

Powdery Mildew Resistance in Selections from Moroccan Barley Landraces

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Thirty barley landraces collected from Morocco in 1985 and 1989, and held in the Polish Gene Bank, IHAR, Radzików, Poland, were screened for resistance to powdery mildew. Fifteen tested landraces (50%) showed powdery mildew resistance reactions and 24 single plant lines were selected. Eighteen lines originating from 13 landraces were tested with 17 isolates of powdery mildew and another six lines originating from six landraces were tested with 23; the isolates were chosen according to their virulence spectra observed on the 'Pallas' isolines differential set. Three lines (E 1090-2-2, E 1110-3-2 and E 1077-1-1) showed resistance to all powdery mildew virulence genes prevalent in Europe. In 21 lines, unknown genes alone or in combination with specific ones were detected. Five different resistance alleles (*Mlat*, *Mla1*, *Mla3*, *Mlg* and *Ml(CP)*) were postulated to be present in the tested lines, alone or in combination: *Mlat* was postulated to be present in nine (~38%) lines; *Mlg* and *Ml(CP)* in two lines, and *Mla1* and *Mla3* in one tested line each. The use of newly identified sources of resistance in barley breeding as a means of controlling powdery mildew is discussed.

KEY WORDS: *Hordeum vulgare*; *Erysiphe graminis*; landraces; resistance genes; germplasm; biodiversity.

INTRODUCTION

Powdery mildew is one of the most destructive foliar diseases of barley. It is caused by the pathogen *Erysiphe graminis* DC. f.sp. *hordei* Em Marchal (syn. *Blumeria graminis* (DC.) Golovin ex Speer f.sp. *hordei*), and is of great economic importance in many major barley production regions, e.g. North America, central and northern Europe (10,33,55). Barley yield losses from powdery mildew can reach 30%, and infection causes reduced quality. Powdery mildew is especially harmful for the production of malting barley (2,21,24,55).

Powdery mildew on barley is one of the most clearly characterized systems of host-pathogen genetic interactions. Since 1907, when Biffen (3) started genetic studies of barley resistance to powdery mildew, more than 100 mildew resistance genes have been identified in barley. In Europe, barley breeders commonly used such resistance genes as *Mla6*, *Mla7*, *Mla9*, *Mla12* and *Mla13* belonging to the *Mla* locus and the resistance alleles *Mlk*, *Mlg*, *Ml(La)*, *Mlh* and *Mlra*. Many of these genes came from barley landraces originating from West Asia, Ethiopia and North Africa, including Morocco (gene *Mlat* – resistance to Atlas) (3,5,32,33). However, virtually all of these genes were gradually overcome by virulent

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rases within 4–5 years when cultivars containing them were planted over a large area (33,46).

In the 19th Century, farmers and landowners (*e.g.* Knight in England, Janasz in Poland, Vilmorin in France) started selection of attractive plants or ears from local populations of crop landraces based upon their phenotypic variation (30,31,56,66). Often only one line was selected as a new cultivar and the landrace from which it was selected, was no longer maintained. This caused within the last 150 years great genetic ‘erosion’ in major crops (7,26). Today in most European countries landraces of major crops, including barley, exist only in gene banks. Domination of pure line varieties of barley and the intensification of nitrogen fertilization are causing significant increases in susceptibility to powdery mildew and other pests and diseases (12,14). In this situation the diversity of landraces which supported agriculture for the past 9000 years is of great value to solve breeding problems including lack of sufficient resistance to barley powdery mildew (20,28,61).

In 1926, Vavilov (60) proposed the region of the Mediterranean Sea as one of the major centers of crop origin. This hypothesis was supported by a high level of crop diversity, including barley, observed in this part of the world (51,60,63,68). According to many studies barley was derived from its wild ancestor, *Hordeum spontaneum* C. Koch. This probably occurred in the region of the Zagros Mountains (western Iran) and the original area of cultivation of *Hordeum vulgare* L. was the region of the Fertile Crescent (the term coined by James Breasted in 1916, referring to the crescent-shaped region of rich farmland that stretched in ancient times from the Mediterranean Sea to the Persian Gulf through the Tigris and Euphrates valleys) (27,36,48,62,68). Recently, the discovery of wild barley in Morocco has been reported (41,42). This finding suggests that the area of Morocco may be the center of origin for cultivated barley and that barley may be a multicentric crop, domesticated along the Mediterranean basin (42,44,45). It is therefore possible that in this region barley co-evolved with the fungus *E. graminis* f.sp. *hordei* over a very long period. Taking this into account, barley landraces collected from Morocco may be a rich source of new genes for resistance to powdery mildew.

The objective of this study was to determine the presence of known and previously unknown powdery mildew resistance genes in lines selected from barley landraces from Morocco.

MATERIALS AND METHODS

Plant material

Seed samples of 19 landraces of *Hordeum vulgare* L. were provided by Dr. W. Podyma (Polish Gene Bank, IHAR, Radzików, Poland). They were collected in Morocco during two expeditions. Eighteen landraces were collected in an expedition organized by the Warsaw Agricultural Academy during April–June 1985, in parts of the Middle, High Atlas and Rif Mountain ranges (53). Another 12 landraces were collected in an expedition organized by the Polish Entomological Society and Plant Breeding and Acclimatization Institute during April and May 1989, in parts of the Middle, High Atlas and Rif Mountain ranges in Morocco, and in Algeria (54). All collected barley landraces were of a spring growth type, had covered kernels and six-row heads. Under Polish conditions they were intermediate in heading date and showed low resistance for lodging.

Pathogen

Thirty-five isolates of *E. graminis* f.sp. *hordei* Em Marchal were used (Table 1). They originated from the collections in Ris National Laboratory, Roskilde, Denmark; Danish Institute for Plant and Soil Science, Lyngby, Denmark; Edigenossische Technische Hochschule – ETH, Zurich, Switzerland (provided by Dr. H.J. Schaerer, ETH); and IHAR, Radzików, Poland. The isolates were chosen according to their virulence spectra which were observed on the ‘Pallas’ isolines differential set (35), provided by Dr. L. Munk (Royal Agricultural and Veterinary University, Copenhagen, Denmark). They were purified by single pustule isolation and were maintained and propagated on young seedlings of the powdery mildew susceptible cv. ‘Manchuria’ (CI 2330). Frequent virulence checks were made to assure the purity of isolates throughout the experiment.

Disease Assessment

After 8–10 days of incubation, the infection types were scored according to a 0–4 scale developed by Mains and Dietz (40). The seedlings were classified into susceptible or resistant groups. Plants scored 0 – 2 were included in the resistant group and plants scored 3 and 4 were included in the susceptible group.

Resistance tests

These tests were conducted during 1994–99 at IHAR, Radzików, Poland. In winter 1994/95 ~30 plants per landrace were evaluated in the greenhouse with a mixture of *E. graminis* f.sp. *hordei* isolates with all virulences known in Europe. Cv. Manchuria was used as the susceptible control. Fifteen (50%) of the tested landraces showed resistance reactions. Five landraces (~33%) were heterogeneous for mildew reaction. From each landrace, one to five resistant plants were selected. Twenty-four single plant lines were obtained. Two lines were assumed to carry Mlo resistance, but they were discarded after microscope investigation proved that they did not show characteristics of Mlo resistance. Eighteen lines originating from 13 landraces were tested with 17 isolates of powdery mildew during winter 1997/98 (Tables 2, 3) and another six lines originating from six landraces were tested with 23 isolates during winter 1998/99 (Tables 2, 4). All these tests were conducted in the IHAR greenhouse. The plants were grown under a 16-h daylength at 16–22°C. The inoculation was carried out when plants were 10–12 days old by shaking or brushing conidia from diseased plants. After 8–10 days of incubation, the disease reaction types evinced by seedlings were scored.

Postulation of resistance alleles

Identification of resistance genes was made by eliminating the resistance genes not present in the tested lines. The next step was to determine the postulated and possible resistance genes (9); this was done on the basis of the gene-for-gene hypothesis (23).

RESULTS

Among 30 investigated landraces from Morocco, 15 (50%) showed resistance for *E. graminis* f.sp. *hordei*. However, most of the landraces (80%) showing resistance originated from the Warsaw Agricultural Academy expedition in 1985. Among 12 landraces collected in the expedition organized by Polish Entomological Society and Plant Breeding and Acclimatization Institute in 1989, only three showed resistance.

TABLE 1. Differential isolates and their infection types on the 'Pallas' differential set

Differential set		Isolates																
Isolines Gene		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
		58-74	59-11	59-12	63-1	A6	D17	EmA30	GE	HL3/5	HL3/6	JEH11	MH1	MH1-2	R13C	R63	R71/1	R86.1
Pallas	<i>Mla8</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
P1	<i>Mla1</i>	0	4	0	4	4	4	4	0	0	0	0	0	0	0	0	0	0
P2	<i>Mla3</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P3	<i>Mla6,Mla14</i>	0	0	0	0	0	0	0	4	4	4	0	4	0	4	4	0	4
P4A	<i>Mla7,Mlk,?</i>	4	4	4	4	0	2	0	0	2	0	4	2	2	2	4	1	2
P4B	<i>Mla7,?</i>	4	4	4	4	1	1	0	0	2	2	4	4	4	2	4	2	2
P6	<i>Mla7,Ml(LG2)</i>	4	4	4	4	0	0	0	1	2	0	4	4	4	2	4	1	2
P7	<i>Mla9, Mlk</i>	4	4	0	4	0	0	0	0	0	0	4	0	0	0	0	0	0
P8A	<i>Mla9, Mlk</i>	4	4	0	4	0	0	0	0	0	0	4	0	0	0	0	0	0
P8B	<i>Mla9</i>	4	4	0	4	0	0	0	0	0	0	4	0	0	0	0	0	0
P9	<i>Mla10, Ml(Du2)</i>	4	4	4	4	0	0	4	0	0	0	4	0	0	1	2	4	0
P10	<i>Mla12</i>	0	0	0	4	0	0	4	0	0	0	0	2	4	4	4	4	0
P11	<i>Mla13, Ml(Ru3)</i>	4	2	0	4	0	0	0	0	0	0	0	4	4	0	4	0	0
P12	<i>Mla22</i>	4	4	4	0	4	4	4	4	4	4	0	4	4	4	4	0	4
P13	<i>Mla23</i>	2	4	1	1	1	1	1	1	2	1	2	2	1	2	1	2	2
P14	<i>Mlra</i>	4	4	4	4	0	4	4	4	4	4	4	0	0	4	4	4	4
P15	<i>Ml(Ru2)</i>	3	4	4	4	4	2	4	2	2	4	2	2	0	4	4	4	2
P17	<i>Mlk</i>	4	4	4	4	0	2	2	2	2	0	4	0	2	2	2	2	2
P18	<i>Mlnn</i>	4	4	4	4	4	4	4	4	4	4	4	3	4	4	4	4	4
P19	<i>Mlp</i>	2	0	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2
P20	<i>Mlat</i>	2	0	2	2	4	2	2	2	2	2	4	2	2	2	2	2	2
P21	<i>Mlg, Ml(CP)</i>	4	4	4	4	0	0	0	4	4	4	0	4	4	0	0	0	0
P22	<i>mlo5</i>	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	3	3	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)	0(4)
P23	<i>Ml(La)</i>	2	4	4	4	3	2	3	2	2	3	3	2	4	3	4	4	4
P24	<i>Mlh</i>	4	4	4	4	0	4	4	4	0	4	4	4	4	4	4	4	4

TABLE 1. Continued

Differential set	Isolates																	
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Isolines Gene	R189	R261	R275	R303	Ru3	TR2	Ry4d	En1/A1	R303.1	E92	59-	SZ/C10	Ra7	Ra9	Ra10	Ra13	Ra16	Ra22
											11.1							
Pallas	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Mia8	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	4	0	0
Mia1	4	0	0	0	0	4	0	0	0	0	0	4	0	4	0	0	0	0
Mia3	4	0	0	0	0	4	0	0	0	0	0	4	0	4	0	0	0	0
Mia6, Mia14	4	0	0	0	0	4	0	0	0	0	0	4	4	4	4	4	4	4
Mia7, Mik, ?	2	4	0	0	0	2	2	4	0	4	4	2	0	4	4	4	4	4
Mia7, ?	2	4	0	0	0	2	2	4	0	4	4	2	0	4	4	4	4	4
Mia7, MI(LG2)	0	4	0	0	0	1	0	4	0	4	4	0	0	2	1	2	4	4
Mia9, Mik	1	4	4	0	0	4	0	0	0	0	0	0	0	0	0	0	4	0
Mia9, Mik	1	4	4	0	0	4	0	0	0	0	0	0	0	0	0	0	4	0
Mia9	4	4	4	0	0	4	0	0	0	0	0	0	0	0	0	0	4	0
Mia10,	0	4	4	4	0	4	4	4	0	4	4	0	0	4	4	4	4	4
MI(Du2)																		
Mia12	0	0	0	0	0	4	4	4	0	4	0	4	0	4	4	4	2	4
Mia13,	0	0	4	0	0	0	0	4	0	0	0	0	0	0	4	4	0	4
MI(Ru3)																		
Mia22	4	0	0	0	4	4	0	4	0	0	4	4	4	0	4	4	0	0
Mia23	1	2	2	1	1	2	2	1	1	2	2	2	2	2	2	1	1	2
Mira	4	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4
Mi(Ru2)	2	4	2	2	2	2	2	4	4	4	4	4	4	4	4	4	4	4
Mik	2	4	4	0	1	4	2	4	2	4	4	0	2	4	4	4	4	4
Minn	4	3	4	0	4	4	4	4	4	4	4	0	4	4	4	4	4	2
Mlp	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	2	0
Mlat	2	4	2	0	2	2	2	2	2	2	2	4	2	2	4	4	2	2
Mig,	0	4	4	3	4	4	4	4	4	4	4	4	0	4	4	4	4	4
MI(CP)																		
mlo5	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)	0(4)	0(4)
MI(La)	2	2	3	3	4	4	4	4	4	4	2	4	4	4	4	4	4	4
Mlh	4	4	4	3	4	4	0	4	4	0	4	4	4	4	4	4	4	4

TABLE 2. Collection site details of 15 barley landraces from Morocco showing resistance to powdery mildew

No.	IHAR No.	Name	Date	Altitude (m)	Province	Site
1	PL 42752	Ex 1068	10.05.1985	1300-1400	Agadir	Agaouz
2	PL 42984	Ex 1077	10.05.1985	1300-1400	Agadir	Agaouz
3	PL 42753	Ex 1079	11.05.1985	1300-1400	Agadir	Agaouz
4	PL 42754	Ex 1084	11.05.1985	1300-1400	Agadir	Agaouz
5	PL 42755	Ex 1086	12.05.1985	1300-1400	Agadir	Agaouz
6	PL 42756	Ex 1090	13.05.1985	1300-1400	Agadir	Agaouz
7	PL 42759	Ex 1095	14.05.1985	1300-1400	Agadir	Timicht
8	PL 42762	Ex 1103	20.05.1985	500-600	Fes	Lesaiss
9	PL 42763	Ex 1110	21.05.1985	500-600	Meknes	15 km E Meknes
10	PL 42765	Ex 1122	22.05.1985	200	Rabat	Tiflet
11	PL 42766	Ex 1132	27.05.1985	300-400	Rabat	Ouazzane
12	PL 42767	Ex 1138	28.05.1985	400-500	Rabat	Ouazzane
13	PL 43341	Ex 2360	20.05.1989	1350	–	Askaun
14	PL 43345	Ex 2383	25.05.1989	1550	–	Azilal
15	PL 43352	Ex 2454	24.06.1989	350	–	Chefchaouen

All 24 lines tested, originating from these 15 landraces, possessed a resistance allele(s) for powdery mildew of barley (Tables 3, 4). Three lines (E 1090-2-2, E 1110-3-2 and E 1077-1-1) which originated from three landraces, showed resistance to all isolates used. Resistance of these lines was characterized by reaction types 2 (mycelium, slight sporulation and chlorosis or necrosis). Generally, the distribution of reaction type scores of all tested lines indicated that ~82% of all reaction types observed were classified as powdery mildew resistant (scores 0, 1 and 2) (Table 5). The most frequent score was 2 (64%); 21 lines (88%) showed this reaction for inoculation with more than 50% of the isolates used. Score 0 was frequent at 13% and two lines showed this reaction for inoculation by most isolates used. The least frequent resistance reaction observed was reaction 1 (~5%).

The distribution of reaction types scores indicates that some tested lines had more than one gene for resistance. In 11 of the tested lines it was impossible to postulate which specific allele(s) for resistance is present. However, the presence of reaction types 0, 1 and 2 in some of these lines indicates that they may have many alleles for resistance.

In 21 lines the presence of an unknown gene, or the combination of an unknown gene with a specific one, was detected (Tables 3, 4). Five different resistance alleles (*Mlat*, *Mla1*, *Mla3*, *Mlg*, and *Ml(CP)*) were postulated to be present in the tested lines, alone or in combination. Allele *Mlat* was the most common in the tested lines, and postulated to be present in nine (~38%) lines. Alleles *Mlg* and *Ml(CP)* were postulated to be present in two, and alleles *Mla1* and *Mla3* in one tested line.

DISCUSSION

For the last 30 years any usage of chemicals (pesticides, fungicides, herbicides, and mineral fertilizers) in agriculture has been increasingly criticized in many developed countries and in general, environmental standards are becoming higher throughout the world (4,25). Therefore, control of powdery mildew will have to focus more and more on ecologically acceptable methods, such as breeding for resistance. In the 20th Century more than 36 alleles for race-specific resistance to powdery mildew alone or in combination

TABLE 3. Infection types of 18 barley landraces listed according to infection by 17 isolates of *Erysiphe graminis* f.sp. *hordei* and their postulated resistance alleles

IHAR No.	Isolates																	Postulated resistance alleles	Possible alleles ^z
	1	2	4	6	8	9	11	12	14	15	16	17	18	19	20	21	24		
	58-74	59-11	63-1	D17	GE	HL 3/5	JEH 11	MH 1	R 13C	R 63	R 71/1	R 86.1	R 189	R 261	R 275	R 303	Ry 4d		
E 1068-2-1	1	4	0	2	2	1	2	2	4	2	1	2	2	4	2	2	2	+?2 ^y	<i>Ml(Ru2)</i>
E 1079-1-1	2	4	1	2	2	2	4	2	2	2	2	2	2	4	2	0	4	+?	<i>Mlat</i>
E 1084-2-1	2	2	1	2	2	2	4	2	2	2	2	2	2	4	2	2	4	+?	<i>Mlat</i>
E 1086-3-4	0	4	0	4	2	2	4	2	4	4	2	4	2	2	2	2	4	+?	<i>Mla7</i>
E 1090-2-4	1	0	0	2	1	2	2	2	2	2	2	2	4	2	2	0	2	<i>Mla3</i> , +?	
E 1090-2-2	0	3	1	1	2	2	2	2	2	2	2	2	2	2	2	0	2	+?	
E 1090-5-4	2	2	2	2	2	2	4	2	2	2	2	2	2	4	2	2	2	<i>Mlat</i>	
E 1095-3-2	0	2	0	2	2	0	0	4	2	2	0	2	2	0	2	0	2	+?	
E 1095-2-3	2	2	2	2	2	2	4	2	2	2	2	2	4	4	2	2	2	<i>Mlat</i> , +?	
E 1103-1-2	4	2	0	2	1	2	4	4	2	2	2	2	2	4	2	0	2	<i>Mlat</i> , +?	
E 1103-3-4	2	2	2	1	0	2	4	2	2	2	2	0	4	4	2	2	2	<i>Mlat</i> , +?	
E 1110-3-2	2	2	0	2	2	2	0	2	2	2	2	2	2	2	2	0	2	+?	
E 1110-2-1	2	2	2	2	2	1	4	2	2	2	2	2	2	4	2	2	2	<i>Mlat</i>	
E 1122-1-2	4	4	2	4	4	4	2	4	2	2	2	2	2	4	2	2	2	<i>Mlg</i> , <i>Ml(CP)</i> , +?	
E 1132-1-1	2	2	2	4	2	2	4	2	2	2	2	2	2	4	2	2	4	+?	<i>Mlat</i>
E 1138-2-3	4	4	2	4	4	2	0	4	2	1	2	2	2	4	2	2	2	<i>Mlg</i> , <i>Ml(CP)</i> , +?	
E 1077-1-1	1	2	1	1	2	2	1	2	2	1	1	2	2	2	1	1	2	+?	
E 2383-1-1	4	2	2	2	2	1	4	2	4	2	2	2	2	4	2	2	4	+?	<i>Mlat</i>

^zResistance alleles which were not eliminated from the reactions of susceptibility and could not be confirmed by the reactions of resistance.^yUnidentified resistance allele, not present in the 'Pallas' isolines set.

TABLE 4. Resistance alleles and infection types of six lines to infection by 23 isolates of *Erysiphe graminis* f.sp. *hordei* and their postulated resistance alleles

IHAR No.	Isolates																							Postulated resistance alleles
	1	3	4	5	7	10	11	13	18	21	22	23	25	26	27	28	29	30	31	32	33	34	35	
	58-74	59-12	63-1	A6	EmA30	HL3/5-1	JEH11	MH1-2	R189	R303	Ru3	TR2	En1/A1	R3031	E92	59-11.1	SZ/C10	Ra7	Ra9	Ra10	Ra13	Ra16	Ra22	
E1079-1-3	2	2	2	2	2	2	4	2	2	2	2	2	2	2	2	2	2	2	2	4	2	2	2	<i>Mlat</i> , + ^z
E1084-1-2	0	0	0	0	0	2		0	0	0	4	2	0	2	0	0	0	0	2	0	0	4	0	+?
E1090-5-5	2	4	4	4	2	2	4	2	2	2	2	2	2	2	2	2	2	2	2	4	4	4	2	<i>Mlat</i> , +?
E2383-1-3	2	2	2	4	2	2	4	4	2	2	2	2	2	2	2	2	4	2	2	4	4	2	2	<i>Mlat</i> , +?
E2454-1-3	0	0	4	4	0	0	0	0	0	0	0	2	0	0	4	0	0	0	0	2	4	0	0	<i>Mla1</i> , +?
E2360-2-3	2	2	2	4	2	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	2	2	<i>Mlat</i>

^zUnidentified resistance allele, not present in the 'Pallas' isolines set.

TABLE 5. Frequency of infection types of 24 lines for isolates of *Erysiphe graminis* f.sp. *hordei*

IHAR No.	Number of isolates that produced infection type					Total
	0	1	2	3	4	
E 1068-2-1	1	3	10	0	3	17
E 1079-1-1	1	1	11	0	4	17
E 1079-1-3	0	0	21	0	2	23
E 1084-1-2	17	0	4	0	2	23
E 1084-2-1	0	1	13	0	3	17
E 1086-3-4	2	0	8	0	7	17
E 1090-2-4	3	2	11	0	1	17
E 1090-2-2	2	2	12	1	0	17
E 1090-5-4	0	0	15	0	2	17
E 1090-5-5	0	0	16	0	7	23
E 1095-3-2	7	0	9	0	1	17
E 1095-2-3	0	0	14	0	3	17
E 1103-1-2	2	1	10	0	4	17
E 1103-3-4	2	1	11	0	3	17
E 1110-3-2	3	0	14	0	0	17
E 1110-2-1	1	0	14	0	2	17
E 1122-1-2	0	0	10	0	7	17
E 1132-1-1	0	0	13	0	4	17
E 1138-2-3	1	1	9	0	6	17
E 1077-1-1	0	8	9	0	0	17
E 2360-2-3	0	0	18	0	5	23
E 2383-1-1	0	1	11	0	5	17
E 2383-1-3	0	0	17	0	6	23
E 2454-1-3	17	0	2	0	4	23

were used in Europe since the first gene, *Mlg*, was introduced on a large scale in the 1930s in Germany. These genes were used in more than 690 cultivars. Twenty-eight of these alleles are closely linked or allelic. This limits greatly the possible number of gene combinations in breeding of new cultivars (5,7,19,33). Also, because of a host erosion of partial resistance during breeding for race-specific resistance (Vertifolia effect), cultivars with resistance genes which lost their value to control powdery mildew effectively had to be discarded (12,13,59). Taking this into account, the introduction of new, unknown genes for resistance to barley powdery mildew is needed.

Barley breeders are seeking gene pools from which new genes can be introduced into existing cultivars in order to improve their stability and their resistance to powdery mildew. Barley landraces, especially those originating from centers of origin for cultivated barley (16,18,58), constitute such a gene pool. This study showed that barley landraces from Morocco are a very valuable source of resistance to powdery mildew. Among 30 investigated barley landraces from Morocco, 15 (50%) showed resistance for *E. graminis* f.sp. *hordei*. However, of 18 landraces collected in 1985 – 13 (72%) showed resistance, and of 12 landraces collected in 1989 – three (25%) showed resistance. This percent of landraces with resistance to powdery mildew is higher than observed in other studies (11,15,20,29,34,37,38,47,50). It is possible that it was due to the fact that different isolates of powdery mildew were used for evaluation of resistant lines.

All 24 single plant lines selected from these landraces possessed a resistance allele(s) for powdery mildew, but only three lines (E 1090-2-2, E 1110-3-2 and E 1077-1-1) showed resistance to all isolates used. The isolates in this experiment had virulences corresponding to all major resistance genes used in the past and currently in Europe. Therefore, it may be concluded that these lines had resistance to all the powdery mildew virulence genes prevalent in Europe. Such lines should be used in barley breeding programs as new and highly valuable sources of resistance to powdery mildew (20). The frequency of powdery-mildew-resistant landraces (Ex 1092, Ex 1110 and Ex 1077) to all isolates of powdery mildew in the present study, 10%, is similar to or higher than that assessed in other studies (11,15,20,29,34,37,38,47,50).

Plant breeders have to deal with the high level of pathogenic variability encountered in natural populations of *E. graminis* f.sp. *hordei* (6,39). In order to increase the durability of effectiveness of resistance genes, many different strategies for deploying resistance genes in barley were developed. The most common of these strategies are multiline cultivars, combining ('pyramiding') different resistance genes into one cultivar and deploying many cultivars with different resistance genes in space or time (13,14,33,64). With these strategies, the new sources of resistance to powdery mildew originating from Moroccan landraces described in this study may also be used.

The most common specific resistance allele was *Mlat*, which was postulated to be present in ~38% of the 21 lines tested. This corresponds with the fact that virulence to *Mlat* is common in the Moroccan mildew population and that the *Mlat* resistance gene was originally described from western North Africa (8,33,65). The presence in barley landraces of a large number of genes different from major resistant genes used in Europe, is in agreement with findings in other studies (11,15,20,29,34,37,38,47,50).

There are great contrasts in the natural conditions in Morocco, due to the country's transitional location between the Mediterranean winter-rain zone and the Sahara desert (52). This is reflected in highly diverse plant material, including barley obtained on Polish germplasm collection missions in 1985 and 1989 (53,54). Observations made by many investigators suggest that due to drought and desertification, barley landraces are subjected to genetic erosion. Because of this, collecting missions in Morocco are highly recommended (21,52,53,54,57,67). The importance of this crop in Morocco is due to the fact that it is often the only one possible under rain-fed conditions and it is cultivated on mountain slopes at elevations higher than suitable for other cereals. Many scientists suggest that barley landraces survive the biotic and abiotic stresses because of their high level of heterogeneity (22,49,52). A high level of heterogeneity was observed also in this study. Five landraces (~33%) were heterogeneous for mildew reaction; this proportion is higher than that reported in other studies (20,50).

On fields of barley landraces, powdery mildew rarely develops to levels that significantly lower the yield. This has been attributed both to the stabilizing effect of the genetic heterogeneity within the landraces and to the presence of resistance sufficient to limit disease development (1,38), and was confirmed in this study. Tests for powdery mildew resistance performed on seedlings usually satisfy the needs of breeders and pathologists. However, the results of these tests do not necessarily predict adult plant resistance and field performance of the selected resistant lines (20).

This study showed that barley landraces from Morocco are very rich sources of resistance to powdery mildew. The findings described herein are generally in agreement

with those of others who have investigated resistance of barley landraces to powdery mildew (11,15,20,29,34,37,38,47,50). In this study new sources of resistance to barley powdery mildew were identified in lines selected from barley landraces from Morocco. These sources confer resistance against all or a large number of powdery mildew virulence genes prevalent in Europe, and may contribute greatly to the diversification of resistance genes in modern barley cultivars.

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REFERENCES

1. Andrivon, D. and de Vallavieille-Pope, C. (1992) Race-specific resistance genes against *Erysiphe graminis* f.sp. *hordei* in old and recent French barley accessions. *Plant Breeding* 108:40-52.
2. Balkema-Boomstra, A.G. and Mastebroek, H.D. (1995) Effect of powdery mildew (*Erysiphe graminis* f.sp. *hordei*) on photosynthesis and grain yield of partially resistant genotypes of spring barley (*Hordeum vulgare* L.). *Plant Breeding* 114:126-130.
3. Biffen, R.K. (1907) Studies on the inheritance of disease resistance. *J. Agric. Sci., Cambridge* 2:109-128.
4. Brown, J.K.M. (1996) Fungicide resistance in barley powdery mildew: from genetics to crop protection. *European and Mediterranean Cereal Rust and Powdery Mildews Conf.* (Lunteren, the Netherlands), pp. 259-267.
5. Brown, J.K.M. and Jørgensen, J.H. (1991) A catalogue of mildew resistance genes in European barley varieties. in: Jørgensen, J.H. [Ed.] *Integrated Control of Cereal Mildews: Virulence Patterns and Their Change*. Risø National Laboratory, Roskilde, Denmark. pp. 263-286.
6. Brown, J.K.M. and Wolfe, M.S. (1990) Structure and evolution of a population of *Erysiphe graminis* f.sp. *hordei*. *Plant Pathol.* 39:376-390.
7. Brush, S.B. (1992) Reconsidering the green revolution: diversity and stability in cradle areas of crop domestication. *Human Ecol.* 20:145-167.
8. Caddel, J.L. (1976) Sources of resistance to powdery mildew of barley in Morocco. *Plant Dis. Rep.* 60:65-68.
9. Caffier, V. and de Vallavieille-Pope, C. (1996) Regional distribution of resistances to powdery mildew in winter and spring barley cultivars grown in the northern part of France. *Plant Breeding* 115:94-100.
10. Ceccarelli, S., Grando, S. and van Leur, J.A.G. (1995) Barley landraces of the fertile crescent offer new breeding options for stress environments. *Diversity* 11:112-113.
11. Czembor, H.J. (1976) Sources of resistance of barley to *Erysiphe graminis* f.sp. *hordei*. *Hodowla Rośl. Aklim. Nasienn.* 20:467-490.
12. Czembor, H.J. and Gacek, E.S. (1990) Selected problems of the disease resistance breeding of cereals. *Biul. Inst. Hodowli Aklim. Rośl.* 173-174:53-62.
13. Czembor, H.J. and Gacek, E.S. (1995) Systems for increasing durability of disease resistance in cereals. *Proc. Second Symp. on Plant Resistance to Diseases, Pests and Unfavorable Environmental Conditions* (Radzików, Poland), pp. 39-48.
14. Czembor, H.J. and Gacek, E.S. (1996) The use of cultivar and species mixtures to control diseases and for yield improvement in cereals in Poland. in: Limpert, E., Finckh, M.R. and Wolfe, M.S. [Eds.] *Integrated Control of Cereal Mildews and Rusts: Towards Co-ordination of Research Across Europe*. Kluwer, Dordrecht, the Netherlands. pp. 177-184.

15. Czembor, H.J., Gacek, E.S. and Kudla, M.M. (1979) Sources of resistance to barley mildew *Erysiphe graminis* f.sp. *hordei*. *Hodowla Rośl. Aklim. Nasienn.* 23:337-355.
16. Czembor, J.H. (1999) Resistance to powdery mildew in barley landraces from Tunisia. *Plant Breeding Seed Sci.* 43(2):(in press).
17. Czembor, J.H. and Czembor, H.J. (1998) Powdery mildew resistance in cultivars of spring barley from Polish Register. *Plant Breeding Seed Sci.* 42(2):87-99.
18. Czembor, J.H. and Czembor, H.J. (1999) Resistance to powdery mildew in barley landraces collected from Jordan. *Plant Breeding Seed Sci.* 44:(in press).
19. Czembor, J.H. and Czembor, H.J. (1999) Powdery mildew resistance in cultivars of winter barley from Polish Register. *Plant Breeding Seed Sci.* 43(1):65-75.
20. Czembor, J.H. and Johnston, M.R. (1999) Resistance to powdery mildew in selections from Tunisian barley landraces. *Plant Breeding* 118(6):(in press).
21. Damania, A.B. (1988) Sampling of cereal diversity in Morocco. *Plant Genet. Res. Newsl.* 72:29-30.
22. Fekadu, A and Parlevliet, J.E. (1997) Variation between and within Ethiopian barley landraces. *Euphytica* 94:183-189.
23. Flor, H.H. (1956) The complementary genetic systems in flax and flax rust. *Adv. Genet.* 8:29-54.
24. Griffiths, E. (1984) Foliar diseases: the damage caused and its effect on yield. in: Wood, R.K.S. and Jellis, G.J. [Eds.] *Plant Diseases: Infection, Damage and Loss*. Blackwell Scientific Publications, Oxford, UK. pp. 149-159.
25. Gullino, M.L. and Kuijpers, L.A.M. (1994) Social and political implications of managing plant diseases with restricted fungicides in Europe. *Annu. Rev. Phytopathol.* 32:559-79.
26. Hammer, K., Knupffer, H., Xhuveli, L. and Perrino, P. (1996) Estimating genetic erosion in landraces – two case studies. *Genet. Res. Crop Evol.* 43:329-336.
27. Harlan, J.R. (1995) Agricultural origins and crop domestication in the Mediterranean region. *Diversity* 11:14-16.
28. Hintum, Th.J.L. von (1996) Core collections in germplasm conservation: Evaluation and use. *Int. Conf. and Int. Barley Genetics Symp.* (University of Saskatchewan, Saskatoon, Saskatchewan, Canada), pp. 113-119.
29. Honecker, L. (1938) Über die physiologische Spezialisierung des Gerstenmeltaues als Grundlage für die Immunitätszucht. *Züchter* 10:169-181.
30. Janasz, A. (1893) Description of a Farm in the Kingdom of Poland Cultivated Chiefly for the Production of Seeds of Improved Agricultural Crops – The World's Colombian Exposition at Chicago. Chicago, IL, USA.
31. Jensen, N.F. (1988) *Plant Breeding Methodology*. John Wiley and Sons, New York, NY.
32. Jørgensen, J.H. (1992) Genes for powdery mildew reaction. *Barley Genet. Newsl.* 22:110-131.
33. Jørgensen, J.H. (1994) Genetics of powdery mildew resistance in barley. *Crit. Rev. Plant Sci.* 13:97-119.
34. Jørgensen, J.H. and Jensen, H.P. (1997) Powdery mildew resistance in barley landrace material. I. Screening for resistance. *Euphytica* 97:227-233.
35. Kølster, P., Munk, L., Stølen, O. and Løhde, J. (1986) Near-isogenic barley lines with genes for resistance to powdery mildew. *Crop Sci.* 26:903-907.
36. Ladizinski, G. (1998) How many tough-rachis mutants gave rise to domesticated barley? *Genet. Res. Crop Evol.* 45:411-414.
37. Lehmann, L. and von Bothmer, R. (1988) *Hordeum spontaneum* and land races as a gene resource for barley breeding. in: Jorna, M.L. and Sloomaker, L.A.J. [Eds.] *Cereal Breeding Related to Integrated Cereal Production*. Pudoc, Wageningen, the Netherlands. pp. 190-194.
38. Leur, J.A.G. van, Ceccarrelli, S. and Grando, S. (1989) Diversity for disease resistance in barley landraces from Syria and Jordan. *Plant Breeding* 103:324-335.

39. Limpert, E. (1987) Barley mildew in Europe: evidence of wind-dispersal of the pathogen and its implications for improved use of host resistance and of fungicides for mildew control. *in*: Wolfe, M.S. and Limpert, E. [Eds.] *Integrated Control of Cereal Mildews: Monitoring the Pathogen*. Martinus Nijhoff, Dordrecht, the Netherlands. pp. 31-33.
40. Mains, E.B. and Dietz, S.M. (1930) Physiologic forms of barley mildew, *Erysiphe graminis hordei* Marchal. *Phytopathology* 20:229-239.
41. Molina-Cano, J.L. and Conde, J. (1980) *Hordeum spontaneum* C. Koch emend Bacht. collected in southern Morocco. *Barley Genet. Newsl.* 10:44-47.
42. Molina-Cano, J.L., Fra-Mon, P., Salcedo, G., Aragoncillo, C., Roca de Togores, F. and Garcia-Olmedo, F. (1987) Morocco as a possible domestication center for barley: biochemical and agromorphological evidence. *Theor. Appl. Genet.* 73:531-536.
43. Molina-Cano, J.L., Gomez-Campo, C. and Conde, J. (1982) *Hordeum spontaneum* C. Koch as a weed of barley fields in Morocco. *Z. Pflanzzücht.* 88:161-167.
44. Molina-Cano, J.L., Moralejo, M., Igartua, E. and Romagosa, I. (1999) Further evidence supporting Morocco as a centre of origin of barley. *Theor. Appl. Genet.* 98:913-918.
45. Moralejo, M., Romagosa, I., Salcedo, G., Sanchez-Monge, R. and Molina-Cano, J.L. (1994) On the origin of Spanish two-rowed barleys. *Theor. Appl. Genet.* 87:829-836.
46. Munk, L., Jensen, H.P. and Jørgensen, J.H. (1991) Virulence and disease severity of barley powdery mildew in Denmark 1974–1989. *in*: Jørgensen J.H. [Ed.] *Integrated Control of Cereal Mildews: Virulence Patterns and Their Change*. Risø National Laboratory, Roskilde, Denmark. pp. 55-65.
47. Negassa, M. (1985) Geographic distribution and genotypic diversity of resistance to powdery mildew of barley in Ethiopia. *Hereditas* 102:113-121.
48. Nesbitt, M. (1995) Clues to Agricultural Origins in the Northern Fertile Crescent. *Diversity* 11:142-143.
49. Nevo, E. (1998) Genetic diversity in wild cereals: Regional and local studies and their bearing on conservation *ex situ* and *in situ*. *Genet. Res. Crop Evol.* 45:355-370.
50. Nover, I. and Lehman, C.O. (1973) Resistenzeigenschaften im gersten- und weizensortiment Gatersleben 17. Prüfung von sommergersten auf ihr verhalten gegen mehltau (*Erysiphe graminis* DC. f.sp. *hordei* Marchal). *Kulturpflanze* 21:275-294.
51. Perrino, P. (1988) The diversity in Vavilov's Mediterranean gene center. *Kulturpflanze* 36:85-105.
52. Perrino, P., Polignano, G.B., Sui-Kwong, J. and Khouya-Ali, M. (1986) Collecting Germplasm in Southern Morocco. *Plant Genet. Res. Newsl.* 65:26-28.
53. Podyma, W. (1988) Sprawozdanie z ekspedycji naukowej do Maroka w 1985 roku w celu zebrania miejscowych odmian roślin uprawnych. *in*: *Roślinne Zasoby Genowe oraz Synteza Materiałów Wyjściowych dla Hodowli, Materiały z Sympozjum, Radzików 15-16.10.1985, Zeszyty Problemowe IHAR, Radzików, Poland*. [Report from expedition to Morocco to collect crop landraces in 1985. *Proc. Symp. on Plant Genetic Resources and Initial Material for Plant Breeding* (Radzikow, Poland, 1985).]
54. Podyma, W. (1989) Collecting Missions – Morocco. *Polish Gene Bank Newsl.* 2:2.
55. Rasmusson, D.C. (1985) Barley. American Society of Agronomy, Crop Science Society of America and Soil Science Society of America, Publishers, Madison, WI, USA.
56. Simmonds, N.W. (1987) Principles of Crop Improvement. Longman Scientific and Technical, New York, NY.
57. Tazi, M., Birouk, A., Fatemi, Z. and Heiffer, P. (1989) Collecting germplasm in Morocco. *Plant Genet. Res. Newsl.* 77:39.
58. Valkoun, J., Robertson, L.D. and Konopka, J. (1995) Genetic resources at the heart of ICARDA mission throughout the Mediterranean region. *Diversity* 11:23-26.
59. Vanderplank, J.E. (1982) Host-Pathogen Interactions in Plant Disease. Academic Press, New York, NY.

60. Vavilov, N. (1926) Origin and Geography of Cultivated Plants. Cambridge Univ. Press, Cambridge, UK.
61. Weltzien, E. (1988) Evaluation of barley (*Hordeum vulgare* L.) landrace populations originating from different growing regions in the Near East. *Plant Breeding* 101:95-106.
62. Willcox, G. (1995) Archeobotanists sleuth out origins of agriculture from early Neolithic sites in the Eastern Mediterranean. *Diversity* 11:141-142.
63. Williams, J.T. (1988) Vavilov's centers of diversity and the conservation of genetic resources. *Plant Gen. Res. Newsl.* 72:6-8.
64. Wolfe, M.S. (1984) Trying to understand and control powdery mildew. *Plant Pathol.* 33:451-466.
65. Yahyaoui, A.H., Reinhold, M. and Scharen, A.L. (1997) Virulence spectrum in populations of barley powdery mildew pathogen, *Erysiphe graminis* f.sp. *hordei* in Tunisia and Morocco in 1992. *Plant Pathol.* 46:139-146.
66. Zeven, A.C. (1996) Results of activities to maintain landraces and other material in some European countries *in situ* before 1945 and what we may learn from them. *Genet. Res. Crop Evol.* 43:337-341.
67. Zine Elabidine, F., Mellas, H. and Rh'rib, K. (1995) Erosion of Morocco's great genetic wealth cause for concern. *Diversity* 11:82-83.
68. Zohary, D. and Hopf, M. (1988) Domestication of Plants in the Old World. Clarendon Press, Oxford, UK.