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Changes in Virulence Frequencies and Higher Fitness of Simple Pathotypes in the Czech Population of *Blumeria graminis* f.sp. *hordei*

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Abstract

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The employment of specific genes, which determine host resistance to avirulent pathotypes of the pathogen, is not recommended for protecting barley against powdery mildew (*Blumeria graminis* f.sp. *hordei*). However, most barley varieties still possess specific resistance genes to this pathogen. The effectiveness of such resistances was determined by assessing virulence frequency using randomly collected Czech population samples of 521 pathogen isolates from the air tested on 29 barley differential varieties over a four-year period. Most virulence frequencies did not show major changes, but the frequencies on the winter cv. Laverda and the spring cv. Kangoo greatly increased. The highest virulence frequency in all four years was on the resistance *Ru2* in Kompolti 4. The period of sampling the air population and associated changes in the proportion of spores that developed on spring and winter varieties with different resistances are one of causes of the changes in virulence frequencies. It was also found out that the virulence complexity of pathotypes with the frequency > 1 was markedly lower than the complexity of pathotypes with the frequency of 1. This could indicate the higher fitness of pathotypes with fewer virulences.

Keywords: barley powdery mildew; *Hordeum vulgare*; population diversity; specific resistances; unnecessary virulences

The area of barley (*Hordeum vulgare* L.) in the Czech Republic has gradually reduced and it is now about half of its peak in 1978–1982. In 2011–2013 the mean annual area of spring barley was 266 000 ha and of winter barley 102 000 ha. Nevertheless, it is still one of the major cereal crops and powdery mildew, induced by the biotrophic airborne fungus *Blumeria graminis* f.sp. *hordei*, is the commonest disease on non-resistant winter and spring barley (Dreiseitl 2011a). The most effective way of protecting crops against major pathogens is genetic resistance. Powdery mildew fungus is one of the most adaptable plant pathogens (McDonald & Linde 2002) and the adoption of non-durable specific genes that determine resistance only to avirulent pathotypes is not recommended (Brown *et al*. 1997).

In June 2014 there were 125 registered barley varieties in the Czech Republic. Out of 70 spring varieties, 45 contained the non-specific resistance *Mlo*. One of the 55 winter varieties did not contain any selected resistance. Thus, 79 out of all currently registered barley varieties contained one or more specific resistances.

The effectiveness of varietal resistance can be studied by evaluating field infections or assessing virulence frequency, but preferably using both methods. A large differential set is used in the Czech Republic to determine the virulence frequency. Its first part is used for the long-term monitoring of virulences to first resistance genes employed in commercial varieties. The second part of the set is used primarily to identify virulence frequencies to resistance genes possessed by currently grown varieties and advanced breeding lines, and the third part of the set is used to check for rare virulences.

This paper presents virulences to resistances possessed by genotypes in the second part of the dif-

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ferential set detected in the Czech Republic during the last four years.

MATERIAL AND METHODS

Collection of isolates. Random population samples of pathogen spores 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. Spores were sampled by driving across the Czech Republic during late May to early June in four years (2011–2014), when tillering of spring barley had usually been 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 & Platz 2012) were placed in 120 mm glass Petri dishes on water agar (0.8%) modified with benzimidazole (40 mg/l) (BWA) – a leaf senescence inhibitor – and inserted in the bottom of the spore sampler. Collected spores settled on leaves while travelling and dishes with detached leaves were replaced for each of the 14 sections of the sampling route, which was about 1000 km in total (Table 1). 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. To multiply inoculum, dishes with leaves and collected spores were incubated for 11–13 days at 19.0 ± 1°C under 12 h artificial light at 30 ± 5 µmol/m^2/s. Conidia from each single-spore colony were sucked into a replaceable tip of a varipipette AW 1000 and then blown off the tip into a micro-settling tower using a 10 ml syringe. Further details of the method used are described in Dreiseitl (2008). By these means dishes with leaf segments of the first part of the differential set were inoculated. After evaluation (results not shown here) the conidia of isolates were used for inoculation of the second part of the differential set and results presented herein.

Table 1. Sampling routes for collecting *Blumeria graminis* f.sp. *hordei* isolates from the air across the Czech Republic

Designation	Sampling route section	Distance (km)
A	Brno–Kroměříž	65
B	Brno–Znojmo	60
C	Brno–Břeclav	50
X	Brno – motorway 1 (90th km)	95
D	Přáslavice–Vyškov	60
E	Přáslavice–Ostrava	65
F	Olomouc–Šumperk	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
Y	Praha–Circle	70

Differentials. A set of 29 barley differential varieties comprising genotypes whose resistance differentiated the pathogen population were selected (Table 2). Of these, 16 varieties were registered in the Czech Republic and five in other countries; six advanced breeding stocks and two standard lines (Kølster *et al*. 1986) were also included. Eleven genotypes were winter and 14 contained unknown resistance(s). In 2014 one of the differentials (Jazz) failed due to a lack of seed.

Production of plant material. About 25 untreated seeds of each susceptible or differential variety were sown in a pot (80 mm diameter) containing a peat-based potting mix. Seedlings were kept in a mildew-proof greenhouse under natural daylight. Leaf segments (20 mm long) of differential varieties were cut from the central part of healthy fully-expanded primary leaves when second leaves were emerging. Three leaf segments of each differential were placed adjacently in a 150 mm glass Petri dish containing BWA with the adaxial surface upward.

Inoculation. Inoculation of the differential set used here was done in a circular metal settling tower of 150 mm diameter and 415 mm in height. For each isolate, a Petri dish with leaf segments from the differential varieties was placed at the bottom of the tower. Conidia of each isolate from a leaf segment 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 conidia of an isolate were blown through a side hole of 13 mm diameter in the upper part of the settling tower over the Petri dish. The inoculum density was about 5–8 conidia per mm^2. The dishes with inoculated leaf segments were kept under described incubation conditions.

Virulence determination and population parameters. Reaction type (RT) according to the response of each differential to a corresponding isolate was

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scored eight days after inoculation on a 0 to 4 scale (Torp *et al.* 1978) where RT 4 or 3–4 were considered virulent to the corresponding resistance gene(s). Descriptive parameters of populations were calculated with the HaGiS program (Hermann *et al.* 1999).

RESULTS

Twenty-three out of the 29 differential cvs were used in all four years (Table 2). Most virulence frequencies did not show large changes during the period, especially those to the resistances of cvs Spilka, Florian, Dubai, Kompolti 4, and P12. Virulence frequencies to the resistances of the other varieties fluctuated more widely, for example, Hulda (2.5–15.3%) or CH-666 (21.5–57.5%). A substantial change was found in the virulence frequency to the resistance of cv. Gilberta – 46.0% in the first year, but only 11.7–23.4% in the following three years. The virulence frequencies to the resistance of cvs Pribina and Annabell declined slightly; conversely, on the winter cvs Venezia and SJ053088 an increase was followed by a decrease in the final year. The virulence frequency to the resist-

Table 2. Virulence frequency of 521 isolates of the Czech population of *Blumeria graminis* f.sp. *hordei* to the resistance of 29 differential varieties from 2011 to 2014

Differential variety	Registration		Growth habit	Resistance	Virulence frequency			
	from	to			2011	2012	2013	2014
Venezia			W	WI-1	0.7 ± 0.7	2.1 ± 1.2	4.7 ± 1.7	2.5 ± 1.3
Spilka	2007	2010	S	Ar U	2.0 ± 1.1	4.2 ± 1.6	1.9 ± 1.1	0.0 ± 0.0
Hulda			S	IM9 Ly Kw Hu4	4.0 ± 1.6	15.3 ± 2.9	8.4 ± 2.3	2.5 ± 1.3
Florian	2008	2013	W	Ln	4.7 ± 1.7	3.4 ± 1.5	2.8 ± 1.3	4.2 ± 1.6
Dubai			W	U	6.7 ± 2.0	4.2 ± 1.6	1.9 ± 1.1	3.3 ± 1.5
Burštyn 2			S	We U	7.3 ± 2.1	12.5 ± 2.7	6.5 ± 2.0	3.3 ± 1.5
KM-2161			S	Ar We U	7.3 ± 2.1	20.1 ± 3.3	8.4 ± 2.3	8.3 ± 2.3
Jazz	2011		S	Ru U	9.3 ± 2.4	19.4 ± 3.2	12.1 ± 2.7	
Vendela	2013		S	Ar U	14.7 ± 2.9	30.6 ± 3.8	20.6 ± 3.3	10.8 ± 2.5
Oowajao			W	Ra U	18.0 ± 3.1	13.9 ± 2.8	10.3 ± 2.5	12.5 ± 2.7
Prosa	1998	2008	S	We U	20.7 ± 3.3	31.3 ± 3.8	29.0 ± 3.7	15.0 ± 2.9
Kangoo	2008		S	Ro	21.3 ± 3.3	17.4 ± 3.1	34.6 ± 3.9	71.7 ± 3.7
Laverda	2007		W	Lv	23.3 ± 3.5	16.0 ± 3.0	50.5 ± 4.1	25.8 ± 3.6
Duet	1999	2009	W	Sp We Ha Dt	26.0 ± 3.6	41.7 ± 4.0	43.0 ± 4.0	30.8 ± 3.8
HE-1051			S	Ru U	32.7 ± 3.8	25.7 ± 3.6	43.0 ± 4.0	38.3 ± 4.0
Signal	1996		S	N81	34.7 ± 3.9	25.0 ± 3.5	28.0 ± 3.7	35.0 ± 3.9
Alinghi	2007		W	IM9	37.3 ± 3.9	20.8 ± 3.3	39.3 ± 4.0	10.8 ± 2.5
CH-666			W	La	41.3 ± 4.0	27.1 ± 3.6	21.5 ± 3.4	57.5 ± 4.0
KM-1998			S	U	42.0 ± 4.0	47.2 ± 4.1	25.2 ± 3.5	18.3 ± 3.2
Gilberta	2006		W	Ra U	46.0 ± 4.1	15.3 ± 2.9	23.4 ± 3.5	11.7 ± 2.6
Pribina	2005	2014	S	Ru Hu4	54.7 ± 4.1	48.6 ± 4.1	44.9 ± 4.1	40.0 ± 4.0
Annabell	2001	2011	S	St	74.7 ± 3.5	75.7 ± 3.5	59.8 ± 4.0	67.5 ± 3.8
Diabas	1977	1982	S	Ly	91.3 ± 2.3	75.7 ± 3.5	88.8 ± 2.6	88.3 ± 2.6
Kompolti 4	1988	1996	W	Ru2	98.0 ± 1.1	91.0 ± 2.3	90.7 ± 2.4	91.7 ± 2.3
Zeppelin	2012		S	U		4.9 ± 1.8	4.7 ± 1.7	0.0 ± 0.0
SJ053088			W	U		8.3 ± 2.3	15.9 ± 3.0	5.0 ± 1.8
P12			S	*Mla22*		44.4 ± 4.1	51.4 ± 4.1	46.7 ± 4.1
RP13029			S	U				3.3 ± 1.5
P09			S	*Mla10*				55.0 ± 4.1

W – winter barley, S – spring barley; U – unknown

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Table 3. Parameters of *Blumeria graminis* f.sp. *hordei* populations in the Czech Republic from 2011 to 2014

Population parameter	2011	2012	2013	2014	All
No. of differentials	24	27	27	26	29
No. of isolates	150	144	107	120	521
No. of isolates of pathotypes with frequency > 1	18	8	2	19	47
No. of pathotypes	140	139	106	110	495
No. of pathotypes with frequency > 1	8	3	1	9	21
Frequency of the most abundant pathotype	4	4	2	3	4
Minimal complexity of isolates	2	2	2	4	4
Maximal complexity of isolates	17	16	14	12	17
Mean of isolate complexity	7.19	7.36	7.67	7.58	7.42
Mean of pathotype complexity	7.36	7.47	7.67	7.74	7.54
Mean of isolate complexity of pathotypes with frequency = 1	7.52	7.53	7.67	7.90	7.64
Mean of isolate complexity of pathotypes with frequency > 1	4.78	4.50	8.00	5.84	5.30
Simple coefficient	0.93	0.97	0.99	0.92	0.95
Richness – Gleason	27.74	27.77	22.47	22.77	
Diversity – Shannon	4.91	4.91	4.66	4.67	

ance of the winter cv. Laverda increased from 23.3% to 50.5% in 2013 with a decline to 25.8% in 2014. The virulence frequency on the spring cv. Kangoo increased from 21.3% in 2011 to 34.6% in 2013 and 71.7% in 2014. The highest virulence frequency during all four years was recorded on *Ru2* carried by cv. Kompolti 4.

In 2011–2014, 521 isolates on 29 differential varieties, and more specifically, 107–150 isolates and 24–28 differentials were studied in individual years (Table 3). The characteristics of the population demonstrate its high diversity throughout. A difference between the lower mean of isolate complexity and higher mean of pathotype complexity was recorded. This difference is better seen when comparing the means of isolate complexity of pathotypes with the frequency of 1 with those with the frequency > 1, when the latter was on average by 30.6% lower than the former.

DISCUSSION

Results from 19 out of the 29 differentials used in this study have been reported previously (Dreiseitl 2011b), including cv. Kompolti 4 carrying the resistance *Ru2*. During the last three decades, the latter resistance gene was the most widely used in winter barley. Therefore, a high virulence frequency to this resistance was expected and confirms previous results. In contrast, a considerable change was recorded in the virulence frequency to the resistance of cv. Gilberta. It was stable in 2009–2011 (41.0–48.6%) (Dreiseitl 2011b) and 2012–2014 (11.7–23.4%) despite an inexplicable change between the two time periods.

Standard lines P09 and P12 (Kølster *et al*. 1986) were the most useful differentials because the virulence frequency to their resistances of around 50% is the maximum differentiating ability of an individual differential. Hence, in terms of population differentiation, it was essential to include both these standards in the differential set. These resistance genes have, however, never been incorporated into any commercial barley cultivar and their virulences are unnecessary. In general, these high frequencies of unnecessary virulences can be explained by an effect of genetic drift or hitch-hiking through virulence association, but the specific situations that have led to this are unknown.

The pathogen populations over the four years were very diversified with 495 pathotypes (= isolates with identical association of studied virulences) among 521 isolates, and the number of pathotypes with the frequency > 1 was not high (21). These 21 pathotypes were represented by only 47 isolates and their virulence complexity was markedly lower than the complexity of pathotypes with the frequency of 1. It could indicate a higher fitness of pathotypes with fewer virulences. This was indeed the case in three out of the four years examined. An exception was in 2013 when only one pathotype with a frequency

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of > 1 was detected in only two isolates, from which no conclusions can be drawn.

Two methods are used to sample populations of airborne pathogens: the first, a classical and more commonly used method based on direct sampling from plants, and the second method based on collecting spores from the air (Benada 1962; Eyal *et al*. 1973; Schwarzbach 1979). Both methods have their advocates. One advantage of the second method is its random sampling and the relative ease of obtaining many isolates. Under constant conditions (not frequently encountered) the number of collected spores also reflects the incidence of the pathogen in that region. A disadvantage is the unknown origin of isolates because the actual source (e.g. variety and growth stage) cannot be determined. Therefore, the aim is to sample at certain growth stages of barley when at least a balanced ratio of spores produced on spring and winter varieties can be expected in the air. However, current climatic conditions sometimes prevent this ideal from being achieved.

The biggest change recorded in this study was the increased virulence frequency to the resistances of cvs Laverda and Kangoo, which were introduced into the Czech Republic in 2008. Both these formerly unknown resistances were identified (Dreiseitl 2011b) and newly designated (Dreiseitl 2011c,d). Laverda is a winter barley cultivar and no virulence to its resistance (*Lv*) (Dreiseitl 2011d) was found among 160 isolates in 2008 (Dreiseitl 2008). However, once cv. Laverda and other cultivars with the new resistance *Lv* began to be grown, the frequency of corresponding virulence increased by directional selection and in the four years after detecting the first virulent pathotype it was present in more than half the isolates. In the final year, however, the frequency of virulence *Lv* declined.

Cv. Kangoo was included in the differential set in the same year as cv. Laverda (Dreiseitl 2008), but no data on its response to the pathogen was published because it was the only spring cultivar in the differential set cv. Kangoo also contains a novel resistance, designated *Ro* (Dreiseitl 2011c). The first isolates virulent to *Ro* were detected in 2008 (Dreiseitl unpublished), before that time the corresponding virulence was probably absent or only rarely present. The frequency of the virulence to *Ro* increased quickly after its widespread use in new cultivars, so by 2013 it was present in almost 35% of isolates and in the final year, in contrast to the virulence *Lv*, increased to nearly 72%.

In 2014, the growth of spring and winter barley was more rapid than usually after a mild winter and an early sowing of spring cereals. Because of weather conditions, however, sampling the population was postponed by almost two weeks and completed on June 5th. On that date, the vegetation of spring barley had reached its peak, while the vegetation of winter barley had already been senescing and spore production low. It is possible, therefore, that a decrease in the frequency of the virulence *Lv* to the resistances of the winter cvs Laverda, Alinghi, Venezia, and SJ053088 is caused by a small proportion of spores arising from winter barley in the pathogen sample. Conversely, a great increase in the virulence frequency to *Ro* in the spring cultivar Kangoo might have resulted from a preponderance of spores originating from spring barley. This might explain too, the increased virulence on CH-666, a winter cultivar but containing one of the most widespread resistances of spring barley rarely found in other winter barley cultivars. The delay in sampling the air population and the associated change in the proportion of spores that developed on spring and winter cultivars possessing various resistances can be one of causes of changes in the determined virulence frequency.

Spring barley cultivars with the resistance *Ro* and varieties of winter barley with *Lv* are now commonly grown in the Czech Republic and in some neighbouring countries, especially Germany, where varieties with both these resistances were developed. The widespread use of these resistances was reflected in the structure of the pathogen population. This situation can be compared with the use of *Ru* in Czech varieties when only 4–7 years had elapsed from the detection of the first pathotype virulent to *Ru* until epidemics broke out on barley cultivars with this resistance in the Czech Republic and Europe (Brückner 1982; Wolfe *et al*. 1992). Experience with the resistance *Ru* and examples of the rapid increase in the frequency of virulences that overcame *Ro* and *Lv* demonstrate the short-term effectiveness of using single specific resistances in widely grown monoculture crops.

The population of powdery mildew is very variable (Wolfe & Schwarzbach 1975) and is conditioned by the effect of evolutionary forces (McDonald & Linde 2002; Flégr 2005) in which directional selection plays a significant role. Wild barley (*H. spontaneum*), which occurs naturally in the centre of diversity of this host, is a rich source of resistance (Dreiseitl & Dinoor 2004) on which a natural centre of the pathogen diver-

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sity has developed (Dreiseitl *et al*. 2006). The centre of pathogen diversity on cultivated barley is Europe (Limpert 1987; Wolfe *et al*. 1992; Hovmøller *et al*. 2000) and is encouraged by many specific resistance genes used (Brown & Jørgensen 1991; Dreiseitl & Križanová 2012; Dreiseitl 2013a,b). The peak of variability was attained in Central Europe due to immigration of wind-borne spores (Dreiseitl 2014a). This variability is still increasing because of the adoption of other specific resistances (Dreiseitl 2011c,d, 2014b). Therefore, the study of the Czech population, which is an integral part of the Central European and European population, is important not only to assess the effectiveness of resistance but also to track the evolution of the global pathogen population.

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