Sources of Resistance to Powdery Mildew in Barley Landraces from Turkey

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Abstract: Powdery mildew on barley, caused by the pathogen *Blumeria graminis* f. sp. *hordei*, occurs worldwide and can result in severe yield loss. Germplasm of barley, including landraces, commercial cultivars, wild relatives and breeding lines are stored in more than 200 institutions. There is a need for characterization of this germplasm in terms of resistance to biotic and abiotic stresses. This is necessary in order to use specific accessions in breeding programs. In the present study, 129 barley landraces originated from Turkey and provided by the ICARDA genebank were tested for resistance to powdery mildew. Seedling resistance tests after inoculation with 19 differentiated isolates of *B. graminis* f. sp. *hordei* were used to postulate the presence of resistance genes. From the 129 landraces studied, plants of 19 (14.7%) of them showed resistance to infection with powdery mildew. Based on preliminary tests from these 19 landraces, 25 resistant single plant lines were selected for testing with differential powdery mildew isolates. Seven lines were resistant to all 19 isolates used. However, only one line (5583-1-4) showed resistance scores of zero against all isolates used. It is likely that this line possesses unknown, but highly effective genes for resistance. In five resistant lines it was not possible to postulate the presence of specific resistance genes. In 19 lines the presence of the genes *Mlp*, *Mlk*, *Mlh*, *Mlg*, *Ml(CP)*, *Mlat*, *Mla3*, *Mla6*, *Mla7* and *Mla22* were postulated. These new sources of highly effective powdery mildew resistance in barley landraces from Turkey could be successfully used in breeding programs.

Keywords: *Hordeum vulgare*; barley; *Blumeria graminis*; powdery mildew; landraces; germplasm; resistance genes; genebank

1. Introduction

Barley (*Hordeum vulgare* L.) is an economically important cereal crop which is known to be drought, cold, and salt tolerant and well-adapted to low-input environmental conditions [1,2]. It is cultivated at high altitudes and commonly under rain-fed conditions. It is often grown in marginal agricultural areas with low annual precipitation, often less than 220 mm [3]. Barley ranks as the fourth crop in the world, after wheat, maize and rice, in terms of the area of cultivation. Almost half of the world’s barley area is in Europe, where barley is second crop after wheat in cultivated area [4].

Germplasm of barley, including landraces, commercial cultivars, wild relatives and breeding lines is very diverse and is stored in more than 200 institutions [5,6]. Barley landraces are an important source of genetic variation and resistance to biotic stresses including powdery mildew [7–9]. Turkey is characterized by the presence of diverse agroecological zones and a long history of agriculture. It is known to be a rich source of barley landraces. They are still planted in this country, and they are characterized by a high level of resistance to biotic and abiotic stresses. There is a need for characterization of this germplasm in terms of resistance to biotic and abiotic stresses. This knowledge is necessary in order to use specific accessions in breeding programs [10–12].
Barley is often infected by barley powdery mildew fungus (*Blumeria graminis* DC. Golovin ex Speer f. sp. *hordei*). Loss of yield caused by this disease can reach up to 30%, with averages of 5–10% [13–16]. Powdery mildew on barley is considered one of the most well-characterized host–pathogen genetic interaction systems. Barley cultivars with effective genes for resistance to powdery mildew have been an efficient means for controlling this disease [17–21]. Barley breeders have used major resistance genes: *Mla6, Mla7, Mla9, Mla12* and *Mla13, Mlk, Mlg, MLa, Mlh* and *Mira*, which originated from landraces as well as from the subspecies *H. vulgare* ssp. *spontaneum*. Durable *mlo*-resistance (gene *mlo*) has been identified in landraces. Since 1984, it has been deployed in many barley cultivars throughout Europe [20,22–24].

Effective controlling of barley powdery mildew is possible by growing genetically resistant barley cultivars. This method of crop protection is relatively inexpensive and it is environmentally friendly. These cultivars started being used from the beginning of the application of modern, intensive methods in barley production because these production methods created favorable conditions for development of this disease [25–30]. Currently, powdery mildew of barley is one of the most common and most widespread disease of barley in Europe and another barley regions of the world, causing significant yield losses [20,21,31].

When a cultivar containing one dominant resistance gene is grown on a large acreage, new virulent *B. graminis* races may occur within 4–5 years. Exceptions are recessive genes for resistance such as *mlf* and *mlo*. However, many factors, e.g., temperature, water stress or light intensity, may affect the use of these genes in breeding programmes [20,22,28]. At least 38 different genes/alleles have been used in varieties grown in Europe [32]. Nevertheless, barley breeders, geneticists and plant pathologists are constantly looking for new, efficient sources of powdery mildew resistance, in order to combine them with those already used in modern cultivars, and to increase their resistance durability [31,33,34].

Most of the original sources of powdery mildew resistance genes came from domesticated cultivars in Europe [25,26,35]. These sources of resistance were easy to be used in breeding but the number of resistance genes was limited. Breeders and geneticists have been looking for new sources of resistance in non-European germplasm. Most of these studies were conducted using collections of landraces and differential sets of powdery mildew isolates [36,37]. Previous studies showed that barley landraces from Turkey are rich sources of genetic diversity for plant breeding, including resistance to pathogens [10–12,38,39].

Identification of powdery mildew resistance genes based on tests performed on seedlings using differential sets of pathogens is effective and sufficient for breeders' and pathologists' needs [25,30,40,41]. This study aimed at detecting sources of powdery mildew resistance in barley landraces from Turkey.

### 2. Materials and Method

#### 2.1. Plant Material

Seed samples of 129 *H. vulgare* L. landraces from Turkey were provided by Dr. J. Valkoun, J. Konopka and Prof. S. Ceccarelli (International Center for Agricultural Research in the Dry Areas—ICARDA, Aleppo, Syria) (Table 1). For 53 landraces, details about the places of collection were known. These landraces originated from 26 provinces: 11 landraces were from Izmir province, 4—Kars, 3—Eskisehir, 3—Agri, 3—Erzincan, 3—Sivas, 3—Mugla, 3—Bilecik, 3—Kayseri, 2—Kutahya and 1 landrace originated from each of the following provinces—Bayburt, Derenizli, Sanli Urfa, Manisa, Van, Mus, Hakkari, Tokat, Icel, Antakya, Gaziantep, Isparta, Adana, Afyon, Usak, and Bursa. They were collected at altitudes from 15 m above sea level in Izmir province, to 1900 m above sea level in Kars province, and 2250 m above sea level in Bayburt province.
2.2. Pathogen

Nineteen differential Bgh (B. graminis f. sp. hordei Em Marschal) isolates with virulence genes corresponding to known resistance genes were used (Table 2). Isolates originated from the collections in Risø National Laboratory, Roskilde, Denmark; Danish Institute for Plant and Soil Science, Lyngby, Denmark; Edgenoissiche Technische Hochschule—ETH, Zurich, Switzerland provided kindly by Dr. H. J. Schaerer (ETH, Zurich, Switzerland) and the Plant Breeding and Acclimatization Institute—National Research Institute (PBAI-NRI) IHAR, Radzikow, Poland. A set of isolines of barley cultivar Pallas with different resistance genes was used [42], provided by Dr. L. Munk (Royal Agricultural and Veterinary University, Copenhagen, Denmark) and on 8 additional cultivars.

Isolate Bgh 33 was the most avirulent isolate. It was avirulent to resistance genes, or their combinations, such as: Mla1, Mla3, Mla6 + Mla14, Mla7 + Mlk +?, Mla7 +?, Mla7 + MILG2, Mla9 + Mlk, Mla9, Mla12, Mla13 + MIRu3, Mla22, Mla23, MIRu2, Mlk, Mlp, Mlat and to resistance genes present in additional cultivars included in a differential set: Benedicte (Mla9,Ml(IM9), Lenka (Mla13,Ml(Ab), Steffi (Ml(St1), Ml(St2), and Kredit Ml(Kr). Isolates Bgh 1, Bgh 29, and Bgh 51 were the most virulent group. Isolate Bgh 51 was virulent to resistance genes or their combinations present in 18 Pallas isolines, Bgh 29 was virulent to resistance genes or their combinations present in 17 Pallas isolines and Bgh 1 virulent to resistance genes or their combinations present in 16 Pallas isolines. They were purified by single pustule isolation and were maintained and propagated on young seedlings of the powdery mildew-susceptible cultivar Manchuria (CI 2330). Virulence checks were conducted to assure the purity of isolates throughout the experiment.

A five-point (0 to 4) reaction type (RT) scale was used, as follows: 0, no visible symptoms; 1, minute necrotic flecks, no mycelial growth and no sporulation; 2, frequent chlorosis, reduced mycelial growth and no or very scarce sporulation; 3, moderate mycelial growth, moderate sporulation, and occasional chlorosis; 4, profuse sporulation of well-developed colonies, 0(4) sparse small colonies originating from the stomatal subsidiary cells [26,43].
Table 1. Collected data of 129 landraces from Turkey.

| No. | ICARDA IG | IHAR No | Longitude (E) | Latitude (N) | Altitude (ppm) | Province |
|-----|-----------|---------|---------------|--------------|----------------|----------|
| 1   | 18,781    | 5177    |                |              |                |          |
| 2   | 18,848    | 5178    | 31 32-E       | N39 27       |                | Eskisehir |
| 3   | 18,849    | 5179    | E31 32-E      | N39 27       |                | Eskisehir |
| 4   | 18,851    | 5180    | E27 11        | N39 07       |                | Izmir    |
| 5   | 19,056    | 5181    |                |              |                |          |
| 6   | 19,058    | 5182    |                |              |                |          |
| 7   | 19,062    | 5183    |                |              |                |          |
| 8   | 19,068    | 5184    | E27 11        | N39 07       |                | Izmir    |
| 9   | 19,077    | 5185    |                |              |                |          |
| 10  | 18,541    | 5186    | E28 38        | N38 33       |                | Manisa   |
| 11  | 19,545    | 5187    |                |              |                |          |
| 12  | 19,546    | 5188    |                |              |                |          |
| 13  | 19,547    | 5189    |                |              |                |          |
| 14  | 19,550    | 5190    |                |              |                |          |
| 15  | 19,562    | 5191    |                |              |                |          |
| 16  | 19,565    | 5192    |                |              |                |          |
| 17  | 19,566    | 5193    |                |              |                |          |
| 18  | 19,568    | 5194    |                |              |                |          |
| 19  | 19,569    | 5195    |                |              |                |          |
| 20  | 19,576    | 5196    | E27 11        | N39 07       |                | Izmir    |
| 21  | 37,224    | 3340    |                |              |                |          |
| 22  | 37,225    | 3341    |                |              |                |          |
| 23  | 37,230    | 3342    |                |              |                |          |
| 24  | 37,234    | 3343    |                |              |                |          |
| 25  | 37,235    | 3344    |                |              |                |          |
| 26  | 37,237    | 3345    |                |              |                |          |
| 27  | 37,239    | 3346    |                |              |                |          |
| 28  | 37,240    | 3347    |                |              |                |          |
| 29  | 37,241    | 3348    |                |              |                |          |
| 30  | 37,242    | 3349    |                |              |                |          |
| 31  | 37,243    | 3350    |                |              |                |          |
| 32  | 37,244    | 3351    |                |              |                |          |
| 33  | 37,246    | 3352    |                |              |                |          |
| 34  | 37,249    | 3353    |                |              |                |          |
| 35  | 37,250    | 3354    |                |              |                |          |
| 36  | 37,251    | 3355    |                |              |                |          |
Table 2. *B. graminis* f. sp. *hordei* isolates used for artificial inoculation and their virulence spectra against resistance genes on differential set of Pallas near-isogenic lines and 8 cultivars.

| No. | Pallas Isolines and Cultivars | Virulence | Bgh Isolates |
|-----|-------------------------------|-----------|--------------|
|     |                               |           | Bgh 1 | Bgh 2 | Bgh 4 | Bgh 8 | Bgh 9 | Bgh 10 | Bgh 11 | Bgh 13 | Bgh 14 | Bgh 24 | Bgh 28 | Bgh 29 | Bgh 31 | Bgh 33 | Bgh 36 | Bgh 40 | Bgh 48 | Bgh 51 | Bgh 57 | Bgh 63 |
| 1   | P1                            | *Mla1*    | 0     | 0     | 4     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 4     | 0     | 0     | 4     | 0     | 0     | 4     | 0     | 0     |
| 2   | P2                            | *Mla3*    | 1     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 4     | 0     | 0     | 4     | 0     | 0     | 4     | 0     | 0     |
| 3   | P3                            | *Mla6, Mla14* | 0     | 0     | 0     | 0     | 4     | 0     | 4     | 0     | 0     | 0     | 0     | 4     | 0     | 4     | 4     | 4     | 4     | 4     | 4     | 4     | 4     |
| 4   | P4A                           | *Mla7, Mlk, +?* | 2     | 2     | 2     | 2     | 2     | 2     | 2     | 2     | 4     | 2     | 4     | 2     | 4     | 0     | 2     | 2     | 2     | 4     | 4     | 4     | 4     |
| 5   | P4B                           | *Mla7, +?* | 4     | 4     | 1     | 0     | 2     | 2     | 4     | 4     | 0     | 2     | 4     | 4     | 4     | 1     | 4     | 4     | 4     | 4     | 4     | 4     | 4     |
| 6   | P6                            | *Mla7, MlL2* | 4     | 4     | 0     | 0     | 2     | 1     | 2     | 4     | 0     | 2     | 2     | 4     | 0     | 4     | 2     | 0     | 4     | 4     | 4     | 4     | 4     |
A five-point (0 to 4) reaction type (RT) scale was as follows: 0, no visible symptoms; 1, minute necrotic flecks, no mycelial growth and no sporulation; 2, frequent chlorosis, reduced mycelial growth and no or very scarce sporulation; 3, moderate mycelial growth, moderate sporulation, and occasional chlorosis; 4, profuse sporulation of well-developed colonies, 0(4) sparse small colonies originating from the stomatal subsidiary cells.
2.3. Landraces and Single Plant-Lines Resistance Tests

First, samples of 30 plants from each of the landraces were tested with the Bgh 33 isolate (the most avirulent one) 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 were inoculated with Bgh isolate by shaking conidia from the susceptible cv. Manchuria. After 8–10 days, infection types were scored. Plants with disease scores of 0 to 1 were classified as highly resistant (R), plants that scored 2 as a moderately resistant (M) and rating of 3 or 4 as susceptible and very susceptible (S). Plants with the score 0(4) possess a resistance gene in locus Mlo. The cultivar Manchurian CI 3230 was used as a susceptible control.

Based on the results of this preliminary experiment, 25 resistant single plant lines from 19 landraces were selected. A highly resistant reaction type was observed on 13 lines, and a moderately resistant reaction type was observed on 11 lines. In 5 landraces, segregation of RT was observed (Table 3). Next, they were grown in greenhouse conditions to obtain seeds for future evaluations using a set of 19 Bgh differential isolates.

Postulation of resistant genes in tested lines was based on a comparison of reaction spectra observed on tested plants and the barley differential set infected with differential Bgh isolates (Table 1). This was performed on the basis of the gene-for-gene hypothesis [44].
Table 3. Resistance of barley (*H. vulgare* L.) lines selected from landraces originating from Turkey to *B. graminis* f. sp. *hordei* isolates after inoculation at the seedling stage.

| No. | ICARDA IHAR No. | Landrace Line | Isolate | Postulated Resistance Genes |
|-----|-----------------|---------------|---------|-----------------------------|
| 1   | 18,781 5177     | 5177 1 1      | BGh 1   | Mlp                         |
| 2   | 18,781 5177     | 5177 1 4      | BGh 2   | Mla7, Milk +?               |
| 3   | 18,849 5179     | 5179 1 1      | BGh 4   | Mla6, +?                    |
| 4   | 19,077 5185     | 5185 1 1      | BGh 8   | [Mla7, Milk+?], [Mlg, Ml(CP)]|
| 5   | 19,077 5185     | 5185 4 3      | BGh 9   | [Mla7, Milk+?], [Mlg, Ml(CP)]|
| 6   | 19,541 5186     | 5186 2 1      | BGh 11  | Mla22                       |
| 7   | 19,547 5189     | 5189 2 1      | BGh 13  | Mla6, +?                    |
| 8   | 19,547 5189     | 5189 3 3      | BGh 14  | Mla7, Milk +?               |
| 9   | 19,550 5190     | 5190 3 1      | BGh 16  | Mla6, +?                    |
| 10  | 25,979 5204     | 5204 3 2      | BGh 17  | Mla3, Milk                  |
| 11  | 37,230 5342     | 5342 1 1      | BGh 18  | Mla6, +?                    |
| 12  | 37,234 5343     | 5343 1 1      | BGh 19  | Mla7, Milk +?               |
| 13  | 37,235 5344     | 5344 1 1      | BGh 20  | Mla6, +?                    |
| 14  | 113,011 5437    | 5437 1 0      | BGh 21  | Mla22                       |
| 15  | 113,020 5439    | 5439 1 1      | BGh 22  | Mla6, +?                    |
| 16  | 113,020 5439    | 5439 5 1      | BGh 23  | Mla6, +?                    |
| 17  | 113,028 5442    | 5442 2 2      | BGh 24  | Mla7, Milk +?               |
| 18  | 113,028 5442    | 5442 3 1      | BGh 25  | Mla7, Milk +?               |
| 19  | 115,940 5470    | 5470 1 1      | BGh 26  | Mla6, +?                    |
| 20  | 115,947 5472    | 5472 1 1      | BGh 27  | Mla6, +?                    |
| 21  | 115,948 5473    | 5473 1 5      | BGh 28  | Mla6, +?                    |
| 22  | 115,958 5475    | 5475 1 1      | BGh 29  | Mla7, Milk +?               |
| 23  | 23,860 5544     | 5544 1 1      | BGh 30  | Mla22                       |
| 24  | 27,267 5583     | 5383 1 4      | BGh 31  | Mla22                       |
| 25  | 27,289 5587     | 5587 2 1      | BGh 32  | Mla22                       |

* nd—no data. A five-point (0 to 4) reaction type (RT) scale was used as follows: 0, no visible symptoms; 1, minute necrotic flecks, no mycelial growth and no sporulation; 2, frequent chlorosis, reduced mycelial growth and no or very scarce sporulation; 3, moderate mycelial growth, moderate sporulation, and occasional chlorosis; 4, profuse sporulation of well-developed colonies, 0(4) sparse small colonies originating from the stomatal subsidiary cells.
3. Results

Plants of 19 (14.7%) of the tested landraces were resistant to infection with Bgh33 isolate in preliminary testing. In five landraces, segregation of RT was observed. Based on preliminary tests from these 19 landraces, 25 resistant, single plant lines were selected for testing with differential isolates. From these lines, seven were resistant to all 19 isolates used. However, only one line (5583-1-4) showed resistance scores of zero against all isolates used (Table 3). In five lines it was not possible to postulate the presence of specific resistance genes. In 19 lines, the presence of the genes Mlp, Mlk, Mlh, Mlg, Ml(CP), Mlat, Mla3, Mla6, Mla7, Mla22 and unknown genes (genes not present in differential set) were postulated.

4. Discussion

Barley landraces from Turkey are a rich source of genetic diversity for plant breeding, including resistance to powdery mildew [10–12,38,39]. This was confirmed in the presented study. Single plant lines selected from 19 (14.7%) of the tested landraces were resistant to infection with powdery mildew.

Resistant lines selected from landraces are a very valuable material for resistance breeding. This kind of germplasm is the simplest source of resistance to use directly in breeding programs. Because of their adaptability to a wide range of conditions, barley landraces are recognized as an important genetic resource for tolerance and resistance to biotic and abiotic stresses. They carry unique traits and are considered a rich resource for resistance breeding and for the expansion of the gene pool [45,46].

Turkey is a rich source of barley genetic diversity because of its geographic location. The south-eastern region of Turkey is at the top of the Fertile Crescent of the Near East, within the centre of origin of cultivated barley [39]. Barley is one of the oldest cultivated plants grown in Anatolia, and it is the second most important cereal crop following wheat. In addition, in Turkey, the ancestor of cultivated barley, Hordeum spontaneum C. Koch, grows naturally, and powdery mildew epidemics occur in the western and southern parts of the country [12]. All these factors lead to conclusion that coevolution of barley powdery mildew was occurring in Turkey for very long time, and that barley landraces from Turkey may be a rich source of resistance to powdery mildew. This was confirmed in the presented study, in which many resistance genes were identified in lines selected from Turkish landraces.

The genetic diversity of barley landraces offers many traits for barley breeding, especially concerning resistance to biotic and abiotic stresses [3,33,47-50]. The genetic heterogeneity within the barley landraces is due to a low level of outcrossing occurring in barley, and farmers’ management of seed [40,51–53]. This genetic heterogeneity was also observed in the presented study, in which five landraces showed segregation of RT.

Many barley landraces collected in Tunisia [27], Morocco [36,54–59], Australia [60], China [61], Greece [62], Jordan [63,64], Egypt [54], Latvia [65], Libya [66], Yemen [67] and Spain [68–72] have been tested for resistance to powdery mildew, and numerous known and unknown specific resistances have been identified. In addition, collections of landraces from many countries have been studied [35,40,73–76]. Results show that the presence of known and unknown powdery mildew resistance genes have been obtained for barley landraces from Turkey [10,38,39]. The present study confirmed that barley landraces from Turkey have numerous known and unknown specific resistances to powdery mildew. In 24 resistant single-plant lines studied, the presence unknown resistance genes and the genes Mlp, Mlk, Mlh, Mlg, Ml(CP), Mlat, Mla3, Mla6, Mla7 and Mla22 were postulated.

Seedling resistance tests were used in order to describe infection types expressed by barley lines after inoculation with differentiated isolates of B. graminis f. sp. hordei. This kind of testing is sufficient for disease-resistance screening. It is used commonly in breeding programmes to postulate the presence of specific resistance genes in modern cultivars.
and to screen germplasm for new sources of effective resistance [36,40,75,76]. However, these kinds of tests are not very useful for identifying and describing partial resistance. For a description of partial resistance there is a need to conduct measurements of resistance characteristics, in addition to the infection type. Furthermore, partial resistance is generally better expressed at the adult plant stage [26,34,77].

Newly identified sources of powdery mildew resistance in 25 single plant lines (originated from 19 landraces) are valuable for barley breeding for resistance. In five lines it was not possible to postulate the presence of specific resistance genes. In 19 lines the presence of the genes Mlp, Mlk, Mlh, Mlg, Ml(CP), Mlat, Mia3, Mia6, Mia7 and Mia22 and unknown genes (not present in differential set) were postulated. Interestingly for barley resistance breeding, seven lines selected from four landraces were resistant to all 19 isolates used in this study. However, the most interesting point from a breeders’ point of view was line 5583-1-4, which showed resistance scores of zero for all isolates used. Most probably this line possesses unknown, yet very effective genes for resistance. Future work will include the genetic study of resistance identified in seven single-plant lines by conducting appropriate crosses and the use of molecular markers [58,59,78,79]. Authors intend to introduce these alleles into elite cultivars of barley to create initial materials for European breeding programmes. This is a necessary step between barley genebank collections and the practical use of barley genetic resources in breeding programmes. The new sources of highly effective powdery mildew resistance described in this study could be successfully used in barley breeding programs.

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