Changes in the Population of *Blumeria graminis* f.sp. *hordei* in the Czech Republic from 2009 to 2010

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Abstract

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Virulences to powdery mildew resistances in barley cultivars mostly carrying unknown resistances were determined in 2009 and 2010. Random spore samples of the airborne pathogen populations originating from winter and spring barley fields were obtained by means of a mobile version of a jet spore sampler by travelling across the Czech Republic. In total 301 isolates were studied, 55 differentials carrying mostly unknown resistances were used and 80 pathotypes were found, of which 26 representing 73.1% of isolates were detected in both years. Virulence frequencies showed a wide range from 0% to 100%. Complexity of the 2010 population slightly increased, mostly due to increasing frequencies of virulence to new resistances, whereas the complexity of virulences to resistances in most other differentials decreased. Pathotype 00027 was the most abundant (10.0%). Diversity of the 2010 population considerably increased due to changes in virulence frequencies.

Keywords: barley; *Hordeum vulgare* L.; powdery mildew resistances; pathogen population; virulence frequencies; diversity parameters

Barley (*Hordeum vulgare* L.) is a widely grown crop in the Czech Republic and powdery mildew caused by the airborne fungus *Blumeria graminis* (DC.) E. O. Speer f.sp. *hordei* emend. É. J. Marchal (anamorph *Oidium monilioides* Link) (= *Bgh*) is its most common disease. In 1989–2000, 40% and 50% of all disease epidemics in winter and spring barley, respectively, were induced by this pathogen. At the same time, high severity of powdery mildew was detected in 20% and 33% of official trials with winter and spring barley, respectively. The disease severity in winter barley accounted for 64% of that determined in spring barley. These findings indicate that winter barley is infected by the powdery mildew pathogen to a lesser extent than spring barley. Nevertheless, powdery mildew dominates also in this crop, whose susceptible cultivars are main sources of the inoculum for spring barley (Dreiseitl 2003a).

Resistant cultivars are an effective and environmentally friendly way of limiting harmful effects of diseases. There are several concepts of attaining and using varietal resistance (Wolfe 2000; Niks & Marcel 2009; Østergård *et al*. 2009; McDonald 2010). However, cultivars whose resistance to the powdery mildew pathogen is based on specific-resistance genes predominate in winter barley and are frequent in spring barley. There is a large number of specific resistances to *Bgh* in barley (Brown & Jørgensen 1991; Dreiseitl *et al.* 2007). Knowledge of the presence of these resistances in individual varieties as well as their effectiveness against the population of the given pathogen is essential for their effective exploitation in breeding and growing.

Specific resistances are identified using molecular markers (Řepková *et al.* 2009a,b; Řepková & Dreiseitl 2010; Teturová *et al.* 2010) or a

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postulation method (Brückner 1964; Torp *et al.* 1978; Jensen *et al.* 1992; Dreiseitl & Rashal 2004; Dreiseitl 2007). Once a marker for a corresponding gene was developed, its use is easy and rapid, but the information obtained is limited. Thus, markers are more suitable for detecting individual genes, it means providing information whether the gene under study is present. It is satisfactory for example in breeding when progenies are selected after crossing. Information obtained by the postulation method is much more complex because it enables to determine whether a related cultivar possesses any specific resistance and how many and which genes are employed. So, the postulation method is more suitable for factual identification of resistance genes.

The ability to identify resistance genes using the postulation method is directly proportional to the existence of available biological material, i.e. standard cultivars representing the widest variation in specific resistances of the given host as well as available isolates representing the widest variation in specific pathogenicity of the given pathogen. Therefore, working gene banks of the host and pathogen have to be continuously supplemented with new genotypes of both organisms.

The objectives of this contribution were to (*i*) determine the frequency of virulences to specific resistances of selected cultivars in order to find an important parameter of the effectiveness of these resistances, (*ii*) compare development of the pathogen population to some resistances, and (*iii*) obtain pathotypes with new virulences or new virulence associations for further experiments focused especially on the identification of unknown resistances.

MATERIAL AND METHODS

Two random samples (2009 and 2010) of the airborne *Bgh* population sampled in the Czech Republic were used for the assessment of frequencies of virulences to powdery mildew resistances in selected barley cultivars and for determination of some other derived characteristics.

Sampling of spores. Spores of the *Bgh* originating from cultivated winter and spring barley fields were obtained by means of a mobile version of a jet spore sampler (Schwarzbach 1979). The sampling of spores was done by travelling across the Czech Republic (Table 1) on May 28, 2009 and June 4, 2009 and from May 28, 2010 to June 6, 2010. In 2009, 144 isolates with identical number of isolates collected in Moravia and Bohemia (72 isolates per

Table 1. Routes of sampling *Blumeria graminis* f.sp. *hordei* in the Czech Republic in 2009 and 2010 and numbers of evaluated isolates

Section of a sampling route	Distance (km)	Number of evaluated isolates	
		2009	2010
Kroměříž – Lipník n. Bečvou	38		12
Kroměříž – Prušánky	75		12
Brno – Osová Bitýška	42		12
Brno – Kroměříž	70	12	12
Brno – Břeclav	51	12	12
Brno – Znojmo	62	12	12
Vyškov – Olomouc – Přáslavice	73	12	12
Přáslavice – Rychaltice	62	12	12
Olomouc – Líbivá	33	12	12
Praha – Avanti (D1 72.5 km)	80	12	6
Praha – Rokycany	72	12	1
Praha – Řevničov	45	12	2
Praha – Lovosice	71	12	7
Praha– Mnichovo Hradiště	62	12	12
Praha – Chlumec nad Cidlinou	71	12	21

Table 2. Codes of barley resistances to the powdery mildew pathogen (according to Boesen *et al*. 1996)

Resistance code	Common name	Resistance code	Common name
Ar	Arabische	Ra	Ragusa
Bw	Borwina	Ro	Roxana
Dr2	Dura	Ri	Ricardo
Ha	Hauters	Ru	Rupee
Hu4	Hulda	SI-I	SI-I
IM9	Ingrid M9	St	Steffi
Kw	Kwan	Tu2	Turkish
Ly	Lyallpur	U	Unknown
Ps	Psaknon	We	Weihenstephan

each) and identical number of isolates per sampling section (12 sections by 12 isolates) were examined. In 2010, 157 isolates, of which 49 isolates originated from Bohemia, were studied.

Differential sets. Extensive sets of differential cultivars containing a lot of specific resistances were used in both years. Resistance codes are given in Table 2. The differential sets were composed of three parts. The first part contained 15 cultivars possessing resistance genes that were used in registered cultivars before 1980, which allow the long-term observation of the population (results are not included in this paper). Differentials possessing resistances in currently grown varieties dominated in the second part. The third part consisted of varieties carrying resistances to which no corresponding virulences have been found in the territory of the Czech Republic. A total of 55 differentials, of which 36 in 2009 and 46 in 2010, were used here. Twenty-seven of them were used in both years (Table 3). Based on the postulation method, it is known that all these cultivars carry mostly different and often unknown specific resistance genes to powdery mildew. However, the knowledge of the presence of these genes in several differentials is still preliminary or incomplete.

Reaction types (RTs) produced by the reaction of each differential to a corresponding *Bgh* isolate were scored nine days after inoculation according to the nine-point 0–4 scale including intertypes (Torp *et al*. 1978). The isolates were assigned numerical designations (Limpert *et al*. 1994) based on their virulence to matching resistances in all 15 differentiating differentials used in both years in the given order (Nos. 40–54) (Table 3). Virulence complexity was calculated as the sum of selected virulence frequencies/100. Parameters for a comparison of both populations were calculated on the basis of virulence patterns of isolates in the set of the same 15 differentials. Descriptive parameters of both populations were calculated by the HaGiS programme (Hermann *et al*. 1999). Further details of the method used including the testing procedure, evaluation, pathotype designation and data analysis are described in Dreiseitl (2008).

RESULTS

Virulence frequency

In 2009, 144 *Bgh* isolates were examined (Table 3). The frequencies of virulence to 36 differentials varied from 0.0% (to resistances in 12 varieties) to 100.0% (to resistances in cvs. Dura and Monaco). One isolate was virulent to cvs. Laurena, Laverda, Souleyka, NORD 02610/24, and NORD 03025/6 (the corresponding virulence frequency = 0.7%). In 2010, 157 pathogen isolates were examined and 46 differentials were used (27 from 2009 and newly 19 others). The virulence frequencies showed the same range from 0% (to resistances in 18 cultivars) to 100% (to resistances in cvs. Dura, Lomerit and Weihenstephan 37/136). No virulence to resistances possessed by differentials Nos. 29–39 and, on the contrary, no avirulence to the resistance of the cv. Dura were detected in either 2009 or 2010.

Virulence complexity

The lowest virulence complexity (2) to resistances of 15 differentials was found in four pathotypes represented by 13 isolates and the highest virulence complexity (10) was found in one isolate only (Table 4). Virulence complexity of the population

Table 3. A differential set of 55 barley cultivars, their resistance and corresponding virulence frequency found in samples of airborne populations of *Blumeria graminis* f.sp. *hordei* in the Czech Republic in 2009 and 2010

No.	Differential variety	Resistance code	Virulence frequency (%)	
			2009	2010
1	Laurena	U	0,7 ± 0.7[a]	
2	NORD 02610/24	U	0.7 ± 0.7	
3	NORD 03025/6	U	0.7 ± 0.7	
4	Souleyka	U	0.7 ± 0.7	
5	Oowajao	U	6.2 ± 2.0	
6	Pribina[b]	Ru U	52.8 ± 4.2	
7	Semper[b]	Ly	80.6 ± 5.3	
8	Babette[b]	St	92.4 ± 2.2	
9	Monaco[b]	Ra	100.0	
10	Himalaya	U		0.0
11	KM 12/2010	U		0.0
12	KM 14/2010	U		0.0
13	KM 2161	U		0.0
14	KM 2929	U		0.0
15	Psaknon	Ps		0.0
16	Sara	Ri Tu2		0.0
17	Hulda[b]	IM9 Ly Kw Hu4		1.3 ± 0.9
18	Florian[b]	U		6.4 ± 2.0
19	Calcule[b]	U		7.6 ± 2.1
20	Prosa[b]	We U		8.9 ± 2.3
21	HE 1051	U		10.2 ± 2.4
22	LAN 0713	U		10.2 ± 2.4
23	HE 454	U		12.7 ± 2.7
24	CE 974	U		17.2 ± 3.0
25	KM 1998	U		29.3 ± 3.6
26	Tocada b[b]	U		69.4 ± 3.7
27	Baub 1910.4	U		89.8 ± 2.4
28	Lomerit[b]	U		100.0
29	Bonita	U	0.0	0.0
30	Br. 4190a1	U	0.0	0.0
31	Camilla	SI-1	0.0	0.0
32	CE 956	U	0.0	0.0
33	HM 407	U	0.0	0.0
34	Klimek	U	0.0	0.0
35	LP 1506.1.96	U	0.0	0.0
36	Pallidum 107	U	0.0	0.0
37	Seljanin 1	U	0.0	0.0
38	SI-1	SI-1	0.0	0.0
39	Venezia	U	0.0	0.0
40	Wendy[b]	U	0.0	10.8 ± 2.5
41	Laverda[b]	U	0.7 ± 0.7	11.5 ± 2.5
42	Spilka[b]	Ar U	1.4 ± 1.0	3.8 ± 1.5
43	Andrey[b]	U	2.1 ± 1.2	12.1 ± 2.6
44	Lilly[b]	U	2.1 ± 1.2	9.6 ± 2.4
45	Burštyn 2	U	2.8 ± 1.4	7.0 ± 2.0
46	Kangoo[b]	Ro	3.5 ± 1.5	12.7 ± 2.7
47	Dubai	U	4.9 ± 1.8	6.4 ± 2.0
48	Alinghi[b]	IM9	26.4 ± 3.7	23.6 ± 3.4
49	Gilberta[b]	Ra U	48.6 ± 4.2	45.9 ± 4.0
50	Signal[b]	U	52.1 ± 4.2	43.3 ± 4.0
51	Meltan[b]	Ru Hu4	52.8 ± 4.2	30.6 ± 3.7
52	Annabell[b]	St	92.4 ± 2.2	78.3 ± 3.3
53	Kompolti 4[b]	Bw	94.4 ± 1.9	92.4 ± 2.1
54	Weihenstephan 37/136[b]	Ha	98.6 ±1.0	100.0
55	Dura[b]	Ra Dr2	100.0	100.0

[a]standard error of binomial distribution; [b]differentials possessing resistances in currently grown cultivars

(mean of isolate complexity) slightly increased from 4.83 in 2009 to 4.88 in 2010. However, virulence complexity of the population to new resistances present in eight differentials (Nos. 40–47) increased more than four times (from 0.18 to 0.74), whereas virulence complexity to resistances in the other differentials (Nos. 48–54) decreased from 4.65 to 4.14. The most frequent pathotypes (21) and also isolates (87 = 28.9%) carried five virulences. In 2009 mean virulence complexity of isolates was 4.83 and mean virulence complexity of pathotypes was 4.98, whereas in 2010 mean virulence complexity of isolates was 4.88 and mean virulence complexity of pathotypes was 5.26.

Table 4. Eighty pathotypes of *Blumeria graminis* f.sp. *hordei* found in the Czech Republic in 2009 and 2010 their virulence complexity and number of respective isolates

Pathotype	Virulence complexity	Number of isolates		Pathotype	Virulence complexity	Number of isolates	
		2009	2010			2009	2010
00005	2		1	00657	7	1	
00006	2	4	6	00677	8		1
00007	3	8	11	01104	3		1
00014	2		1	01107	5		1
00015	3	1	2	01117	6		1
00016	3	2	2	01317	7		1
00017	4		8	03107	6		3
00023	3	1		03117	7		1
00025	3	3		03126	6		1
00027	4	16	14	03127	7	1	3
00037	5	9	10	03137	8		3
00046	3	1	1	03167	8		1
00047	4	14	4	03537	9	1	1
00056	4	1	2	03577	10	1	
00057	5	12	2	04047	5	2	2
00065	4	1		04053	5	1	
00067	5	10	5	04075	6		1
00077	6	9	3	04077	7		2
00135	5	2		04247	6		1
00207	4		2	04267	7	1	1
00216	4	1		04657	8		1
00217	5	1		07145	7		1
00235	5	1		07167	9		1
00257	6	1	1	20006	3		1
00267	6		1	20046	4	1	
00404	2		1	30006	4		3
00407	4	3	1	30007	5		1
00415	4		1	30016	5		3
00416	4	1	2	30025	5		1
00417	5	6	2	30046	5		1
00427	5	2	4	30047	6		3
00437	6	3	6	30406	5		1
00446	4		2	30416	6		3
00447	5	2	2	30456	7		1
00456	5		1	40007	4	1	
00457	6	3	2	40017	5		1
00467	6	2	1	40037	6		3
00477	7	12	3	40047	5	1	
00617	6	1		40125	5		1
00637	7		1	44044	4		1

Pathotype distribution

In 2009 and 2010, 40 and 66 pathotypes were found out, respectively, of which 20 and 31 pathotypes, respectively, showed frequencies higher than 2. In total, 301 isolates were studied that belonged to 80 pathotypes (Table 4). Twenty-six pathotypes (32.5%) were found out in both years and they represented 220 isolates (73.1%). Out of them, 127 isolates (88.2% of the given population) were detected in 2009 and 93 isolates (52.2%) in 2010. Fifty-four pathotypes (67.5%) represented by 81 isolates (26.9%) were found out only in one of the two years. In both years, pathotype 00027 was the most abundant, comprising in total 30 isolates (= 10.0% of all isolates studied) and showing virulence complexity 4. Pathotype 00017 was not found out in 2009, whereas in 2010 it was the fourth most abundant represented by eight isolates. Virulence spectra of the 12 most abundant pathotypes are shown in Table 5.

Diversity parameters

All parameters shown in Table 6 indicate a considerable increase in the diversity of the 2010 population in comparison with the 2009 population. It is documented by the values of diversity components such as richness (Gleason), which reflects a number of pathotypes, and evenness (Shannon), which gives the evenness of their proportions, as well as by more complex characteristics of diversity such as Shannon and Simpson diversity indexes.

DISCUSSION

In Europe more than 50% of the global area of barley is grown (FAOSTAT 2010). Both spring and winter forms are grown on large areas, which creates so-called "green bridge" favourable for all, but especially obligate pathogens. Also, climatic conditions in most parts of the continent are evidently favourable for the reproduction of *Bgh*, and therefore powdery mildew is the most widespread disease of barley there.

The whole continent is the only epidemiological unit for airborne pathogens where they can spread without any apparent restriction. The Czech Republic, where a quickly changing collection of

Table 5. Virulence spectra of 12 most abundant pathotypes of *Blumeria graminis* f.sp. *hordei* found in the Czech Republic in 2009 and 2010 to resistance of seven selected differential cultivars

Differential cultivar	Abundant pathotypes of *Blumeria graminis* f.sp. *hordei* and their virulence spectra											
	00006	00007	00017	00027	00037	00047	00057	00067	00077	00417	00437	00477
Alinghi										+	+	+
Gilberta			+		+		+		+	+	+	+
Signal				+	+			+	+		+	+
Meltan						+	+	+	+			+
Annabell		+	+	+	+	+	+	+	+	+	+	+
Kompolti 4	+	+	+	+	+	+	+	+	+	+	+	+
Weihenstephan 37/136	+	+	+	+	+	+	+	+	+	+	+	+

+ = virulence

Table 6. Diversity parameters of *Blumeria graminis* f.sp. *hordei* population in the Czech Republic in 2009 and 2010

Diversity parameter	2009	2010
No. of isolates	144	157
No. of pathotypes	40	66
No. of pathotypes with frequency > 1	20	31
Mean of isolate complexity	4.83	4.88
Mean of pathotype complexity	4.98	5.26
Simple match/mismatch coefficient	0.28	0.42
Richness – Gleason	7.85	12.86
Evenness – Sheldon	0.86	0.91
Diversity – Shannon	3.18	3.83
Diversity – Simpson	0.95	0.97

both domestic and foreign varieties is grown, is situated in the heart of Europe. A critical role in the domestic *Bgh* population is played, besides the other evolutionary forces, by directional selection, effecting also genetic draft (hitchhiking) and gene/genotype flow (migration). Therefore, the *Bgh* population can be characterised by both high diversity and dynamic changes (Dreiseitl 2003b).

Thirty-six varieties were used for the study of the 2009 population presented herein. However, nine of them were not used in 2010 for the following reasons. Among 160 isolates no isolate with matching virulence to cv. Laverda was detected in 2008 (Dreiseitl 2008). In 2009, such an isolate was found which was simultaneously virulent to other four differentials with unknown resistance (cvs. Laurena, Souleyka, NORD 02610/24, and NORD 03025/6). Thus, all these five cultivars are supposed to possess identical or similar resistance, therefore, only cv. Laverda was used in 2010. Cv. Oowajao could not be employed due to a lack of seed. In 2009, csv. Pribina and Meltan exhibited identical or very similar reaction types to all isolates. This indicates their identical or very similar resistance, therefore, only cv. Meltan was used in 2010. In the meantime, the resistance in cv. Semper was found to be the same as in P04B in the first part of the differential set, and the resistance in cv. Babette was found to be identical to that in cv. Annabell (Dreiseitl unpublished). No isolate avirulent to cvs. Monaco and Dura was detected. Therefore, only cv. Dura remained in the set because it is more probable to find a rare avirulent isolate on it since it carries, besides the common gene *Mlra*, another resistance gene *Ml*(*Dr2*).

In 2010, 19 varieties were newly included in the differential set, mainly those with newly determined unknown resistances (Dreiseitl unpublished). Among them it was also cv. Lomerit that was supposed to carry the gene *Mla8* based on its resistance spectrum containing only one avirulent pathotype (Dreiseitl 2007). However, new findings confirmed a different resistance in cv. Lomerit (Dreiseitl unpublished), and therefore this cultivar was included in the differential set again.

Some differentials, or at least cultivars with identical or similar resistance, were used for the study of the domestic population also in preceding years. The proportion of isolates virulent to the resistance possessed by cv. Florian was 1.3% in 2008 (Dreiseitl 2008), whereas it amounted to 6.4% in 2010. The frequency of virulence to the resistance in cv. Lomerit was identical (100%) in both years. There was a rapid increase in the frequency of virulence to the resistance of cv. Laverda (0% in 2008, 0.7% in 2009 and 11.5% in 2010), which is obviously related to the migration of individuals of the examined population from neighbouring countries, especially from Germany, where cultivars with the relevant resistance were grown earlier, and with extending areas under corresponding cultivars in the Czech Republic. In 2000 as well as in 2009 and 2010, 100% of isolates virulent to the resistance Ra were found out, however five avirulent isolates were detected in 2002 documenting that *Vra* is not fixed in the European population (Dreiseitl 2004). A very high

frequency of virulence has also been found to the resistance Ha. However, some sporadic avirulent isolates have been detected (0.3% in 2002, 1.5% in 2004, and 1.4% in 2009) while no avirulent isolate was found in 2010. Virulence to the resistance of cv. Gilberta has been stable in recent years (45.6% in 2008, 48.6% in 2009 and 45.9% in 2010). An increased frequency of virulence to the resistance St (cv. Babette) was determined in the first year studied in this paper (76.3% in 2008, 92.4% in 2009, and 78.3% in 2010). It should be noticed that two cultivars with this resistance (cvs. Babette and Annabell) were included in the differential set in 2009 and identical virulence frequency was determined on both of them. A considerably lower virulence frequency was found out only on cv. Alinghi (48.8% in 2008, 26.4% in 2009, and 23.6% in 2010).

A higher complexity of pathotypes in comparison with a lower complexity of isolates in both years, especially in 2010, reflects the fact that the frequency of isolates with the below-average value of this character was higher than the frequency of isolates with above-average complexity. A considerable increase in this difference in 2010 as well as a considerable increase in diversity of this population reflects an increase in the frequency of virulence to new resistances present in differentials Nos. 40–47. Consequently, relevant new pathotypes were characterised by higher complexity, but the frequency of the corresponding isolates was low. The population diversity was also increased by a considerable decrease in the frequency of virulence to the resistance of cv. Annabell, from 92.4% to 78.3%. The resultant values of diversity were then corrected by a decrease in the frequency of virulence to the resistance of cv. Meltan and other changes in virulence frequencies.

A large number of isolates with new virulences and new virulence associations were found which are suitable for the identification of resistance genes and that are able to replace some currently used isolates from the working gene bank of the pathogen. For this purpose, 14 isolates from the 2009 population (Dreiseitl & Adamcová 2011) and eight isolates from the 2010 population have been conserved. However, due to the current exchange of the gene bank these isolates will also be earlier or later replaced by new isolates with a higher resolving ability.

No isolate virulent to the resistances possessed by 18 of the 55 differentials used has been found. Most of them carry an unknown resistance to the given pathogen. Thus, it is possible that these differentials possess a large number of new fully effective resistance genes. However, repeating the following story of cultivars with the resistance Ro cannot be excluded. In the last two decades, powdery mildew resistance has been investigated in a large number of barleys. Apart from those with the Mlo resistance, 29 spring barley varieties were fully resistant to all isolates used and many new resistance genes were expected in them. Later, 22 of these cultivars were studied and surprisingly at least 18 of them have the same resistance designated according to cv. Roxana Ro (Dreiseitl 2011).

Results of this contribution demonstrate that fully effective resistances are highly vulnerable, especially those based on one gene. As an example, the resistance of cv. Laverda can be shown. No isolate virulent to this cultivar was found in 2008, the first virulent isolate was detected in 2009 and 18 such isolates (virulence frequency = 11.5%) were found in 2010. The rate of increasing the proportion of virulent individuals in the pathogen population is then directly proportional to the rate of decreasing the effectiveness of the relevant resistance. Combining two or more fully effective resistances in one variety can delay the emergence of virulent individuals. However, it is necessary to use also other options of achieving more durable resistance of grown varieties.

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