POWDERY MILDEW RESISTANCE IN SELECTIONS FROM BARLEY LANDRACES COLLECTED IN JORDAN, EGYPT, LIBYA AND TUNISIA

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Eight barley (*Hordeum vulgare* L.) landraces were tested for resistance to powdery mildew (*Blumeria graminis* f. sp. *hordei*) and new sources of resistance were identified. Landraces were collected in 5 expeditions in 4 countries: Jordan (2 landraces), Egypt (2 landraces), Libya (3 landraces) and Tunisia (1 landrace). Seed samples of these landraces were kindly provided by International Centre for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. In 1998 all tested landraces showed resistance to natural infection of powdery mildew in IHAR, Radzików, Poland. From these landraces 18 single-plant lines were selected and tested at the seedling stage with 23 differential isolates of powdery mildew. The isolates were chosen according to their virulence spectra as observed on the 'Pallas' isoline differential set and on 8 additional differential cultivars. These isolates had collectively virulences to all major resistance genes used in the past and currently in Europe. Six lines (155-2-1, 469-2-5, 805-2-3, 806-1-1, 806-2-2, 806-3-4) showed resistance to all isolates used. These lines were characterised by resistance reaction type 2 which was observed for inoculation with most isolates. However, expression of infection types 0, 1 and 2 for the isolates tested indicated that some of these lines may have more than one allele for resistance. Twelve (66.7%) lines expressed infection type 2 for inoculation with more than 50% of the isolates. Only 2 lines showed resistance infection type 0 for most isolates used. About 86.1% of all infection types observed among tested lines were classified as powdery mildew resistance. The most frequent (66.4%) resistant infection type was 2. The infection type 0 (immunity) occurred with frequency 16.8% and infection type 1 (hypersensivity) with frequency of 2.9%, respectively. In 15 tested lines it was impossible to determine which specific allele or alleles for resistance are present. Allele *Mlat* was postulated to be present in 2 lines in combination with other unknown gene or genes. The presence of allele combination of *Mla13*, *Ml(Ru3)* was postulated in one line. The use of identified sources of resistance to powdery mildew in barley breeding was discussed.

barley; *Erysiphe graminis* f. sp. *hordei*; genetic resources; genes for resistance; *Hordeum vulgare*; landraces; powdery mildew; West Asia and North Africa Region

INTRODUCTION

Barley (*Hordeum vulgare* L.) is the fourth most important cereal crop in the world, after wheat, maize and rice. In European Union (EU) barley is the second (after wheat) most important cereal crop with about 32% (about 10 898 000 ha) of EU total cereals acreage. In the Czech Republic barley is of great economic importance and it is grown on 543 696 ha (34.9% of total cereals acreage) (Rasmusson, 1985; Dreiseitl, Jurečka, 1996, 1997; Atzema, 1998; Anonymous, 2000). In West Asia and North Africa (WANA) region barley is often grown in marginal agricultural areas with low annual precipitation (often less than 220 mm). Landraces in this area are important as they are often the only rain-fed crop possible and they are cultivated on mountain slopes at elevations higher than other cereals (Rasmusson, 1985; Ceccarelli, Grando, 1999; Ceccarelli et al., 2000).

Powdery mildew, caused by the pathogen *Erysiphe graminis* (DC.) Golovin ex Speer f. sp. *hordei* Em. Marchal (synamorph *Blumeria graminis* DC. f. sp. *hordei* Em. Marchal), is one of the most destructive foliar diseases of barley in central and western Europe, WANA region, Japan and the eastern and southern barley producing areas of North America (Rasmusson, 1985; Czembor, 1996; Atzema, 1998). In countries where mildew is a problem, yield losses in experimental tests usually exceed 25%, although average losses in barley production are smaller and about 10% (Zwatz, 1987; Schally et al., 1995; Atzema, 1998). Yield reduction is due to loss of functional green leaf area, reduced root growth, reduced kernel weight, smaller numbers of kernels per spike and tillers per plant. Reduction in quality characteristics is particularly detrimental for malting barley (Wolfe, 1984; Wolfe, McDermott, 1994).

The total number of about 280 000 of barley accessions (many of them landraces) is estimated to be in *ex situ* germplasm collections world-wide (Knüpffer, Hintum, 1995). Barley landraces constitute a rich genetic resource, and many examples of their successful use have been reported (Alemayehu, 1995; Valkoun et al., 1995; Czembor, 1996; Jørgensen, Jensen, 1997). However only for less than 2 per cent of barley landraces the attempts were made to identify powdery mildew resistance genes using differential lines and isolates. These types of studies were mostly conducted in Germany, Denmark and Sweden and on smaller scale in other countries, such as Czech Republic, The Netherlands, USA and Poland (Honecker, 1938; Ralski, Mikolajewicz, 1958; Brückner, 1964; Nover, Lehmann, 1973; Wiberg, 1974; Czembor, 1976, 1996, 1999, 2000; Czembor et al., 1979; Lehmann, von Bothmer, 1988; Negassa, 1985; Leur et al., 1989; Leijerstam, 1996; Jørgensen, Jensen, 1997; Lehmann et al., 1998; Czembor, Czembor, 1999a; Jönsson, Lehmann, 1999). Based on these raports it may be assumed that barley landraces collected in Mediterranean region may possess mildew resistance genes different from those which already have been introduced into barley cultivars. Such genes would be of value in the further diversification of resistance genes available to breeding programs (Czembor, 1996, 1999, 2000; Jørgensen, Jensen, 1997).

About 80 years ago Vavilov proposed that the Mediterranean region is major centre of crop origin. This hypothesis is supported by the richness of crop diversity, including barley, of this part of the world. In the most accepted theory, postulated by Körnicke and Werner (1885), barley was derived from its wild ancestor *H. spontaneum* C. Koch. when Neolithic men selected spikes with tough rachis (Perrino 1988; Bothmer et al., 1995; Williams, 1995; Ladizinsky, 1998; Zohary, 1999). The original area of cultivation and the centre of origin of *H. vulgare* L. is assumed to be the area of the Fertile Crescent. The term Fertile Crescent coined by James Breasted in 1916 refers to a crescent-shaped region of the rich farmland that stretches from the Mediterranean Sea to the Persian Gulf through the Tigris and Euphrates valley (Nesbitt, 1995; Willcox, 1995). Archaeological evidences indicate the earliest signs of cultivation of barley in this region in the 9th millennium B. C. (Tell Mureybet, Syria) and its domestication around 8000 B.C. (Jerycho, Israel). Also most probably barley was the first domesticated cereal and until around 2000 B.C. it was more commonly grown and higher valued than wheat in such ancient countries as Egypt and Summer (Williams, 1988; Harlan, 1995; Willcox, 1995; Haywood et al., 1997).

Wild progenitors of barley were exploited in Fertile Crescent (e.g. Nahal Oren in Israel, Abu Hureira in Syria – 12 000 B.C.) for at least several thousand years before the appearance of domesticated barley. During this time wild barley was harvested in premature stage before shattering seed and this is practised until now in some mountain regions (e.g. Nepal) (Bothmer et al., 1995; Willcox, 1995; Haywood et al., 1997). The wild barley species *H. spontaneum, H. bulbosum*, and *H. murinum* grow abundantly in this region often on the edge of a cultivated fields with *H. vulgare* (Bothmer et al., 1995; Hawkes, 1995). These species are represented by populations greatly varying in morphology and growth habits. The *H. bulbosum* and *H. murinum* are introgressing occasionally with *H. spontaneum* and *H. spontaneum* may cross with domesticated barley (Eyal et al., 1973; Bothmer et al., 1995; Hadjichristodoulou, 1995; Asfaw, 1999). The

mentioned *Hordeum* species in WANA region annually support outbreaks of powdery mildew of barley (Eyal et al., 1973; Czembor, 1996). The concept of correlated host-pathogen evolution implies that genetic diversity in the populations of the indigenous *Hordeum* species is matched by diversity in populations of *E. graminis* f. sp. *hordei*. This concept was proved to be true in many studies (Eyal et al., 1973; Wolfe, 1988; Jana, Nevo, 1991; Finckh, Wolfe, 1997a; Brown, 1999). Consequently, barley landraces collected from Jordan, Egypt, Libya and Tunisia may be source of the resistance to powdery mildew due to their high degree of diversification resulting from the long co-evolution with populations of pathogen.

The objective of this study was to determine the identity of powdery mildew resistance genes in selections from barley landraces collected in Jordan, Egypt, Libya and Tunisia.

MATERIAL AND METHODS

Plant material

Eight barley landraces were used in this study (Table I). Seed samples of landraces were kindly provided by Dr. J. Valkoun and Prof. S. Ceccarelli (International Center for Agricultural Research in the Dry Areas – ICARDA, Aleppo, Syria). The landraces were collected between 1981–1990 during 5 expeditions (ICARDA collection code JOR 81-3, JOR 85, EGY 87, LBY 81, TUN 90-2) in Jordan, Egypt, Libya and Tunisia. Under Central Poland field conditions the landraces showed low resistance to lodging and were intermediate in heading date.

Pathogen

Twenty-three isolates of *E. graminis* f. sp. *hordei* were used in this study (Table II). The isolates were kindly provided by Dr. H. J. Schaerer (ETH, Zurich, Switzerland) and originated from collections of the Risø National Laboratory, Roskilde, Denmark; Danish Institute for Plant and Soil Science, Lyngby, Denmark and Edigenossische Technische Hochschule – ETH, Zurich, Switzerland. In addition 4 isolates from collection in Plant Breeding and Acclimatization Institute – IHAR, Radzików, Poland were used. The isolates were chosen according to differences in virulence spectra that were observed on 'Pallas' isoline differential set (Kolster et al., 1986) kindly provided by Dr. L. Munk (Royal Agricultural and Veterinary University, Copenhagen, Denmark) and on 8 additional differential cultivars. Isolates were purified by single pustule isolation. Young seedlings of the cultivar 'Manchuria' (CI 2330) were used to maintain and propagate all isolates used. Isolates were

I. Site of collection of 8 barley landraces showing resistance to powdery mildew

IHAR No.	ICARDA No.	Country of origin	ICARDA Collection code	Collection date	Altitude	Province	Site
133	ICB 31526	Jordan	Jor 81-3	5. 1981	500	Irbid	Madaba
155	ICB 31549	Jordan	Jor 85	21. 5. 1985	650	Mafraq	Al Mansoura 5 km W of Mafraq
460	ICB 32538	Egypt	Egy 87	23. 4. 1987	60	Marsa Matrruh	Al Nigela, 12 km N of Al Nigela
469	ICB 32547	Egypt	Egy 87	23. 4. 1987	30	Marsa Matrruh	Sidi Barrani, 2 km E Sidi Barrani
792	ICB 37536	Libya	Lby 81	10. 6. 1981	390	Albaida	Al Qaniu
805	ICB 37549	Libya	Lby 81	14. 6. 1981	130	Darnah	48 km E Darnah in direction to Tobruq
806	ICB 37550	Libya	Lby 81	14. 6. 1981	20	Al Qubbah	25 km W Darnah on the coast road
888	ICB 37749	Tunisia	Tun 90-2	5. 1990	30	–	Bouterfes

II. Differential isolates and their infection types on Pallas isolines set and on 8 additional cultivars

Differential set		Isolates																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Pallas isolines and cultivars	gene	58-74.1	59-12	63-1a	A6c	D17-1	EmA30.1	HL3/5.c	JEH11-2	MH1-3	R189.1	R303a	Ru3.2	TR2-2	En1/A1	R303.2	E92-1	59-11.2	SZ/C10a	Ra7	Ra9-1	Ra10-2	Ra16a	Ra22-2
Pallas	*Mla8*	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
P1	*Mla1*	0	0	4	4	4	0	0	0	0	0	0	0	4	0	0	4	0	0	0	0	4	0	0
P2	*Mla3*	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	4	0	4	0	0	0
P3	*Mla6, Mla14*	0	0	0	0	0	4	4	0	2	4	0	4	0	0	0	4	0	4	4	4	4	4	4
P4A	*Mla7, Mlk, +?*	4	4	4	0	0	0	0	4	2	1	1	0	4	4	0	4	4	0	0	4	4	4	4
P4B	*Mla7, +?*	4	4	4	0	1	0	0	4	4	0	0	1	4	4	0	4	4	2	0	2	2	4	4
P6	*Mla7, MlLG2*	4	4	4	0	0	0	0	4	4	0	0	0	2	4	0	4	4	0	0	1	1	4	4
P7	*Mla9, Mlk*	4	0	4	0	0	0	0	4	0	0	0	0	4	0	0	0	0	0	0	0	0	4	0
P8A	*Mla9, Mlk*	4	0	4	0	0	0	0	4	0	0	0	0	4	0	0	0	0	0	0	0	0	4	0
P8B	*Mla9*	4	0	4	0	0	0	0	4	0	2	0	0	4	0	0	0	0	0	0	0	0	4	0
P9	*Mla10, MlDu2*	4	4	4	0	0	0	0	4	0	0	4	0	4	4	4	4	2	0	0	4	4	4	4
P10	*Mla12*	0	0	4	0	0	4	0	0	2	0	0	0	4	4	0	4	0	4	0	4	4	0	4
P11	*Mla13, MlRu3*	4	0	4	0	0	0	0	0	4	0	0	0	0	4	0	0	0	0	0	0	4	0	4
P12	*Mla22*	4	4	0	4	4	4	4	0	4	4	0	4	4	4	0	0	4	4	4	0	4	0	0
P13	*Mla23*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
P14	*Mlra*	4	4	4	0	4	4	4	4	0	4	4	4	4	4	4	4	4	4	4	0	4	4	4
P15	*Ml(Ru2)*	2	4	4	4	2	4	2	4	2	4	4	4	4	4	4	4	4	4	4	0	4	4	4

Differential set		Isolates																						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Pallas isolines and cultivars	gene	58-74.1	59-12	63-1a	A6c	D17-1	EmA30.1	HL3/5.c	JEH11-2	MH1-3	R189.1	R303a	Ru3.2	TR2-2	En1/A1	R303.2	E92-1	59-11.2	SZ/C10a	Ra7	Ra9-1	Ra10-2	Ra16a	Ra22-2
P17	*Mlk*	4	4	4	2	2	2	2	4	2	2	0	2	4	4	2	4	4	2	2	4	4	4	4
P18	*Mlnn*	4	4	4	4	4	4	4	4	4	2	2	4	4	4	4	4	4	2	4	4	4	2	2
P19	*Mlp*	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
P20	*Mlat*	0	2	2	4	2	2	2	4	2	2	2	2	4	2	2	2	2	4	2	2	4	2	2
P21	*Mlg, Ml(CP)*	4	4	4	0	0	0	4	0	4	0	4	4	4	4	4	4	4	4	0	4	4	0	4
P22	*mlo5*	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	3	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)
P23	*Ml(La)*	0	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
P24	*Mlh*	4	4	4	2	4	4	4	4	4	4	4	4	4	4	4	2	4	4	4	4	4	4	4
Benedicte	*Mla9, Ml(IM9)*	0	0	4	0	0	0	0	0	4	0	4	0	4	4	0	4	0	0	0	4	4	0	4
Lenka	*Mla13, Ml(Ab)*	0	0	4	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	4	0	4
Gunnar	*Mla3, Ml(Tu2)*		0	3	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	
Steffi	*Ml(St1), Ml(St2)*	0	0	2	0	0	0	4	0	4	4	4	0	2	4	0	0	2	2	0	4	2	4	4
Kredit	*Ml(Kr)*		2	4	0	0	0	0	2	4	0	4	1	2	4	2	4	1	2	0	2	4	2	4
Jarek	*Ml(Kr), +?*	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	2
Trumph	*Mla7, Ml(Ab)*	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Borwina	*Ml(Bw)*	2	4	4	4	3	4	2	4	4	2	4	4	4	4	4	4	2	4	2	4	4	4	4
Manchuria	–	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4

tested frequently on host differentials to assure their purity throughout the experiment.

Inoculation and Disease Assessment

In greenhouse tests the plants were grown with 16 h light and 8 h dark at 16–22 °C. During this testing the plants were grown in plastic pots (5 cm upper diameter) filled with a mixture of Radzików sandy soil and peat in a 3 : 1 ratio. At least 10 plants from each selected line were tested together with seedlings of the cultivar 'Manchuria' CI 2330 (used as susceptible control) and differential set (to assure the purity of the isolates). The inoculation was carried out when plants were 10–12 days old (two leaf stage) by shaking or brushing conidia from diseased plants. After 8–10 days of incubation the disease reaction types showed by seedlings were scored on the primary leaf of the seedlings. This scoring was done according to a 0–4 scale adopted from Mains and Dietz (1930) (Table III). This scale was broadened by including score 0(4) describing infection type characteristic for gene *mlo*. This modification was done, because this gene was not known in the time of developing of this scale (*mlo* gene was described in 1942) and because this gene is of great importance in Europe (it is present in about 20% of cultivars grown in Central Europe) (Schwarzbach 1997, 1998; Atzema, 1998; Czembor, Czembor, 1998, 2000). Seedlings were classified into susceptible or resistant groups. Plants with infection types 0–2 were classified as resistant, while plants that scored 3 and 4 were classified as susceptible.

Resistance tests

This investigation was conducted during 1998–2000 at IHAR, Radzików, Poland. During summer 1998 about 90 plants per each of 8 landraces were grown in the field (Table I). These plants were evaluated for reaction to natural infection of *E. graminis* f. sp. *hordei* and from each landrace 1–5 resistant plants were selected. In October 1998 progeny of selected plants (about 30 plants per line) were grown in the greenhouse and tested again for resistance to powdery mildew using isolate R 303a. R 303a isolate represented the most avirulent isolate available allowing the expression of a maximum number of resistance genes. During this testing from progeny of each single-plant line again 1-5 resistant plants were selected and 18 lines were created. These tests showed that lines selected from 3 landraces were heterogenous for mildew reaction. During the same winter (1998–1999) selected plants were propagated in the greenhouse. Next, during summer 1999 these single-plant lines were propagated under field conditions. During the winter

III. Description of infection types and codes used (adapted from Mains and Dietz, 1930)

Infection type	Symptoms
0	No visible symptoms (immunity).
0(4)	Sparse small colonies originating from the stomatal subsidiary cells.
1	Necrotic flecks
2	Frequent chlorosis. Reduced mycelial growth. No or very scare sporulation.
3	Moderate mycelial growth
4	Profuse sporulation of well developed colonies and sometimes green islands.

of 1999–2000 these lines were tested in greenhouse with 23 isolates (including R 303a) (Table IV).

Postulation of resistance alleles

Hypotheses about the specific resistance genes present were made from the comparison of the reaction spectra of the tested lines with those of differential lines. The lines giving the same reaction spectra with all isolates were classified in the same group. Identification of resistance genes was made by eliminating resistance genes not present in tested lines. The next step was determination of postulated and possible resistance genes present and was done on the basis of the gene for gene hypothesis. In the case when a compatible reaction (scores 3 and 4) was observed with one given isolate, it meant that the cultivar did not possess the resistance alleles for which the isolate was avirulent. Incompatible reactions (scores 0–2) with isolates possessing only one avirulence allele among the remaining possible resistance alleles made it possible to postulate that the matching resistance allele was present (Flor, 1956; Dreiseitl, Steffenson, 1996b, Dreiseitl et al., 1996; Dreiseitl, Jørgensen, 2000).

RESULTS

All 8 tested barley landraces (at least one plant) expressed resistance to natural infection of *E. graminis* f. sp. *hordei* occurred in Central Poland. Also all 18 single-plant lines derived from these landraces expressed resistance to powdery mildew (Table IV). Six lines (155-2-1, 469-2-5, 805-2-3, 806-1-1, 806-2-2, 806-3-4) showed resistance to all isolates used. These lines were characterised by resistance reaction type 2 which was observed for inoculation with most isolates. However, expression of infection types 0, 1 and 2 for

IV. Resistance alleles and infection types of 18 lines to infection by 23 isolates of *E. graminis* f. sp. *hordei*

No.	Lines	Isolates																					Postulated resistance alleles	Possible alleles[1]
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23		
		58-74.1	59-12	63-1a	A6c	D17-1	EmA30.1	HL3/5.c	JEH11-2	MH1-3	R189.1	R303a	Ru3.2	TR2-2	En1/A1	R303.2	E92-1	59-11.2	SZ/C10a	Ra7	Ra9-1	Ra10-2	Ra16a	Ra22-2		
1	133-1-1	2	2	2	4	0	0	2	4	2	2	2	2	2	1	2	2	2	4	2	2	4	2	2	*Mlat, +?*[2]	
2	155-1-1	2	2	2	4	0	0	2	4	2	2	2	2	2	0	2	2	2	4	2	2	4	2	2	*Mlat, +?*	
3	155-2-1	2	2	2	0	0	0	2	0	2	0	2	2	2	2	2	2	2	2	0	2	2	2	2	*+?*	
4	155-3-2	0	2	2	2	2	4	2	2	4	4	2	4	0	0	2	2	2	4	2	4	4	4	4	*+?*	*Mla6, Mla4, +?*
5	155-4-1	0	0	0	0	0	4	2	2	4	4	0	2	0	0	2	4	2	2	0	2	2	2	2	*+?*	*Mla6, Mla4, +?*
6	155-4-5	0	0	0	2	0	4	2	0	4	4	0	2	0	0	0	4	0	2	0	0	2	2	0	*+?*	*Mla6, Mla4, +?*
7	460-1-3	4	4	2	2	4	2	4	2	4	0	1	4	1	2	1	2	4	2	2	2	2	2	2	*+?*	
8	469-2-5	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	2	2	2	2	2	2	2	*+?*	
9	792-1-2	2	2	2	4	2	2	2	2	4	2	2	1	2	2	2	2	2	4	2	2	4	2	2	*+?*	
10	792-2-1	1	0	2	2	0	0	2	2	1	0	0	0	2	0	0	0	1	4	0		1	0	0	*+?*	
11	805-1-2	0	0	2	2	0	4	4	0	4	4	0	4	0	0	0	4	0	4	4	4	4	4	4	*+?*	*Mla6, Mla14, +?*
12	805-2-3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2		2	2	2	*+?*	
13	805-3-1	2	2		2	2	2	2	2	2	2	1	4	2	2	2	2	0	2	0	2	2	2	2	*+?*	
14	806-1-1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	*+?*	
15	806-2-2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	*+?*	
16	806-3-4	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	*+?*	
17	888-1-5	2	0	4	0	0	0	0	0	2	0	0	0	0	4	0	0	0	0	0	0	4	0	4	*Mla13, MlRu3*	
18	888-2-1	2	2	2	2	2	2	0	2	2	2	2	2	2	0	2	2	2	4	2		4	2	2	*Mlat, +?*	

[1] Resistance alleles which were not eliminated from the reactions of susceptibility and could not be confirmed with the reactions of resistance
[2] Unidentified resistance allele, not present in the 'Pallas' isolines set

V. Infection type frequencies of 18 barley lines evaluated for reaction to 23 isolates of *E. graminis* f. sp. *hordei*

No.	Lines	No. of isolates that produced each infection type				
		infection type				
		0	1	2	3	4
1	133-1-1	2	1	16	0	4
2	155-1-1	3	0	16	0	4
3	155-2-1	6	0	17	0	0
4	155-3-2	3	0	10	0	10
5	155-4-1	9	0	10	0	4
6	155-4-5	13	0	6	0	4
7	460-1-3	1	3	12	0	7
8	469-2-5	0	0	23	0	0
9	792-1-2	0	1	18	0	4
10	792-2-1	11	5	5	0	1
11	805-1-2	9	0	2	0	12
12	805-2-3	1	0	21	0	0
13	805-3-1	2	1	18	0	1
14	806-1-1	0	0	23	0	0
15	806-2-2	0	1	22	0	0
16	806-3-4	0	0	23	0	0
17	888-1-5	17	0	2	0	4
18	888-2-1	2	0	18	0	2
Percentage		16.8	2.9	66.4	0	13.9

the isolates tested indicated that some of these lines may have more than one allele for resistance. This was based on the assumption that different resistance genes may condition different infection types.

The distribution of infection types indicated that 12 (66.7%) lines expressed infection type 2 for inoculation with more than 50% of the isolates. Only 2 lines showed resistance infection type 0 for most isolates used. About 86.1% of all infection types observed among tested lines were classified as powdery mildew resistant. The most frequent (66.4%) resistant infection type was 2. The infection type 0 (immunity) occurred with frequency 16.8% and infection type 1 (hypersensitivity) with frequency of 2.9%, respectively.

Conclusions about presence of putative known genes in the lines were made by checking infection types patterns of the isolates expressed by tested lines with those expressed on differential lines (Tables I, IV). Based on this analysis of data, it was concluded that allele *Mlat* was postulated to be present in 2 lines in combination with other unknown gene or genes. The presence of allele combination *Mla13*, *Ml(Ru3)* was postulated in one line. However, in 15 tested lines it was impossible to determine which specific allele or alleles for resistance are present. Most probably these lines possess genes not represented in differential used in the present experiment.

DISCUSSION

Geneticists, plant pathologists and breeders working with barley are constantly looking for gene pools from which new genes can be introduced into existing cultivars in order to improve their resistance to major diseases including powdery mildew. Such gene pool are barley landraces, especially those originated from origin centres of barley, such as Mediterranean region, and most of the powdery mildew resistant genes used commercially (e.g. *Mla1*, *Mla3*, *Mla6*, *Mla7*, *Mla9*, *Mla12*, *Mla13*, *Mlat*, *Mlk*, *Mlg*, *Mlh* and *Mlra*) are derived from these landraces (Czembor, 1976; Kolster et al., 1986; Jørgensen, 1994). This was confirmed in this study. All 8 investigated landraces expressed resistance to natural infection of *E. graminis* f. sp. *hordei* in Central Poland. Testing of 18 single-plant lines with 23 differential isolates showed that all these lines possessed a resistance allele or alleles for powdery mildew. However, only six lines (155-2-1, 469-2-5, 805-2-3, 806-1-1, 806-2-2, 806-3-4) showed resistance to all isolates used. These lines were characterised by resistance reaction type 2, which was observed for inoculation with most isolates. Based on the fact that isolates used in this experiment had collectively virulences to all major resistance genes used in the past and currently in Europe, it may be concluded that these lines showed high level of resistance to the powdery mildew virulence genes occurring in Europe. Therefore this germplasm should be very useful in barley breeding programs as new sources of resistance to powdery mildew. The frequency of landraces possessing resistance to all isolates of powdery mildew in the present study was 50% and is higher than that found in other studies (Honecker, 1938; Ralski, Mikolajewicz, 1958; Brückner, 1964; Nover, Lehmann, 1973; Wiberg, 1974; Czembor, 1976, 1996, 1999, 2000; Czembor et al., 1979; Negassa, 1985; Lehmann, von Bothmer, 1988; Leur et al., 1989; Leijerstam, 1996; Jørgensen, Jensen, 1997; Lehmann et al., 1998; Czembor, Czembor, 1999a; Jönsson, Lehmann, 1999). This may relate to differences in various methods and isolates of powdery mildew used for screening landraces for resistance among the different studies.

Many barley landraces display high level of genetic diversity and in some studies more than 50% of tested landraces were found to be genotypic mixtures (Bernardo et al., 1997; Demissie, Bjørnstad, 1997; Asfaw, 1999). The genetic heterogeneity within the barley landraces is due to a low level of outcrossing occurring in barley (Alard, 1988; Hadjichristodoulou, 1995). This was confirmed in this study by the fact that 3 landraces (37.5%) were heterogeneous in preliminary tests for mildew reaction. Similar or lower powdery mildew resistance heterogeneity of barley was observed in other studies (Nover, Lehmann, 1973; Czembor, 1996). All countries from which originated tested landraces are characterised by big contrast in their natural conditions due to mountainous character of their topography and different climate due to the transitional location between the Mediterranean winter-rain zone and the Sahara desert. These environmental conditions allow for the expression of a wide array of genes and a wide diversity of wild and domesticated barley (Negassa, 1985; Czembor, 1996; Asfaw, 1999). Collection missions in Mediterranean countries are recommended because landraces of major crops in these countries are subject to genetic erosion due to drought and desertification (Perrino et al., 1986; Anishetty et al., 1995; Valkoun et al., 1995; Zine Elabidine et al., 1995).

The used fungicides and resistant cultivars are available for the effective control of powdery mildew. During last thirty years fungicide control of *E. graminis* f. sp. *hordei* has been used to reduce the severity of powdery mildew in the field. However, many pathotypes of *E. graminis* f. sp. *hordei*, that are resistant to commonly used fungicides, have been identified. Also, fungicide cost and environmental concerns regarding pesticide use have led to a gradual reduction in their use for control of powdery mildew (Brown, Kane, 1994; Gullino, Kuijpers, 1994; Brown, 1996). Breeding for resistance, as an alternative approach to control of powdery mildew, has been very successful, inexpensive and environmentally safe (Czembor, Czembor, 1998, 1999b, 2000).

Genetic studies of barley resistance to powdery mildew started by Biffen (1907) have resulted in characterization of the powdery mildew/barley genetic interactions. Currently, powdery mildew on barley is considered as one of the best known system of host-pathogen genetic interactions and about 100 mildew resistance genes have been identified in barley cultivars, landraces and wild or related *Hordeum* species (Jørgensen, 1994; Czembor, 1996). In Europe, the use of specific resistance genes to control barley powdery mildew began in the 1930s with the work of Honecker and

it was stimulated by an extraordinarily heavy attack of this pathogen in Germany in 1929. In the 20th century, about 36 genes for specific resistance have been used in Europe in more than 700 cultivars since the first gene, *Mlg*, was introduced on a large scale in the 1930s (Wolfe, Schwarzbach, 1978; Brown, Jørgensen, 1991; Jensen, Jørgensen, 1991; Czembor, Czembor, 1998, 1999b, 2000). However, resistance conferred by most of these genes has not been effective for more than a few years with the exception of genes *mlo* and *Ml(La)* (Schwarzbach, 1997, 1998; Munk et al., 1991; Atzema, 1998). This was caused by high level of pathogenic variability encountered in natural populations of *E. graminis* f. sp. *hordei*. In many investigations it was proved that *E. graminis* f. sp. *hordei* is able to develop many new races and that its spores are spread by wind eby the million over large distances across Europe (Věchet, Kocourek, 1986; Dreiseitl, Steffenson, 1996a; Dreiseitl, 1997, 1998; Limpert et al., 1999; Hovmøller et al., 2000).

Many strategies for effective use of resistance genes in order to increase their durability were developed. Such strategies are: use of multiline cultivars, combining ('pyramiding') different resistance genes into one variety and deploying many cultivars with different resistance genes over space (e.g. cultivar mixtures) and time (winter versus spring barley) (Czembor, Gacek, 1990, 1995; Finckh et al., 1996; Finckh, Wolfe, 1997a, b, 1998). However, there are resistance genes which have not been exploited, and new sources of resistance are still being found in barley landraces and wild relatives (Dreiseitl, Bockelman, 1997, 1998; Czembor, 1999, 2000; Dreiseitl, 1999). Such new sources of resistance to powdery mildew have been described in this study.

Modern plant breeding started in the second half of 19th century when a few farmers and landowners (e.g. Knight in England, Rimpau in Germany, Janasz in Poland, Vilmorin in France) started selection of attractive plants from landraces based upon their phenotypic variation (Janasz, 1893; Jensen, 1988; Zeven, 1996). During this activity often only one line was selected as a new cultivar and the landrace from which this line was selected was no longer maintained. This caused within the last 100 years great genetic erosion in major crops including barley. The subject of conservation of landraces for the first time was discussed at the Agriculture and Forestry Congress in Vienna in 1890 but without results. In 1927, 37 years later, during the International Agricultural Congress in Rome, it was recommended that participants should start the conservation of landraces in their native countries and organise Gene Banks (Zeven, 1996). The large scale landrace cultivation of barley in Europe practically ceased in the 1950s and today in most European countries landraces of major crops exist only in Gene Banks

(Hammer et al., 1996; Jana, 1999; Ceccarelli et al., 2000). However, in the Mediterranean region (especially in West Asia and North Africa), farmers still rely on landraces because powdery mildew and other diseases rarely develop to levels that significantly damage the yield (Ceccarelli et al., 1987, 1995, 2000; Czembor, 1996; Ceccarelli, Grando, 1999). Most probably it is due to the stabilising effect of intermediate resistance in landraces, which is sufficient to control the limited disease development (Leur et al., 1989; Alemayehu, 1995; Ceccarelli, Grando, 1999). This corresponds with the fact that majority (66.4%) of sources described in the present study expressed intermediate resistance (infection type 2) for most isolates used. Also this is in agreement with results in other studies (Honecker, 1938; Ralski, Mikolajewicz, 1958; Brückner, 1964; Nover, Lehmann, 1973; Wiberg, 1974; Czembor, 1976, 1996, 1999, 2000; Czembor et al., 1979; Negassa, 1985; Lehmann, von Bothmer, 1988; Leur et al., 1989; Leijerstam, 1996; Jorgensen, Jensen, 1997; Lehmann et al., 1998; Czembor, Czembor, 1999a; Jönsson, Lehmann, 1999). Probably landrace populations evolved intermediate resistance mechanism because its lower cost in terms of energy requirement in comparison to immunity (infection type 0) (Smedegaard-Petersen, Stolen, 1980; Negassa, 1985). Also immunity is much more effective selective medium for the corresponding virulence than other types of resistance. Consequently intermediate resistance in landraces enabled them to survive at an optimum level (Negassa, 1985; Czembor, 1996; Atzema, 1998).

Infection type 2 is different from infection types conferred by most of powdery mildew resistance genes used in Europe. These genes confer mostly infection type 0 and 1 (Brown, Jørgensen, 1991; Dreiseitl, Steffenson, 1996b; Dreiseitl et al., 1996; Dreiseitl, Jørgensen, 2000). Barley accessions expressing intermediate resistance to a wide-array of isolates, as observed for 12 lines (66.78%) in this study, provide a more stable resistance in barley cultivars to powdery mildew (Parlevliet, 1993; Zadoks, 1993; Czembor, Gacek, 1995). Good example of this is deployment of *Ml(La)* resistance gene conferring 2 or 3 infection types. This resistance gene has been effective for more than 10 years, despite the fact that it has been present in many barley cultivars throughout Europe (Munk et al., 1991; Jørgensen, 1994).

In most selected lines the presence of unknown genes alone or in combinations with known genes were postulated. Presence of a high number of unknown genes in barley landraces is in agreement with findings from other studies (Honecker, 1938; Ralski, Mikolajewicz, 1958; Brückner, 1964; Nover, Lehmann, 1973; Wiberg, 1974;

Czembor, 1976, 1996, 1999, 2000; Czembor et al., 1979; Negassa, 1985; Lehmann, von Bothmer, 1988; Leur et al., 1989; Leijerstam, 1996; Jørgensen, Jensen, 1997; Lehmann et al., 1998; Czembor, Czembor, 1999a; Jönsson, Lehmann, 1999). These genes for resistance to powdery mildew should be a relatively easy incorporated into a barley breeding programs by crossing lines (Jana, 1995; Czembor, 1996). Also, by using barley landraces in breeding programs it is possible often to incorporate other desirable agronomic traits, e.g. good adaptation to dry land conditions (Ceccarelli et al., 1995, 2000; Hadjichristodoulou 1995; Ceccarelli, Grando, 1999; Havaux, Tardy, 1999).

Determination of powdery mildew resistance genes based on tests performed on seedlings using isolates with different virulence spectra is effective and sufficient for breeders' and pathologist' needs (Dreiseitl, 1996; Dreiseitl, Steffenson, 1996b; Czembor, Czembor, 1998, 1999b, 2000; Dreiseitl, Jørgensen, 2000). However, it may not always predict adult plant resistance. Because of this screening germplasm for disease resistance should be conducted using seedlings and adult plants. This was done in the present study. Confirmation of putative resistance genes or alleles can only be established through evaluation of progeny from crosses and backcrosses among appropriate genotypes. Also different levels of partial resistance in tested lines may influence the postulation of presence of specific resistance genes (Jørgensen, 1994; Czembor, 1996).

In general, results of this study are in agreement with those of other investigators, in which barley landraces possessed mildew resistance genes different from genes present in cultivated varieties (Honecker, 1938; Ralski, Mikolajewicz, 1958; Brückner, 1964; Nover, Lehmann, 1973; Wiberg, 1974; Czembor, 1976, 1996, 1999, 2000; Czembor et al., 1979; Negassa, 1985; Lehmann, von Bothmer, 1988; Leur et al., 1989; Leijerstam, 1996; Jørgensen, Jensen, 1997; Lehmann et al., 1998; Czembor, Czembor, 1999a; Jönsson, Lehmann, 1999). This investigation identified new sources of resistance to barley powdery mildew in lines selected from barley landraces collected in Jordan, Egypt, Libya and Tunisia. These new sources confer resistance to all or a large number of powdery mildew virulence genes prevalent in Europe and may contribute significantly to the diversity of the powdery mildew resistance gene pool available for barley breeders.

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CZEMBOR, J. H. (Plant Breeding and Acclimatization Institute, Plant Breeding and Genetics Department, Radzików, Blonie, Poland):

Odolnost vůči padlí travnímu ve výběru z krajových odrůd ječmene získaných z Jordánska, Egypta, Libye a Tuniska.

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Bylo testováno osm krajových odrůd ječmene (*Hordem vulgare* L.) na odolnost vůči padlí travnímu (*Blumeria graminis* f. sp. *hordei*) a byly zjištěny nové zdroje odolnosti. Krajové odrůdy byly odebrány na pěti expedicích ve čtyřech zemích: Jordánsko (2 krajové odrůdy), Egypt (2 krajové odrůdy), Libye (3 krajové odrůdy) a Tunisko (1 krajová odrůda). Vzorky semen těchto krajových odrůd nám dodalo Mezinárodní centrum pro zemědělský výzkum v suchých oblastech (ICARDIA), Aleppo, Sýrie. V roce 1998 projevily všechny testované krajové odrůdy odolnost vůči přirozené infekci způsobené padlí travním v IHARu, Radzików, Polsko. 18 jednotlivých linií bylo odebráno a testováno z těchto krajových odrůd ve stadiu semenáčů s 23 různými izoláty padlí travního. Izoláty byly vybrány podle spektra virulence, jak byly sledovány na diferenční skupině izolínu „Pallas" a na 8 dalších diferenčních kultivarech. Tyto izoláty měly všechny virulence vůči veškerým hlavním genům odolnosti, které byly použity v minulosti i současnosti v Evropě. Šest linií (155-2-1, 469-2-5, 805-2-3, 806-1-1, 806-2-2, 806-3-4) prokázalo odolnost vůči všem použitým izolátům. Tyto linie byly charakterizovány podle typu reakce odolnosti 2, jaká byla zjištěna u většiny izolátů. Vyjádření typu infekce 0, 1 a 2 pro testované izoláty naznačuje, že některé z těchto linií mohou mít víc než jednu alelu odolnosti. Dvanáct (66,7 %) linií mělo typ infekce 2 pro inokulaci u více než 50 % izolátů. Jenom dvě linie měly typ odolnosti vůči infekci 0 pro většinu použitých izolátů. Asi 86,1 % všech zjištěných typů infekce mezi testovanými liniemi bylo identifikováno jako odolnost vůči padlí travnímu. Nejčastější typ (66,4 %) odolnosti vůči infekci byl typ 2. Typ infekce 0 (imunita) se vyskytoval s frekvencí 16,8 %, resp. typ infekce 1 (hypersenzitivita) s frekvencí 2,9 %. U 15 testovaných linií nebylo možné určit přítomnost specifické alely nebo alel pro odolnost. Předpokládalo se, že se alela *Mlat* vyskytuje ve dvou liniích v kombinaci s dalším neznámým genem nebo geny. Přítomnost kombinace alely *Mla12*, *Ml(Ru3)* se předpokládala u jedné linie. Bylo zjišťováno použití identifikovaných zdrojů odolnosti vůči padlí travnímu v pěstování ječmene.

ječmen; *Erysiphe graminis* f. sp. *hordei*; genetické zdroje; geny odolnosti; *Hordeum vulgare*; krajové odrůdy; padlí travní; region západní Asie a severní Afriky

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