

RESISTANCE TO POWDERY MILDEW IN BARLEY LANDRACES FROM MOROCCO

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SUMMARY

A total of 44 accessions of barley landraces from Morocco were screened for resistance to powdery mildew. Nineteen of the tested landraces showed resistance reactions and 45 lines were selected. Sixteen of these lines were tested at the seedling stage with 17, and another 29 lines with 23 differential isolates of powdery mildew respectively. Six lines (170-1-3, 172-3-2, 173-1-2, 181-3-5, 201-3-2, 201-3-3) were identified that have resistance to all the prevalent European powdery mildew virulence genes. It was postulated that 3 different resistance alleles (*Mlat*, *Mla6*, and *Mla14*) are present in the tested lines either alone or in combination. Among the tested lines 8 (18.0%) had one specific gene for resistance and 37 (82.0%) had a combination of different genes for resistance. Among specific resistance alleles the most common was *Mlat* whose presence was postulated in 20 (44.4%) of the tested lines. The distribution of reaction type indicated that about 79.0% of all reaction types observed were classified as powdery mildew resistance (scores 0, 1 and 2). The majority (65.0%) of resistance reaction types observed in the tested lines was intermediate reaction type 2. The use of new effective sources of resistance from Moroccan barley landraces for diversification of resistance genes for powdery mildew in barley cultivars is discussed.

Key words: barley landraces, *Erysiphe graminis* f.sp. *hordei*, genetic resources, *Hordeum vulgare*, mildew resistance.

INTRODUCTION

Barley (*Hordeum vulgare* L.) is widely grown in many major production regions of the crop around the world and is often attacked by the barley powdery mildew fungus (*Erysiphe graminis* DC. f.sp. *hordei* Em Marchal - synonym *Blumeria graminis* DC. Golovin

ex Speer f.sp. *hordei*). The primary effect of barley powdery mildew is reduced yield, which can reach up to 20% in Europe and 30% in North Africa (Rasmusson 1985; Corazza 1991; Zine Elabidine 1992; Ceccarelli *et al.*, 1995). In addition, powdery mildew is lowering quality characteristics such as 1000-kernel weight. This reduction in quality is particularly detrimental for malting barley (Griffiths, 1984; Rasmusson, 1985; Balkema-Boomstra and Masterbroek, 1995).

Powdery mildew on barley is one of the most clearly characterized systems of host-pathogen genetic interactions. Since 1907, when Biffen started studying the genetics of barley resistance to powdery mildew, more than 100 mildew resistance alleles have been identified. In Europe, the use of specific resistance genes to control barley powdery mildew began in the 1930s with the work of Honecker. Since that period, barley breeders have used such resistance alleles as *Mla6*, *Mla7*, *Mla9*, *Mla12* and *Mla13* belonging to the *Mla* locus and the resistance alleles *Mlk*, *Mlg*, *MlLa*, *Mlh* and *Mlra*. Many of these alleles derived from the barley landrace populations from West Asia, Ethiopia and North Africa (Biffen, 1907; Honecker, 1938; Brown and Jørgensen, 1991; Jørgensen, 1994). However, virtually all of these genes were gradually overcome by virulent races about 5 years after cultivars containing them were used on a large acreage. Exceptions to this are cultivars with *Mlo* resistance and the *Ml(La)* resistance gene. The *Ml(La)* resistance gene have been effective for more than 10 years (Munk *et al.*, 1991). Despite the fact that since 1979 *Mlo* resistance has been deployed in many barley cultivars throughout Europe, there is no known virulence for *mlo* genes (Atzema, 1998; Czembor and Czembor, 1998).

In the nineteenth century, a few outstanding farmers, landowners and scientists (*e.g.* Knight in England, Strampelli in Italy, Janasz in Poland, Vilmorin in France) started selecting attractive plants from populations of crop landraces based upon their phenotypic variation (Simmonds, 1987; Janasz, 1893; Bianchi, 1995; Zeven, 1996). However, in this activity often only one line was selected as a new cultivar and the landrace from which it was selected was no longer maintained. This caused great genetic erosion in major crops

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(Brush, 1992; Hammer *et al.*, 1996). The subject of conservation of landraces for the first time was discussed at the Agriculture and Forestry Congress at 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 to organize the conservation of landraces in their native countries (Zeven, 1996, 1998).

There exist many examples of the successful use of landraces to solve breeding problems including lack of sufficient resistance to diseases (Perrino, 1995; Hintum, 1996; Hodgkin, 1998). This is possible because landraces of major crops including barley are available in Gene Banks. The total number of barley accessions worldwide is estimated to be about 280,000 (Knüpffer and Hintum, 1995). Barley breeders are constantly using these genetic resources including sources of resistance to powdery mildew. Most powdery mildew resistance genes used in modern cultivars of barley are from landraces maintained in Gene Banks. Most of these landraces originated from West Asia, Ethiopia and North Africa including Morocco (gene *Mlat* – resistance Atlas) (Czembor, 1976; Jørgensen, 1994; Czembor, 1996; Jørgensen and Jensen, 1997).

The high level of crop diversity, including barley, observed in the Mediterranean Sea region lead Vavilov in 1926 to propose this region as one of the major centers of crop origin (Vavilov, 1926; Perrino, 1988; Williams, 1988; Valkoun *et al.*, 1995). In the most widely accepted theory, postulated in 1885 by Körnicke and Werner, barley was derived from its wild ancestor *Hordeum spontaneum* C. Koch when Neolithic men selected spikes with tough rachis (Körnicke and Werner 1885; Zohary and Hopf 1988; Ladizinsky 1998). Most probably it happened in the Zagros Mountain region (western Iran). The original area of *Hordeum vulgare* L. cultivation was the Fertile Crescent (a term coined by James Breasted in 1916 which refers to a crescent-shaped region of rich farmland that stretched, in ancient times, from the Mediterranean Sea to the Persian Gulf through the Tigris and Euphrates valley) (Zohary and Hopf, 1988; Nesbitt, 1995; Willcox, 1995). Recently, the discovery of wild barley in Morocco has been reported (Molina-Cano and Conde, 1980; Molina-Cano *et al.*, 1982). This finding suggests that North Africa may be the possible center of origin of cultivated barley and that it may be a multicentric crop, domesticated along the Mediterranean basin (Molina-Cano *et al.*, 1987; Moralejo *et al.*, 1994; Molina-Cano *et al.*, 1999). Taking this into account, barley landraces collected from Morocco may be a rich source of new genes for resistance to powdery mildew due to their high degree of diversification resulting from the long coevolution with popula-

tions of pathogen.

The aim of the present investigation was to identify powdery mildew resistance genes in lines selected from barley landraces from Morocco.

MATERIALS AND METHODS

Plant materials. Seed samples of forty four *H. vulgare* L. landraces were kindly provided by Dr. J. Valkoun (International Center for Agricultural Research in the Dry Areas – ICARDA, Aleppo, Syria). They were collected in Morocco during May, June and July in 1985 (ICARDA collection code MAR85). All of them were of a spring growth type, had six row heads and covered kernels. Generally under Polish conditions, they had low resistance for lodging and were intermediate in heading date.

Pathogen. Thirty-five isolates of *E. graminis* f.sp. *hordei* Em Marschal were used (Table 1). They came from the collections in the Risø National Laboratory, Roskilde, Denmark; Danish Institute for Plant and Soil Science, Lyngby, Denmark, Edigenossische Technische Hochschule – ETH, Zurich, Switzerland kindly provided by Dr. H.J. Schaerer (ETH, Zurich, Switzerland) and IHAR Radzików, Poland. The isolates were chosen according to the virulence spectra observed on the 'Pallas' isolines differential set (Kølster *et al.*, 1986), kindly provided by Dr. L. Munk (Royal Agricultural and Veterinary University, Copenhagen, Denmark). They were purified by single pustule isolation, maintained and propagated on young seedlings of the cultivar 'Manchuria' (CI 2330). This was carried out in greenhouse isolation rooms. Isolates were tested frequently on host differentials to assure their purity 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 (1930) (Table 2). The seedlings were classified into susceptible or resistant groups. Plants scoring 0-2 were included in the resistant group and plants scoring 3 and 4 were included in the susceptible group.

Resistance tests. This investigation was carried out during 1996-99 at IHAR Radzików, Poland. In winter 1996/97 about 30 plants per landrace were evaluated in the greenhouse with the R 303 isolate of *E. graminis* f.sp. *hordei*. R 303 represented the most avirulent isolate available allowing the expression of a maximum number of resistance genes. The cultivar 'Manchuria' was used as a susceptible control.

Table 1. Differential isolates used and their infection types on 'Pallas' differential set.

Differential set	Isolates																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Gene	58-74	59-11	59-12	63-1	A 6	D 17	7	8	GE	9	10	11	12	13	14	15	16	17
Pallas	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
<i>Mla8</i>	0	4	0	4	4	4	4	0	4	0	0	0	4	0	0	0	0	0
<i>Mla1</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mla3</i>	0	0	0	0	0	0	0	4	4	4	4	0	4	0	4	4	0	4
<i>Mla6, Mla14</i>	4	4	4	4	0	2	0	0	2	0	0	4	2	2	2	4	1	2
<i>Mla7, Mlk, ?</i>	4	4	4	4	1	1	0	0	0	2	4	4	4	4	2	4	2	2
<i>Mla7, ?</i>	4	4	4	4	0	0	0	1	1	0	4	4	4	4	2	4	1	2
<i>Mla7, MILG2</i>	4	4	4	4	0	0	0	0	0	0	4	4	0	0	0	0	0	0
<i>Mla9, Mlk</i>	4	4	0	4	0	0	0	0	0	0	4	4	0	0	0	0	0	0
<i>Mla9, Mlk</i>	4	4	0	4	0	0	0	0	0	0	4	4	0	0	0	0	0	0
<i>Mla9</i>	4	4	0	4	0	0	0	0	0	0	4	4	0	0	0	0	0	0
<i>Mla10, MIDu2</i>	4	4	4	4	0	0	4	0	0	0	4	4	0	0	1	2	4	0
<i>Mla12</i>	0	0	0	4	0	0	4	0	0	0	0	0	2	4	4	4	4	0
<i>Mla13, MI(Ru3)</i>	4	2	0	4	0	0	0	0	0	0	0	0	4	4	0	4	0	0
<i>Mla22</i>	4	4	4	0	4	4	4	4	4	4	4	0	4	4	4	4	0	4
<i>Mla23</i>	2	4	1	1	1	1	1	1	1	2	1	2	2	1	2	1	2	2
<i>Mra</i>	4	4	4	4	0	4	4	4	4	4	4	4	0	0	4	4	4	4
<i>MI(Ru2)</i>	3	4	4	4	4	2	4	2	2	4	4	2	2	0	4	4	4	2
<i>Mlk</i>	4	4	4	4	0	2	2	2	2	0	4	4	0	2	2	2	2	2
<i>Minn</i>	4	4	4	4	4	4	4	4	4	4	4	4	3	4	4	4	4	4
<i>Mlp</i>	2	0	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2
<i>Mlat</i>	2	0	2	2	4	2	2	2	2	2	2	4	2	2	2	2	2	2
<i>Mlg, MI(CP)</i>	4	4	4	4	0	0	0	4	4	4	0	0	4	4	0	0	0	0
<i>mlo5</i>	0(4)	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)
<i>MI(La)</i>	2	4	4	4	3	2	3	2	2	2	3	3	2	4	3	4	4	4
<i>Mlb</i>	4	4	4	4	0	4	4	4	4	0	4	4	4	4	4	4	4	4

(continued)

Table 2. Description of infection types and codes used (Mains and Dietz, 1930).

Infection type	Macroscopic symptoms
0	no visible symptoms (immunity)
1	necrotic flecks, usually minute chlorosis often present no mycelial growth. No sporulation (hypersensitivity)
2	necrotic flecks, often with chlorosis reduced mycelial growth. No or scarce sporulation
3	necrotic flecks or small necrotic areas frequent chlorosis moderate mycelial growth, moderate sporulation
4	profuse sporulation of well developed colonies and sometimes green islands

Nineteen of the tested total 44 landraces showed resistance reactions (Table 3). From 1 to 5 resistant plants per each landrace were grown in the greenhouse to obtain their seed. Forty-five single plant lines were created. Sixteen of these lines were tested with 17 isolates of powdery mildew during winter 1997/98 (Table 4). An-

other 29 lines were tested with 23 isolates during winter 1998/99 (Table 5). Both of these testings were conducted in the IHAR Radzików greenhouse. The plants were grown with 16 h light and 16-22°C range of temperature. 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 shown by seedlings were scored.

Postulation of resistance alleles. Hypotheses on the specific resistance genes present were made by comparing the reaction spectra of the tested lines with those of differential lines. The lines with the same reaction spectra for 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 to determine the postulated and possible resistance genes. It was done on the basis of the gene for gene hypothesis. 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; Czembor, 1996).

Table 3. Site of collection of 19 barley landraces from Morocco showing resistance to powdery mildew.

IHAR number	ICARDA number	Altitude	Province	Site
163	ICB 31864	700	Tiznit	Merekht, 20km S of Tiznit
166	ICB 31867	300		2-3km S of Fask
169	ICB 31870	450	Tiznit	Oua-Bell oasis
170	ICB 31871	500		10km S of Tiggan
171	ICB 31872	500		Tigane oasis
172	ICB 31873	600		Tougria oasis, near Azzargazzane
173	ICB 31874	600	Tiznit	Tata town, INRA Station
174	ICB 31875	650	Tiznit	Tata town, domestic garden
178	ICB 31879	600		Trhite oasis
179	ICB 31880	450		Oued Mellah
181	ICB 31882	700		Alougum Oasis
182	ICB 31883	1200		Ait Abdelah, by Oued
184	ICB 31885	1250		near Bleida, by Oued
189	ICB 31890	600		Tamgrout, Oued Drea
190	ICB 31891	600	Ourzazate	Tagounite, Oued Drea
198	ICB 31899	900		Ouriz, Oued Draa
199	ICB 31900	1100	Ourzazate	Ourzazate
201	ICB 31902	1400	Tiznit	Imitek between Dades and Tinerhir
202	ICB 31903	1300	Tiznit	Timadriouine, near of Imiter

Table 4. Resistance alleles and infection types of 16 lines to infection by 17 isolates of *E. graminis* f.sp. *bordei*.

IHAR number	Isolates																	Postulated resistance alleles	Possible alleles ¹
	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	JEH11	MH 1	R13C	R63	R71/1	R86.1	R189	R261	R275	R303	Ry 4d		
169-2.5	2	2	0	2	4	2	0	4	2	4	2	4	2	2	2	0	2	+ ²	Mla6, Mla14
170-1.3	0	2	0	2	2	2	0	2	2	2	2	2	2	2	2	0	2	+ ²	
170-2.2	0	4	2	4	4	4	0	2	0	1	2	0	2	4	1	2	2	+ ²	
172-1.4	0	2	0	1	4	2	0	0	0	1	0	0	4	2	2	0	2	+ ²	
172-3.2	0	2	1	2	2	1	0	2	2	1	1	2	0	2	2	0	2	+ ²	
173-1.2	2	0	1	1	0	1	0	2	0	0	0	0	0	0	2	0	0	+ ²	
174-3.2	2	2	0	2	4	2	0	4	4	2	0	2	0	2	4	1	2	+ ²	
174-2.2	0	2	2	4	4	4	0	4	2	4	2	2	4	2	4	2	4	+ ²	
178-1.4	4	2	2	2	4	2	0	4	4	4	4	4	4	2	2	2	4	+ ²	
178-3.1	4	2	2	4	2	2	4	2	2	2	2	2	2	4	1	2	2	+ ²	Mlat
189-3.4	0	2	2	4	2	1	4	2	2	2	4	2	2	2	2	2	4	+ ²	Mlat
198-1.5	2	2	2	2	2	1	4	2	2	2	2	2	4	2	2	2	4	+ ²	Mlat
199-1.3	2	2	2	2	2	2	2	2	2	2	2	1	2	4	2	2	4	+ ²	Mlat
201-3.2	2	2	1	2	1	1	1	2	0	2	2	1	1	2	1	1	2	+ ²	Mla6, Mla14, Mlk
201-2.2	2	2	2	2	2	2	4	2	2	2	1	2	2	4	2	2	2	Mlat, + ²	
202-1-1	1	2	2	2	2	1	2	0	2	2	2	2	2	4	2	2	2	Mlat, + ²	

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.

Table 5. Resistance alleles and infection types of 29 lines to infection by 23 isolates of *E. graminis* f.sp. *borderi*.

IHAR number	Isolates																							Postulated resistance alleles	Possible alleles ¹
	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	A	Em	HL	JEH	MH	R	Ru	TR	En1	R30	E	59-11.1	SZ/	Ra	Ra	Ra	Ra	Ra	Ra	Ra	Ra		
			6	A30	3/5-1	11	1-2	189	303	3	2	/A1	3.1	92	11.1	C10	7	9	10	13	16	22	22		
163-2-1	2	2	1	4	2	4	2	2	2	1	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat</i>	
163-2-5	4	2	2	4	2	4	2	2	2	0	2	1	2	2	4	4	2	2	4	4	4	2	2	+? ²	
166-3-1	2	4	2	0	2	4	1	0	4	1	2	2	2	2	2	2	2	2	2	2	2	2	1	+?	
169-1-2	0	2	0	4	4	0	4	0	4	0	4	0	4	4	4	4	4	4	4	4	4	4	4	+? ²	
169-2-1	0	0	0	4	4	0	4	0	4	0	0	0	0	4	0	4	4	4	4	4	4	4	4	<i>Mlat6, Mlat14, +?</i>	
170-1-4	1	2	2	0	2	2	4	2	0	2	0	2	2	2	2	4	2	2	4	2	4	2	2	<i>Mlat, +?</i>	
170-3-4	2	2	2	2	2	2	2	2	0	2	0	0	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat, +?</i>	
170-5-5	2	2	2	4	2	4	2	2	2	2	2	1	2	2	2	4	2	4	4	4	4	2	2	<i>Mlat</i>	
171-2-1	2	0	0	4	2	2	2	2	2	2	0	0	2	2	2	2	2	2	2	2	2	2	2	<i>Mlat</i>	
172-3-5	0	2	0	2	2	4	2	2	0	2	0	0	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat, +?</i>	
174-1-4	2	2	2	4	2	0	2	2	2	2	2	2	2	2	4	0	4	2	4	4	4	2	2	<i>Mlat, +?</i>	
179-2-1	2	2	2	4	2	4	2	2	2	2	2	2	2	4	4	4	2	2	4	4	4	2	2	<i>Mlat</i>	
181-3-5	2	2	2	2	2	0	2	1	2	2	0	2	2	2	2	2	2	2	2	2	2	2	0	0	+?
182-1-1	2	2	2	2	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat, +?</i>	
182-2-1	2	2	2	2	4	2	4	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat, +?</i>	
182-3-2	2	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat</i>	
182-4-3	2	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat</i>	
184-2-1	2	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	4	4	4	4	2	2	+?	
184-2-2	2	2	2	4	2	4	2	2	2	1	2	2	2	2	2	4	2	2	4	4	4	1	2	<i>Mlat</i>	
189-1-1	2	2	2	4	2	4	2	2	2	2	2	0	2	2	2	4	2	2	4	2	2	2	2	<i>Mlat, +?</i>	
189-2-1	2	2	4	4	2	2	2	2	2	2	2	2	2	2	2	4	2	2	4	4	2	4	2	<i>Mlat, +?</i>	
189-3-3	2	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat</i>	
190-3-2	2	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	1	<i>Mlat</i>	
198-1-3	2	2	2	4	0	2	4	2	2	2	0	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat, +?</i>	
199-2-1	2	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat</i>	
201-2-3	2	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat</i>	
201-3-3	1	2	0	0	2	2	2	2	1	2	2	2	2	2	2	4	2	2	4	2	2	2	2	+?	
202-1-2	4	2	2	4	2	4	2	2	2	2	2	2	2	2	2	4	2	2	4	4	4	2	2	<i>Mlat</i>	
202-2-1	4	2	2	2	2	2	2	2	0	2	0	0	2	2	4	2	2	4	4	4	4	2	2	<i>Mlat</i>	

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.

RESULTS

All 45 tested lines possessed a resistance allele or alleles for powdery mildew of barley (Table 4, 5). However, only 6 lines (170-1-3, 172-3-2, 173-1-2, 181-3-5, 201-3-2 and 201-3-3) originating from 5 landraces (170, 172, 173, 181 and 201) were resistant to all isolates used. One of these lines (173-1-2) showed reaction type 0 and the other 5 lines showed reaction type 2 for most isolates used respectively. The distribution of reaction type readings indicate that 79% of all reaction types observed were classified as powdery mildew resistance (score 0, 1 and 2) (Table 6). The majority (65.0%) of resistance reaction types observed in tested lines was intermediate resistance reaction type 2. Thirty-six lines (80.0%) had scores 2 and 3 lines (6.6%) had score 4 for more than 50% isolates used respectively.

In 24 (53.3%) tested lines it was impossible to determine which specific gene or genes for resistance are present (Table 4, 5). Most probably these lines possessed alleles not present in the 'Pallas' isolate differential set. In 13 (30.0%) lines the presence of unknown genes in combination with specific ones were detected. The distribution of reaction type readings indicate the minimum number of genes involved because different genes for resistance may condition different reaction types. Based on this assumption, it may be concluded that most tested lines had many genes for resistance. It was postulated that 3 different resistance alleles (*Mlat*, *Mla6* and *Mla14*) are present in the tested lines either alone or in combination. Among tested lines 8 (18.0%) had one specific gene for resistance and 37 (82.0%) had a combination of different genes for resistance. Alleles *Mla6*, *Mla14* were postulated to be present in line 169-2-1. The most common resistance allele in tested lines was *Mlat*. This allele was present in 20 (44.4%) tested lines.

DISCUSSION

Powdery mildew is now one of the most common and most widespread disease of barley. However for a long time this disease was not important for barley production (Honecker, 1938; Wolfe and Schwarzbach, 1978). The first devastating epidemic of barley powdery mildew was observed in Europe on winter barley in 1901 and on spring barley in 1903 (Wolfe and Schwarzbach, 1978). It happened at the advent of modern agricultural methods such as the large scale cultivation of uniform varieties, the use of high crop densities and the application of nitrogen fertilizers (Wolfe and Schwarzbach, 1978; Wolfe, 1984). The main means of

controlling powdery mildew are fungicides and growing of resistant varieties. However, future strategies for the control of powdery mildew will have to focus increasingly on ecologically acceptable methods as the use of any chemicals (pesticides, fungicides, herbicides, and mineral fertilizers) in agriculture is increasingly criticized in many developed countries. Such a method is breeding for resistance. This method is considered also as relatively inexpensive and convenient for the farmer because the use of fungicides requires investment in machinery, labor and special training (Czembor and Gacek, 1990; Gullino and Kuijpers, 1994; Czembor and Gacek, 1995; Brown, 1996; Jacobsen, 1997).

However breeding barley for resistance to powdery mildew is faced with a highly mobile pathogen, whose gene-pool forms an almost infinite source of genetic variation (Müller *et al.*, 1996; O'Hara and Brown, 1997; Hovmøller *et al.*, 2000). A number of genes for specific resistance have been used in commercial barley varieties since the first gene, *Mlg*, was introduced on a large scale in the 1930s in Germany (Wolfe and Schwarzbach, 1978; Jørgensen, 1994; Wolfe and MacDermott, 1994). In the 20th century in Europe, more than 700 cultivars of barley have been used with different combinations of 36 alleles for race-specific resistance to powdery mildew. However, 28 of these alleles are closely linked or allelic, which limits the possible number of gene combinations in breeding new varieties (Czembor and Gacek, 1990; Brown and Jørgensen, 1991; Jørgensen, 1994; Wolfe and McDermott, 1994). All these genes were successively overcome by the appearance of pathotypes with matching virulence. These varieties had to be discarded because they were far too disease susceptible to be of any further value. This susceptibility was due to a host erosion of partial resistance during breeding for race-specific resistance (*Vertifolia* effect) (Vanderplank, 1982; Czembor and Gacek, 1990).

This study demonstrate the practical advantages of preserving the genetic diversity of barley in the form of landraces. Among 92 investigated landraces from Morocco, 41 (45%) showed resistance for *E. graminis* f.sp. *bordei*. However, only 6 (170-1-3, 172-3-2, 173-1-2, 181-3-5, 201-3-2, 201-3-3) from 79 lines originating from these landraces were resistant to all isolates used. These lines had resistance to all powdery mildew virulence genes prevalent in Europe. This conclusion is based on the fact that isolates used in this experiment had virulences corresponding to all major resistance genes used in the past and currently in Europe. Taking this into account, they should be used in breeding of barley as a new sources of resistance to powdery mildew. The frequency of powdery mildew resistant landraces (170, 172, 173, 181, 201) in the present study,

Table 6. Infection types frequencies of 45 lines for isolates of *E. graminis* f.sp. *hordei*.

IHAR number	Number of isolates that produced infection type (0, 1, 2, 3 or 4)					Total
	0	1	2	3	4	
163-2-1	0	2	16	0	5	23
163-2-5	1	1	14	0	7	23
166-3-1	2	4	13	0	4	23
169-1-2	6	0	1	0	16	23
169-2-1	10	0	1	0	12	23
169-2-5	3	0	10	0	4	17
170-1-3	4	0	13	0	0	17
170-1-4	3	1	16	0	3	23
170-2-2	4	2	6	0	5	17
170-3-4	3	0	17	0	3	23
170-5-5	0	1	16	0	6	23
171-2-1	4	0	16	0	2	22
172-1-4	8	2	5	0	2	17
172-3-2	4	4	9	0	0	17
172-3-5	5	0	14	0	4	23
173-1-2	11	3	3	0	0	17
174-1-4	2	0	16	0	5	23
174-2-2	2	0	7	0	8	17
174-3-2	4	1	8	0	4	17
178-1-4	1	0	7	0	9	17
178-3-1	0	1	12	0	4	17
179-2-1	0	0	15	0	8	23
181-3-5	4	1	18	0	0	23
182-1-1	0	0	19	0	4	23
182-2-1	0	0	18	0	5	23
182-3-2	0	0	18	0	5	23
182-4-3	0	0	18	0	5	23
184-2-1	0	0	15	0	6	21
184-2-2	0	3	15	0	5	23
189-1-1	1	0	18	0	4	23
189-2-1	0	0	19	0	3	22
189-3-3	0	0	18	0	5	23
189-3-4	1	1	11	0	4	17
190-3-2	1	0	17	0	5	23
198-1-3	2	0	16	0	5	23
198-1-5	0	1	13	0	3	17
199-1-3	0	1	14	0	2	17
199-2-1	0	0	17	0	5	22
201-2-2	0	1	14	0	2	17
201-2-3	0	0	18	0	5	23
201-3-2	1	8	8	0	0	17
201-3-3	2	2	19	0	0	23
202-1-1	1	2	13	0	1	17
202-1-2	0	0	17	0	6	23
202-2-1	3	0	15	0	5	23

5.4 per cent, is similar to or higher than that assessed in other studies (Honecker, 1938; Nover and Lehmann, 1973; Czembor, 1976; Czembor *et al.*, 1979; Negassa, 1985; Lehmann and von Bothmer, 1988; Leur *et al.*, 1989; Czembor, 1996; Jørgensen and Jensen, 1997; Czembor, 1999; Czembor and Czembor, 1999a). This may be caused by using the various methods for screenings landraces for resistance.

Incorporating genes for resistance to powdery mildew originated from landraces into a barley breeding program should be a relatively easier when mutants or wild barley are used. A good example of this is the introduction of Mlo resistance into modern European barley cultivars. All twenty five different *mlo* alleles with the exception of *mlo11* were obtained by mutagenesis. However, almost all barley cultivars with Mlo resistance have the same allele *mlo11* which originated from the Ethiopian landrace L92 (Jørgensen, 1992a, b, 1994; Pickering *et al.*, 1995). Furthermore undesirable agronomic traits that are usually derived from wild relatives do not have to be bred out when using landraces as a source of powdery mildew resistance. Using barley landraces in breeding programs has also another advantage, which is the incorporation of desirable agronomic traits *e.g.* good adaptation to dry land conditions (Ceccarelli *et al.*, 1987, 1991, 1995; Yahyaoui *et al.*, 1996; Lakew *et al.*, 1997).

Morocco is characterized by contrasts in its natural conditions due to the transitional location between the Mediterranean winter-rain zone and the Sahara desert (Perrino *et al.*, 1986). This is reflected in very diverse plant material including barley obtained on germplasm collection missions. Collecting missions in Morocco are highly recommended because barley landraces in this country are subject to genetic erosion due to drought and desertification (Perrino *et al.*, 1986; Damania, 1988; Tazi *et al.*, 1989; Zine Elabidine *et al.*, 1995). Barley is one of the most important cereal crops in the North Africa including Morocco. It is grown as landraces in marginal, low-input, drought-stressed environments both for grain and straw (Ceccarelli *et al.*, 1987, 1995; Czembor, 1996). It is presumed that they survive the fluctuations of biotic and abiotic stresses because of their high level of heterogeneity (Demissie and Bjørnstad, 1996; Yitbarek *et al.*, 1998). This was confirmed in the present study by the fact that six landraces (about 15%) were heterogeneous for mildew reaction. This percentage of observed powdery mildew resistance heterogeneity of barley landraces is similar to or lower than that described in other studies (Nover and Lehmann, 1973; Czembor, 1996, 1999; Czembor and Czembor, 1999a).

In the farming system which uses landraces, pow-

dery mildew rarely develops to levels that significantly damage 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 control the limited disease development (Leur *et al.*, 1989; Andrivon and Vallavielle-Pope, 1992). This was confirmed in this study. The most frequently observed score in tested lines was 2 (65.0%) and 36 lines (80.0%) showed this reaction for inoculation with more than 50% isolates used. This is different from the resistance reaction conferred by most powdery mildew resistance genes used in Europe which confer mostly reaction type 0 and 1 (Brown and Jørgensen, 1991; Jensen *et al.*, 1992; Jørgensen, 1992a; Jørgensen, 1994; Czembor and Czembor, 1998, 1999b). In most selected lines (83.3%) the presence of unknown genes alone or in combination with specific ones were detected. Among specific resistance alleles the most common was allele *Mlat* which was postulated in 20 (44.4%) tested lines. This is in agreement with the fact that virulence to *Mlat* is very common in the Moroccan mildew population and that *Mlat* resistance gene was originally described from western North Africa (Caddel, 1976; Jørgensen, 1994; Yahyaoui *et al.*, 1997). The presence of a high number of unknown genes in barley landraces is in agreement with findings in other studies (Honecker, 1938; Nover and Lehmann, 1973; Czembor, 1976; Czembor *et al.*, 1979; Negassa, 1985; Lehmann and von Bothmer, 1988; Leur *et al.*, 1989; Czembor, 1996; Jørgensen and Jensen, 1997; Czembor, 1999; Czembor and Czembor, 1999a).

Crucial to the efficiency of breeding for resistance is the durability of the resistance genes. It may be increased by using many different strategies for deploying resistance genes in barley. Most common of these strategies are: multiline cultivars, combining different resistance genes into one cultivar and deploying many cultivars with different resistance genes in space (*e.g.* cultivar mixtures) or time (winter versus spring barley) (Jørgensen, 1983; Jørgensen, 1994; Czembor and Gacek, 1995; Gacek, 1996). In last twenty years, new sources of resistance to powdery mildew were found in barley landraces and wild barley. New sources of resistance, including sources described in this study, may be used by barley breeders in new cultivars employing different strategies (Wolfe, 1984; Jørgensen, 1994; Jørgensen and Jensen, 1997).

Determination of powdery mildew resistance genes based on tests performed on seedlings is effective and sufficient for the needs of breeders and pathologists (Jørgensen, 1981; Brown and Jørgensen, 1991; Jensen *et al.*, 1992; Jensen and Jørgensen, 1992a; Czembor and Czembor, 1998, 1999b). Generally, confirmation of re-

sistance composition can only be established by a test for allelism through crosses and backcrosses among appropriate hosts (Czembor, 1996; Heitefuss *et al.*, 1997). Also different levels of partial resistance in tested lines may influence conclusions concerning the postulated presence of specific resistance genes (Jørgensen, 1994; Czembor, 1996).

This study confirmed the findings of other investigators that many barley landraces possess mildew resistance genes different from genes present in cultivated varieties (Honecker, 1938; Nover and Lehmann, 1973; Czembor, 1976; Czembor *et al.*, 1979; ; Negassa, 1985; Lehmann and von Bothmer, 1988; Leur *et al.*, 1989; Czembor, 1996; Jørgensen and Jensen, 1997; Czembor, 1999; Czembor and Czembor, 1999a). New effective sources of resistance described in this study may increase the diversity of the powdery mildew resistance genes present in barley cultivars in Europe.

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