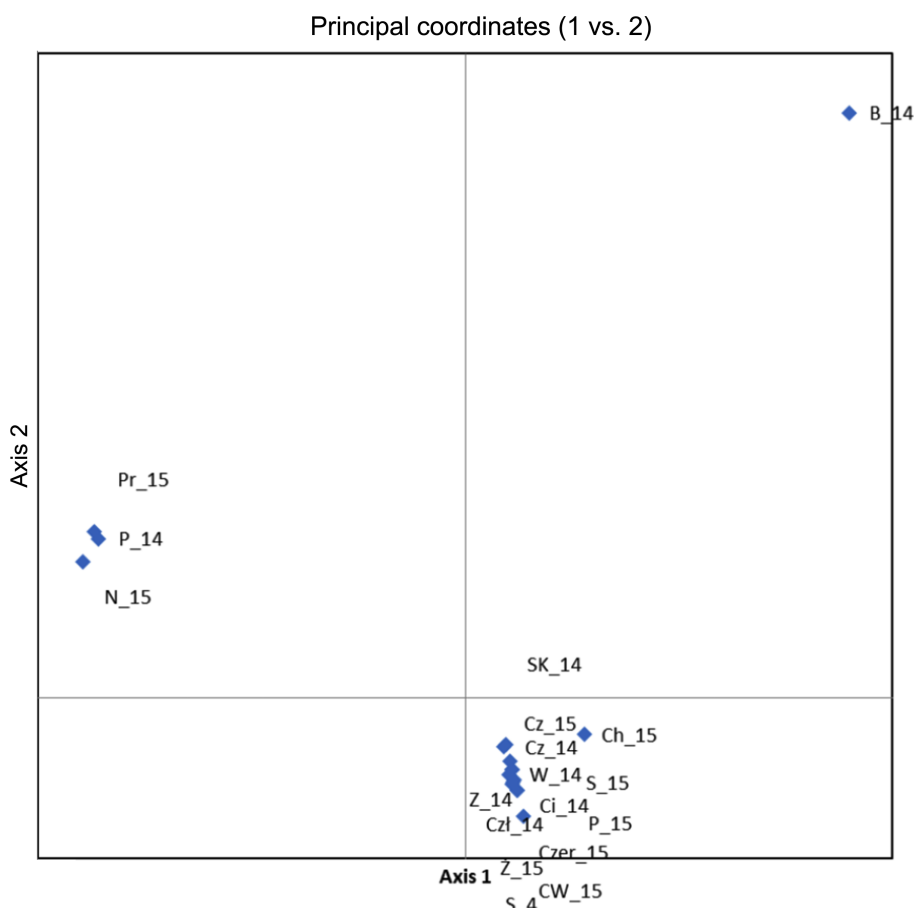

Principal coordinates (1 vs. 2)

Fig. 3. Principal coordinate analysis of group of isolates from different localizations: B_14, Białka 2014; Cz_14, Czesławice 2014; SK_14, Sępólno Krajeńskie 2014; W_14, Warmia near Koszalin; Z_14, Zambrów 2014; Czł_14, Człuchów 2014; P_14, Polanowice 2014; S_14, Strzelce 2014; Ci_2014, Cisów 2014; CW_15, Cisia Wola 2015; Czer_15, Czerwin 2015; Cz_15, Czesławice 2015; Ch_15, Choryń 2015; Nowosiółki_15, Nowosiółki 2015; P_15, Polanowice 2015; Pr_15, Prusice 2015; S_15, Strzelce 2015; Ż_15, Żalno 2015.
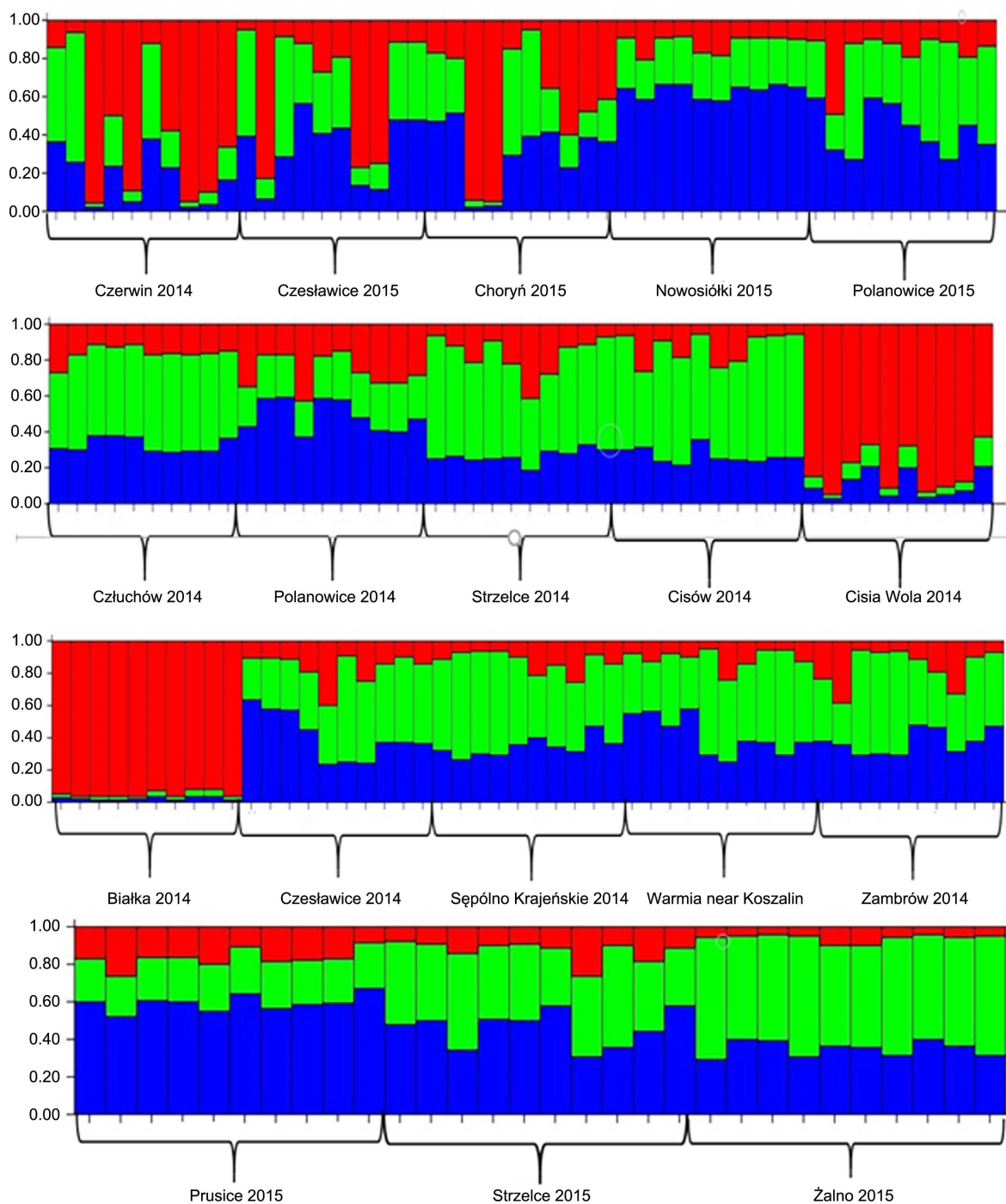
Fig. 4. Structural analysis of 180 *Blumeria graminis* f. sp. *avenae* isolates. Individual bars represent one single isolate from particular locations. Each localization is represented by 10 single-spore isolates.

by single isolates from the population collected in 2015 at Czesławice and Choryń. The second cluster (green) was characteristic of the population collected in 2014, and the third (blue) grouped isolates belonging to the population collected in 2015 (Fig. 4).

Discussion

Interactions between the host plant and the pathogen are very complex and dynamic. Understanding the fundamen-

tals and complexity of this process is useful for achieving long term and effective resistance under different environmental conditions. Therefore, for oat resistance breeding to be effective, systematic studies on pathogen population structure, and changes in virulence over time and space are necessary. They allow to control and limit the occurrence of the pathogen by selecting the most optimal resistance genes that provide a high level of protection for many years under various environmental conditions. This type of research is conducted on the populations of *Blumeria graminis* f. sp. *hordei* in barley (Dreiseitl and Kosman, 2013; Kokina et al., 2014; Komínková et al., 2016) and *Blumeria graminis* f. sp. *tritici* in wheat (Abdelrhim et al., 2018; Liu et al., 2015). It allows to select effective resistance genes in a given area and their application in breeding programs. The number of studies focusing on this problem with respect to *Bga* population is very small; moreover, the published data come from the second half of the 20th century. Jones and Griffiths (1952) made the first attempts to characterize oat powdery mildew virulence by examining the resistance level of oat cultivars. Further research regarding pathogenicity by Hayes and Catling (1963) and Hayes and Jones (1966) allowed the identification of five breeds of *Bga* with different levels of virulence in relation to control forms carrying equal resistance genes for this pathogen. Roderick et al. (2000) conducted studies on the virulence of powdery mildew in oats in 1991-1998, and showed that there were very few effective resistance genes in oat, and that the frequency of virulence followed classical gene-for-gene principles. Recent studies on the characteristics of *Bga* population was carried out in 2010-2013 in Poland by Okoń and Ociepa (2017). The studies presented in this work are their continuation, allowing to track virulence dynamics in *Bga* population in the subsequent years. Okoń and Ociepa (2017) found that the highest level of virulence was observed for the *Pm1*, *Pm3*, and *Pm6* genes. In the present study, the tested isolates also overcame the resistance conditioned by these genes. Virulence frequency for these genes ranged from 65% to 100% from 2010 to 2015, and the dynamics of changes remained at the level of 10% for *Pm3*, 15% for *Pm1*, and 35% for *Pm6*. In 2015, a significant decrease in the virulence against the *Pm6* gene was observed. However, virulence at the level of 65% still classified this gene as ineffective. The *Pm1*, *Pm3*, and *Pm6* genes have been used in breeding programs and introduced into oat for many years (Hsam et al., 1997, 1998; Kowalczyk et al., 2004; Okoń et al., 2016). The high pressure of cultivars with these genes could have overcame their resistance by new, more virulent races of the pathogen.

It was found in the experiment described by Okoń and Ociepa (2017) and in the current that *Pm2*, *Pm4*, and *Pm5* were good resistance genes. All tested isolates were avirulent against them during the years 2010-2015. It has been confirmed that these sources of resistance are valuable over a long period of time and in different geographical regions of Poland. Among the genes tested, *Pm7* deserved special attention. Many previous studies showed that *Pm7* was highly resistant both in seedlings and adult plant stages (Hsam et al., 1997, 1998; Okoń, 2015). However, prior (Okoń and Ociepa, 2017) and present research identified isolates that overcame the resistance of this gene. Host-pathogen tests have shown that the cultivar Canyon have a source of resistance with a different profile than the genes described so far (Okoń, 2015). However, Herrmann and Mohler (2018) indicated that this cultivar contained the *Pm7* gene. For this reason, the set of control lines used in this study included the APR122 line and cultivar Canyon carrying the *Pm7* gene. The obtained results indicated a different reaction of the studied isolates to these genotypes, which could suggest the presence of two variants of the *Pm7* gene. Therefore, both genotypes should be included in the control set for the subsequent studies on *Bga* virulence. Monitoring changes in pathogen virulence for this gene is important because it is present in many cultivars, especially in Germany (Herrmann and Mohler, 2018). Moreover, even small changes in virulence may suggest that the pathogen's adaptation process may lead to a decrease in immunity conditioned by this gene.

The number of genotypes in the differential set is very important in studies aimed at characterizing the pathogen population. Okoń and Ociepa (2017) used a set of seven lines and control varieties, which resulted in the identification of seven different pathotypes and slight differentiation of the analyzed population. The control set in the present study was extended by two forms, which allowed to detect a greater number of pathotypes and a slightly greater diversity of the pathogen population. Extending the control set with recently identified genotypes carrying new resistance genes will provide more reliable results, and in turn more precise conclusions. This was confirmed by numerous studies conducted in the populations of barley and wheat pathogens. A study of Dreiseitl and Kosman (2013) based on 20 control lines identified 27 different pathotypes in the population of *B. graminis* f. sp. *hordei* in South Africa. The parameters of population diversity were significantly higher than those obtained in our study on a set of nine control genotypes. Similarly 16 control genotypes allowed the identification of 15 different pathotypes in *B. graminis* f. sp. *tritici* population in Lithuania and Ukraine (Traskovetskaya et al., 2019).

Based on STRUCTURE and PCoA, all studied isolates were divided into three groups, which confirmed that *Bga* populations in Poland were not very diverse despite the fact that they were collected from different locations across the country. This could also be due to the slow rate of pathogen evolution during these two years.

The summary of studies from 2010-2015 has demonstrated that the dynamics of changes in *Bga* population is low. However, continuous observations of the pathogen population are important aspect of research on oat resistance, considering widespread cultivation of cultivars with specific resistance genes and climate changes. This contributes to a better wintering of powdery mildew and passing the full cycle of sexual reproduction, resulting in the emergence of new allelic systems in the pathogen population (Elad and Pertot, 2014; Gupta et al., 2018; Tang et al., 2017; Yáñez-López, 2012).

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

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