Selections from barley landrace collected in Libya as new sources of effective resistance to powdery mildew (*Blumeria graminis* f.sp. *hordei*)

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ABSTRACT

Powdery mildew on barley (*Hordeum vulgare* L.) caused by the pathogen *Blumeria graminis* f.sp. *hordei* occurs worldwide and can result in severe yield loss. Because agronomical methods to control the disease are not completely effective, cultivars with genetic resistance are needed. Therefore, there is a need to describe new sources of genes that confer resistance to barley powdery mildew. This study was conducted to determine the genetic basis of resistance to powdery mildew in three selections 995-1-1, 995-1-2, 995-1-3 from barley landrace 995 (ICB 112840) collected in Al Aziziyah district, Tripolitania, Libya. Landrace originated from International Center for Agricultural Research in the Dry Areas – ICARDA, Aleppo, Syria. To determine the number of genes, the types of genes action and the gene loci in tested lines two types of crosses were made: (1) the lines were crossed to the susceptible cultivar Pallas, (2) the lines were crossed with Pallas isoline P22 carrying gene *mlo5*. The parents and progeny F_2 were evaluated with isolate R303.1 for the powdery mildew resistance. Based on segregation ratios we found that resistance in these three selections was determined by a single recessive gene allelic to the *Mlo* locus occurring in Pallas isoline P22. In addition tested lines showed resistance reaction type 0(4) characteristic only for genes *mlo*. The value of new identified sources of highly effective powdery mildew resistance to breeding programs and barley production is discussed.

Keywords: *Hordeum vulgare*; *Blumeria graminis*; barley landraces; Mlo resistance; powdery mildew

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 11 000 000 ha) of EU total cereals acreage. In the Czech Republic barley is of great economic importance and it is grown on about 550 000 ha (about 35% of total cereals acreage) (Dreiseitl and Jurečka 1996, 1997, Anonymous 2001). Almost 70% of this area is covered by spring barley, which is used for malt production (30%) and animal feeding (Ovesná et al. 2001). 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 (Ceccarelli and Grando 1999, Ceccarelli et al. 2000).

Fungus *Blumeria graminis* (D.C.) Golovin ex Speer f.sp. *hordei* Em. Marchal (synamorph *Erysiphe graminis* D.C. f.sp. *hordei* Em. Marchal.) is considered one of the most destructive foliar pathogens of barley. In countries where mildew is a problem, yield losses in experimental tests usually exceed 25%. However, average annual losses in barley production in Central Europe, including Czech Republic, are about 10% (Zwatz 1987, Czembor and Czembor 2001).

The incorporation of new genes for powdery mildew resistance into barley cultivars has been useful in combating powdery mildew. However, the resistance conferred by most of these genes has not been maintained for more than a few years with one exception, which is the Mlo resistance (Dreiseitl and Jørgensen 2000, Czembor and Czembor 2001). The Mlo resistance is a unique type of resistance because it is monogenic and non-race-specific. Recessive alleles at the *Mlo* locus condition penetration resistance of barley of attacked epidermal cells by rapid deposition of large callose-containing appositions (papillae) in the epidermal cell wall, directly subtending the attacking fungal appressoria. This infection type is characteristic only for *mlo* alleles and is designed as 0(4) (Jørgensen 1992, Atzema 1998, Lyngkjær et al. 2000).

Mlo resistance has become a very important source of powdery mildew resistance in barley because there is no known virulence for these genes. However many factors e.g. temperature, water stress or light intensity may affect the expression of this gene (Atzema 1998, Schwarzbach 1998, 2001, Lyngkjær et al. 2000). Negative pleiotropic effects that were common when *mlo* was used in earlier crosses have been overcome by recent breeding and this type of resistance is presently utilised with increasing intensity in spring barley production. During last 20 years, the Mlo resistance has been deployed in many barley cultivars throughout Europe. It is estimated that about 20% spring barley cultivars grown in Central Europe carry Mlo resistance (Atzema 1998, Schwarzbach 1998, Czembor and Czembor 2001).

A knowledge concerning the inheritance of resistance to diseases, including barley powdery mildew, is valuable for planning crosses in breeding programs, identifying resistance genes, and developing genetic markers to as-

sist in selection (Jahoor et al. 1991, Czembor and Talbert 1997). Since 1930, when isolates of powdery mildew with different virulence genes were identified by Mains and Dietz (1930), specific isolates (usually 1–3 isolates) were used for screening collections of barley for genes for resistance (Jørgensen 1994, Czembor and Johnston 1999). However for a total number of about 280 000 of barley accessions (most of them landraces) which is estimated to exist world-wide in *ex situ* germplasm collections (Knüpffer and Hintum 1995) only less than 2 percent attempts have been made to identify powdery mildew resistance genes using differential lines and isolates (Czembor 1996, 2001). Identification 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 (Brückner 1964, Dreiseitl et al. 1996, Dreiseitl 1999, Dreiseitl and Jørgensen 2000). However, confirmation of putative resistance genes or alleles can only be established through the evaluation of progeny from crosses among appropriate genotypes (Jørgensen 1994, Czembor and Johnston 1999, Czembor and Czembor 2001).

Vavilov (1926) proposed that the region of Mediterranean Sea is major center 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 (Bothmer et al. 1995, Ladizinsky 1998, Zohary 1999). The original area of cultivation of *H. vulgare* L. is assumed to be the area of the Fertile Crescent. According to archaeological evidence, barley was cultivated in this region in the ninth millennium B.C. (Willcox 1995, Zohary 1999). However, in 1980, wild barley was discovered in Morocco, and it was postulated that Morocco was a possible center of origin for cultivated barley (Molina-Cano and Conde 1980, Molina-Cano et al. 1987). It was suggested that barley may be a multicentric crop, domesticated along the Mediterranean basin (Molina-Cano et al. 1999, Moralejo et al. 1994). Based on the concept of correlated host-pathogen evolution, barley landraces collected from Morocco may be a rich source of new powdery mildew resistance genes resulting from the long co-existence of barley with populations of pathogen (Wolfe 1988, Jana 1999).

The purpose of this research was to conduct inheritance study to determine the number of genes and the types of gene action in three selections from Libyan barley landrace 995 (ICB 112840). Results are compared with previous study in which the gene *mlo* was postulated to be present in these selections based on test using 23 differential isolates (Czembor 2000).

MATERIAL AND METHODS

Plant material. Seed samples of *Hordeum vulgare* L. landrace 995 (ICB 112840) were provided by Dr. J. Valkoun and Prof. S. Ceccarelli (International Center for Agricultural Research in the Dry Areas – ICARDA, Aleppo, Syria). It was collected in Al Aziziyah district, Tripolitania, Libya during 1982 (ICARDA collection code LBY82). Under Central Poland field conditions, it showed low resistance for lodging and was intermediate in heading date.

During 1996–1998 from this landrace, three single plant lines 995-1-1, 995-1-2, 995-1-3 were selected. During winter 1998–1999, these selections were tested with 23 isolates of *B. graminis* f.sp. *hordei* (Czembor 2000).

Pathogen. The isolate (R303.1) of *B. graminis* f.sp. *hordei* provided kindly by Dr. H. J. Schaerer (ETH Zurich, Switzerland) was used. It was purified by single colony isolation and was maintained and propagated on young seedlings of the powdery mildew susceptible cultivar Manchuria (CI 2330). The virulence spectrum of this isolate was determined based on observation of its infection types on the Pallas isoline differential set (Kølster et al. 1986), provided kindly by Dr. L. Munk (Royal Agricultural and Veterinary University, Copenhagen, Denmark). This isolate was chosen for this experiment because it was the most avirulent isolate available.

Inoculation and disease assessment. All tests for powdery mildew resistance of generation F_2 were conducted in the greenhouse. In these tests, the plants were grown with 16 h light and 8 h dark at 16–22°C. The plants were grown in 6-cm-diameter plastic pots filled with a mixture of Radzików sandy soil and peat in a 3:1 ratio. Tested plants were always grown together with seedlings of the cultivar Manchuria CI 2330 (used as a susceptible control) and the Pallas isoline differential set. 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 of seedlings were scored on the primary leaf of the seedlings. This scoring was done according to a 0–4 scale adapted from Mains and Dietz (1930).

Postulation of resistance alleles. To determine the number of genes, the types of genes action and the gene loci in tested lines two types of crosses were made: (1) the lines were crossed to the susceptible cultivar Pallas, (2) the lines were crossed with Pallas isoline P22 carrying gene *mlo5*. These crosses were made during February 2000 in the greenhouse. During 2000–2001, the seeds from F_1 and F_2 generations were obtained. In March 2001, seedlings of parents and F_2 generations were evaluated for the powdery mildew resistance with isolate R303.1 as described above. A χ^2 analysis was performed to test consistency of fit between observed and expected ratios of resistant and susceptible plants.

RESULTS

Segregation studies. The F_2 progeny derived from three crosses between selections from barley landrace 995 and susceptible cultivar Pallas gave a good fit to the 1:3 (resistant: susceptible) ratio (Table 1). This indicated

that powdery mildew resistance of these three lines is controlled by a recessive allele of a single gene. No segregates were observed in the F_2 generation of crosses between three selections and Pallas isoline P22 carrying gene *mlo5*. Based on these results it may be assumed that the genes for resistance in these lines are allelic to the *Mlo* locus occurring in Pallas isoline P22.

Resistance reaction studies. Resistance reaction type observed on F_2 progeny and tested lines was designed as 0(4). This reaction was described as no visible signs of infection except for an occasional infection type 4 (compatible) mildew colonies. These colonies were also about 30–60% of size in comparison to susceptible control. Young leaves with 168 young colonies of tested lines (121 colonies) and F_2 progeny (47) were also investigated under microscope. It was observed that mildew colonies originated from successful infection in the subsidiary cells next to the stomata on the barley epidermis. However, on one occasion (colony originated from tested line) it was observed that colony originated from short cell in contact with stomata. Based on these observations the presence of *mlo* allele in selections from landrace 995 was postulated.

DISCUSSION

The genetic analysis showed in this study proved the presence of spontaneous Mlo resistance in barley landrace 995 (ICB 112840) collected in Al Aziziyah district, Tripolitania, Libya. This finding is in agreement with the results of the previous study in which the putative presence of this resistance was postulated based on tests using 23 differential isolates (Czembor 2000). This is the first rapport about discovery of spontaneous Mlo resistance in barley landrace originating from a country other than Ethiopia (Jørgensen 1971, 1992) and Turkey (Czembor and Frese 2001, unpubl. data). Additionally, it was observed that mildew colonies originated from successful infection in the subsidiary cells next to the stomata on the barley epidermis with only one exception in which colony originated from short cell in contact with stomata. This is in agreement with observations concerning origin of colonies on Mlo resistant plants made by other investigators (Atzema 1998, Schwarzbach 1998). Results of this study demonstrate practical advantages of preserving the genetic diversity of barley in the form of landraces to control barley powdery mildew.

The primary way of controlling powdery mildew is to cultivate genetically resistant barley varieties (Dreiseitl and Jørgensen 2000, Czembor 2001, Czembor and Czembor 2001). This is not expensive and environmentally safe barley protection measure and it was used from the beginning of modern, intensive methods in barley production (Czembor 1996). Currently, powdery mildew of barley is one of the most common and most widespread diseases of barley causing significant yield losses. However, this disease opposite to leaf rust was, for a long time, not important factor in barley production. In Europe, the first devastating epidemic of barley powdery mildew was observed in Germany on winter barley in 1901 and on spring barley in 1903 (Wolfe and Schwarzbach 1978). Most probably, it happened because German farmers introduced modern agricultural methods. These methods included the use of high crop densities, the application of nitrogen fertilizers and on the large-scale cultivation of uniform varieties (Wolfe and Schwarzbach 1978, Wolfe 1984). Genetic studies of barley resistance to powdery mildew started about 100 years ago (Biffen 1907) and have resulted in characterisation of more than 100 sources of mildew resistance in barley cultivars, landraces and wild or related *Hordeum* species. The use of specific resistance genes to control barley powdery mildew began in the 1930s (after heavy barley losses due to powdery mildew in 1929) with the work of Honecker and during this time the first gene, *Mlg*, was introduced on a large scale (Honecker 1938, Czembor 1996). In the 20th century, about 36 genes for specific resistance have been used in Europe in more than 700 cultivars (Brown and Jørgensen 1991, Czembor and Czembor 2001). However, resistance conferred by most of these genes has not been effective for more than a few (4–6) years with the exception of alleles *mlo* (Schwarzbach 1998, Hovmøller et al. 2000, Lyngkjær et al. 2000). This was caused by high level of pathogenic variability encountered in natural populations of *B. graminis* f.sp. *hordei* (Dreiseitl and Steffenson 1996a, b, Dreiseitl 1997, 1998). Many investigations showed that *B. graminis* f.sp. *hordei* is able to develop many new races and that its spores are spread by wind over large distances across Europe (Schwarzbach 1979, 1987, Věchet

Table 1. Reaction of progeny F_2 derived from crosses between three selections (995-1-1, 995-1-2, 995-1-3) with the cultivar Pallas and Pallas isoline P22 to the R303.1 isolate of *B. graminis* f.sp. *hordei*, expected ratios, χ^2 and probability (*P*)

Parents		Infection type on parents		Observed frequency of plants		Hypothesis	χ^2	P
P1	P2	P1	P2	susceptible	resistant			
995-1-1	× Pallas	0(4)	4	219	77	3:1	8.58	0.687
	× P22	0(4)	0(4)	0	367	0:1		
995-1-2	× Pallas	0(4)	4	220	71	3:1	9.58	0.813
	× P22	0(4)	0(4)	0	352	0:1		
995-1-3	× Pallas	0(4)	4	286	98	3:1	10.58	0.814
	× P22	0(4)	0(4)	0	357	0:1		

and Kocourek 1986, Limpert et al. 1999). Because of this, the durability of resistance genes may be increased by use of multiline cultivars, by combining (pyramiding) different resistance genes into one variety and by deploying many cultivars with different resistance genes in space (cultivar mixtures) or time (winter versus spring barley) (Wolfe and McDermott 1994, Finckh et al. 1999, Jalli et al. 1999). In addition, there are still many resistance genes that have not been exploited so far, and new sources of resistance are still being found in barley landraces and barley wild relatives (Jørgensen 1994, Dreiseitl and Bockelman 1997, 1998, Czembor 2001).

North Africa, including Libya, is characterised by big contrast in its natural conditions because of their mountainous topography and big contrasts in climate (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, Alemayehu 1995, 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, Valkoun et al. 1995, Zine Elabidine et al. 1995, Hammer et al. 1996).

Mlo resistance was first identified in 1942 in an *X*-ray induced mutant (M66) in the German variety Haisa (Jørgensen 1992). Since 1942, Mlo resistance was more than 150 times independently induced by mutation. About 1970, it was also discovered as a spontaneous gene in barley landraces from Ethiopia collected by German expeditions in the 1930s. In 1985, Negassa described Mlo resistant barley landraces collected in southern Ethiopia (Jørgensen 1971, 1994, Negassa 1985, Schwarzbach 1998). Currently 25 different *mlo* resistance alleles are known. All of them with exception of *mlo11* were produced by mutagenesis (Jørgensen 1994, Schwarzbach 1998). The first in Europe Mlo resistant barley variety Atem (released in The Netherlands in 1979) derived its resistance (*mlo11*) from the Ethiopian landrace L92. Almost all barley varieties with Mlo resistance have the same allele *mlo11* with one important exception: Alexis (*mlo9*). This proves that in contrary to the mutants, barley landrace were the most important sources of Mlo resistance (Atzema 1998, Schwarzbach 1998). Perhaps a just important role may play the new source of this resistance described in the present study. In addition, 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 (Hadjichristodoulou 1995, Ceccarelli and Grando 1999, Havaux and Tardy 1999, Ceccarelli et al. 2000).

In recent years, Mlo resistance has become a very important source of durable powdery mildew resistance in Europe and more than 100 cultivars with gene *mlo* were registered in Europe during 1979–2001 (Czembor and Czembor 2001, Schwarzbach 2001, personal commun.). Consequently, the new source of highly effective powdery mildew resistance described in this study should be successfully used in barley breeding programs. Use of this newly described sources of mlo resistance should significantly increase yield stability of barley cultivars registered in Central Europe including the Czech Republic. Future work will concentrate on introduction of allele or alleles at locus *Mlo* occurring in selections from landrace 995 (ICB 112840) into elite cultivars of barley.

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ABSTRAKT

Novošlechtění pocházející z místní rasy ječmene odebrané v Libyi jako nové zdroje účinné rezistence proti padlí (*Blumeria graminis* f. sp. *hordei*)

Padlí na ječmeni (*Hordeum vulgare* L.), které způsobuje patogen *Blumeria graminis* f. sp. *hordei*, se vyskytuje po celém světě a může vést k vážným ztrátám výnosů. Jelikož agrotechnická opatření zaměřená na kontrolu ztrát způsobených touto chorobou nejsou zcela účinná, jsou žádány odrůdy s geneticky založenou rezistencí. Je proto třeba charakterizovat nové zdroje genů, které předávají rezistenci k padlí ječmene. Tuto studii jsme uskutečnili s cílem stanovit genetické založení rezistence k padlí u tří novošlechtění 995-1-1, 995-1-2, 995-1-3, pocházejících z místní rasy ječmene 995 (ICB 112840), odebrané v okrese Al Aziziyah v provincii Tripolitanie v Libyi. Místní rasa pocházela z Mezinárodního centra pro zemědělský výzkum v suchých oblastech ICARDA sídlem v Aleppu v Sýrii. Ke stanovení počtu genů, typu působení genů a lokusů genů u testovaných linií jsme provedli křížení dvojího typu: (1) jednotlivé linie jsme zkřížili s náchylnou odrůdou Pallas, (2) jednotlivé linie jsme zkřížili s izolinií P22 odrůdy Pallas nesoucí gen *mlo5*. Rodiče i potomstvo F_2 jsme hodnotili na rezistenci k padlí pomocí izolátu R303.1. Na základě poměrů štěpení jsme zjistili, že rezistence u těchto tří novošlechtě-

ní byla určena jednotlivou alelou recesivního genu v lokusu *Mlo*, vyskytující se v izolinii P22 odrůdy Pallas. Kromě toho testované linie vykazovaly reakci rezistence typu 0(4) typickou pouze pro geny *mlo*. Diskuse se týká přínosu nových zjištěných zdrojů vysoce účinné rezistence vůči padlí pro šlechtitelské programy a produkci ječmene.

Klíčová slova: *Hordeum vulgare*; *Blumeria graminis*; místní rasy ječmene; rezistence Mlo; padlí

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