Identification of barley powdery mildew resistances in gene bank accessions and the use of gene diversity for verifying seed purity and authenticity

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Abstract

Human activities including those in crop gene banks are subject to errors, especially during seed multiplication and maintenance of seed germination. Therefore, the most serious problem of gene banks is authenticity of the accessions and their genotypic purity. There are many methods for determining the identity of varieties, but comparisons between current data and past records are not easy since the latter are often missing. Breeding barley resistant to powdery mildew caused by Blumeria graminis f. sp. hordei (Bgh) was traditionally based on incorporating major genes into new varieties and the results have been published. Our goal was to identify resistance genes to powdery mildew in accessions of the Czech spring barley core collection and compare these data with earlier information to establish the authenticity of the accessions. Two hundred and twenty-three accessions of the collection including 665 single plant progenies were tested. Sixty-four selected reference isolates of Bgh representing the world diversity of the pathogen were used for resistance tests. Twenty-two known resistance genes were postulated either separately or in combinations. In the collection, 151 homogeneous accessions were found, but the resistances of nine of them were inconsistent with published data and in 12 accessions their authenticity is doubtful. The remaining 72 accessions were heterogeneous and comprised 176 resistance genotypes, 54 of which were probably mechanical admixtures of other varieties. There are several pathogens of cereals, e.g. rusts and mildews, against which many resistance genes in host crops have also been exploited. Knowledge of these resistances can assist in maintaining pure and genuine stocks in gene banks. Seed purity and the authenticity of accessions can subsequently be checked with more advanced methods.

Introduction

Barley (Hordeum vulgare L.) is one of most important cereal crops in the world. Genetic resistance in cultivated plant species plays an essential part in disease management and plant
genetic resources are key to improving crops. Gene banks contain vast collections of varieties, but there are often groups of similar genotypes. Therefore, model collections, so-called core collections, have been created [1–3], which should provide as much genetic diversity as possible in a limited number of genotypes.

Human activity can result in errors and in gene banks these can cause problems relating to seed multiplication when each reproductive cycle comprises several operations where genotype contamination can occur especially after repeated cycles. To counter such errors gene banks implement standardized procedures, but in the past such procedures were not sufficiently elaborated and even with these techniques errors are still possible.

Varieties deposited in gene banks are mostly used for research and breeding and any genotype contamination creates more work for investigators; unintentional use of admixtures or misnamed varieties compromises the results [4,5]. Hence, the authenticity and genotypic purity of accessions in gene banks is essential. There are many methods available for determining varietal identity [6–8], including sequencing methods [9,10]. However, such refined methods may create more confusion if they are used on unverified varieties.

Powdery mildew, caused by the fungus *Blumeria graminis* (D.C.) Golovin ex Speer f. sp. *hordei* Em. Marchal (*Bgh*), is a worldwide disease that can cause frequent epidemics of barley particularly in Central Europe [11]. To combat this, genetic resistance is an efficient and environmentally acceptable way of limiting its effect on yield and quality.

Breeding barley resistant to mildew, particularly in Europe, was traditionally based on major genes. The sources of resistance were at first landraces [12–14], but were later superseded by wild barley (*Hordeum vulgare* subsp. *spontaneum*) obtained from its centre of diversity [15]. The utilization of resistance genes in breeding has been closely monitored [16–18], summarized [19] and subsequently updated [20,21]. With the change in gene bank personnel and management it is now opportune to reconsider the current state of stored accessions.

Our goal was, therefore, i) to check the homogeneity of accessions included in the Czech core collection of spring barley regarding major resistance genes to powdery mildew, ii) to identify resistance genes to powdery mildew in the accessions, and iii) based on previously published resistance data, to verify the authenticity of the accessions and, in the case of any inconsistencies, to identify those accessions of doubtful authenticity.

**Materials and methods**

**Plant material and pathogen isolates**

We tested all 223 accessions of the Czech spring barley core collection including 665 single plant progenies. For resistance tests we used 64 selected reference isolates of *Bgh* from our gene bank of the pathogen collected in 12 countries in all non-polar continents over a period of 63 years (1953–2016) which represent the world diversity of the pathogen (S1 Table). Before inoculation we checked isolates for their purity, verified the correct pathogenicity phenotype on standard barley lines [22] and multiplied on leaf segments of susceptible variety Stirling [23].

**Testing procedure**

We sowed about 60 seeds of each accession in two pots (80 mm diameter) filled with a garden peat substrate and placed them in a mildew-proof greenhouse under natural daylight. Then we cut leaf segments 15 mm long from the central part of healthy fully-expanded primary leaves when second leaves were emerging. We placed three segments adjacent to each other along with four segments of the susceptible Stirling oriented diagonally and with adaxial surfaces facing upward in a 150 mm Petri dish on water agar (0.8%) containing benzimidazole (40 mg L⁻¹)—a
leaf senescence inhibitor. For testing single plant progenies, we planted seed from one spike in a pot and used a leaf segment from each.

For isolate inoculation, we used a cylindrical metal settling tower of 150 mm diameter and 415 mm in height and we placed a dish with leaf segments at the bottom of the tower. We shook conidia of each isolate from a leaf segment of the susceptible variety with fully developed pathogen colonies onto a square piece (40 x 40 mm) of black paper to visually estimate the amount of inoculum deposited. Then we rolled the paper to form a blowpipe and we blew conidia of an isolate through a side hole of 13 mm diameter in the upper part of the settling tower over the Petri dish at a concentration of ca. 8 conidia mm$^{-2}$. The dishes with inoculated leaf segments were incubated at 18±2°C under artificial light (cool-white fluorescent lamps providing 12 h light at 30±5 μmol m$^{-2}$ s$^{-1}$).

**Evaluation**

Eight days after inoculation, we scored response types (RT = phenotype of barley variety x pathogen isolate interaction) on the central part of the adaxial side of leaf segments on a scale 0–4, where 0 = no visible mycelium or sporulation, and 4 = strong mycelial growth and sporulation on the leaf segment [17]. An RT0(3) representing RT0 with presence of a few mildew colonies was added [24]; generally, RTs 0–3 and 0(3) were considered resistant, but a typical RT of each resistance gene was also taken into account. We tested each accession with a minimum of two replications. If there were significant differences in RTs between replications, we carried out additional tests. A set of 64 RTs provided a response type array (RTA) for each accession. Based on the gene-for-gene model [25], we postulated the resistance genes in accessions by comparing the RTAs with previously determined RTAs of standard barley genotypes possessing known resistance genes.

**Assessment of results**

The authenticity of genotypes was assessed by comparing the results of their resistance recorded in this project with published data obtained around the time of registration of commercial varieties. The basic source of information was a catalogue containing information on the registration of these mostly European varieties [19]. In addition, information relating to their pedigree and the year of their registration or the acquisition date by the gene bank was used.

**Results**

First tests of 223 spring barley accessions showed that 90 of them had pure seed and were homogeneous. For each of the remaining 133 heterogeneous accessions we harvested five single plants and 665 progenies were re-tested. In 61 varieties, all five progenies had identical RTAs, although in the original accessions they were heterogeneous. In the remaining 72 sets different RTAs were found, which represented 176 genotypes. In 45 sets we detected two different genotypes, in 22 sets three and in 5 sets four genotypes. There were 327 accession × powdery mildew resistance genotypes in the core collection (Table 1).

In total there were 63 RTAs (excluding 27 RTAs that had unknown resistances) and 13 isolates were sufficient to separate them (S2 Table). Twenty-two known $Ml$ resistance genes ($a1$, $a3$, $a6$, $a7$, $a8$, $a9$, $a12$, $a13$, $Ab$, $at$, $g$, $h$, $He2$, $Ch$, $IM9$, $k1$, $La$, $Lo$, $mlo$, $p1$, $ra$ and $Ru2$), occurring either separately or in combinations were identified. Among the most frequent resistance genes found in 327 genotypes were $Mla8$ (in 99 genotypes) and $Mlg$ (in 75 genotypes); 43 genotypes contained no resistance genes (= none). We also observed a higher frequencies of $Ml$ genes $La$ (32), $He2$ (29), $Ch$ (24), $a7$ (22), $k1$ (21) and $a13$ (20). The total frequency of the
Table 1. Specific resistance genes against *Blumeria graminis* f. *sp.* *hordei* in 223 accessions of varieties included in the Czech core collection of spring barley.

| Code | Variety         | Country | Ml resistance gene | Category |
|------|-----------------|---------|--------------------|----------|
| 0446 | Abyssinian 1102 | ETH     | a8, He2            | e        |
| 0446 | Abyssinian 1102 | ETH     | a7, g              | e        |
| 0446 | Abyssinian 1102 | ETH     | none               | e        |
| 0448 | Abyssinian 1113 | ETH     | a6                 | c        |
| 2043 | Abyssinian 21   | ETH     | a8, k1             | c        |
| 2043 | Abyssinian 21   | ETH     | g, k1              | c        |
| 1231 | Adonia          | DEU     | a6, h, ra          | a        |
| 1231 | Adonia          | DEU     | p1                 | a        |
| 1231 | Adonia          | DEU     | p1, at             | a        |
| 1231 | Adonia          | DEU     | a12, u             | e        |
| 0760 | Agio            | NLD     | none               | b        |
| 2182 | Akcent          | CSK     | a7, La             | a        |
| 2182 | Akcent          | CSK     | a3                 | e        |
| 1986 | Akta Abed       | DNK     | a7                 | a        |
| 0911 | Algerian        | DZA     | a1, at             | a        |
| 2202 | Amalia          | AUT     | a9, g, u           | a        |
| 2342 | Amulet          | CSK     | a13, La            | a        |
| 1437 | Apex            | NLD     | mlo                | a        |
| 1103 | Aramir          | NLD     | a12, g             | a        |
| 0824 | Archer          | GBR     | a8                 | e        |
| 2240 | Arra            | FIN     | a8                 | b        |
| 0738 | Asplund         | SWE     | a8                 | b        |
| 0334 | Asse            | DEU     | ra, u              | e        |
| 0334 | Asse            | DEU     | a8                 | e        |
| 1537 | Athos           | FRA     | a12, g             | a        |
| 2343 | Atribut         | CSK     | mlo                | a        |
| 2245 | Attiki          | GRC     | p1                 | a        |
| 2245 | Attiki          | GRC     | p1, g              | a        |
| 2245 | Attiki          | GRC     | g, La              | e        |
| 0754 | Aurore          | FRA     | a8                 | b        |
| 0969 | Australische Fruehe | AUS | a8 | b |
| 0969 | Australische Fruehe | AUS | Ch | b |
| 1481 | Azuma Mugi      | JPN     | Ru2                | b        |
| 1953 | Bai Liu Leng    | CHN     | u                  | b        |
| 0939 | Balder Ohra     | SWE     | Ch                 | a        |
| 2140 | Ballerina       | DEU     | a12, g, k1         | a        |
| 0516 | Bavaria Ackermanns | DEU | Ch, He2 | c |
| 2162 | Beladi          | EGY     | a8, u1             | d        |
| 2162 | Beladi          | EGY     | a8, u2             | d        |
| 1171 | Beta 6 Kora     | HUN     | a8                 | b        |
| 1171 | Beta 6 Kora     | HUN     | k1                 | c        |
| 0667 | Bethge II       | DEU     | a8                 | b        |
| 0557 | Bethges III     | DEU     | a8                 | b        |
| 1024 | Bigo            | NLD     | Ch                 | b        |
| 0719 | Binder Abed     | DNK     | g, He2             | a        |
| 2012 | Bingo Carlsberg | DNK     | a13                | a        |
| 2012 | Bingo Carlsberg | DNK     | a12, g             | e        |

(Continued)
| Code | Variety                        | Country | Ml resistance gene | Category |
|------|-------------------------------|---------|-------------------|----------|
| 2012 | Bingo Carlsberg               | DNK     | a12, g, La        | e        |
| 2040 | Black Hull-Less               | USA     | u                 | a        |
| 2307 | Blondie                       | SWE     | a12, La           | a        |
| 2307 | Blondie                       | SWE     | a12, u            | a        |
| 1083 | Bode                          | NOR     | a8                | b        |
| 0012 | Bohatytr                      | CSK     | a8                | b        |
| 1014 | Bolivia                       | USA     | u                 | d        |
| 0070 | Branisovicky C                | CSK     | a8                | b        |
| 0070 | Branisovicky C                | CSK     | Ch, He2           | b        |
| 2434 | Brenda                        | DEU     | mlo               | a        |
| 0576 | Breustedts Harzer Imperial    | DEU     | a8                | b        |
| 2516 | Buck                          | CAN     | none              | d        |
| 0718 | Carlsberg                     | DNK     | a8                | a        |
| 2298 | Cask                          | GBR     | a13               | c        |
| 0057 | Ciechovicky Hanacky           | CSK     | a8, He2           | b        |
| 0636 | Ceres                         | FRA     | a8                | b        |
| 0636 | Ceres                         | FRA     | none              | b        |
| 0636 | Ceres                         | FRA     | g                 | c        |
| 0637 | Ceresia Ackermans             | DEU     | g                 | a        |
| 0637 | Ceresia Ackermans             | DEU     | a9, g             | e        |
| 0637 | Ceresia Ackermans             | DEU     | Ch                | e        |
| 0851 | Clermont                      | FRA     | Ch                | b        |
| 0908 | Club Marriout                 | EGY     | a8, u             | d        |
| 0908 | Club Marriout                 | EGY     | ra, Ch            | d        |
| 1472 | Combi                         | DEU     | a7, g             | a        |
| 1472 | Combi                         | DEU     | a9                | e        |
| 0757 | Commander                     | FRA     | a8, u             | d        |
| 2408 | Cooper                        | GBR     | a1, La            | a        |
| 2452 | Cork                          | GBR     | a1, Ab            | a        |
| 0241 | Danubia Ackermans             | DEU     | none              | a        |
| 0241 | Danubia Ackermans             | DEU     | Ch                | b        |
| 0241 | Danubia Ackermans             | DEU     | a8                | e        |
| 0241 | Danubia Ackermans             | DEU     | g                 | e        |
| 0347 | Denso                         | DNK     | a8                | a        |
| 0201 | Deuce                         | CAN     | a7, u             | d        |
| 0166 | Diamant                       | CSK     | a8                | b        |
| 0166 | Diamant                       | CSK     | a8, He2           | b        |
| 0166 | Diamant                       | CSK     | a7                | e        |
| 0166 | Diamant                       | CSK     | mlo               | e        |
| 0298 | Dinky                         | BEL     | a9, k1, La        | a        |
| 0298 | Dinky                         | BEL     | a8, k1            | c        |
| 0032 | Dobrovicky Starocesky         | CSK     | a8                | b        |
| 0032 | Dobrovicky Starocesky         | CSK     | a8, He2           | b        |
| 0032 | Dobrovicky Starocesky         | CSK     | Ch                | b        |
| 0032 | Dobrovicky Starocesky         | CSK     | none              | b        |
| 0538 | Dometzkoer Paradies Nackte    | DEU     | a8, He2           | b        |
Table 1. (Continued)

| Code  | Variety                | Country  | ML resistance gene | Category |
|-------|------------------------|----------|--------------------|----------|
| 0512  | Donaria Ackermanns     | DEU      | Ch, He2            | a        |
| 0899  | Doneckij 9             | SUN      | a12                | d        |
| 0065  | Dregervu               | CSK      | a8                 | b        |
| 0123  | Druzba                 | SUN      | a7, g, La          | c        |
| 0123  | Druzba                 | SUN      | g                  | c        |
| 2146  | Duckbill               | GBR      | none               | d        |
| 0900  | Early Chevalier        | CAN      | Ch                 | b        |
| 0900  | Early Chevalier        | CAN      | none               | b        |
| 0575  | Ebstorfer Nacktgerste | DEU      | none               | b        |
| 0527  | Egelfinger Monarchia   | DEU      | a8                 | b        |
| 0075  | Ekonom                 | CSK      | a8                 | b        |
| 0780  | Emir                   | NLD      | a8                 | e        |
| 0780  | Emir                   | NLD      | none               | e        |
| 0450  | Entresole              | BOL      | a8, u              | b        |
| 0450  | Entresole              | BOL      | none               | d        |
| 1350  | Esperance No. 227/1960 | FRA      | a8                 | c        |
| 2528  | Falcon                 | CAN      | Ch                 | d        |
| 2528  | Falcon                 | CAN      | none               | d        |
| 1128  | Franzista              | DEU      | a8, La             | d        |
| 0759  | Frisia Breustedts      | DEU      | a8, u              | d        |
| 0657  | Gerda                  | DEU      | a7, g, k1          | e        |
| 0657  | Gerda                  | DEU      | a8                 | e        |
| 0657  | Gerda                  | DEU      | g                  | e        |
| 0765  | Glattgrannige von Vilmorin | USA | none               | b        |
| 0765  | Glattgrannige von Vilmorin | USA | g                  | c        |
| 1003  | Golden Promise         | GBR      | a8                 | a        |
| 1607  | Goldmarker             | GBR      | a6, La             | a        |
| 2244  | Grammos                | GRC      | Ch                 | b        |
| 0517  | Granat Breustedts      | DEU      | a8, u              | c        |
| 0413  | Gull Svalofs           | SWE      | Ch                 | a        |
| 0507  | Hadostreng             | DEU      | a8, u              | d        |
| 0523  | Haisa I Heines         | DEU      | Ch                 | b        |
| 0523  | Haisa I Heines         | DEU      | none               | b        |
| 0090  | Hana                   | CSK      | a8, He2            | a        |
| 0090  | Hana                   | CSK      | g, He2             | c        |
| 0002  | Hanacky Jubilejni      | CSK      | a8                 | b        |
| 0002  | Hanacky Jubilejni      | CSK      | a8, He2            | b        |
| 0013  | Hanacky Kargyn         | CSK      | a8                 | b        |
| 0689  | Hanna                  | CSK      | g                  | a        |
| 0168  | Harbine                | USA      | none               | b        |
| 2572  | Heris                  | CZE      | mlo                | a        |
| 2024  | Hermine                | FRA      | a7, g, k1          | a        |
| 1169  | Hero                   | USA      | a8, u              | b        |
| 1169  | Hero                   | USA      | Ch                 | b        |
| 1169  | Hero                   | USA      | none               | b        |
| 1255  | Hiproly                | ETH      | none               | b        |

(Continued)
| Code | Variety      | Country | Ml resistance gene | Category |
|------|--------------|---------|--------------------|----------|
| 1255 | Hiproly ETH  | ETH     | a12                | d        |
| 1993 | Hockey GBR   | GBR     | a12, La            | a        |
| 0854 | Hunter IRL   | IRL     | a8                 | a        |
| 0876 | Husky CAN    | CAN     | Ch                 | b        |
| 0876 | Husky CAN    | CAN     | none               | b        |
| 2349 | Chariot GBR  | GBR     | mlo                | a        |
| 2126 | Charkovskii 91 | SUN  | a7, k1             | c        |
| 0923 | Chevallier GBR | GBR  | a8                 | b        |
| 0923 | Chevallier GBR | GBR  | Ch                 | b        |
| 0923 | Chevallier GBR | GBR  | none               | b        |
| 1152 | Chevron USA  | USA     | g, h               | a        |
| 1152 | Chevron USA  | USA     | h, u               | a        |
| 0023 | Chlumecky CSK | CSK  | a8                 | b        |
| 2188 | Icare FRA    | FRA     | a13, g, La         | c        |
| 0529 | Isaria Ackermanns DEU | DEU  | Ch, He2            | b        |
| 0671 | Isaria Nova  | DEU     | a8, He2            | b        |
| 0671 | Isaria Nova  | DEU     | a6                 | e        |
| 0671 | Isaria Nova  | DEU     | a6, g              | e        |
| 2038 | Ishtar CHN   | CHN     | a8                 | b        |
| 2038 | Ishtar CHN   | CHN     | none               | b        |
| 2164 | Izmir 9 TUR  | TUR     | g                  | c        |
| 2164 | Izmir 9 TUR  | TUR     | g, at              | c        |
| 0158 | Jantar CSK   | CSK     | g                  | a        |
| 0158 | Jantar CSK   | CSK     | a8                 | e        |
| 2395 | Jelen YUG    | YUG     | a7, g, La          | a        |
| 0132 | Kasticky CSK | CSK     | a8                 | b        |
| 1478 | Kilta FIN    | FIN     | none               | d        |
| 2508 | Klinta LVA   | LVA     | a8, La             | a        |
| 0085 | KM 1192 CSK  | CSK     | a8, La             | e        |
| 0085 | KM 1192 CSK  | CSK     | a8                 | e        |
| 0515 | Kneifels Vollkorn DEU | DEU  | a8, He2            | b        |
| 0089 | Koral CSK    | CSK     | a13, g             | a        |
| 0093 | Krajova St. Hrozenkov CSK | CSK   | a8                 | b        |
| 0104 | Krystal CSK  | CSK     | a13, g             | a        |
| 0568 | Lada DDR    | DDR     | a12                | a        |
| 0568 | Lada DDR    | DDR     | a8, He2            | e        |
| 2026 | Lapac YUG   | YUG     | Ch                 | b        |
| 2026 | Lapac YUG   | YUG     | none               | b        |
| 2026 | Lapac YUG   | YUG     | a9, g              | e        |
| 0826 | Lion USA    | USA     | none               | b        |
| 2460 | Logan USA   | USA     | a8, k1             | a        |
| 2460 | Logan USA   | USA     | a1, g              | e        |
| 1428 | Lud GBR     | GBR     | g, La              | a        |
| 2340 | Lumar CSK   | CSK     | a1, g, k1          | a        |
| 1507 | Lyallpur 3647 IND | IND  | a7, k1             | a        |
| 0704 | Maja Abed DNK |       | a8                 | a        |
| 0704 | Maja Abed DNK |       | g, He2             | e        |
| Code | Variety         | Country | ML resistance gene | Category |
|------|-----------------|---------|--------------------|----------|
| 2153 | Malebo          | AUS     | a8, k1             | e        |
| 1002 | Malteria Heda   | ARG     | a8                 | a        |
| 1002 | Malteria Heda   | ARG     | a6, La             | e        |
| 1002 | Malteria Heda   | ARG     | a7, g, k1          | e        |
| 2034 | Manchuria       | USA     | none               | a        |
| 0766 | Mansholts Tweetijge | NLD | none               | b        |
| 0745 | Maskin          | NOR     | a8, He2            | e        |
| 0865 | Maytorpe        | GBR     | a8                 | a        |
| 0592 | Mehlaresistente II Firlbecks | DEU | g                 | a        |
| 0592 | Mehlaresistente II Firlbecks | DEU | g, He2            | a        |
| 0147 | Merkur          | CSK     | g                  | a        |
| 0699 | Midas           | GBR     | a6                 | a        |
| 1155 | Monte Cristo    | IND     | a9, k1             | a        |
| 1155 | Monte Cristo    | IND     | a1                 | e        |
| 1155 | Monte Cristo    | IND     | a13                | e        |
| 2047 | Murasski Mochi  | USA     | u                  | d        |
| 1216 | Nadja           | DDR     | a7, k1, La         | c        |
| 1216 | Nadja           | DDR     | a8                 | e        |
| 2313 | Nagrad          | POL     | g, La              | a        |
| 2313 | Nagrad          | POL     | a13                | e        |
| 2456 | Namoi           | AUS     | Ch                 | a        |
| 0042 | Nolc-Dregeruv Imperial A | CSK | a8              | b        |
| 0086 | Nolc-Dregeruv Velerany | CSK | a8              | b        |
| 2220 | Nomad           | GBR     | a9, La, u          | a        |
| 0004 | Novodvorsky Hanacky | CSK | a8              | b        |
| 2394 | Novosdaski 406  | YUG     | a13, g            | d        |
| 2394 | Novosdaski 406  | YUG     | a7                | d        |
| 2394 | Novosdaski 406  | YUG     | g, La             | d        |
| 0074 | Novum           | CSK     | a13, g            | a        |
| 2285 | Nugget          | GBR     | a13, La           | a        |
| 1025 | Oderbrucker     | USA     | none              | a        |
| 0514 | Oderlangauer Kneifelgerste | DEU | a8              | b        |
| 0514 | Oderlangauer Kneifelgerste | DEU | none            | b        |
| 2329 | Odesskij 131    | SUN     | a7, g, La         | c        |
| 0201 | Odesskij 9      | SUN     | g, La             | e        |
| 2015 | Odissej        | SUN     | a12               | c        |
| 2015 | Odissej        | SUN     | a13, g            | e        |
| 0792 | Olli            | FIN     | none              | b        |
| 2076 | Olont           | MNG     | a8                | b        |
| 2112 | Omskij 13709    | SUN     | a7, k1            | c        |
| 2112 | Omskij 13709    | SUN     | mlo               | e        |
| 0101 | Opal            | CSK     | a8                | e        |
| 0101 | Opal            | CSK     | a7, La            | e        |
| 0005 | Opavsky Kneiffl | CSK     | a8                | b        |
| 1273 | Otra            | FIN     | a7, La            | e        |
| 0621 | Otterbacher     | AUT     | a8, He2           | b        |
| 1027 | Palestine 10    | EGY     | a8, k1, La        | a        |
| Code | Variety         | Country | Ml resistance gene | Category |
|------|----------------|---------|--------------------|----------|
| 2365 | Pannonia       | AUT     | mlo                | a        |
| 1467 | Patty          | FRA     | a12, g             | a        |
| 2371 | Pax            | CSK     | a13, La            | a        |
| 0848 | Peatland       | USA     | none               | b        |
| 0935 | Peruvian       | USA     | at                 | a        |
| 2292 | Phantom        | DDR     | a13, g             | a        |
| 2093 | Pirogovskij    | SUN     | a8                 | c        |
| 0680 | Plena          | DDR     | g                   | c        |
| 0680 | Plena          | DDR     | g, He2, Lo         | c        |
| 0821 | Plumage Archer | GBR     | a8                 | e        |
| 2135 | Princesse      | DEU     | a3, g, La          | a        |
| 2135 | Princesse      | DEU     | a3, g              | b        |
| 2135 | Princesse      | DEU     | g                   | b        |
| 0834 | Prior          | AUS     | a8                 | a        |
| 2524 | Prosa          | AUT     | g, u               | a        |
| 0079 | Proskowtzuv    | CSK     | a8, He2            | b        |
| 0079 | Proskowtzuv    | CSK     | g                   | e        |
| 0866 | Provost        | GBR     | none               | a        |
| 0617 | Pumper 6 ZLG   | AUT     | h                  | b        |
| 1243 | Quantum        | AUT     | a12, La, g         | e        |
| 0605 | Ragusa 415     | YUG     | ra, Lo             | a        |
| 0605 | Ragusa 415     | YUG     | p1, ra, Lo         | e        |
| 0017 | Ratborsky      | CSK     | a8                 | b        |
| 1915 | Research       | AUS     | a8                 | a        |
| 2101 | Roxane         | FRA     | a12, g, u          | a        |
| 1299 | RTG Valticky   | CSK     | a8, He2            | b        |
| 1299 | RTG Valticky   | CSK     | a12                | e        |
| 1299 | RTG Valticky   | CSK     | a13                | e        |
| 1299 | RTG Valticky   | CSK     | g                   | e        |
| 0059 | Rubin          | CSK     | a1                 | a        |
| 1622 | Rupee          | IND     | u                  | e        |
| 0756 | Sarah          | FRA     | none               | a        |
| 2354 | Saxo           | DNK     | mlo                | a        |
| 0594 | Saxonia Malz Imperial | DEU | a8 | b |
| 0163 | Selekeni Hanacky VIII. | CSK | g, h | b |
| 0163 | Selekeni Hanacky VIII. | CSK | g, He2 | b |
| 0163 | Selekeni Hanacky VIII. | CSK | at | e |
| 0054 | Semicicky Hospodarsky | CSK | a8 | b |
| 0054 | Semicicky Hospodarsky | CSK | none | b |
| 0054 | Semicicky Hospodarsky | CSK | a1 | e |
| 2266 | Senor          | DNK     | a13                | a        |
| 0626 | Schwarzenberg Gerste 21 | DEU | a6, g | c |
| 1285 | Sinaji Mugi    | JPN     | none               | b        |
| 0197 | Sladar         | CSK     | a8                 | b        |
| 0197 | Sladar         | CSK     | none               | b        |

(Continued)
Table 1. (Continued)

| Code  | Variety                        | Country b | ML resistance gene | Category c |
|-------|--------------------------------|-----------|--------------------|------------|
| 0008  | Slovensky Dunajsky Trh         | CSK       | a8                 | b          |
| 0055  | Spartan                        | CSK       | a9, k1             | a          |
| 0055  | Spartan                        | CSK       | a6, g              | e          |
| 0702  | Stella Svalof                 | SWE       | a8                 | b          |
| 0702  | Stella Svalof                 | SWE       | none               | b          |
| 1054  | Stephan                        | CAN       | g                  | c          |
| 0010  | Stupicky Hanacky               | CSK       | a8                 | b          |
| 0007  | Stupicky Plnozrnnny            | CSK       | a8                 | b          |
| 1046  | Sudan                          | USA       | none               | b          |
| 1165  | Sulu                           | AUS       | k1                 | a          |
| 0383  | Tamina                         | DDR       | a13                | a          |
| 1339  | Tellus                         | SWE       | g                  | a          |
| 1339  | Tellus                         | SWE       | a12                | e          |
| 0548  | Thaya Loosdorfer               | AUT       | a8                 | b          |
| 2376  | Torcal                         | ESP       | g, u               | a          |
| 0234  | Trebi                          | USA       | a8                 | b          |
| 1097  | Triple Awn Lemma               | USA       | Ch                 | e          |
| 0011  | Triumph                        | CSK       | a8                 | b          |
| 0011  | Triumph                        | CSK       | none               | b          |
| 1019  | Trumpf                         | DDR       | a7, k1, La         | d          |
| 1019  | Trumpf                         | DDR       | a13, g             | e          |
| 1019  | Trumpf                         | DDR       | a9                 | e          |
| 0572  | Tschermaks                     | AUT       | Ch, He2            | b          |
| 0572  | Tschermaks                     | AUT       | none               | b          |
| 0572  | Tschermaks                     | AUT       | g, He2             | d          |
| 1969  | Turk                           | TUR       | none               | b          |
| 1969  | Turk                           | TUR       | IM9, Lo            | e          |
| 0262  | Umanskij                       | SUN       | none               | b          |
| 0564  | Union Firlbecks                | DEU       | g, He2             | a          |
| 0019  | Valticky                       | CSK       | a8, He2            | b          |
| 0880  | Varde                          | NOR       | none               | b          |
| 1651  | Vega Abed                      | DNK       | a13                | e          |
| 0264  | Viner                          | SUN       | a8                 | b          |
| 0264  | Viner                          | SUN       | none               | b          |
| 0264  | Viner                          | SUN       | g                  | e          |
| 2364  | Viva                           | AUT       | a9, u              | a          |
| 1251  | Voldagsen ST. 824/44           | DEU       | u                  | d          |
| 1251  | Voldagsen ST. 824/44           | DEU       | a9                 | e          |
| 2328  | Vybor                          | SUN       | a8                 | d          |
| 2328  | Vybor                          | SUN       | none               | d          |
| 0521  | Weihenstephaner Mehltresistante| DEU       | g                  | a          |
| 0562  | Wisa Breuns                    | DEU       | g, He2             | a          |
| 0842  | Wong                           | CHN       | g                  | d          |
| 0849  | Woodrow                        | USA       | a8                 | b          |
| 0707  | Ymer                           | SWE       | a8                 | a          |

(Continued)
known genes determined in all 327 genotypes was 406. In addition, in 27 of these genotypes we noted an unknown resistance combined with at least one (18 cases) and, in three cases, two known resistance genes. In some genotypes, we detected “additional” \( Ml \) genes closely linked to alleles of the \( Mla \) locus (\( aAl2, a14, aEm2 \), etc.). Such genes are not shown and discussed further because in most of the remaining genotypes that were expected to contain “additional” genes, this could not be conclusively established.

All 327 genotypes were divided into five categories, of which the first category (a) includes the genotypes whose identified resistance was consistent with published data (97 genotypes). The second category (b) of 109 genotypes were those whose determined resistance is consistent with the resistance of the given variety (e.g. ‘none’ resistance gene or \( Mla8 \) in the case of the older varieties), and those for which there were no data challenging their identity. The third category (c) is represented by 30 genotypes for which there are no previous published data. The fourth category (d) includes 28 genotypes where there are doubts about their authenticity, and the fifth category (e) comprises 63 genotypes whose resistance is inconsistent with published data.

Among 223 accessions of the collection, we found 151 homogeneous accessions, but the resistance of nine of them was inconsistent with published data, and 12 of those remaining have doubtful authenticity. In 72 heterogeneous accessions represented by 176 accession × powdery mildew resistance genotypes, 54 genotypes had a resistance that is inconsistent with published data. These have clearly resulted from mechanical admixtures. Regarding the other 16 heterogeneous genotypes there are doubts as to their authenticity.

**Discussion**

The first European commercial variety of spring barley intentionally bred for the incorporation of a mildew resistance (\( Mlg \)), was the German variety \( \text{Union} \) registered in 1955 [18]. Union was followed by varieties possessing other specific resistance genes of which there are now several dozens. These are present either singly or in combinations [19,26] and have influenced the composition and increased complexity of the Central European population of the pathogen [27,28]. In 1979 the first commercial variety (\( \text{Atem} \)) with the \( mlo \) non-specific resistance gene was registered [29] and this resistance has become dominant in spring barley varieties [21,26]. Thus, barley resistance to powdery mildew conditioned by many major genes is highly diverse with a progressive utilisation of individual genes in commercial varieties that has been extensively reported.

**Discrepancies among homogeneous accessions**

In \( \text{Triple Awn Lemma} \), \( MlCh \) was found, which is completely ineffective except against one isolate that we used, while Nover and Lehmann [30] recorded high resistance in this variety

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**Table 1.** (Continued)

| Code* | Variety                | Country* | \( Ml \) resistance gene | Category* |
|-------|------------------------|----------|--------------------------|-----------|
| 0037  | Zidlochovicky Gloria   | CSK      | \( a8 \)                 | b         |

*Identification number of the Czech gene bank of spring barley.

*Country of origin: ARG—Argentina, AUS—Australia, AUT—Austria, BEL—Belgium, BOL—Bolivia, CAN—Canada, CSK—Czechoslovakia, CZE—Czech Republic, DDR—East Germany, DEU—Germany, DNK—Denmark, DZA—Algeria, EGY—Egypt, ESP—Spain, ETH—Ethiopia, FIN—Finland, FRA—France, GBR—Great Britain, GRC—Greece, HUN—Hungary, CHN—China, IND—India, IRL—Ireland, JPN—Japan, LVA—Latvia, MNG—Mongolia, NLD—Netherlands, NOR—Norway, POL—Poland, SUN—Soviet Union, SWE—Sweden, TUR—Turkey, USA—United States of America, YUG—Yugoslavia.

*Category: a—genotypes whose identified resistance was consistent with published data; b—genotypes for which the observed resistance is probably consistent with previous data, and those for which there were no data to indicate an erroneous designation; c—insufficient data to validate genotype identity; d—genotypes for which the data indicate a discrepancy in genotype authenticity; e—genotypes whose recorded resistance is inconsistent with published data.

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conditioned by a combination of the \textit{Mla9} and \textit{Mlk1} genes \cite{14}. In \textit{Archer}, \textit{Maskin} and \textit{Plumage Archer}, we identified \textit{Mla8}, but in the catalogue \cite{19} there is no mention of a resistance gene (= none). The results included in the catalogue are based on the study that focused particularly on the detection of \textit{Mla8} \cite{31}. In \textit{Vega Abed}, \textit{Mla13} was uncovered while the catalogue states \textit{Mlla}, and in \textit{Rupee}, which is a known source of the \textit{Ml} genes, \textit{a13 (= aRu1)}, \textit{Ru2}, \textit{aRu3}, \textit{aRu4}, a different unknown resistance was detected. In the Australian variety \textit{Malebo}, we established the presence of \textit{Mla8} and \textit{Mlk1}, while Dreiseitl and Platz \cite{23} found only \textit{Mla8}. It is possible that \textit{Malebo} was composed of two lines, one of which was described in the previous research and the other was the one we investigated. \textit{Otra} contained \textit{Mla7} and \textit{Mlla}, while this variety was reported as being susceptible in Latvia \cite{32}, and confirmed by Hovmöller et al. \cite{33}. \textit{Odesskij 9} is a selection from an unknown variety which was acquired for the gene bank in 1958. The fact that we found both \textit{Mlg} and \textit{Mlla} in this variety poses questions about its authenticity as the first known variety with \textit{Mlla} (Vada) was registered in 1963.

\textbf{Discrepancies among heterogeneous accessions}

We identified 37 heterogeneous accessions with incorrect genotypes. In this report we will focus on six accessions in which none of the genotypes consistently corresponded with previous data. Progenies of \textit{Abyssinian 1102} contained three genotypes, but none of them possesses \textit{mlo}, which is present in the genuine Abyssinian 1102 \cite{29}. Furthermore, \textit{mlo} is often naturally present only in Ethiopian barleys. In accessions marked as \textit{Asse}, we found two genotypes, but neither carried \textit{Mlg} specified in the catalogue. Similarly, two genotypes were uncovered in \textit{Emir}, neither of which was \textit{Mla12}, although \textit{Emir} is known as a source of the latter, and the accepted code of this resistance (\textit{Em}) was derived from this variety. Moreover, although in \textit{Gerda Mla6} is listed together with \textit{Mlg} in the catalogue we did not find evidence to confirm this. \textit{KM 1192} is the original source of the resistance used for the first time in \textit{Kredit} after which the resistance is named \textit{Mlk}\textit{kr} \cite{20}. However, in the \textit{KM 1192} accession we recorded two different lines (\textit{Mla8} and \textit{Mla8}, \textit{Mlla}). In \textit{Opal} (Czech), there were two genotypes (\textit{Mla7}, \textit{Mlla} and \textit{Mla8}), while the original one contained \textit{Mla6} and \textit{Mlla} \cite{20}. \textit{Mla8} is present in a number of varieties, for example in Danish \textit{Opal} \cite{19}.

\textbf{Identical designation of different varieties}

\textit{Sarah}, which originated from France and was described as an alternative rather than spring type, was lodged in the gene bank in 1974. We obtained no evidence of a resistance gene, which could be supported by the fact that \textit{Sarah} was selected from Champagner. In England, \textit{Mla12} was reported in winter \textit{Sarah} \cite{34}, and in Germany an unknown resistance was observed possibly in another winter form of \textit{Sarah} \cite{35}.

In \textit{Commander}, deposited in the gene bank in 1958, \textit{Mla8} and another unknown resistance was revealed. In a set of Australian barleys a variety with the same name was studied \cite{23}. However, it was registered much later (2004) and its two lines carried \textit{Mlg}, \textit{Mlg} \textit{a} and \textit{Mlg}, \textit{Mlla}.

\textit{Wong} (China) is a known source of the resistance gene that is named after it–\textit{MlWo} \cite{36}. On the other hand, there are spring and winter varieties also known as \textit{Wong} and it is not clear which of them is the true source of this gene. Schwarzbach and Fischbeck \cite{18} identified \textit{MlWo} in two winter varieties, whereas in our tests \textit{Wong} carried \textit{Mlg}.

No specific resistance gene was found in either \textit{Manchuria} or \textit{Oderbrucker}, which is a selection from Manchuria. In Poland Manchuria was used in the pathogen survey as a susceptible variety \cite{33}. On the other hand, Wiberg \cite{14} states that Manchuria (C.I. 2610) has genes that are identical with those in Algerian (\textit{Mla1}, \textit{Mlat}). Therefore, Manchuria that was the
subject of our research and in Poland, as well as the Manchuria from which Oderbrucker was selected, differs from the Manchuria studied by Wiberg [14].

In Esperance No. 227/1960, we detected Mla8, while Brückner [13] and Schwarzbach and Fischbeck [18] mention that Esperance has a typical and phenotypically very different resistance gene. It seems that Esperance and Esperance No. 227/1960 are different varieties.

Anomalies

Adonia. According to the catalogue [19], Adonia as well as its parents are winter types. We found four genotypes with the following Ml resistance genes: a6, h, ra; p1; p1, at and a12, u. The pedigree of Adonia is Espe × Stamm729 × Vogelsanger Gold × Inka. Schwarzbach and Fischbeck [18] studied Adonia and reported a combination of Mla6 and Mlh. The catalogue mentions the resistance of their three parents (Espe-Mla, Inka-Mlh and Vogelsanger Gold-Mla6, Mlh, Mlra). The combination of Ml genes specified for Adonia thus corresponds to the genes carried by two of the parents and is identical to that (Mla6, Mlh, and Mlra) in one of the three characterised genotypes [37] and in one of the four genotypes studied here. However, all these genes occur more frequently in winter rather than spring varieties [38].

Mlp1, which was present in two Adonia genotypes and two of the three previously described genotypes [37], is one of the oldest known resistance genes [12], although its presence in commercial varieties is rare. This gene was also detected in one of the three genotypes of Seljanin (Mlp1, Mla6) whose parent is Adonia (Adonia × Perf × Muronec). We can confirm, therefore, the presence of Mlp1 in both Adonia and its daughter Seljanin. Nevertheless, the question of why the detection or specification of the Adonia line carrying Mlp1 was not mentioned by Schwarzbach and Fischbeck [18] remains open.

Hanna. We recorded the presence of Mlg in Hanna and Binder Abed (a selection from Hanna bred in 1913). Nover and Lehmann [30] also state that Hanna (C.I. 906) contains Mlg. C.I. 906 is a selection from C.I. 34 (Hanna pedigree) which was collected in Austria in 1900 (at that time the Czech Republic was a part of the Austrian empire). Also in Selekcni Hanacky VIII, which is again a selection of the original regional Hana variety (Hanna), three genotypes were found, two of which carry Mlg. However, the catalogue states that Mla8 is in both these varieties.

The name Hanna (Hana) is derived from the name of a fertile region of the Czech Republic (Hana) and traditionally an area where high quality malting barley has been grown. Therefore, the name has been assigned to several varieties of different crop species including barley. The Hanna carrying the resistance gene that was named after this variety, Mlh [14], and Heils Hanna carrying Mla8 [36], after which the code of this resistance (HH) was named, belong to this group.

In 1973 another derivative Hana, in which no resistance gene was recorded [20], but which could carry Mla8, was registered in the Czech Republic. This Hana was screened by us and we uncovered two genotypes, namely one with Mla8 (which is regarded as genuine) and the other with Mlg, which had not been found in this variety before [20].

In Hanna, we confirmed the presence of Mlg found in this variety by Nover and Lehmann [30]. We also detected Mlg in selections from Hanna (Hana), namely Binder Abed and Seleckni Hanacky VIII. It seems highly likely that the Hanna we tested did possess Mlg and could be one of the original sources of this gene revealed here.

Nadja and Trumpf. For Nadja, Brown and Jørgensen [19] note the presence of Mla7 and Trumpf is named Triumph with the genes Mla7, MlAb, and MlTr3. We uncovered two genotypes for Nadja together with four genotypes in the Trumpf accession. In each of these varieties there was one genotype carrying Mla7 and in both there was an identical combination of Mla7, Mk1, and Mla, which differs from the catalogue data.
Conclusions

The goal of our study of heterogeneous accessions was to identify the resistance(s) contained in these accessions. By examining five individually harvested plants of each accession we reliably established all resistances, but we could not find genotypes that occurred less frequently. This explains why we came across identical resistances in each of the 61 sets of plant progenies of the 133 heterogeneous accessions.

Dreiseitl [39] studied heterogeneous wild barleys (H. vulgare subsp. spontaneum) maintained in the ICARDA gene bank. For each of the 128 accessions five plant progenies were tested. Forty-four accessions were composed of two genotypes, 25 accessions of three genotypes, 10 accessions of four and two accessions comprised five genotypes. A total of 260 genotypes were found, equalling 2.03 genotype per accession. We tested 133 accessions in the same manner and detected 237 genotypes, i.e. 1.78 genotype per accession on average.

Wild barley is well-known for its high resistance diversity [39–43] and its diversity in the gene bank might have arisen from collecting bulked heterogeneous samples along with outcrossing in the field because of its open flowering nature [44]. It is surprising, therefore, that the value of the average number of genotypes in one accession of the core collection (1.78) was similar to the value in the collection of wild barley (2.03).

The most frequent gene found in 99 genotypes was Mla8, which is detectable only with pathotypes appearing in Japan [45]. The actual frequency of Mla8 must be even higher since only Race 1, which is avirulent to many specific resistance genes including Mlg, was available for its detection. Mla8 is often accompanied by MlHe2—we revealed this combination in 15 genotypes. However, in nine genotypes with MlHe2 we also found Mlg, which masks Mla8. Hence, in these nine genotypes Mlg and MlHe2 could be accompanied by Mla8. The latter gene could also be present in the absence of MlHe2 in some genotypes containing Mlg.

Jørgensen and Jensen [31] studied the presence of Mla8 in 63 European varieties of spring barley bred in the first half of the 20th century and identified Mla8 in 40 of them. In addition, Mla8 occurs frequently in Australian [23] and Chinese varieties [46] and elsewhere. As well as this gene and in the absence of any specific resistance gene (none), older varieties of spring barley may naturally have carried MlHe2 and MlCh, and South Asian barleys [46] possess MlRu2 too (formerly designated as MlBw). The older varieties were often bred by bulk selection from landraces or after cross-breeding and no subsequent selection for undetected resistances. This explains why the existence of two or more genotypes (lines) may not be mechanical admixtures but may be an inherent feature of these varieties. A good example is the domestic landrace Dobrovicky Starocesky, in which there were four genotypes (none, MlCh, Mla8 and Mla8, MlHe2) and all of them could be considered as the original progenies.

Plant progenies used in this research will serve as the basis for multiplying genotypically pure varieties. In the future we will replace accessions that are not genuine, and whose authenticity is in doubt, with well-characterised accessions from other gene banks. We will then test them using similar methods to verify their identity. Accessions with unknown resistances will be subject to further studies.

Our investigation of the core collection has confirmed earlier findings that accessions in gene banks are often contaminated or even confused with other genotypes [4]. In addition, we have demonstrated that identifying barley resistance genes to powdery mildew is an effective although not totally reliable tool that can reveal such errors. To expand our abilities, there are several pathogens of cereals, particularly rusts and mildews, against which many resistance genes in host crops have also been utilized [47–51]. Knowledge and identification of these genes can lead to the purification of accessions in gene banks. Seed purity and accession authenticity can subsequently be checked by more advanced and less laborious methods.
Supporting information

S1 Table. Origin of 64 *Blumeria graminis* f. sp. *hordei* isolates used for response tests of 223 varieties in the Czech spring barley core collection.

S2 Table. Sixty-three response type arrays produced by 13 selected *Blumeria graminis* f. sp. *hordei* isolates on 223 varieties of the Czech spring barley core collection.

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