Cereal Research Communications (2020) 48:179–185
https://doi.org/10.1007/s42976-020-00021-4

ORIGINAL PAPER

Evaluating barley landraces collected in North Africa and the Middle East for powdery mildew infection at seedling and adult plant stages

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Received: 30 August 2019 / Accepted: 15 January 2020 / Published online: 4 February 2020

Abstract

Barley (*Hordeum vulgare* L.) is one of the most widely grown cereal crops. Numerous pathogens impair the amount and quality of the grain yield. *Blumeria graminis* f. sp. *hordei* (*Bgh*) is a fungal pathogen causing powdery mildew, a widespread and economically important foliar disease. Since there is a limited number of known resistance genes, efforts of scientists and breeders are focused on searching for new sources of resistance. Barley landraces are a known, but still underexploited source of diversity. A set of 79 barley landraces collected in North Africa and the Middle East was tested against powdery mildew at seedling and adult plant stages. Under a controlled environment, 50% of accessions showed resistance conditioned by major genes. Among them, seven accessions showed broad resistance to *Bgh* isolates that were virulent to most of the known resistance genes. The field experiments carried out under natural infection over several years indicated all accessions as potential sources for resistance breeding. Twelve landraces were found to be medium resistant or resistant during all six seasons. This report relates to barley landraces as a promising source of potentially novel resistance to powdery mildew.

Keywords *Hordeum vulgare* · *Blumeria graminis* f. sp. *hordei* · Resistance genes

Introduction

Barley (*Hordeum vulgare* L.) is the fourth most important cereal crop according to harvesting area (http://www.fao.org/faostat). It is resistant to harsh environmental conditions, such as soil salinity, high altitude and low rainfall (von Bothmer et al. 2003a), and is used for feeding and malting purposes. The challenge is to control over 250 pathogens infecting the barley crop (Singh et al. 2019). Most of them are a significant economic problem through reduction of the crop quality and yield. Prevention of crop loss is one of the goals of food security (Savary et al. 2012). Powdery mildew caused by *Blumeria graminis* (D.C.) Golovin ex Speer f. sp. *hordei* Em. Marchal (*Bgh*) is one of the most important barley diseases. *Bgh* is an airborne fungus which causes yield loss of up to 50%, while average losses are about 10–20% (Tratwal and Weber 2006). In contrast to chemical agents, resistance breeding is an economically effective and environmentally friendly method of controlling the spread of the pathogen.

Several race-specific major resistance genes were already mapped on the barley genome: *Mla*, *Mlat*, *MlGa*, *Mlk*, *Mlnn*, *Mlra* on chromosome 1H; *MlLa* and *MlMor* on 2H; *Mlg* and *MlBo* on 4H; *Mlj* on 5H; *Mlh* on 6H; and *mlt* and *Mlf* on 7H (Jørgensen 1994; Schönfeld et al. 1996; Chełkowski et al. 2003; Piechota et al. 2019). Some of them, as well as other major resistance genes with unknown location on the barley genome, like *Ml(Ab)*, *Ml*(*Lv*); *Ml(Lo)* and *Ml(St)*, have been introduced to modern European cultivars (Dreiseitl 2017a). Resistance conditioned by major genes is non-durable. Newly appearing fungal pathotypes can overcome resistant genes in a few years. Also the effectiveness of pyramiding two or more major genes is limited in time (Dreiseitl 2003, 2011). The recessive allele *mlo* carries non-race-specific resistance to *Bgh*. It is widely used in elite cultivars due to its durability and lack of selection pressure to the pathogen population.

Communicated by H. Grausgruber.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s42976-020-00021-4) contains supplementary material, which is available to authorized users.

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In the face of the limited available gene pool, searching for new resistance sources is in the interests of scientists and breeders. The selection process has narrowed the gene pool of modern crops (Wulff and Dhugga 2018), so exploration should extend beyond cultivars (Pietrusińska et al. 2018). Barley landraces could be promising as they were cultivated according to traditional practices and not subjected to strong selection pressure. They are highly diverse and heterogeneous populations with a variable gene pool (Camacho Villa et al. 2005). Landraces belong to the primary gene pool and can be easily used in breeding programs. The lack of crossing barriers reduces breeding costs and efforts (von Bothmer et al. 2003b; Yun et al. 2006). The aim of this study was to select promising sources of powdery mildew resistance in North African and Middle East barley landraces.

Materials and methods

Plant material

A set of 79 spring barley landraces from the collection of the Plant Breeding and Acclimatization Institute – National Research Institute (Radzików, Poland) was screened for resistance to *Bgh*. All accessions were obtained from The International Centre for Agricultural Research in the Dry Areas (ICARDA) collection (Table 1). Barley landraces originated from North Africa and the Middle East and included 27 accessions from Algeria, 14 from Jordan, six from Egypt, six from Morocco, six from Libya, one from Tunisia and 19 of unknown origin.

Pathogen isolates

Six barley *Bgh* isolates, Bgh27, Bgh133, Bgh111, Bgh131, Bgh4714, Bgh314, collected in Poland, were used for artificial inoculation at the seedling stage. The isolates have a known virulence spectra according to the Pallas near-isogenic lines: Pallas (*Mla8*), P01(*Mla1*), P02 (*Mla3*), P03 (*Mla6*, *Mla14*), P04B (*Mla7, +?*), P06 (*Mla7*, *MlLG2*), P07 (*Mla9*, *Mlk*) P08B (*Mla9*), P09 (*Mla10*, *MlDu2*), P10 (*Mla12*), P11 (*Mla13*, *Ml(Ru3)*), P12 (*Mla22*), P13 (*Mla23*), P14 (*Mlra*), P15 (*Ml(Ru2)*), P17 (*Mlk*), P18 (*Mlnn*), P19 (*Mlp*), P20 (*Mlat*), P21 (*Mlg*, *Ml(CP)*), P23 (*MlLa*), P24 (*Mlh*) (Kølster et al. 1986); and cultivars Borwina (*Ml(Bw)*), Iron (*Ml(1-B-53)*), Steffi (*Ml(St1)*, *Ml(St2)*), Lenka (*Mla13, Ml(Ab)*), Gunnar (*Mla3, Ml(Tu2)*) and Triumph (*Mla7, Ml(Ab)*) (Table 2, Table S1*). All isolates were freshly propagated on the susceptible barley variety Manchuria CIho 2330.

Seedling resistance screening

Seedling tests were performed for resistance against each of six *Bgh* isolates: Bgh27, Bgh133, Bgh111, Bgh131, Bgh4714, Bgh314. For each test ca. 25 seeds per barley accession were sown. They were grown under controlled chamber conditions with a 16/8 h day/night photoperiod and a 22/16 °C temperature regime. Seedlings with a fully expanded first leaf (DC: 12 (Zadoks et al. 1974)) were inoculated with *Bgh* by shaking conidia from the susceptible cv. Manchuria. After 8–10 days, infection types were scored according to a 5-level scale (Mains and Dietz 1930), where 0, 1 and 2 represented resistant plants and 3 and 4 represented susceptible plants. Postulation of resistant genes was based on a comparison of reaction spectra designated on landraces and the barley differential set (Table S1). In case of a mixed reaction against *Bgh* isolate, postulation was performed for the resistance score. Possibility of resistance to Avr genes was concluded on the basis of the gene-for-gene hypothesis (Flor 1956). The infection response spectrum of each landrace was compared with the *Bgh* virulence spectrum previously found on the set of barley differential varieties.

Adult plant resistance screening

Barley landraces were screened for adult plant resistance under natural infection conditions. Plants were field grown in Radzików, central Poland (52° 13′ 38″ N, 20° 36′ 55″ E) during six seasons: 2010–2013, and 2016–2017. Plants were sown in a 2-m plot with 20 cm row spacing and 7 cm distance between seeds. Susceptible Manchuria was sown every 20 rows as a disease spreader. Disease symptoms were scored on adult plants at the flowering stage (DC: 60–69; Zadoks et al. 1974) according to a 9-level scale, were 1 indicates a very susceptible reaction and extreme infection of the entire plant and 9 indicates a totally resistant plant without visible symptoms of infection (Dreiseitl 2003, 2011) and the lowest infection score per accession and per season was recorded.

Results

Seedling resistance screening

Among 79 barley landraces, 39 (49%) showed resistance to at least one *Bgh* isolate tested (Table 3). Among them, two accessions (701, 720) were resistant to five isolates, four (695, 719, 737, 740) to four, five to three, and 15 were resistant to two isolates. Postulation of resistance genes

Table 1 Origin of barley landraces and results of resistance tests against *B. graminis* f. sp. *hordei* infection at seedling and adult plant stage

Accession	ICARDA ID	Origin	Seedling av *Bgh*[a]	Adult plant score[b]		Accession	ICARDA ID	Origin	Seedling av *Bgh*	Adult plant score	
				Min.	Mean					Min.	Mean
612	116139	Algeria	0	5	7	747	119144	Jordan	0	3	5
613	116141	Algeria	0	5	7	748	119145	Jordan	2	5	7
621	116150	Algeria	0	5	7	749	119147	Jordan	2	3	6
622	116154	Algeria	0	3	5	753	119153	Jordan	2	5	7
623	116160	Algeria	0	3	6	761	119164	Jordan	1	3	6
624	116162	Algeria	0	3	5	766	119170	Jordan	0	3	6
628	116166	Algeria	0	5	6	772	119176	Jordan	0	3	6
631	116171	Algeria	0	5	7	695	118542	Libya	4	3	6
633	116175	Algeria	0	5	5	784	120662	Libya	1	3	6
636	116180	Algeria	0	3	6	789	120667	Libya	0	3	6
643	116189	Algeria	0	5	6	792	120670	Libya	0	3	6
646	116199	Algeria	0	5	6	793	120671	Libya	1	3	6
651	116221	Algeria	1	5	7	794	120672	Libya	3	3	6
652	116222	Algeria	0	5	6	601	116081	Morocco	2	3	6
666	118512	Algeria	0	3	5	602	116082	Morocco	0	3	6
667	118513	Algeria	0	3	5	603	116083	Morocco	0	3	6
668	118514	Algeria	1	3	6	692	118538	Morocco	0	3	5
669	118515	Algeria	0	3	5	693	118539	Morocco	1	3	6
670	118516	Algeria	0	5	6	694	118540	Morocco	3	5	7
671	118517	Algeria	0	5	6	691	118537	Tunisia	1	3	5
672	118518	Algeria	0	5	6	698	118606	un[c]	3	3	6
673	118519	Algeria	0	3	6	700	118608	un	2	3	6
681	118527	Algeria	0	3	5	701	118609	un	5	3	4
683	118529	Algeria	0	3	5	703	118620	un	2	3	6
684	118530	Algeria	0	3	6	704	118621	un	2	3	6
686	118532	Algeria	0	3	6	705	118622	un	1	3	6
687	118533	Algeria	0	3	6	707	118624	un	0	5	6
605	116130	Egypt	2	3	5	712	118629	un	2	3	5
606	116131	Egypt	0	3	5	717	118634	un	1	3	5
607	116132	Egypt	0	3	5	718	118635	un	1	3	5
610	116135	Egypt	0	3	5	719	118636	un	4	3	6
647	116217	Egypt	2	5	7	720	118637	un	5	3	6
648	116218	Egypt	2	5	7	724	118641	un	2	3	5
660	118357	Jordan	0	3	6	725	118642	un	1	3	6
735	119130	Jordan	2	3	5	727	118644	un	2	5	7
737	119133	Jordan	4	3	7	728	118645	un	2	3	5
739	119135	Jordan	1	3	6	729	118646	un	3	3	6
740	119136	Jordan	4	3	6	730	118647	un	3	5	7
742	119139	Jordan	1	3	5	732	118649	un	0	3	6
744	119141	Jordan	0	3	5						

[a]Number of avirulent powdery mildew isolates out of six used for artificial inoculation

[b]Minimum and mean infection scores (1–2: susceptible; 3–4: medium susceptible; 5–6: medium resistant; 7–9: resistant) noted during 6-years field trial under natural inoculation

[c]Unknown origin

was feasible for seven accessions. For all resistant landraces resistance to Avr genes was estimated. Presumption indicated 11 accessions (605, 695, 701, 704, 720, 735, 737, 740, 748, 749, 753) carrying putative resistance to at least

Table 2 *B. graminis* f. sp. *hordei* isolates used for artificial inoculation and their virulence spectra against barley resistance genes

Bgh isolates	Virulence[a]
Bgh27	*a7; a8; a10; Ab; CP; Du2; g; h; La; ra*
Bgh133	*a1; a3; a6; a7; a8; a9; a12; a13; a14; a22; Ab; at; CP; g; h; IM9; LG2; ra; Ru3*
Bgh111	*a6; a7; a8; a9; a10; a12; a13; a14; Ab; Bw; CP; Du2; g; IM9; k; La; nn; ra; Ru2; Ru3; St1; St2*
Bgh131	*a1; a3; a6; a7; a8; a9; a10; a12; a14; Ab; Bw; Du2; h; IM9; k; La; nn; ra; Ru2; St1; St2*
Bgh314	*a1; a7; a8; a9; a10; a12; a13; Ab; CP; Du2; g; h; IM9; k; La; LG2; nn; ra; Ru2; Ru3*
Bgh4714	*a1; a7; a8; a9; a10; a12; a13; Ab; Bw; CP; Du2; g; h; IM9; k; La; LG2; nn; ra; Ru2; Ru3; St1; St2; 1-B-53*

[a]Tested for pathogenicity on differential genotypes carrying different *Ml* genes: *a1, a3, a6, a7, a8, a9, a10, a12, a13, a14, a22, Ab, at, Bw, CP, Du2, g, h, IM9, k, La, LG2, nn, ra, Ru2, Ru3, St1, St2, 1-B-53*

nine Avr genes. Two accessions (701, 720) probably carried resistance to 20 Avr genes. For two landraces (739, 742) it was impossible to indicate any known resistance, but they showed an incompatible reaction against one of the *Bgh* isolates used. Some of the accessions revealed a heterogenic reaction and contained resistant and susceptible plants against at least one *Bgh* isolate tested. A mixed reaction was observed for 27 landraces, which is 37% of all tested barleys and 67% of accessions resistant to *Bgh* isolates at the seedling stage.

Adult stage screening

The set of 79 barley landraces was tested under field conditions during six seasons. The lowest infection scores noted during the trial were: 5 (medium resistance) recorded for 21 (26%) landraces and 3 (which is medium susceptible) observed for 58 (74%) accessions (Table 1). Average infection scores calculated for six seasons were: 7 (resistant) for 13 (16%) accessions, 5–6 (medium resistant) for 65 (82%) accessions, and 4 (medium susceptible) for one accession. A set of 12 (612, 613, 621, 631, 647, 648, 651, 694, 727, 730, 748, 753) accessions showed an average score of 7 (resistant) with the lowest score of 5 (medium resistant). These accessions were medium resistant or resistant during all six seasons.

Discussion

Blumeria graminis is a highly adaptive and fast propagating fungal pathogen. New pathotypes, which emerge easily and fast, may manifest virulence to resistance genes currently used in crops. To retard erosion of resistance, gene pyramiding as well as major and minor gene combinations are used. The limited number of known genes carrying resistance to *Bgh* inspires the effort to discover new potential resources.

Landraces are crucial for resistance breeding and to restore diversity among the resistance gene pool (Akem et al. 2000). Variable genotypes throughout the population and lack of strong selection pressure support genetic differentiation. Previous reports identified barley landraces as potential sources of resistance (Czembor 2000, 2002; Comadran et al. 2009; Newton et al. 2010; Spies et al. 2012). Resistance genes revealed in landraces were successfully introduced to modern cultivars. The best known and used is the *mlo* recessive allele, which was first identified in an Ethiopian landrace. Other examples are *Mlg*, originating from the German landrace Weihenstephan; and variants revealed in the multiallelic locus *Mla*: *Mla3* carried by the Uruguayan landrace Ricardo, and *Mla12* from Arabische (Jørgensen 1994). Since *Bgh* isolates collected in Africa revealed higher diversity than European fungi (Dreiseitl and Kosman 2013; Jensen et al. 2013), barley landraces originating from that region are suspected to be variable in *Bgh* resistance loci. Additionally, landraces originating from regions of barley diversification and domestication, such as North Africa and the Middle East, exhibit a diversity of resistance genes due to long-term coevolution with the pathogen (Camacho Villa et al. 2005; Morrell and Clegg 2007). Screening of Jordanian barley landraces allowed the selection of 165 lines resistant to *Bgh* (Abdel-Ghani et al. 2008). A collection of 131 barley lines originating from Morocco exhibited seedling resistance (Czembor 2000, 2002).

In this report seedling tests showed that 50% of the investigated accessions harbored major resistance genes (Table 3). The *Bgh* isolates used for inoculation covered most of the known and used genes (Jørgensen 1994; Dreiseitl 2014), so it can be presumed that these accessions carry new resistance genes. Six accessions (695, 701, 719, 720, 737, 740) have a broad spectrum of resistance and may be of interest to breeders. Some of the accessions revealed mixed infection types after inoculation with *Bgh* isolates. Since the landraces are non-homogeneous dynamic populations, mixed reaction within plants is expected. Progeny of these accessions should be selected according to the resistance trait before further testing. Previous reports showed the mixed reaction of barley landraces against *Bgh* (Dreiseitl 2017b). In the present research, postulation of resistance genes was feasible for seven landraces (Table 3), whereas possible resistance to Avr

Table 3 Set of barley (*H. vulgare* L.) landraces which revealed resistance to at least one *B. graminis* f. sp. *hordei* isolate after inoculation at the seedling stage

Hv	*Bgh* isolates						Postulated R genes[c]	Possibly resistance to *Bgh* Avr genes[d]
	Bgh27	Bgh133	Bgh111	Bgh131	Bgh4714	Bgh314		
701	0[a]	2	2+4[b]	2	4	2		*a1, a9, a10, a12, a13, Bw, CP, Du2, g, h, IM9, k, La, LG2, nn, Ru2, Ru3, St1, St2, 1-B-53*
720	2	2	2	2	4	1		*a1, a9, a10, a12, a13, Bw, CP, Du2, g, h, IM9, k, La, LG2, nn, Ru2, Ru3, St1, St2, 1-B-53*
695	2+4	2+4	2	2+4	4	4		*a1, a9, a10, a12, a13, CP, Du2, g, h, IM9, La, LG2, nn, Ru2, Ru3*
737	1	1	2	4	4	2		*a9, a10, Bw, Du2, h, IM9, k, La, nn, Ru2, St1, St2*
740	1	1	2	4	4	2		*a9, a10, Bw, Du2, h, IM9, k, La, nn, Ru2, St1, St2*
704	1	1	4	4	4	4		*a9, a10, a12, Du2, IM9, k, La, nn, Ru2*
605	0+4	1+4	4	4	4	4		*a9, a10, a12, Du2, IM9, k, La, nn, Ru2*
735	2+4	1+4	4	4	4	4		*a9, a10, a12, Du2, IM9, k, La, nn, Ru2*
748	1	1	4	4	4	4		*a9, a10, a12, Du2, IM9, k, La, nn, Ru2*
749	1	1+4	4	4	4	4		*a9, a10, a12, Du2, IM9, k, La, nn, Ru2*
753	1+4	2	4	4	4	4		*a9, a10, a12, Du2, IM9, k, La, nn, Ru2*
703	2	4	2+4	4	4	4		*a1, a9, a12, h, IM9*
719	4	2	2	1+4	4	1+4		*a10, CP, Du2, g, h*
601	2	4	4	2+4	4	4		*a9, a12, a13, CP, IM9*
724	0	4	4	0	4	4	*Mla13, Ml(Ab)*	*a9, a12, a13, CP, IM9*
727	2+4	4	4	2+4	4	4		*a9, a12, a13, CP, IM9*
728	1	4	4	2+4	4	4		*a9, a12, a13, CP, IM9*
698	1	1	2	4	4	4		*a1, a9, a10, a12*
694	2	4	2	4	4	2		*a1, a12, h*
794	0	4	0	4	4	0+2		*a1, a12, h*
729	1	4	2	4	4	1+4		*a1, a12, h*
693	4	2+4	4	4	4	4	*MlLa*	*a10, Du2, La*
651	1	4	4	4	4	4		*a9, a12, IM9*
705	0+4	4	4	4	4	4	*Mla9, Ml(IM9)*	*a9, a12, IM9*
793	0+4	4	4	4	4	4	*Mla9, Ml(IM9)*	*a9, a12, IM9*
718	1+4	4	4	4	4	4		*a9, a12, IM9*
725	2	4	4	4	4	4		*a9, a12, IM9*
647	41	4	2+4	2	4	4		*CP, g, h*
700	4	4	2+4	0	4	4		*CP, g, h*
712	4	4	2+4	4	4	1+4		*CP, g, h*
730	4	4	1	2	4	1		*CP, g, h*
648	4	4	4	2+4	4	2		*CP, g*
784	4	4	4	2+4	4	4		*CP, g*
717	4	4	4	2+4	4	4	*Mlg, Ml(CP)*	*CP, g*
691	4	4	2	4	4	4		*h*
668	4	4	2+4	4	4	4	*Mlg, Ml(CP)*	*h*
761	4	4	2+4	4	4	4	*Mlg, Ml(CP)*	*h*
739	4	4	4	4	4	2		?
742	4	4	4	4	4	2+4		?

[a]Infection score according to 5-level scale; 0, 1 and 2 represent resistant plants, 3 and 4 –susceptible

[b]Mixed reaction after inoculation, accession contained resistant and susceptible plants

[c]Based on a comparison of reaction spectra designated on landraces and barley differential set

[d]Based on gene-for-gene hypothesis, resistance not eliminated during tests

was estimated for 38 seedling resistant landraces. In previous data presented by Czembor (2000, 2002), reaction of 66 (50%) lines selected from barley landraces were unique and distinguished from other known genes. Nevertheless, for 99 (76%) accessions the *Mlat* gene was postulated or supposed. The latter author used in the experiments a more diverse set of *Bgh* isolates that were more accurate. The six *Bgh* isolates used in this study had broad virulence spectra and allowed expression of the maximum number of resistance genes but are less informative than the full differential *Bgh* set.

Since major genes are usually overcome in a few years, field resistance determined by minor quantitative genes is more promising. It has longer durability and is effective against various pathotypes. That kind of resistance increases during continuous cultivation and quantitative minor genes are still diversifying and changing (Jensen et al. 2012). The multiyear trial examined resistant landraces under different weather conditions and variable pathogen pressure. A set of 12 (612, 613, 621, 631, 647, 648, 651, 694, 727, 730, 748, 753) accessions revealed a good level of resistance during six seasons. These accessions could be valuable material for a more detailed analysis and a good source for resistance breeding. Additionally, selected landraces were collected from the area of barley origin and domestication. Field resistance maintained by long-term coevolution with a pathogen is valuable and economically important for farmers and breeders (Jensen et al. 2012).

This multiyear study did not reveal consistent field resistance to natural pathogen pressure with seedling resistance against artificial inoculation in a climate chamber. Reaction patterns were variable among growth stages. Expression of quantitative resistance becomes more visible at the adult stage and against multipathotype infection. Previous data identified wild barley (*H. vulgare* ssp. *spontaneum*) genotypes resistant at seedling stage and highly susceptible at adult stage under field conditions (Dreiseitl and Bockelman 2003). Nevertheless, all landraces resistant to at least three *Bgh* isolates (701, 720, 695, 719, 737, 740, 698, 694, 729, 794, 730) at the seedling stage were at least medium resistant at the adult stage.

According to Dreiseitl (2017b) searching for and detecting new resistance is desirable for its utility in breeding programs, for easier identification of minor resistance genes frequently masked by major genes and for improving knowledge of resistance. New resistance genes can be useful by combining them with other known genes or partial Mlo resistance in barley cultivars. That approach makes resistance more durable and inhibits Mlo resistance erosion (Dreiseitl 2017b). Six-year field trials and artificial testing against highly virulent powdery mildew isolates, presented in this report, provided the list of barley landraces resistant to *B. graminis* f. sp. *hordei*.

Acknowledgements The authors thank to Professor Henryk Czembor for significant and valuable advices provided in their work with barley–powdery mildew pathosystem. The research was conducted within program "Creation of scientific basis for biological improvement and plant genetic resources protection as source of innovation and support of sustainable agriculture and national food security", Project No. 3-2-00-0-02 (PW task 2.2): "Broadening of barley gene pool" supported by The Ministry of Agriculture and Rural Development Poland.

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