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Great pathotype diversity and reduced virulence complexity in a Central European population of *Blumeria graminis* f. sp. *hordei* in 2015–2017

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Abstract Powdery mildew caused by the airborne fungus *Blumeria graminis* f. sp. *hordei* is one of the main diseases of barley (*Hordeum vulgare*) throughout the world. In Europe spring and winter barley is widely grown under high-input management and with European-bred varieties containing resistance genes to *B. graminis* f. sp. *hordei*. The pathogen is wind-borne and in Central Europe spores can be blown in from any direction. Thus, in this region directional selection can maintain and expand virulences arising from local mutations or introduced from other parts of the continent. In this paper, 309 isolates were studied and, based on the reaction to 32 differential varieties, assigned to 279 pathotypes (Simple index = 0.903). Complexity ranged from 5 to 18 virulences, where the most frequent (56) were isolates characterized by nine virulences. In 2016 and 2017, eight additional differential varieties revealed that the population was highly diverse and 226 isolates were represented by 224 pathotypes (Simple index = 0.982). This illustrates the importance of genetic recombination in the formation of this pathogen population. There was a gradual decrease in virulence frequencies to some resistances resulting in a reduced average virulence complexity from 11.30 in 2015 to 9.26 in 2017. The cause might be attributed to a decreased area of varieties with the particular resistances leading to a weakening of directional selection. New virulences to resistances contained in Camilla, Sara and E-388/01 were detected over the same period.

Keywords Barley · *Hordeum vulgare* · Powdery mildew · Resistance genes · Virulence frequency

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Powdery mildew caused by the airborne ascomycete fungus *Blumeria graminis* (DC.) E. O. Speer, f. sp. *hordei* emend. É. J. Marchal (anamorph *Oidium monilioides* Link) is one of the most common diseases of barley (*Hordeum vulgare* L.). *Blumeria graminis* f. sp. *hordei* is also a model organism when studying host-pathogen interactions (Collins et al. 2003; Schweizer and Stein 2011; Panstruga and Spanu 2014; Lu et al. 2016; Menardo et al. 2017).

The largest areas and highest concentration of barley are in Europe, where winter and spring forms are sown under highly intensive management systems. Favourable climatic conditions for pathogen development and the availability of host tissues throughout the year result in annual infections of powdery mildew (Dreiseitl 2011a), causing yield losses and reduced quality of susceptible cultivars (Murray and Brennan 2010).

The disease can be effectively controlled using genetic resistance, which is an inexpensive and environmentally-friendly method of control. Honecker (1931) founded barley powdery mildew resistance breeding in Europe and subsequent research has resulted in commercial

varieties with many resistance genes (Brown and Jørgensen 1991). A diverse source of resistance derived from wild barley (*Hordeum vulgare* subsp. *spontaneum* (C. Koch.)) has since been exploited (Dreiseitl 2014a). A list of known barley resistance genes was published by Jørgensen (1994) and new resistances have recently been detected in cultivated varieties (Dreiseitl 2011b, c, d) and wild barley (Dreiseitl 2017a, b).

There are several methods of evaluating, selecting and using varietal resistance (Wolfe 2000; McDonald 2010; Burdon et al. 2016; Lof et al. 2017). Varieties with specific resistance genes still predominate in winter barley and the *mlo* gene has been backcrossed into modern spring barley cultivars (Dreiseitl 2017c). A knowledge of the presence of these resistances in individual varieties, as well as their effectiveness against populations of the pathogen, is an aid for exploiting resistances in breeding and cultivation (Brown 2006).

Over the last decades the European population of *B. graminis* f. sp. *hordei* has mostly reproduced on host varieties containing specific resistances and, because there are no barriers preventing the gene flow of airborne pathogens, the continent is considered as a metapopulation (epidemiological unit). Central Europe comprises nine countries, of which only the Czech Republic is entirely landlocked and spores can enter from the surrounding countries. Thus, within this population directional selection allows the maintenance of multiple windborne virulences from adjacent areas or locally via mutation leading to a high virulence complexity by the second half of the 1990s (Hovmøller et al. 2000). Since that time novel specific resistances have been incorporated into commercial varieties (Dreiseitl 2011b, c, d, 2016), but gradually overcome by newly emerging virulences (Dreiseitl 2015a) whose frequencies rapidly increase (Dreiseitl 2015b).

The objectives of this research were: (i) to determine the composition of the pathogen populations over a 3-year period, (ii) to analyse changes in the main parameters of the population structure, and (iii) to obtain pathotypes with new virulences and virulence combinations for further experiments to identify unknown resistances.

Material and methods

Differentials and production of plant material

A set of 50 barley differential varieties comprising genotypes carrying different resistances against *B. graminis* f. sp. *hordei* were selected (Table 1). Of these, 14 standard lines (Kølster et al. 1986), 20 commercial varieties and 16 other genotypes, mostly advanced breeding stocks were included.

About 25 untreated seeds of each differential or susceptible barley variety were sown in a pot (80 mm diameter) filled with a gardening peat substrate and placed in a mildew-proof greenhouse under natural daylight. Plants were grown until primary leaves were fully expanded, when the secondary leaves were emerging.

Collection of isolates

Random samples of pathogen populations originating from cultivated spring and winter barley fields collected from the air were obtained by means of a jet spore sampler (Schwarzbach 1979) mounted on the roof of a car. Conidiospores were collected by driving across the Czech Republic in 3 years (2015–2017) during late May to early June, when tillering of spring barley had usually ended and winter barley was at the ear emergence stage. Freshly detached healthy and fully-expanded primary leaves of the susceptible barley variety Stirling (Dreiseitl and Platz 2012) were placed in 120 mm glass Petri dishes on water agar (0.8%) containing benzimidazole (40 mg L^{-1}) (BWA) - a leaf senescence inhibitor - and inserted in the bottom of the spore sampler. The collected spores settled on detached leaves while travelling and dishes were replaced for each section of the sampling route, which was annually about 1000 km (Table 2). During sampling, dishes with fresh as well as with exposed leaves were kept in a refrigerator at about 8 °C. After sampling, exposed leaves were transferred to glass Petri dishes of 150 mm diameter with fresh BWA.

Multiplication of isolates and inoculation

To multiply inoculum, dishes with leaves and collected spores were incubated for 11 to 13 days at 19.0 ± 1 °C under artificial light (cool-white fluorescent lamps providing 12 h light at 30 ± 5 μmol/m^2/s). Conidia from each single-spore colony were sucked into a replaceable tip of an AW 1000 varipipette and then blown off the tip through a hole in the central part of the upper cap into a circular metal micro-settling tower 200 mm high using a 10 ml syringe. 15 mm long leaf segments of differential varieties and the susceptible Stirling were cut from the central part of healthy primary leaves. Two segments of each variety of the first part of the differential set

Table 1 Barley differential varieties, their resistance genes and corresponding virulence frequencies found in a Central European population of *Blumeria graminis* f. sp. *hordei* in 2015–2017

No.	Differential variety	Main *Ml* resistance gene(s)	Growth type	Virulence frequency (%)		
				2015	2016	2017
1	P01	*a1*	s[b]	50.6 ± 5.5[d]	44.8 ± 4.9	44.6 ± 4.5
2	P02	*a3*	s	18.1 ± 4.2	14.3 ± 3.4	9.9 ± 2.7
3	P03	*a6*	s	98.8 ± 1.2	99.0 ± 1.0	100.0
4	P04B	*a7*	s	90.4 ± 3.2	70.5 ± 4.5	71.9 ± 4.1
5	P08B	*a9*	s	19.3 ± 4.3	14.3 ± 3.4	10.7 ± 2.8
6	P09	*a10*	s	56.6 ± 5.4	34.3 ± 4.6	47.1 ± 4.5
7	P10	*a12*	s	97.6 ± 1.7	96.2 ± 1.9	92.6 ± 2.4
8	P11	*a13*	s	51.8 ± 5.5	46.7 ± 4.9	38.8 ± 4.4
9	P12	*a22*	s	49.4 ± 5.5	43.8 ± 4.8	32.2 ± 4.2
10	P15	*Ru2*	s	90.4 ± 3.2	94.3 ± 2.3	73.6 ± 4.0
11	P17	*k1*	s	49.4 ± 5.5	46.7 ± 4.9	45.5 ± 4.5
12	P20	*at*	s	21.7 ± 4.5	22.9 ± 4.1	23.1 ± 3.8
13	P21	*g*	s	91.6 ± 3.0	86.7 ± 3.3	84.3 ± 3.3
14	Annabell	*St*	s	77.1 ± 4.6	80.0 ± 3.9	58.7 ± 4.5
15	Camilla	*SI-1*	s	1.2 ± 1.2	1.0 ± 1.0	1.7 ± 1.2
16	Dubai	*u*[a]	w[c]	4.8 ± 2.3	5.7 ± 2.3	6.6 ± 2.3
17	E-388/01	*u*	s	1.2 ± 1.2	0	0.8 ± 0.8
18	Florian	*Ln*	w	3.6 ± 2.0	1.0 ± 1.0	1.7 ± 1.2
19	HE1051	*a13, u*	s	41.0 ± 5.4	28.6 ± 4.4	20.7 ± 3.7
20	Kangoo	*Ro*	s	81.9 ± 4.2	69.5 ± 4.5	63.6 ± 4.4
21	Laverda	*Lv*	w	26.5 ± 4.8	21.0 ± 4.0	15.7 ± 3.3
22	Oowajao	*u*	w	9.6 ± 3.2	12.4 ± 3.2	7.4 ± 2.4
23	Pop	*u*	s	2.4 ± 1.7	7.6 ± 2.6	1.7 ± 1.2
24	Pribina	*a13, Hu4*	s	41.0 ± 5.4	32.4 ± 4.6	28.9 ± 4.1
25	Psaknon	*p1*	s	1.2 ± 1.2	1.9 ± 1.3	0.8 ± 0.8
26	Sara	*a3, aTu2*	s	1.2 ± 1.2	0	0
27	SBCC097	*u*	s	2.4 ± 1.7	1.0 ± 1.0	0.8 ± 0.8
28	Signal	*N81*	s	37.3 ± 5.3	31.4 ± 4.5	28.9 ± 4.1
29	SK4770–7	*u*	s	1.2 ± 1.2	0	0
30	Spilka	*u*	s	2.4 ± 1.7	1.0 ± 1.0	0
31	Venezia	*Ve*	w	1.2 ± 1.2	2.9 ± 2.7	8.3 ± 2.1
32	Zeppelin	*u*	s	7.2 ± 2.8	8.6 ± 2.7	5.8 ± 2.1
33	Alinghi	*IM9*	w		16.2 ± 3.6	21.5 ± 3.7
34	Black Heart	*u*	s		41.0 ± 4.8	33.1 ± 4.3
35	Burštyn 2	*u*	s		1.9 ± 1.3	2.5 ± 1.4
36	Hulda	*a7*, *k1*, *IM9*, *Hu4*	s		0	3.3 ± 1.6
37	KM1998	*u*	s		11.4 ± 3.1	14.0 ± 3.2
38	P23	*La*	s		21.9 ± 4.0	26.4 ± 4.0
39	Prosa	*g*, *u*	s		11.4 ± 3.1	14.9 ± 3.2
40	Ricus	*u*	w		17.1 ± 3.7	9.1 ± 2.6
41	A222	*a11*	w			3.3 ± 1.6
42	KM2161	*u*	s			6.6 ± 2.3

Table 1 (continued)

No.	Differential variety	Main *Ml* resistance gene(s)	Growth type	Virulence frequency (%)		
				2015	2016	2017
43	SC101-12A	*u*	s			1.7 ± 1.2
44	Bonita	*u*	w	0	0	0
45	NORD07017/69	*u*	w	0	0	0
46	NORD12/1122	*u*	s	0	0	0
47	SJ123063	*u*	s	0	0	0
48	SY412–329	*u*	s	0	0	0
49	KM14/2010	*u*	s	0	0	
50	SJ048311	*u*	w	0		

[a] *u* = unknown, [b] s = spring, [c] w = winter, [d] standard error

represented by Pallas near-isogenic lines (Table 1, differential varieties no. 1–13) and the susceptible Stirling were placed adjacently with the adaxial surface upward on BWA in 90 mm plastic Petri dishes and inoculated in the micro-settling tower.

After evaluation of the first part of the differential set the conidiospores of isolates produced on Stirling were used for the second inoculation. For each isolate, a 150 mm glass Petri dish with three leaf segments of each variety of the rest of the differential set was placed at the bottom of a settling tower 415 mm in height. Conidia of each isolate from a leaf segment of Stirling with fully developed pathogen colonies were shaken onto a square piece (40 × 40 mm) of black paper to visually estimate the amount of inoculum deposited. This was then gently rolled to form a blowpipe and the conidia of an isolate were blown through a side hole in the upper part of the settling tower over the Petri dish. The inoculum density was about 5–8 conidia mm^{-2}. The dishes with inoculated leaf segments were kept under the described incubation conditions.

Table 2 Sampling route sections for collecting air-borne spores of *Blumeria graminis* f. sp. *hordei* across the Czech Republic in 2015–2017

Designation	Sampling route section	Distance (km)
A	Brno - Kroměříž	65
B	Brno - Znojmo	60
C	Brno - Břeclav	50
D	Přáslavice - Vyškov	60
E	Přáslavice - Ostrava	65
F	Olomouc - Šumperk	50
G	Kroměříž - Otrokovice - Přerov	55
H	Prostějov - Kroměříž - Přerov	50
I	Praha - Motorway 1 (90th km)	90
K	Praha - Plzeň	80
L	Praha - Petrohrad	75
M	Praha - Lovosice	75
N	Praha - Turnov	80
O	Praha - Hradec Králové	85
X	Brno - Motorway 1 (90th km)	95
Y	Praha (circle)	70
Z	Kroměříž - Strážnice	60

Virulence determination and pathotype designation

The response type (RT) based on the reaction of each differential to an isolate was scored 8 days after inoculation on a scale of 0 to 4 (Torp et al. 1978) where RT 4 or 3–4 (= strong mycelial growth and strong sporulation on leaf segments) were considered virulent to the corresponding resistance gene(s). A set of RTs provided a response type array (RTA) for each isolate.

The numerical designations of RTAs were based on their virulence / avirulence patterns to the set of 32 differential varieties ranked in the order shown in Table 1 and divided into ten triplets and the two last varieties on their own. Each of the digits indicates virulence to the three differentials of the respective triplet. If virulence to a corresponding variety was detected, the first differential is given the value 1 (2^0), the second differential has the value 2 (2^1), and the third differential 4 (2^2). Therefore, each digit can have a value from 0 (no virulence to any of the three differentials) up

to 7 (1 + 2 + 4), denoting virulence to each of the three varieties. The resulting number (reverse-octal) defines the virulence / avirulence patterns of isolates and their pathotype classification (Gilmour 1973; Limpert and Müller 1994). The HaGiS program was used for transcription of the RTAs into octal notation (Herrmann et al. 1999). In 2016 eight and in 2017 an extra three additional differential varieties were used and the results were numerically designated.

Statistical analysis

Standard error (SE) of virulence frequency was calculate as follows:

$$SE = p\,(p-1)/n$$

p virulence frequency
n number of isolates

In this contribution virulence frequency and standard error are presented in percentages.

Simple index (SI).

SI number of pathotypes / number of isolates

Results

Differential varieties

In 2015, 39 differentials were used (Table 1); seven of these were unsuitable since all the isolates were avirulent to their resistances. In 2016, one non-differentiating variety was omitted and eight new differentials were added; 10 out of 46 varieties did not differentiate the population for the same reason as above. In 2017, one non-differentiating variety was also removed and three varieties added; nine out of 48 varieties could not differentiate the population - eight were avirulent and one (P03) virulent on all isolates. In 2015, 2016 and 2017 32, 36 and 39 varieties, respectively, differentiated the population. A total of 50 differentials were used, 37 of which were used in all 3 years, but five of them did not differentiate within any of the populations.

Virulence frequency (VF)

Virulence frequencies ranged from 0 to 100% in all 3 years, and several of the differentials had similar VFs over the same time period (see Table 1 for full data). In 2015, 2016 and 2017 no virulence (VF = 0%) was recorded to the resistances of seven, ten and eight differential varieties, respectively. In 2017, five of the varieties with VFs of 0% were common to the previous 2 years and seven varieties the same as in 2016; a VF of 100% was found to the resistance of P03.

Diversity of isolates

All isolates from populations 2015–2017 were tested on 32 common differential varieties and their virulence / avirulence phenotypes encoded into 11-digit numbers of reverse octal notation (Supplementary Table S1). Based on the response of 83 isolates of the 2015 population they belonged to 77 pathotypes (Table 3), six of which were present as two isolates. Among 105 isolates from 2016, there were 104 pathotypes; the pathotype 40,513,020,010 was represented by two isolates. In 2017, 121 isolates belonged to 116 different pathotypes, with five of the pathotypes composed of two isolates.

Six pathotypes (41,513,040,000, 45,121,020,000, 5,151,302,000, 53,513,020,010, 55,133,020,010 and 57,133,020,012), including 13 isolates, were common to the 2015 and 2016 populations, one pathotype (41513020000) with two isolates was common to the 2015 and 2017 populations and three pathotypes (4,111,102,000, 45,133,000,010 and 45,133,020,000), including six isolates, were common to the 2016 and 2017 populations. Four pathotypes (41,513,020,010, 44,133,020,000, 54,131,020,000 and 55,133,020,000), comprising 14 isolates were found in all three populations. A total of 309 isolates belonging to 279 pathotypes were studied (Simple index = 0.903); of these pathotypes, 256 had one isolate, 18 had two isolates, three (44,133,020,000, 54,131,020,000 and 55,133,020,010) had three isolates and two (41,513,020,010 and 55,133,020,000) had four isolates.

In addition to the 32 common varieties, eight extra differentials were used in 2016 and 2017. In the numerical designation of the pathotype, virulence / avirulence to such differentials is contained in the three digits following the first dash. These additional differentials enabled the resolving of 226 isolates in both these years and 224 pathotypes were recorded (Simple index =

Table 3 Number and complexity of isolates, and number and frequency of pathotypes found in a Central European population of *Blumeria graminis* f. sp. *hordei* in 2015–2017

Year	No. isolates	Complexity of isolates	No. pathotypes	Frequency of pathotypes			
				1	2	3	4
2015	83	11.30	77	71	6		
2016	105	10.20	104	103	1		
2017	121	9.26	116	111	5		
All	309	10.13	279	256	18	3	2

0.982). A total of 222 pathotypes of these had only one isolate and two with two isolates, where pathotype 41,113,020,010–100 included two isolates (2017) and pathotype 41,513,020,010–000 had one isolate in each of the 2016 and 2017 populations. In 2017, there were three additional differential varieties and in the numerical designation of the pathotypes, the three virulences are contained in the digit following the second dash. However, these three varieties no longer differentiated the two aforementioned pathotypes (Supplementary Table S1).

Complexity of the isolate virulence

The complexity of virulences (number of virulences) to 32 common differential varieties ranged from 5 (in the 40,113,000,000, 41,110,000,001 and 51,011,000,000 isolates) up to 17 and 18 (75,333,135,010, and 55,733,235,012 respectively). The most frequent were isolates characterized by nine virulences (56 isolates) (Table 4).

Change in the population

In the 2015–2017 populations, a decrease in VFs to the *Ml* resistance genes *a1*, *a3*, *a7*, *a9*, *a12*, *a13*, *k1*, *g*, and *Ro*, *Lv*, *Hu2* and *N81* was observed (Table 1). This gradual decrease in VFs resulted in a reduced average complexity of the isolate virulence to 32 common differential varieties, from 11.30 in 2015, 10.20 (2016) to 9.26 in 2017 (Table 3). At the same time new virulences to the resistances contained in the differential varieties Camilla (monitored since 2009), Sara (in 1999 and then since 2010), and E-388/01 (since 2013) were recorded.

Selection of isolates for the pathogen gene bank

Of the 309 isolates, six were included in the working pathogen gene bank for further experiments relating to the detection and postulation of resistance genes in barley varieties (Table 5).

Discussion

Disease resistance genes are postulated on the basis of specific interactions of the host varieties with pathogen isolates of known virulences (Kolmer 2003; Zhang et al. 2010; Goyeau and Lannou 2011; Lu et al. 2016; Dreiseitl 2017c). The number of resistances, and their combinations that can be identified depends on the availability of appropriate biological material, i.e. standard host varieties representing specific resistances as well as pathogen isolates that include virulences or avirulences to these resistances. Therefore, gene banks of the host and pathogen must be continuously supplemented with new genotypes.

Table 4 Virulence complexity and corresponding frequency of 309 *Blumeria graminis* f. sp. *hordei* isolates collected in a Central European population in 2015–2017

Virulence complexity	No. isolates	Virulence complexity	No. isolates
5	3	12	31
6	17	13	27
7	18	14	16
8	43	15	7
9	56	16	3
10	42	17	1
11	44	18	1

Table 5 Isolates of *Blumeria graminis* f. sp. *hordei* selected from a Central European population in 2015–2017 and saved in a gene bank of the pathogen

Isolate	Matching virulence (V) / avirulence (Av)
A-1/2015	V Pop and Zeppelin
A-2/2015	V Camilla and E-388/01
K-3/2015	V Psaknon, Spilka and Venezia
M-4/2015	V Sara, Av Saturn and Laverda
O-11/2016	V SBCC097
M-8/2017	High complexity of required virulences

Six isolates were included in the gene bank of the pathogen and have been used since their acquisition. Among them there are isolates with the following characteristics: 1. New virulences to Camilla, E-388/01 and Sara; 2. Virulence to the recently discovered resistance SBCC097 (Silvar et al. 2013); 3. A new virulence to a previously unknown resistance Venezia (Dreiseitl 2018); 4. New combinations of virulences as well as high complexity of virulences to new resistances (Dreiseitl 2011b, c, 2016). It is not clear whether these pathotypes originated from mutations in the Czech Republic or are sourced from neighbouring countries.

Regarding possible migration of the rare pathotypes there are two examples. At the end of 1980, the first pathotype virulent on varieties containing the widely-adopted *Mla13* gene (Brückner 1982) was detected in the Czech Republic. In 1985, an epidemic of mildew appeared that infected these varieties in particular, and in 1986 the first pathotype virulent to *Mla13*, which came from the Czech population, was detected in England (Wolfe et al. 1992). This was quite unexpected since the prevailing wind to spread the pathogen is from west to east (Limpert 1987).

On the other hand, the variety Gunnar with identical resistance to Sara, was already registered in Denmark in 1981 (Brown and Jørgensen 1991). We used Sara as a differential variety initially in 1999 and annually since 2010. However, the first and, so far, sole virulent isolate was detected as recently as 2015, despite the prevailing westerly wind direction. Hence, for virulent pathotypes successfully to migrate over longer distances, they probably need a suitable host with a corresponding resistance grown along the migratory path.

In addition to the findings of the new virulences, changes in the frequencies of individual virulences were also detected although these were not dramatic. For example out of 32 differentials used in the 3 years, 19 differential varieties contain resistances present in the currently or previously grown varieties. Among these, two showed an increase in VF to *Mlat* (P20) of 1.4% and to *Mla6* from 98.8% up to 100.0% - only minor deviations from their stable levels. *Mla6* was widely used in spring varieties in the Czech Republic (Dreiseitl 2003) and also in other parts of Europe (Brown and Jørgensen 1991) and is now one of the most frequently occurring genes in varieties of winter barley (Dreiseitl 2017c). Despite the detection of VF 100.0% in the last monitored year, it cannot be expected that *Va6* has been fixed in the given population; the increase in the two aforementioned VFs (*Vat* and *Va6*) amounted in total 2.6%. A decrease in the sum of VFs to the resistances of the remaining 17 differentials amounted to 178.1% (1.781 virulences), namely from 1.9% to *MlLn* (Florian) up to 19.2% to *MlSt* (Annabell).

The cultivated area of varieties with specific resistances has declined because of the increasing area of cultivars with Mlo non-specific durable resistance and the diversification of specific resistances in other varieties. Hence, the directional selection of the pathogen in host varieties with specific resistance genes is weakening. This decrease in the frequency of most virulences may indicate that the pathogen pays a fitness penalty for its virulence (Brown 2015). On the other hand, the permanently high VF to *Mla10* (P09) or *Mla22* (Hovmøller et al. 2000; Dreiseitl 2015b), which have never been used in commercial varieties, are exceptions.

To compare population diversity, a simple index can be adopted. The survey in Table 6 demonstrates that the diversity of the Central European population of *B. graminis* f. sp. *hordei* is very high compared with other populations of the pathogen on the globe. This might be due to the year-round availability of host plants for inoculum production, i.e. high concentrations of winter- and spring-sown crops grown on conditions favorable for pathogen development. These factors unlock the potential for a rapid evolutionary development

Table 6 Comparisons of diversity expressed by the Simple index among biotrophic airborne pathogen populations on cereals

Host plant	Pathogen population	Area	Year(s)	Reference	Simple index
Barley	*Blumeria graminis* f. sp. *hordei*	Central Europe	2016 and 2017	this contribution	0.982
Barley	*Blumeria graminis* f. sp. *hordei*	China	2006	Zhu et al. 2010	0.113
Barley	*Blumeria graminis* f. sp. *hordei*	South Africa	2004 and 2007	Dreiseitl and Kosman 2013	0.237
Barley	*Blumeria graminis* f. sp. *hordei*	Australia	2010 and 2011	Dreiseitl et al. 2013	0.075
Barley	*Blumeria graminis* f. sp. *hordei*	Morocco	2009	Jensen et al. 2013	0.847
Wheat	*Blumeria graminis* f. sp. *tritici*	Egypt	2014	El-Shamy et al. 2016	0.324
Wheat	*Blumeria graminis* f. sp. *tritici*	Poland	2009	Czembor et al. 2014	0.896
Wheat	*Blumeria graminis* f. sp. *tritici*	U.S.A.	2005	Parks et al. 2008	0.396
Rye	*Blumeria graminis* f. sp. *secalis*	Germany	2011–2013	Miedaner et al. 2016	0.700
Oats	*Blumeria graminis* f. sp. *avena*	Poland	2012	Okoň and Ociepa 2017	0.300
Triticale	*Blumeria graminis*	Poland	2009	Czembor et al. 2014	0.068
Triticale	*Blumeria graminis*	Germany	2007–2009	Klocke et al. 2013	0.392
Wheat	*Puccinia triticina*	U.S.A.	2009	Kolmer et al. 2011	0.069
Wheat	*Puccinia triticina*	France	1999–2002	Goyeau et al. 2006	0.127
Wheat	*Puccinia triticina*	Spain	1998–2000	Martínez et al. 2005	0.625
Wheat, barley	*Puccinia striiformis* f. sp. *tritici*	U.S.A.	2008	Wan and Chen 2012	0.112
Rye	*Puccinia recondita* f. sp. *secalis*	Germany	2000–2002	Miedaner et al. 2012	0.383
Oats	*Puccinia coronata* f. sp. *avenae*	U.S.A.	2006–2009	Carson 2011	0.654

of the pathogen (McDonald and Linde 2002; Dreiseitl 2014b; Komínková et al. 2016). Furthermore, the wide spectrum of host resistances in cultivated varieties (Brown and Jørgensen 1991) is a requisite for directional selection of newly mutated or migrated virulences.

The diversity of the Czech population is also higher compared to other forms of mildew and rusts on cereals. But, unlike rusts, *B. graminis* has no intermediate host and sexual as well as asexual reproduction takes place exclusively on the host. New virulences, generated by mutations or introductions from adjacent regions are quickly combined with existing genotypes by genetic recombination. The enormous diversity of pathotypes, where nearly each isolate belonged to a different pathotype, is indicative of this phenomenon. The pathogen then has a potential rapidly to adapt to all specific resistances and reflects the diversity of host resistances within its population.

Monitoring pathogen populations in combination with resistant cultivar deployment can prolong the lifespan of individual specific resistances and lead to a reduction in pesticide applications (Walters et al. 2012). Breeding of new varieties should focus on attaining durable resistance, for example by the *mlo* gene which widely occurs in many European spring varieties (Dreiseitl 2017c). For winter barley varieties that are mostly susceptible, an option is pyramiding genes with minor effect (quantitative resistance) (Niks et al. 2015) and has proved effective in breeding resistance to *B. graminis* f. sp. *tritici* in intensively-grown winter wheat in the United Kingdom (Brown 2015).

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

Human and animals rights Research do not involve human participants nor animals.

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