ISSN 1392-3196 / e-ISSN 2335-8947
Zemdirbyste-Agriculture, vol. 101, No. 4 (2014), p. 419–424
DOI 10.13080/z-a.2014.101.053

The peculiarities of genetic structure of the *Blumeria graminis* f. sp. *hordei* population in Lithuania

Inese KOKINA[1], Grazina STATKEVICIUTE[2], Alge LEISTRUMAITE[2], Isaak RASHAL[3]

[1]Institute of Systematic Biology, Daugavpils University
Vienības 13, Daugavpils, Latvia
E-mail: inese.kokina@biology.lv

[2]Institute of Agriculture, Lithuanian Research Centre for Agriculture and Forestry
Instituto 1, Akademija, Kėdainiai distr., Lithuania

[3]Institute of Biology, University of Latvia
Miera 3, Salaspils, Latvia

Abstract

In 2010, samples of *Blumeria graminis* f. sp. *hordei* both in sporulation and cleistothecia were collected in Lithuania from spring barley variety 'Dina'. Eighty monopustule isolates were tested on differentials with well-known resistance genes. Frequencies of virulence genes, virulence complexity and pathotypes were detected. Virulence frequencies showed a wide range from 0 to 90%. The clear tendency of virulence increasing for *Vla* in cleistothecia was observed during the growing season of the pathogen. No virulences were found against resistances, which were present in the line *SI1*, as well as no matching virulence was found for the resistance gene *mlo* in Lithuania in 2010. Wide diversity of the population is confirmed by the present of high number of detected pathotypes. In the samples in sporulation, the pathotype *a6 a7 a9 a12 k la* was the most abundant and the dominant pathotype in cleistothecia was *a7 a9 a12 k la*. In comparison with 2000, significant changes in virulence genes frequencies, complexity and pathotypes were detected in 2010.

Key words: barley, *Blumeria graminis* f. sp. *hordei*, complexity, pathotype, resistance, virulence.

Introduction

Powdery mildew fungi are parasites that cause disease on a wide range of important crops. The grass powdery mildew fungus is classified into eight *formae speciales* (ff. spp.) based on the strict host specialization (Wyand, Brown, 2003). Barley powdery mildew caused by *Blumeria graminis* f. sp. *hordei* is one of the most devastating diseases (Naghavi et al., 2007), which can cause serious yield losses. The pathogen is a wind-borne and obligate biotrophic pathogen, often used as a model in understanding host-parasite interaction (Dreiseitl, Wang, 2007). The disease can be controlled easily with fungicides, but it may represent a serious threat for barley produced in low input and organic agriculture (Dreiseitl et al., 2006; Kokina, Rashal, 2008). Genetic resistance is an effective, economically sound and safe alternative to fungicide application (Dreiseitl, 2008). Plant resistance (*R*) genes, which induce host defenses against powdery mildews, encode proteins that recognize avirulence (AVR) molecules from the parasite in a gene-for-gene manner (Skamnioti et al., 2008). Partial resistance is characterized by a compatible interaction in all growth stages, but a lower frequency of infection, a longer latent period, or lower rate or shorter period of a spore production (Jørgensen, 1994).

The evolutionary potential of a pathogen population is reflected in its population genetic structure. Pathogen populations with a high evolutionary potential are more likely to overcome genetic resistance than pathogen populations with a low evolutionary potential (McDonald, Linde, 2002). Recombinations and efficient dispersal contribute high adaptation potential for *Blumeria graminis* f. sp. *hordei*. Airborne migration of spores also favours the spread of new genotypes, which can travel over large distances (Limpert, 1987). A high level of pathogenic variability in local populations has been demonstrated in many studies (Limpert, 1987; Czembor, 2010; Kokina, Rashal, 2012).

Agricultural land constitutes 53% of the total area in Lithuania. Among cereals, spring barley is the second most widely grown crop after winter wheat. Winter barley hardly survives Lithuanian winters; in 2010 it comprised only about 6% of the total barley area (Statistical Yearbook of Lithuania, 2011). Some investigations have been done on the field resistance of spring barley varieties to powdery mildew in Lithuania,

when Lithuania-registered genotypes, new genotypes for initial breeding and genotypes from collections of genetic resources were tested (Liatukas, Leistrumaitė, 2007). The recent study concerning genetic peculiarities of the population of the causal agent of barley powdery mildew in Lithuania was done in 2000 (Kokina, Rashal, 2002). The overall goal of this study was to evaluate virulence frequencies, distribution of virulence genes, dominant pathotypes and their complexity in the population of *Blumeria graminis* f. sp. *hordei* from Lithuania in 2010.

Material and methods

Eighty isolates of powdery mildew causal agent *Blumeria graminis* f. sp. *hordei*, used in this study, were collected from the spring barley variety 'Dina' in Lithuania in 2010 both in sporulation and cleistothecia. Sampling size and dates are presented in Table 1.

Table 1. Sampling date and number of pathogen samples collected in Lithuania in 2010

Sampling date	Phase of the pathogen	Number of isolates
13 July	conidia	40
4 August	cleistothecia	40

Samples of barley leaves with well-developed vegetative sporulation or cleistothecia were used. Collected conidia spores were settled on detached healthy and fully-expanded primary leaves of the susceptible barley variety 'Otra'. Samples of cleistothecia were stored at a temperature of 4–8°C. Isolates were purified by single colony isolation. The standard set of differentials was used for testing single colonies (Table 2).

Table 2. Set of differentials used for detection of virulence genes in powdery mildew causal agent *Blumeria graminis* f. sp. *hordei* samples collected in Lithuania in 2010

Differentials	Main resistance genes
P01	*Mla1*
P02	*Mla3*
P03	*Mla6*
P04B	*Mla7*
P08B	*Mla9*
P10	*Mla12*
P11	*Mla13*
P17	*Mlk*
P23	*MlLa*
SI1	*Ml(SI)*
'Steffi'	*Ml(St1)*, *Ml(St2)*
'Goldie'	*Mla12*, *MlLa*, *U*
'Meltan'	*Mla13*, *Ml(Im9)*, *Ml(Hu4)*

Each differential was grown in the laboratory conditions at 24°C, photoperiod 10 h for 12–14 days and for further inoculation the central part of healthy primary leaves was used. Leaf segments of each differential, approximately 25 mm long, were placed on the 0.7% water agar with 35 ppm benzimidazole (Dreiseitl, 2004). For inoculation of the leaf segments the microinoculation technique was used (Dreiseitl, 1998). Conidia from each single isolate were shaken onto differentials. Incubation of inoculated segments of differentials was carried out under 18–20°C in light with a photoperiod of 10 h. After 7–10 days of incubation, the disease reaction types of differentials were scored according to a 0–4 scale (Jørgensen, 1994). For type of infection, characterized by segregated colonies originating from the stomatal cells and expressed when the gene *mlo* is present, symbol 0(4) (i.e. infection type 0 with a few colonies corresponding to infection type 4) was used. Isolates that produced infection type 0–3 were considered as avirulent on the corresponding differentials. Infection type 4 only was defined as virulent on the corresponding differentials. Virulence frequency, complexity (virulence gene number per genotype) and pathotypes or combinations of virulence genes in genotypes were calculated. Statistical significance of differences between virulence frequencies was evaluated using the *Student t*-test at $\alpha = 0.05$.

Results and discussion

In 2010, 80 monopustule isolates were obtained for study of the Lithuanian population of *Blumeria graminis* f. sp. *hordei*. Virulence frequencies of *Va1*, *Va3* and *Va13* were middle and varied from 35% to 42.5% and from 37.5% to 47.5% in sporulation and cleistothecia, respectively (Fig. 1).

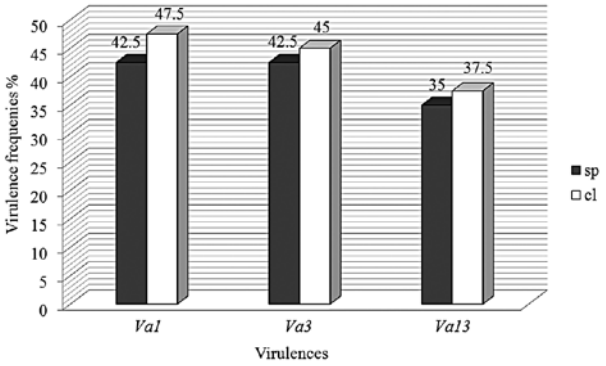

Figure 1. Virulence frequencies of *Va1*, *Va3* and *Va13* in sporulation (sp) and cleistothecia (cl) phases in Lithuania in 2010

Some increasing of virulences mentioned above in cleistothecia was detected. The virulence frequency detected on the *Va6*, *Va7*, *Va9*, *Va12*, *Vk* and *VLa* ranged from 60% to 90% (Fig. 2). The clear tendency of virulence increasing for *Vla* from 70% in sporulation to 90% in cleistothecia was observed during growing season of the pathogen.

The virulence frequency detected on the varieties 'Steffi', 'Goldie' and 'Meltan' ranged from 15% to 25% (Fig. 3).

All differencies among virulences in sporulation and cleistothecia were statistically significant, except

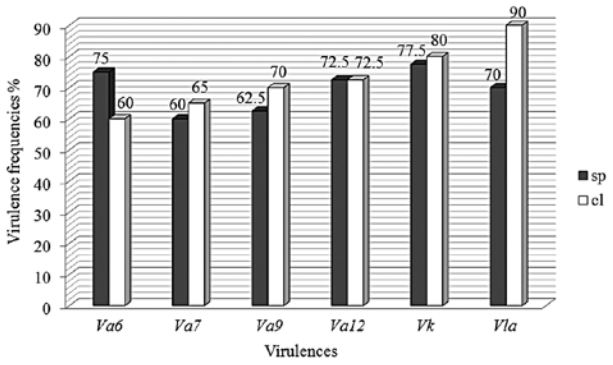

Figure 2. Virulence frequencies of *Va6*, *Va7*, *Va9*, *Va12*, *Vk* and *VLa* in sporulation (sp) and cleistothecia (cl) phases in Lithuania in 2010

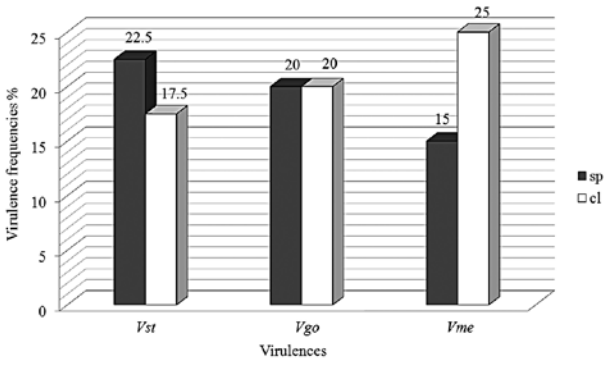

Figure 3. Virulence frequencies of *Vst*, *Vgo* and *Vme* in sporulation (sp) and cleistothecia (cl) phases in Lithuania in 2010

for *Va12* (Table 2) and *Vgo* (Table 3). In contrast, no virulences were found against resistances, which were present in the line *SI1*.

Long-term changes in virulence in *Blumeria graminis* f. sp. *hordei* in Lithuania in 2010 can be examined by comparing current results with the data obtained in 2000 (Kokina, Rashal, 2002). In 2010, we found considerably higher frequency of virulences for resistance genes *Mla1*, *Mla3* and *Mla13* common in European barley varieties. One of the main reasons for considerable increasing of correponding virulences *Va1*, *Va3* and *Va13* during last 10 years in Lithuania could be explained by propagation of the pathogen spores according to the main wind direction with an average speed of 110 km per year (Limpert, 1987). During the recent years, a clear tendency to higher frequencies of the virulences *Va1*, *Va3* and *Va13* in Europe was observed (Dreiseitl et al., 2006; Dreiseitl, 2008), including Latvia (Kokina, Rashal, 2008). Consequently, data observed in 2010 showed that the corresponding resistance genes *Mla1*, *Mla3* and *Mla13* lost their effectiveness in Lithuania as well.

In comparison with 2000, in 2010 some decreasing of virulences *Va6*, *Va7*, *Va9* and *Va12* was detected in Lithuania. The virulence frequency for *Vk* practically did not change. In contrast, *Vla* frequency was markedly higher, especially in phase of cleistothecia. Overall, high virulences of genes mentioned above proved ineffectiveness of the corresponding resistance genes *Mla6*, *Mla7*, *Mla8*, *Mla9*, *Mla12*, *Mlk* and *Mlla* in Lithuania at the moment like in other populations of the pathogen in Europe (Hovmøller et al., 2000; Dreiseitl et al., 2006; Kokina, Rashal, 2008).

During last ten years, virulence frequency of *Vme* considerably increased from 6.6% in 2000 to 25% in cleistothecia in 2010. The corresponding resistance of the variety 'Meltan', which in fact is controlled by three genes (*Mla13*, *Ml(Im9)*, *Ml(Hu4)*) is still effective. Based on the data obtained, further increasing of the virulence *Vme* in the pathogen population can be forecast. Similar tendency to considerable increasing during last decade was observed for *Vst* and *Vgo* from 1.3–2.6% in 2000 to approximately 20% in 2010. In the 20th century, approximately 40 alleles for race-specific resistance to powdery mildew, either alone or in combination, have been used in Europe. Resistance genes *Mla6*, *Mla7*, *Mla9*, *Mla12* and *Mla13* belonging to the *Mla* locus and the resistance alleles *Mlk*, *Mlg*, *MlLa*, *Mlh* and *Mlra* have been used in approximately 700 varieties (Jørgensen, 1994). All these genes are gradually overcome by virulent races within four to five years when varieties containing them are grown on a large acreage (Wolfe, McDermott, 1994). This occurs because the causal agent of barley powdery mildew is able to develop new genotypes which rapidly spread across Europe on susceptible barley varieties.

In 2010, no matching virulence was found for the resistance gene *mlo* in Lithuania. Barley *mlo* resistance has remained highly effective since 1979, when commercial spring barley varieties with the resistance were first released. Currently, this resistance is the most used resistance in spring barley grown throughout Europe (Lyngkjær et al., 2000; Kokina et al., 2008). Some surveys pointed out that isolates that appeared virulent on *mlo* in the virulence test could not be propagated on barley line with *mlo*. The apparent virulence of these isolates may have been to some environmental factors causing breakdown of the resistance in some of the differentials plants with *mlo* (Dreiseitl et al., 2006; Makepeace et al., 2007).

Identification of new sources of resistance to barley powdery mildew is important in relation to disease resistance management. Barley line *SI1* with unknown resistance genes, which is defined as a new source of resistance (Hovmøller et al., 2000), was also included in the set of differentials. In 2010, not any isolate of the pathogen from Lithuanian population break down resistance factors from *SI1*.

Wide diversity of the population is confirmed by the present results by the high number of detected pathotypes. In 2010, 26 pathotypes in sporulation and 21 pathotypes in cleistothecia were found (Table 3). In samples in sporulation the pathotype *a6 a7 a9 a12 k la* was the most abundant (25.0%). The mentioned pathotype was present in the samples from cleistothecia too, but with considerably lower frequency (12.5%). The dominant pathotype in cleistothecia was *a7 a9 a12 k la*

with the frequency 15%. This pathotype was not present in sporulation at all, likewise pathotypes *a6 a7 a9 a12 a13 k la* and *a1 a3 a9 k la*. The pathotype *a1 a3 a6 a7 a9 a12 a13 k la st go me* which overcomes resistances of 12 out of 13 differentials occurs in cleistothecia only with considerable frequency (7.5%) in the population. Pathotypes *a1 a3 a6 a7 a9 a12 a13 k* and *a3 a6 a12 la st* were present in sporulation only with frequencies 10% and 5%, respectively. A significant finding is a new pathotype *a1 a3 a13* which appeared both in sporulation (5.0%) and cleistothecia (7.5%) and which was not detected in 2000 in Lithuania (Kokina, Rashal, 2002). The mentioned pathotype was also detected in Latvia (first time in 2001) with considerable frequencies (till 7%) (Kokina, Rashal, 2004).

Table 3. Dominant pathotypes and their frequencies in the pathogen population in sporulation and cleistothecia phases in Lithuania in 2010

Dominant pathotypes	Frequencies %	
	sporulation phase	cleistothecia phase
a6 a7 a9 a12 k la	25.0	12.5
a1 a3 a6 a7 a9 a12 a13 k	10.0	–
a1 a3 a13	5.0	7.5
a3 a6 a12 la st	5.0	–
a7 a9 a12 k la	–	15.0
a6 a7 a9 a12 a13 k la	–	7.5
a1 a3 a9 k la	–	7.5
a1 a3 a6 a7 a9 a12 a13 k la st go me	–	7.5
Total number of pathotypes	26	21
Mean complexity	5.95	6.30

Note. Pathotypes were calculated for virulence genes *Va1*, *Va3*, *Va6*, *Va7*, *Va9*, *Va12*, *Va13*, *Vk*, *VLa*, *VSI*, *VSt*, *VGo* and *VMe*; "–" – pathotype was not present in corresponding phase.

Most of the popular spring barley varieties grown in Lithuania carry *mlo* gene, therefore they exhibit full resistance to powdery mildew. However, variety 'Beatrix' carrying other than *mlo* resistance genes is also available on the market. It has *Mlg*, *Ml(CP)*, *MlLa*, *Mla12*, *Mla17* resistance genes. Variety 'Beatrix' has been registered in the National Variety List since 2007 (Lithuanian National List of Plant Varieties, 2011), and it exhibited a high resistance to powdery mildew in variety trials, carried out by State Plant Service in 2005–2006, but in recent years distributing companies have recommend fungicide spray for disease control.

The adaptation of the pathogen population in Lithuania, like in others (Dreiseitl et al., 2006; Kokina, Rashal, 2008) also resulted in huge increase in its virulence complexity against corresponding resistance genes. The maximal detected complexity was 8 in 2000 (Rashal et al., 2000) and 12 in 2010 (Fig. 4). The mean isolate complexity was approximately 6 virulences per genotype with none considerable changes in sporulation and cleistothecia.

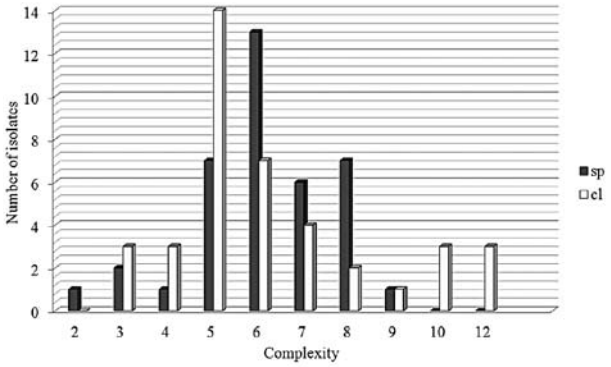

Figure 4. Distribution of virulence complexity in the population of powder mildew causal agent *Blumeria graminis* f. sp. *hordei* in sporulation (sp) and cleistothecia (cl) phases in Lithuania in 2010

This study revealed the ability of *Blumeria graminis* f. sp. *hordei* to adapt and produce new pathotypes with high complexity. Based on the increasing isolate complexity over the last decade in Lithuania, it can be assumed that individual use of new resistance genes in new varieties will lead to quick overcoming of its resistance. Pyramiding of resistance genes is advisable for success. On the other hand, further long-term investigations of the pathogen evolution are necessary.

Conclusions

1. Barley powdery mildew resistance genes *Mla1*, *Mla3* and *Mla13* have lost their effectiveness in Lithuania.

2. High frequences of virulences genes *Va6*, *Va7*, *Va8*, *Va9*, *Va12*, *Vk* and *Vla* in Lithuanian population of powder mildew causal agent *Blumeria graminis* f. sp. *hordei* proved ineffectiveness of the corresponding barley resistance genes *Mla6*, *Mla7*, *Mla8*, *Mla9*, *Mla12*, *Mlk* and *Mlla*.

3. Increasing of the virulence complexity in Lithuanian population of *Blumeria graminis* f. sp. *hordei* was detected in 2010 in comparison with 2000.

4. In 2010, in Lithuania no matching virulence was found for the barley powdery mildew resistance gene *mlo*, as well as no virulences were found against resistances, which are present in the line *SI1*.

Received 20 12 2013
Accepted 16 05 2014

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ISSN 1392-3196 / e-ISSN 2335-8947
Zemdirbyste-Agriculture, vol. 101, No. 4 (2014), p. 419−424
DOI 10.13080/z-a.2014.101.053

Miltligės sukėlėjo (*Blumeria graminis* f. sp. *hordei*) Lietuvos populiacijos genetinės struktūros ypatybės

I. Kokina[1], G. Statkevičiūtė[2], A. Leistrumaitė[2], I. Rashal[3]

[1]Daugpilio universiteto Sisteminės biologijos institutas, Latvija
[2]Lietuvos agrarinių ir miškų mokslų centro Žemdirbystės institutas
[3]Latvijos universiteto Biologijos institutas

Santrauka

Miltligės sukėlėjo *Blumeria graminis* f. sp. *hordei* grybienos su konidijomis ir kleistotecių ėminiai buvo surinkti Lietuvoje 2010 m. nuo veislės 'Dina' vasarinių miežių. Aštuoniasdešimties monoizoliatų virulentiškumas įvertintas naudojant diferencinį miežių rinkinį su gerai žinomais atsparumo genais ir nustatyti virulentiškumo genų dažniai, virulentiškumo kompleksiškumas bei patotipai. Virulentiškumo dažniai svyravo nuo 0 iki 90 %. Pastebėta ryški *Vla* virulentiškumo didėjimo tendencija kleistoteciuose. 2010 m. Lietuvoje nenustatytas virulentiškumas atsparumo genams, esantiems vasarinių miežių linijoje *SI1*, taip pat nerasta virulentiškumas *mlo* atsparumo genui. Miltligės populiacijos genetinės įvairovės aukštą lygį patvirtino didelis kiekis nustatytų patotipų. Dažniausiai pasitaikantis patotipas micelio su sporomis ėminiuose buvo *a6 a7 a9 a12 k la*, o kleistoteciuose dominavo *a7 a9 a12 k la* patotipas. Lyginant su 2000 m., 2010 m. nustatyti reikšmingi virulentiškumo genų dažnių, kompleksiškumo ir patotipų pokyčiai.

Reikšminiai žodžiai: atsparumas, *Blumeria graminis* f. sp. *hordei*, kompleksiškumas, miežiai, patotipas, virulentiškumas.