Adaptation of *Blumeria graminis* f.sp. *hordei* to barley resistance genes in the Czech Republic in 1971–2000

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ABSTRACT

Results of scoring the resistance of 35 selected spring barley varieties to powdery mildew, exhibiting high powdery mildew severity, in 307 variety trials of the Central Institute for Supervising and Testing in Agriculture were analysed. The varieties can be divided into two groups: the varieties that could not induce any changes in the pathogen population (the varieties with no effective resistance gene and varieties carrying gene *mlo*) and the varieties possessing major resistance genes [a total of 12 *Ml*-genes: *a1, a3, a6, a7, a9, a12, a13, at, k1, La, g* and *(Kr)*] to which the pathogen population adapted in 1971–2000. The time slope of decreasing resistance of varieties is described. The importance of individual evolutionary forces (mutations, migration, direct selection, indirect selection and recombinations) for the erosion of efficiency of respective major resistance genes and the effects of pathogen adaptation on population complexity and diversity are discussed.

Keywords: *Hordeum vulgare*; *Blumeria graminis* f.sp. *hordei*; spring barley; powdery mildew; genetic resistance; adaptation; evolutionary forces

Barley (*Hordeum vulgare* L.), both spring and winter form, is the second widely grown crop in the Czech Republic and powdery mildew is its commonest disease (Dreiseitl and Jurečka 1996, 1997). On average 33% of the spring barley area planted with non-resistant varieties are heavily infected by powdery mildew (Dreiseitl and Jurečka 2003). Growing resistant varieties is the most rational way of controlling this disease on barley. Basic demands made on genetic resistance are efficiency and sufficient durability at least for the natural lifetime of the variety.

Durability of disease resistance is affected by the evolutionary potential of pathogen population. Powdery mildew on barley is caused by the pathogenic fungus *Blumeria* (syn. *Erysiphe*) *graminis* f.sp. *hordei* (= *Bgh*). This pathogen possesses a mixed reproduction system, with at least one sexual cycle per growing season followed by asexual reproduction during the epidemic phase, and a high potential for gene flow. With regard to sufficiently durable resistance, *Bgh* ranks among evolutionarily highly risky pathogens (McDonald and Linde 2002).

The effect of individual adaptation mechanisms on the breakdown of barley resistance controlled by selected genes was examined in part recently (Dreiseitl 2000a, b, 2001b, 2003). The objective of this paper is to elucidate the erosion of barley variety resistance due to the pathogen adaptation conditioned by effects of individual evolutionary forces in a more comprehensive way.

MATERIAL AND METHODS

Results of scoring the powdery mildew resistance of spring barley varieties in variety trials conducted by the Central Institute for Supervising and Testing were analysed.

Years. Results of variety trials for 30 years (1971–2000) were used: registration trials lasted for 18 years (1971–1988) and trials of registered varieties for 12 years (1989–2000).

Locations. The trials were conducted at 37 locations across the Czech Republic (for details see Dreiseitl and Jurečka 2003).

Trials. Nine hundred twenty-three field trials were conducted (year × location × variant), but only results of the trials with high powdery mildew severity were used in this study (307 trials). Basic data on these trials are given in Table 1, for further details see Dreiseitl and Jurečka (2003).

Varieties. A total of 144 spring barley varieties (the term variety is used for both registered varieties and candidates for registration) were included in the trials. Data on the resistance of 35 selected and another 9 additional varieties were used (Table 2). The most resistant and the most susceptible varieties in each year are listed in Table 3. Commercial names are given to registered varieties also in the years of their registration testing (for further details see Dreiseitl and Pařízek 2003).

Major genes of resistance. The following results obtained at identification of major genes of resistance to powdery mildew in spring barley varieties were used: Brown and Jørgensen (1991), Dreiseitl (1997), Dreiseitl and Jørgensen (2000), Dreiseitl (unpublished).

Scoring scale. A common 1–9 scale for scoring the resistance of barley to powdery mildew in the field was used; 1 = the variety is very susceptible (extreme infection of entire plants by powdery mildew), 9 = the variety is fully resistant (plants are free of visible symptoms of powdery mildew infection).

The article was elaborated within project 522/00/1062 supported by the Grant Agency of the Czech Republic.

Scoring procedure. In 1971–1988, the resistance of each variety was characterised by one value. In 1989–2000, the resistance of varieties was scored in 2 to 4 replications whose means are used.

RESULTS

Results of scoring the powdery mildew resistance of spring barley varieties tested in variety trials of the Central Institute for Supervising and Testing in Agriculture were analysed. From a total number of 144 varieties included in these trials from 1971 to 2000, 35 varieties were selected. To characterise their genetic resistance, only results of scoring the resistance of these varieties in the trials with high powdery mildew severity (307 out of the total number of 923 trials) were selected. The results comprise 2 884 data on the resistance of varieties to this disease (Table 1).

Varieties with no effective major resistance gene. This group comprises the varieties Dvoran, Diamant, Hana and Tolar. All of them constantly exhibited low resistance. Diamant and Hana were the most susceptible varieties in the period of 1971–1976, except 1972 (Table 2).

Mlg. Gene *Mlg* alone is present in Favorit only within the examined varieties. It ranked among the varieties exhibiting low resistance in 1971–1983. In 1977, Favorit (together with Rapid – see below) became the most susceptible variety (Table 3). The resistance of Favorit remained markedly below average in the following six years. In 1972, however, II/61-FUDII possessing gene *Mlg* became the most susceptible variety earlier than Favorit. *Mlg* as a gene that is present together with other genes given below in the varieties Elgina, Rapid, Koral,

Table 1. Data on variety trials with spring barley (Central Institute for Supervising and Testing in Agriculture)

Year	A	B	C	D	E	F	G	%
1971	23	17 (6)*	529	10	230	6	60	26
1972	32	15 (8)*	736	19	437	6	114	36
1973	28	9 (8)*	476	14	238	6	84	35
1974	36	10	360	14	140	8	112	80
1975	42	14	588	21	294	10	210	71
1976	39	12	468	5	60	9	45	75
1977	32	15	480	3	45	9	27	60
1978	34	16	544	6	96	11	66	69
1979	35	18	630	8	144	11	88	61
1980	34	18	612	8	144	12	96	67
1981	35	17	595	17	289	10	170	59
1982	34	15	510	3	45	10	30	67
1983	35	17	595	13	221	12	156	71
1984	35	18	630	5	90	10	50	56
1985	35	18	630	8	144	11	88	61
1986	32	19	608	8	152	10	80	53
1987	34	17	578	16	272	7	112	41
1988	28	21	588	21	441	8	168	38
1989	31	14	434	10	140	11	110	79
1990	26	16	416	3	48	12	36	75
1991	24	15	360	5	75	12	60	80
1992	21	14	294	3	42	11	33	79
1993	24	11	264	10	110	9	90	82
1994	27	18	486	10	180	12	120	67
1995	32	21	672	18	378	14	252	67
1996	31	24	744	9	216	13	117	54
1997	31	21	651	15	315	9	135	43
1998	32	19	608	10	190	8	80	42
1999	25	21	525	10	210	7	70	33
2000	16	35	560	5	175	5	25	14
	923	(127)	16 171	307	5 561	(35)	2 884	51.9

A – total number of trials, B – number of varieties included in the trials, C – total number of data (A × B),
D – number of trials with high powdery mildew severity, E – number of data obtained in trials with high disease severity (B × D),
F – number of varieties included in this study, G – number of data used in this study, % – G/E.100
* number of varieties that were included in two types of trials

Table 2. Varieties of spring barley, their resistance genes and powdery mildew resistance in field trials of the Central Institute for Supervising and Testing in Agriculture with high powdery mildew severity

Variety	*Ml*-genes	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Dvoran	*a8*[1, 4]	5.20	4.68	5.18	4.57																										
Elgina	*a7*, *g*[2]	**8.90**	**8.58**	8.43	7.14																										
Diamant	*a8*[1, 4]	**3.90**	3.87	**4.07**	**3.50**	**3.52**																									
Hana	*a8*[1, 4]	4.85	3.84	4.89	4.21	4.19	**4.80**																								
Ametyst	*a6*, *a14*[1, 4]	7.20	6.42	6.86	4.93	5.38	5.20	4.33																							
Favorit	*g*[1]	5.00	4.66	4.14	4.93	5.19	6.20	**3.67**	4.83	4.78	5.38	4.65	5.33	4.31																	
Atlas	*a7*, *k1*[1]				5.79	5.67	5.80	5.00	4.83																						
Rapid	*a6*, *a14*, *g*[1]				4.93	5.67	6.00	**3.67**	5.33	4.33	5.13																				
Trumpf	*a7*, *(Ab)*, *(aTr3)*[2]					**8.86**	8.40	7.67	7.17	5.44																					
Diabas	*a7*[1]					5.29	5.80	4.33	**4.33**	3.67	**4.25**																				
Spartan	*a9*, *k1*[1]					8.38	8.60	8.00	8.17	7.11	7.75	4.53	5.67	**3.38**																	
Koral	*a13*, *g*[1]					7.81	**8.80**	**9.00**	**9.00**	8.33	8.50	**8.71**	**9.00**	8.54	8.80	7.13	5.50														
Opal	*a6*, *a14*, *La*[1, 4]							7.33	6.83	6.22	7.13	6.24	8.00	4.85	3.60	4.38															
ST-6984	*a6*, *a14*, *at*[3, 4]								7.50	6.89	8.13	7.76																			
Zefir	*a12*, *g*[1]								7.00	5.56	6.00	**3.24**	**5.00**	3.92	**2.80**	**3.00**	**2.50**														
Krystal	*a13*, *g*[1]								8.17	7.89	**8.63**	8.59	9.00	8.15	**9.00**	7.38	5.50	6.00	4.81	**3.95**	**3.67**	4.54									
Rubin	*a1*[1]									6.22	7.38	7.76	9.00	6.62	5.60	6.63	5.25	6.00	5.38	5.79	5.70	6.16	5.93	4.37	4.56	4.05	**4.51**				
Kredit	*(Kr)*[1]										8.25	8.00	8.67	7.69																	
Mars	*a3*, *g*[1]										7.25	6.59	8.33	6.38	5.60	5.13	5.00	5.56	6.05												
Zenit	*a13*[1]												8.67	**8.62**	8.80	6.38	5.50	5.25	4.67												
Jaspis	*a6*, *a14*, *at*, *La*[1]													6.00	7.20	4.88	4.25	4.94	5.48	5.21	6.10	4.72	5.27	–	5.01	4.44					
Orbit	*a6*, *a14*, *at*, *La*[1]													5.54	4.40	7.25	4.63	5.19	5.62	4.72	5.33	4.76	4.93	**4.07**	4.59	4.39	4.77				
Jarek	*(Kr)*, *La*[1]														8.80	7.25	6.50	–	–	5.57	4.70	–	–	–	6.23	5.71	5.47				
Novum	*a13*, *g*[1]															**8.25**	6.25	5.88	5.29	4.37	4.03	**3.36**	**4.87**	4.81	5.33	5.58	5.91	4.97	5.45	5.00	
Terno	*a9*, *La*[1]																		5.05	5.41	6.87	5.26	4.93	–	5.64	4.82	5.42				
Svit	*a13*, *at*[1]																			6.12	6.43	6.36	7.83	5.95	5.66	5.14					
Ladik	*a12*[1]																			6.16	6.27	5.70	6.27	5.49	5.77	5.56	5.57				
Sladko	*a7*, *La*[1]																			**6.40**	6.93	5.86	7.43	5.81	5.53	5.13	5.06	5.07			
Akcent	*a7*, *La*[1]																			5.99	6.67	6.32	6.93	6.50	6.93	6.18	6.34	5.73	5.87	4.83	4.40
Forum	*mlo*, *a8*[1, 4]																				**7.10**	**7.50**	**8.67**	**8.28**	**7.78**	**8.43**	**8.98**	**8.69**	**8.23**	**8.94**	8.94
Pax	*a13*, *La*[1]																					6.06	5.43	4.34	4.95	5.06	5.39	**4.02**	**3.86**	**3.74**	
Lumar	*a1*, *k1*, *g*[1]																									**3.79**	4.57	4.24	4.18		
Kompakt	*a13*, *La*[1]																									5.07	5.69	5.30	4.20	4.32	**4.14**
Pejas	*a13*, *at*[1]																										5.69	5.62	5.15	5.28	5.22
Tolar	*a8*[1, 4]																											5.34	5.23	4.93	4.80
Resistant[I]	–	**8.90**	**8.58**	[b]**9.00**	[b]**8.79**	**8.86**	**8.80**	**9.00**	**9.00**	[c]**8.89**	**8.63**	**8.71**	**9.00**	**8.62**	**9.00**	**8.25**	[e]**8.25**	[e]**6.69**	[g]**6.86**	**6.40**	**7.10**	**7.50**	**8.67**	**8.28**	**7.78**	**8.43**	**8.98**	**8.69**	**8.23**	**8.94**	[i]**9.00**
Susceptible[II]	–	**3.90**	[a]**3.06**	**4.07**	**3.50**	**3.52**	**4.80**	**3.67**	**4.33**	[d]**3.44**	**4.25**	**3.24**	**5.00**	**3.38**	**2.80**	**3.00**	**2.50**	[f]**3.31**	[f]**2.48**	**3.95**	**3.67**	**3.36**	**4.87**	**4.07**	[h]**4.33**	**3.79**	**4.51**	**4.02**	**3.86**	**3.74**	**4.14**
Mean[III]	–	5.49	4.93	5.78	5.44	5.76	6.62	5.71	6.61	6.29	7.21	6.71	8.11	6.58	7.16	6.13	5.24	5.32	5.09	5.38	5.79	5.57	6.02	5.37	5.53	5.20	5.96	5.91	6.30	6.57	6.82

[1]Dreiseitl and Jørgensen 2000, [2]Brown and Jørgensen 1991, [3]Dreiseitl 1997, [4]Dreiseitl unpublished

– testing the variety was interrupted, [I]most resistant variety, [II]most susceptible variety, [III]mean of all varieties included in the trials in the respective year

[a]II/61-FUDII (*Mlg*[4]), [b]KM-1192 [*(Kr*[1]*)*], [c]Karat (*Mla13*[1]), [d]BR-638 (not identified), [e]CE-396 (*mlo*[3]), [f]HE-3527 (*Mla7*[3]), [g]BR-3011 (*Mla3*[3]), [h]Malvaz [*(Kr*[1]*)*], [i]Nordus (*mlo*[a])

Zefir, Krystal, Mars, Novum and Lumar had a negligible effect on the resistance of these varieties in the field, and therefore its presence will not be mentioned any more.

Mla6. The variety Ametyst exhibited above-average resistance in 1971–1973. A considerable decrease in resistance of both varieties possessing gene *Mla6* (also Rapid) was found in 1974, and Rapid (together with Favorit) became the most susceptible variety in 1977.

Mla7. Elgina (Germany) was the most resistant among all the examined varieties in 1971 and 1972. A decrease in its resistance was recorded in 1974. In 1975, another German variety Trumpf (possessing other two resistance genes in addition to gene *Mla7*) exhibited the highest resistance that did not decrease significantly until 1979. The variety Atlas carries genes *Mla7* and *Mlk1*. Despite of this, Atlas was much less resistant in 1974 than Elgina and its resistance decreased in the following years, similarly like in Diabas. Diabas was the most susceptible variety in 1978 and 1980. HE-3527 (*Mla7*) was included in the trials in 1987 and 1988 and became the most susceptible variety for all of the 30 years.

Mla9. Spartan ranked among the most resistant varieties in the period of 1975–1978. An extremely rapid decrease in its resistance was found in 1981, and it became the most susceptible variety in 1983.

Mla12. Zefir exhibited moderate resistance in 1978–1980. Its resistance rapidly decreased in the same year as in Spartan (1981), so Zefir became the most susceptible variety in 1981–1986 (except for 1983 when Spartan was the most susceptible).

Mla13. Koral was included in the trials in 1975. In the following 10 years (1976–1985), the varieties possessing gene *Mla13* were the most resistant (Koral, Karat, Krystal, Zenit, Perun and Novum). The resistance of Koral, Krystal and Zenit considerably decreased in 1985 and this trend continued in 1986 (Koral, Krystal and Novum)

Table 3. A survey of the most resistant and most susceptible spring barley varieties to powdery mildew in the trials of the Central Institute for Supervising and Testing in Agriculture

Year	Most resistant variety		Most susceptible variety	
	name	resistance genes	name	resistance genes
1971	Elgina	*Mla7*, *Mlg*[1]	Diamant	*Mla8*[2,4]
1972	Elgina	*Mla7*, *Mlg*	II/61-FUDII	*Mlg*[4]
1973	KM-1192	*Ml(Kr)*[2]	Diamant	*Mla8*[2,4]
1974	KM-1192	*Ml(Kr)*	Diamant	*Mla8*
1975	Trumpf	*Mla7*, *Ml(Ab)*, *MlaTr3*[1]	Diamant	*Mla8*
1976	Koral	*Mla13*, *Mlg*[2]	Hana	*Mla8*[2,4]
1977	Koral	*Mla13*, *Mlg*	Rapid, Favorit	*Mla6*, *Mlg*[2]; *Mlg*[2]
1978	Koral	*Mla13*, *Mlg*	Diabas	*Mla7*[2]
1979	Karat	*Mla13*[2]	BR-638	not found
1980	Krystal	*Mla13*, *Mlg*[2]	Diabas	*Mla7*[2]
1981	Koral	*Mla13*, *Mlg*[2]	Zefir	*Mla12*, *Mlg*[2]
1982	Koral, Krystal	*Mla13*, *Mlg*[2]	Zefir	*Mla12*, *Mlg*
1983	Zenit	*Mla13*[2]	Spartan	*Mla9*, *Mlk1*[2]
1984	Krystal, Perun	*Mla13*, *Mlg*[2]; *Mla13*[2]	Zefir	*Mla12*, *Mlg*[2]
1985	Novum	*Mla13*, *Mlg*[2]	Zefir	*Mla12*, *Mlg*
1986	CE-396	*mlo*[3]	Zefir	*Mla12*, *Mlg*
1987	CE-396	*mlo*	HE-3527	*Mla7*[3]
1988	BR-3011	*Mla3*[3]	HE-3527	*Mla7*
1989	Sladko	*Mla7*, *MlLa*[2]	Krystal	*Mla13*, *Mlg*[2]
1990	Forum	*mlo*, *Mla8*[2,4]	Krystal	*Mla13*, *Mlg*
1991	Forum	*mlo*, *Mla8*	Novum	*Mla13*, *Mlg*[2]
1992	Forum	*mlo*, *Mla8*	Novum	*Mla13*, *Mlg*
1993	Forum	*mlo*, *Mla8*	Orbit	*Mla6*, *MlLa*, *Mlat*[2]
1994	Forum	*mlo*, *Mla8*	Malvaz	*Ml(Kr)*[2]
1995	Forum	*mlo*, *Mla8*	Lumar	*Mla1*, *Mlk1*, *Mlg*[2]
1996	Forum	*mlo*, *Mla8*	Rubin	*Mla1*[2]
1997	Forum	*mlo*, *Mla8*	Pax	*Mla13*, *MlLa*[2]
1998	Forum	*mlo*, *Mla8*	Pax	*Mla13*, *MlLa*
1999	Forum	*mlo*, *Mla8*	Pax	*Mla13*, *MlLa*
2000	Nordus	*mlo*[4]	Kompakt	*Mla13*, *MlLa*[2]

[1] Brown and Jørgensen 1991, [2] Dreiseitl and Jørgensen 2000, [3] Dreiseitl 1997, [4] Dreiseitl unpublished

and more slowly also in subsequent years; these varieties (Krystal and Novum) became the most susceptible in 1989–1992. (Already in 1988 six out of the seven most susceptible varieties possessed gene *Mla13*; Table 2 shows only less susceptible varieties Krystal and Zenit; however, susceptible varieties possessing *Mla13* were surpassed in susceptibility in that year by the above-mentioned extremely susceptible HE-3527.) The most susceptible varieties were also represented by those carrying gene *Mla13* (Pax and Kompakt) in 1997–2000.

Ml(Kr). In 1973–1974, KM-1192 was included in the trials and became the most resistant variety. Kredit, which was included in the trials in 1980–1983, belonged to the most resistant, together with the varieties possessing gene *Mla13*. The variety Jarek exhibited a significant decrease in resistance in 1985, similarly like the varieties carrying gene *Mla13*, and in 1994 Malvaz became the most susceptible variety.

Mla1. Rubin exhibited resistance slightly above average for 14 years. In 1993, the resistance of this variety significantly decreased. Lumar and Rubin became the most susceptible variety in the successive year.

Mla3. Mars was included in the trials in 1980–1988 and its resistance varied around the average of the studied varieties. In 1988, BR-3011 (*Mla3*) was included in the trials and became the most resistant variety. It exhibited the third lowest resistance level among all of the most resistant varieties for the 30 years.

Mlk1. Gene *Mlk1* is present in several examined varieties, always in addition to other resistance genes. The above-mentioned Czech variety Atlas was the first variety to possess this gene (in addition to gene *Mla7*). Atlas was considerably less resistant than Elgina (*Mla7*, *Mlg*) already in the first year of its testing, and during the next four years its resistance was only slightly higher than in Diabas (*Mla7*). Gene *Mlk1* is also present in the varieties Spartan and Lumar, and it seems to have contributed to resistance only little at that time.

MlLa. Gene *MlLa* is present in several examined varieties, always in addition to other resistance genes, for the first time in Opal (*Mla6*, *MlLa*). Its resistance was only moderate in 1978–1982, however markedly higher than in the varieties Ametyst and Rapid (*Mla6*). A higher decrease in the resistance of variety Opal was assessed in 1983. The variety Sladko (*Mla7*, *MlLa*) became the most resistant variety in 1989 even though it exhibited the lowest resistance level among the most resistant varieties for the 30 years. In 1993, the variety Orbit as the first of those possessing gene *MlLa* became the most susceptible variety. Some varieties carrying gene *MlLa* (Sladko, Akcent, Terno and Jarek) exhibited after 1993 higher resistance than it would have been based on other genes possessed by them. The varieties Pax and Kompakt, however, became the most susceptible varieties in 1997–2000.

Mlat. Gene *Mlat* is present in several examined varieties, always in addition to other resistance genes. It was possessed for the first time by the variety ST-6984 (*Mla6*, *Mlat*). The resistance of ST-6984 was markedly higher than that of Ametyst and Rapid (*Mla6*) and higher than that of Opal (*Mla6*, *MlLa*) in 1978–1981. Orbit became the most susceptible variety in 1993. The variety Svit (*Mla13*, *Mlat*) exhibited slightly above-average resistance in 1989–1994 and the variety Pejas (*Mla13*, *Mlat*) higher resistance than it would have been on the basis of the gene *Mla13* itself.

mlo. Salome (Germany) was the first variety to possess this gene. It was included in the trials in 1983 and 1984, and exhibited high resistance (it is not listed in Table 2). In 1986–1988, CE-396 was included in the trials and became the most resistant variety in the first two years. The variety Forum was tested in the trials since 1990 and it was the most resistant variety nearly till the end of the studied period (the most resistant variety in 2000 was Nordus-*mlo* with a negligible, and apparently random difference in comparison with Forum).

DISCUSSION

The occurrence (qualitative aspect) and frequency (quantitative aspect) of matching virulence in the pathogen population define the efficiency of a resistance gene. The expression of variety resistance in the field is affected by the environment and especially by the actual inoculation potential of the pathogen (Dreiseitl and Pařízek 2003). If the pathogen is absent, all varieties appear to be resistant, and under such conditions, a potential change in resistance is impossible to determine. Therefore, only data on the resistance of varieties from trials with high powdery mildew severity were used in this study (Dreiseitl and Jurečka 2003).

The varieties can be divided into two groups: those that could not induce any changes in the pathogen population (the varieties without a resistance gene and the varieties possessing gene *mlo*) and the varieties carrying the above-mentioned resistance genes to which the *Bgh* population could adapt (Dreiseitl and Jørgensen 2000).

There was no variety without a resistance gene to powdery mildew among the examined varieties. Such varieties are rare in Europe. However, the varieties designated as those missing an effective resistance gene are often varieties possessing *Mla8* only. The European population of *Bgh* is characterised by 100% frequency of matching virulence on this gene. Therefore, the presence of gene *Mla8* in the examined as well as other European varieties could be detected using Race I originating from Japan (Jørgensen and Jensen 1983, Dreiseitl unpublished). The 100% frequency of virulence does not allow the pathogen population to adapt. Therefore, the varieties possessing gene *Mla8* exhibited high susceptibility stable over time.

The varieties carrying gene *mlo* have been grown in Europe since 1979 on large planted areas (Jørgensen 1992). No virulence on this gene has been found until now and it is not supposed to be so in the nearest future either. The varieties possessing gene *mlo* exhibited high and stable resistance and they did not cause any detectable changes in the pathogen population.

A qualitative change, that means the occurrence of the first individuals virulent on a certain resistance gene, is a result of mutation in the pathogen population in the studied territory or virulence immigration from another territory. Decreasing efficiency of specific resistance based on major genes is a quantitative change. It occurs most frequently due to direct selection of virulent pathotypes on varieties with corresponding resistance. So direct selection is the main cause of increasing the frequency of matching virulence in the pathogen population.

A typical example of direct selection is the breakdown of resistance conditioned by gene *Mla13*. Denmark (since 1972) and former Czechoslovakia (since 1978) were among the first countries to grow varieties possessing gene *Mla13*. In contrast to a low proportion of the planted area of varieties possessing *Mla13* in Denmark (Munk et al. 1991), the proportion of such varieties exceeded 55% of the spring barley area in the Czech Republic and Slovakia already in 1983 (Dreiseitl 1993). However, these varieties resistant till that time, in spite of their percentage of the harvesting area, were grown under conditions of high inoculation potential that was produced by winter barley varieties that were not resistant to powdery mildew (Dreiseitl and Jurečka 2003). A large size of the pathogen population, together with a high percentage of the varieties possessing gene *Mla13* induced a strong selection pressure in the pathogen population. A rapid direct selection of virulent pathotypes accompanied by a rapid decrease in the resistance of the corresponding varieties was only a logical consequence of this state. Considering the variety resistance, adaptation of the pathogen population to gene *Mla13* was the most important change within the entire host-pathogen system. Owing to subsequent emigration of virulent pathotypes (Dreiseitl 2001b), it became an event of European importance (Wolfe et al. 1992). The mentioned process from development of virulent individuals due to mutation (Brückner 1982) through intensive direct selection of virulent pathotypes to total breakdown of resistance conditioned by gene *Mla13* (Dreiseitl and Pařízek 2003) took place in the domestic territory.

A similar situation was in the following case. The most dramatic breakdown was recorded in the resistance controlled by gene *Mla9* (Spartan). The planted area of Spartan variety increased very rapidly and it reached 32% of the spring barley area in 1980 (Dreiseitl 1993). Next year, an epidemic of powdery mildew attacked especially Spartan and other barleys possessing gene *Mla9*. Besides gene *Mla9* Spartan also possesses resistance gene *Mlk1* (Dreiseitl and Jørgensen 2000). At the same time, gene *Mlk1* was also overcome even though it was a new gene in the Czech Republic (gene *Mlk1* was carried by the variety Atlas for the first time; however, Atlas was registered only a year before Spartan and occupied a negligible planted area).

A critical role of direct selection accompanied by more or less extensive immigration of virulent pathotypes can also be assumed in resistances controlled by genes *Mla1*, *Mla6*, *Mla7* and *MlLa*. Slower breakdown of resistance conditioned by gene *Mla1* was obviously related to balanced growing of a single variety possessing this gene (Rubin) whose proportion did not exceed 10% of the spring barley planted area until 1990 (Dreiseitl 1993). After this year, the planted area of this variety enlarged (direct selection of virulent pathotypes also increased) and a considerable decrease in the resistance of Rubin variety below the average of the examined varieties was recorded in 1993.

Direct selection undoubtedly played a primary role also in the breakdown of resistance controlled by gene *Mlg*. However, extensive immigration of virulent pathotypes seems to have significant effects on the breakdown of this resistance. Gene *Mlg* was the first resistance gene to powdery mildew incorporated into a domestic variety (Merkur). The breakdown (not shown in Table 2) of resistance conditioned by gene *Mlg* was obviously influenced by both the direct selection of virulent pathotypes in the territory of the Czech Republic and immigration of virulent pathotypes from Germany where the use of gene *Mlg* and direct selection of virulent pathotypes started. Therefore Favorit possessing gene *Mlg* later was susceptible after 1970.

There is no doubt that an increase in the virulence frequency *Va3* in the Czech population of *Bgh* from 7% in 1992 (Dreiseitl and Schwarzbach 1994) to 13% in 1995 (Dreiseitl and Steffenson 2000) and to 24% in 2000 (Dreiseitl unpublished) was caused by migration. Mars is the only barley variety possessing resistance gene *Mla3* grown in the Czech Republic for the time being. It was registered in 1983 and two years later, Mars achieved its largest planted area (nearly 24 000 ha = 3.4% of total barley area) (Dreiseitl 1993). During the following period, the area planted with Mars decreased very quickly, and since 1990 Mars has been registered for seed production for export only. Although no barley carrying resistance gene *Mla3* is grown in the territory of the Czech Republic, the frequency of corresponding virulence *Va3* has significantly increased. Seed of Mars was exported mostly to Hungary, where this variety was grown. That probably caused a high frequency of *Va3* (38%) found in 1996 in the south of Slovakia (Križanová 1997). Besides Hungary, the varieties possessing resistance gene *Mla3* (Sewa, Dorina, Korinna and Baronesse) were grown in Germany and Rodos variety in Poland (Dreiseitl 1996). So there is no direct selection of *Va3* in the Czech Republic, but in adjacent countries. Due to wind dispersal (migration) the virulence frequency increases not only in the population created by direct selection but also in its surroundings.

Important changes in the pathogen population are also induced by indirect selection. It is obviously the case of the breakdown of resistances controlled by genes *Mla12* and *Ml(Kr)*. In the Czech Republic, gene *Mla12* was present in the variety Zefir for the first time (Dreiseitl and Jørgensen 2000). This variety was registered in 1981, i.e. in the same year when its resistance dramatically decreased. Its planted area was negligible in 1981 (Dreiseitl 1993). The resistance of Zefir decreased in the same year when the resistance of Spartan drastically declined. The joint breakdown of these different resistances must be explained as the (above-described) direct selection of pathotypes virulent on the resistance genes of Spartan variety (*Mla9*, *Mlk1*) at the simultaneous indirect selection (hitch-hiking) of (obviously associated) virulence *Va12*. A similar situation was also recorded in the breakdown of resistance controlled by gene *Ml(Kr)*. The varieties with this resistance (KM-1192 and Kredit) ranked among the most resistant varieties at the time of their inclusion in the trials. Resistance gene *Ml(Kr)* is original, therefore it was designated according to the first variety (Kredit) that possessed it (Dreiseitl and Jørgensen 2000). Kredit was registered in 1984 and a year later (1985) the resistance of Jarek variety [*Ml(Kr)*, *MlLa*] dramatically decreased. It was in the same year when a high decrease in resistance controlled by gene *Mla13* was recorded. There is no doubt that resistance *Ml(Kr)* also broke down due to indirect selection of pathotypes possessing *V(Kr)* in association with the breakdown of resistance *Mla13*.

Gene *Mlat* was present in Europe for the first time in our domestic varieties Jaspis and Orbit, both registered in 1986 (Dreiseitl and Jørgensen 2000). However, previously in the period of including these varieties in the trials (Table 2), their resistance was low (excesses in the resistance of the variety Jaspis in 1984 and particularly of the variety Orbit in 1985 can be explained by a failure of seed identity). It documents the abundant presence of a gene of unnecessary virulence *Vat* in the pathogen population prior to growing these first European varieties possessing gene *Mlat*.

Fast adaptation of the pathogen to variety resistance is also facilitated by the high recombination ability of *Bgh* fungus. Among 295 isolates obtained from the air in the territory of the Czech Republic in 2001, 41 isolates exhibited virulence on the original gene *Ml(N81)* (Brückner 1986) for the first time possessed by the variety Maridol, which was registered in 1999 (Dreiseitl and Jørgensen 2000). These 41 isolates belonged to 33 different pathotypes (Dreiseitl 2003). It is an evidence for the high recombination ability of the pathogen and importance of the sexual stage to create high population diversity.

It can be concluded that practical durability of any resistance is limited by adaptability of the pathogen population. Two basic preconditions facilitates fast adaptation and dramatic breakdown of resistance in the field. Firstly, a portion of pathotypes virulent for the corresponding resistance reaches a sufficient level (mostly due to direct or indirect selection on the cultivar possessing a respective resistance gene or due to immigration of virulent pathotypes) and secondly, the conditions of the year are favourable for the development of disease epidemic (Dreiseitl and Jurečka 2003).

All the above-mentioned evolutionary forces act in the direction of increasing the virulence frequency on individual major resistance genes (decreasing the virulence frequency is quite rare). It leads to an increase in the complexity (accumulation of virulence genes) of individuals in the pathogen population. It was found that the population complexity to 12 out of the 14 major resistance genes (except *Mla8* and *mlo*) increased from the estimated value of 0.90 in 1971 to the assessed value of 8.73 in 2001 (Dreiseitl 2002), whereas the critical increase in the complexity was apparently till 1987. Such an increase in virulence complexity brings about a decrease in the diversity of pathogen population (Dreiseitl 2001a), but only when considering the presented virulences examined for a long time (Limpert and Dreiseitl 1996). At present, barley varieties possessing some new resistance genes are introduced to which the pathogen population successfully adapts again (Dreiseitl unpublished). Due to the increasing virulence frequency to these new resistance genes, both the complexity and diversity of pathogen population continue to increase.

Acknowledgement

I thank the Central Institute for Supervising and Testing in Agriculture that I could use the results of scoring the resistance of spring barley varieties to powdery mildew in this study.

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Received on December 13, 2002

ABSTRAKT

Adaptace *Blumeria graminis* f.sp. *hordei* ke genům odolnosti ječmene v ČR v letech 1971–2000

Byly analyzovány výsledky hodnocení odolnosti 35 vybraných odrůd ječmene jarního k padlí travnímu v 307 odrůdových pokusech Ústředního kontrolního a zkušebního ústavu zemědělského, které se vyznačovaly silným výskytem padlí travního. Odrůdy lze rozdělit do dvou skupin: odrůdy, které nemohly vyvolat změny v patogenní populaci (odrůdy bez účinného genu odolnosti a odrůdy obsahující gen *mlo*) a odrůdy nesoucí geny specifické odolnosti [celkem 12 *Ml*-genů: *a1*, *a3*, *a6*, *a7*, *a9*, *a12*, *a13*, *at*, *k1*, *La*, *g* a *(Kr)*], na které se ve sledovaném období patogenní populace adaptovala. Je dokumentováno snižování odolnosti odrůd a diskutován podíl jednotlivých adaptačních mechanismů (evolučních sil), jako mutace, migrace, přímý výběr, nepřímý výběr a rekombinace, na erozi účinnosti jednotlivých genů specifické odolnosti, jakož i vliv adaptace patogena na komplexnost a diverzitu patogenní populace.

Klíčová slova: *Hordeum vulgare*; *Blumeria graminis* f.sp. *hordei*; jarní ječmen; padlí travní; genetická odolnost; adaptace; evoluční síly

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