Powdery mildew resistance of barley accessions from Dagestan

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Abstract. Powdery mildew caused by the parasitic fungus Blumeria graminis (DC.) Golovin ex Speer f. sp. hordei Marchal is one of the most common diseases of barley. Growing resistant varieties can significantly minimize harmful effects of the pathogen. The specificity in the interaction between the fungus and its host plant requires a continuous search for new donors of the resistance trait. The powdery mildew resistance of 264 barley accessions from Dagestan and genetic control of the trait in resistant forms were studied under field and laboratory conditions. Forty-seven barley lines carrying previously identified powdery mildew resistance genes were also examined. During three years, the experimental material was evaluated under severe infection pressure at the Dagestan Experiment Station of VIR (North Caucasus, Derbent). Juvenile resistance against the Northwest (St. Petersburg, Pushkin) pathogen population was evaluated in a climatic chamber. The genetic control of B. graminis resistance in the selected accessions was studied with the application of hybridological and molecular analyses. The level of genetic diversity of Dagestan barley for effective resistance to powdery mildew is very low. Only two accessions, VIR-23787 and VIR-28212, are resistant against B. graminis at both seedling and adult plant stages. The high-level resistance of breeding line VIR-28212 originating from barley landrace VIR-17554 (Ep-80 Abyssinien) from Ethiopia is controlled by the recessive gene mlo11. Accession VIR-17554 is heterogeneous for the studied trait, with the powdery mildew resistant genotypes belonging to two varieties, dupliatrum (an awnless phenotype) and nigrinudum (an awned phenotype). In accession VIR-23787, a recessive resistance gene distinct from the mlo11 allele was identified. This accession is supposed to be protected by a new, effective pathogen resistance gene.

Key words: barley landraces; Blumeria graminis f. sp. hordei; durable resistance; genes.

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Устойчивость образцов ячменя из Дагестана к мучнистой росе

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Аннотация. Мучнистая роса (возбудитель Blumeria graminis (DC.) Golovin ex Speer f. sp. hordei Marchal) — одно из самых распространенных заболеваний ячменя. Возделывание устойчивых сортов может существенно ограничить вредоносность патогена. Специфичность взаимодействия гриба с растением-хозяином обусловливает необходимость постоянного поиска новых доноров устойчивости. Носителями эффективных генов устойчивости к патогену часто являются образцы местного ячменя. В полевых и лабораторных экспериментах оценили потенциал изменчивости 264 образцов ячменя из Дагестана по устойчивости к B. graminis и изучили генетический контроль признака у выделившихся форм. Исследовали также 47 линий ячменя, несущих ранее идентифицированные гены устойчивости к мучнистой росе. В течение трех лет с использованием балльной шкалы экспериментального материала оценивали на жестком инфекционном фоне в условиях Дагестанской опытной станции Всероссийского института генетических ресурсов растений им. Н.И. Вавилова (Северный Кавказ, г. Дербент). Установили, что генетическое разнообразие ячменей Дагестана по эффективной устойчивости к мучнистой росе весьма невелико. Лишь образцы к-23787 и к-28212 устойчивы к дагестанской популяции B. graminis. В течение трех лет с использованием балльной шкалы экспериментального материала оценивали на жестком инфекционном фоне в условиях Дагестанской опытной станции Всероссийского института генетических ресурсов растений им. Н.И. Вавилова (Северный Кавказ, г. Дербент). Установили, что генетическое разнообразие ячменей Дагестана по эффективной устойчивости к мучнистой росе весьма невелико. Лишь образцы к-23787 и к-28212 устойчивы к дагестанской популяции B. graminis в фазе цветения и к петербургской популяции патогена — в фазе двух листьев. Две географически очень разобщенные популяции гриба оказались идентичны по вирулентности к линиям с ранее идентифицированными генами устойчивости к мучнистой росе. Высокая устойчивость селек-
Introduction

Powdery mildew caused by the parasitic fungus *Blumeria graminis* (DC.) Golovin ex Speer f. sp. *hordei* (Marchal) is one of the most common and harmful diseases of barley. The pathogen predominantly affects leaves, leaf sheath, and stems throughout the growing season. In the infected plants, photosynthetic activity of leaves is being decreased while water loss and respiration intensity are being increased, which results in growth retardation, reduced tillering ability, and decreasing seed mass and grain number per spike. Yield reduction caused by powdery mildew can reach 30 %, with an average of 5–10 % across all regions (Balkema-Boomstra, Masterbroek, 1995; Gong et al., 2013).

Selection of resistant plant genotypes is a radical and environment friendly way to combat the disease. Unfortunately, the pathogen is characterized by differential interaction with the host plant genotype. This means that the ubiquitously observed genetic uniformity of cultivated varieties creates conditions for adaptive microevolution of the fungus.

In barley, numerous powdery mildew resistance genes designated by various symbols have been identified, most of them are alleles at the loci *Mla* and *Mlo*. Thus, 39 alleles at the *Mla* (Mildew resistance locus *a*) (chromosome 1H) and 44 alleles at the *Mlo* (Mildew resistance locus *o*) locus (chromosome 4H) are known (Jørgensen, 1994; Seeholzer, 2009; Reinstädler et al., 2010; Kusch, Panstruga, 2017). However, most alleles are ineffective against the causative agent. The allele *mlo11* is practically the only effective gene that confers durable resistance to the pathogen. barley landraces often possess effective genes for resistance against phytopathogens. For example, a study of 925 Ethiopian barley accessions has revealed 15 accessions harboring the *mlo11* allele, and 59 forms whose resistance to *B. graminis* was controlled by effective genes distinct from the *mlo11* (Abdullaev et al., 2019).

Since recently, the attention of researchers is drawn to Dagestan, a region of ancient agriculture. In a small area, with a row to row spacing of 15 cm and row length of 1 m. Spring barley cultivar Temp (VIR-22055, Krasnodar region) sown after each 20 accessions was used as a control. Resistance to disease was evaluated at the heading stage and at the milk-ripe stage and expressed as infection type (IT) in the following scale (Lokstov et al., 2012):

**IT 1** – resistance is very low – pustules cover all leaves and internodes in abundance, including the upper ones; a lesion can capture an ear;

**IT 3** – low resistance – pustules in bulk develop mainly on the lower leaves and internodes; individual scattered pustules are observed on the upper leaves;

**IT 5** – medium resistance – a moderate number of pustules on the lower leaves and internodes;

**IT 7** – high resistance – single small pustules on the lower leaves and internodes, pustules can be more numerous, but small;

**IT 9** – very high resistance – no pustules are visible.

To exclude the presence of known powdery mildew resistance genes in barley accessions from Dagestan, the seedling resistance test was performed. Fungal inoculum was propagated on plants grown in a Barnstead 845-2 climatic chamber at a 12-hour photoperiod and a temperature of 16 °C (day), 13 °C (night).

et al., 2005). Powdery mildew resistance of Dagestan barleys has not yet been studied.

This study is aimed at evaluating variability potential of barley accessions from Dagestan for resistance to *B. graminis*, and at elucidating genetic control of the trait in the selected resistant forms.

Material and methods

The material used in the study included 264 barley accessions (187 spring, 76 winter, and one facultative) from Dagestan (Supplementary 1), among them the landraces (228 accessions) prevailed whereas only 36 accessions represented cultivars and breeding lines. The studied forms belong to the two subspecies: six-row barley (subsp. *vulgare*) and two-row barley (subsp. *distichon*) and represent 29 botanical varieties. Some accessions were registered in the collection of the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) as populations involving up to five varieties. Forty-seven barley lines carrying previously identified powdery mildew resistance genes were also studied (Supplementary 2).

Field trials were carried out at the Dagestan Experiment Station of VIR (DES VIR, Derbent; latitude 41°59’03.3”N, longitude 48°19’47.7”E) in 2012–2014. Accessions were sown in the third decade of October in the field plots of 1 m² area, with a row to row spacing of 15 cm and row length of 1 m. Spring barley cultivar Temp (VIR-22055, Krasnodar region) sown after each 20 accessions was used as a control. Resistance to disease was evaluated at the heading stage and at the milk-ripe stage and expressed as infection type (IT) in the following scale (Lokstov et al., 2012):

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1 Supplementary materials 1–2 are available at http://www.bionet.nsc.ru/vogis/download/pict-2021-25/appx10.pdf
The Northwest (St. Petersburg, Pushkin) population of the fungus was used for inoculation. The population was collected from a susceptible barley cultivar Belogorsky (VIR-22089, Leningrad region). Twenty seeds of each of resistant accessions and 47 barley lines carrying previously identified powdery mildew resistance genes were sown on water-moistened cotton in plastic trays, placed in a climatic chamber, and after a week the seedlings were inoculated through shaking conidia on them from plants strongly affected by powdery mildew. Infection types were scored using 0–4 point scale (Mains, Dietz, 1930) as follows:

- **IT 0** – highly resistant, no mycelium evident. Chlorotic or necrotic spots may be developed by some varieties;
- **IT 1** – very resistant, slight to moderate mycelial development, but with little or no sporulation. Chlorotic or necrotic spots may develop in some varieties;
- **IT 2** – moderately resistant, moderate mycelial development, accompanied by limited sporulation. Chlorotic or necrotic areas may be formed;
- **IT 3** – moderately susceptible. Moderate to abundant mycelial development, accompanied by sporulation;
- **IT 4** – very susceptible. Abundant mycelial development, accompanied by abundant sporulation.

To specify resistance genes, we have estimated segregation ratios in the F₂ hybrid populations obtained from crossing resistant accessions with a susceptible variety (VIR-15033). For allelic testing, the resistant accessions were crossed with each other, as well as with near-isogenic line Ingrid (cultivar Belogorsky) which was sown along with F₂ plants. At the two-leaf stage, the seedlings were inoculated with the Northwest pathogen population (collected near St. Petersburg). Hybrids from the crossings of resistant accessions and a susceptible tester were evaluated for resistance at the time of death of susceptible parental form. The assessment of allelic relations among powdery mildew resistance genes was carried out at the time of death of susceptible control (cultivar Belogorsky) which was sown along with F₂ plants in the same tray. Plants exhibiting infection type similar to that of either the susceptible parent or the control (IT scores of 3 or 4 according to the 0–9 point scale (Mains, Dietz, 1930)) were classified as homozygous susceptible (S). The resistant test plants similar in infection type to the resistant parental form (IT scores of 0–1).

For identifying the *mlo11* gene, the PCR markers (Table 1) developed by P. Piffanelli et al. (2004) were used. Total DNA was isolated from 7-day-old seedlings according to the method of D.B. Dorokhov and E. Kloke (1997). Amplification was carried out in a 25 μl volume reaction mixture containing 50–100 ng of genomic DNA, 1 × reaction buffer, 2 mM MgCl₂, 0.25 mM dNTPs, 0.25 μM of each primer, 1 U Taq DNA polymerase (Dialat Ltd). PCR was conducted on a MyCycler thermal cycler (Bio-Rad, USA). The protocol consisted of an initial cycle of denaturation at 94 °C for 5 min, followed by 35 cycles (94 °C for 30 s, 60 °C for 30 s and 72 °C for 1.5 min). Final extension was done at 72 °C for 10 min. Amplification products were analyzed by electrophoresis on 1.5 % agarose gels and visualization under ultraviolet light. Fragment size was estimated using FastRuler™ SM1113 DNA-marker (Fermentas).

### Table 1. Primers used in the study (Piffanelli et al., 2004)

| Primer | Sequence (5′–3′) |
|--------|-----------------|
| ADUP7  | CTCAGCCTGCCCACCATGTCGCGAAAAAGGG |
| Mlo6   | CATCTACTAGTACGTACC |
| Mlo10  | GTCTGGCACCCTAAGTAGCAG |

### Results

In 2012–2014, the epiphytotic disease development was observed at the DES VIR: the susceptible control cultivar Temp exhibited the IT score of 3 according to the 0–9 point scale (Loskutov et al., 2012). At a severe infection pressure, five accessions whose IT scores did not exceed 7 points have been initially isolated; in 2014 only two accessions (VIR-23787 and VIR-28212) were resistant (Table 2).

Forty-seven barley lines carrying previously identified powdery mildew resistance genes were evaluated under laboratory conditions and in the field experiments at the DES VIR. Twelve lines have been shown to be resistant to the pathogen in the field and laboratory experiments. According to the information documented at the VIR Department of Oat, Rye and Barley Genetic Resources, the landrace accession VIR-23787 is of unknown pedigree, and line VIR-28212 originated from Ethiopian spring barley accession VIR-17554.

Thus, a comparative analysis of infection types of powdery mildew resistant accessions VIR-23787 and VIR-28212, and lines resistant to the Dagestan and St. Petersburg populations of *B. graminis* (see Table 3) has shown that these accessions might be protected either by the recessive gene(s) *mlo* or dominant *Mla*.
To determine the number of genes conferring resistance, the F₁ and F₂ hybrids obtained from crossing resistant accessions VIR-23787 and VIR-28212 with susceptible tester VIR-15033 were evaluated for resistance at the seedling stage. The parental genotypes VIR-23787 and VIR-28212 were resistant to the Northwest pathogen population with the IT score of 1, whereas F₁ hybrid plants were susceptible to the pathogen (IT score of 4). Phenotypic segregation in the F₂ populations fitted the expected ratio 1R: 3S (Table 4). We suggest that accessions VIR-23787 and VIR-28212 possess recessive genes conferring powdery mildew resistance at the seedling stage. Analysis of F₂ hybrid progenies derived from reciprocal crosses between the resistant (VIR-28212) and susceptible (VIR-22055) accessions did not reveal an effect of the maternal or paternal genotype on the segregation pattern (χ² = 0.60 and χ² = 0.65).

We have also analyzed segregation for pathogen resistance of the F₂ hybrids obtained from crossing accession VIR-17554 from Ethiopia (a putative donor of disease resistance in the line VIR-28212) and susceptible cultivar Belogorsky (VIR-22089). The results indicated that accession VIR-17554 also carries a single recessive gene for *B. graminis* resistance (see Table 4).

| Cross combination | Total number of plants | The ratio of phenotypes (R:S) | χ² | p |
|------------------|-----------------------------|---------------------------|-----|---|
| VIR-15033 × VIR-23787 | 244 | 51:193 | 1:3 | 2.48 | 0.10−0.20 |
| VIR-15033 × VIR-28212 | 935 | 244:691 | 1:3 | 0.60 | 0.25−0.50 |
| VIR-28212 × VIR-15033 | 223 | 61:162 | 1:3 | 0.65 | 0.25−0.50 |
| VIR-17554 × VIR-22089 | 433 | 93:340 | 1:3 | 2.87 | 0.05−0.10 |

Note. χ²₀.₀₅ = 3.84.
fragments with primer pairs ADUP7-Mlo6 and Mlo6-Mlo10 respectively is usually an indication of the presence of the mlo11 allele. Genotypes carrying the mlo11 allele were found in accessions VIR-17554 and VIR-28212 (see the Figure). No carriers of the mlo11 allele were detected among the 20 plants analyzed in accession VIR-23787, therefore this form is protected by another resistance gene.

**Discussion**

The results of the study indicate a rather low level of genetic diversity for powdery mildew resistance within the studied set of Dagestan barley accessions. Five accessions (VIR-23787, VIR-28212, VIR-28211, VIR-28212, VIR-30781) were selected for powdery mildew resistance in 2012 and 2013. However, in the past years their susceptibility is enhanced, which may be due to changes of the population structure. Only two accessions, VIR-23787 and VIR-28212, were resistant to the Dagestan population of *B. graminis* at the adult stage and to the St. Petersburg population of the pathogen at the seedling stage respectively. It is interesting that two geographically very distant populations of the fungus turned out to be identical in virulence to the tester lines (see Table 3).

It was somewhat surprising, that accession VIR-28212 was protected by the effective resistance gene mlo11, which was introgressed from VIR-17554 (Ep-80 Abyssinien). This accession, which has entered the VIR collection from the German Gene Bank in 1949, turned out to be heterogeneous for resistance (eight resistant plants out of the ten studied). Plants belonging to the variety *nigrinudum* are most likely a result of genetic contamination in consequence of the cross-pollination, which is quite typical for Ethiopian barley.

Durable non-specific resistance of barley to *B. graminis* is associated with mutations at the *Mlo* locus on the long arm of chromosome 4 (Jørgensen, 1992). The resistance of *mlo* mutants is associated with physiological processes which prevent successful penetration of the pathogen into epidermal cells of the host plant (Ge et al., 2016). Carriers of the recessive *mlo* allele are characterized by leaf damage which is considered as a manifestation of premature cell death symptoms after cell wall appositions (callose deposits on adult leaves), observed even in the absence of the pathogen (Skou et al., 1984). Despite a number of limitations associated with negative pleiotropic effects leading to yield decrease, the use of *mlo* alleles (mostly *mlo11* and, in part, *mlo9*) in barley breeding programs provided durable protection against *B. graminis* in the regions with temperate humid climate. Currently, 75 % of modern spring barley varieties in Europe are protected by the *mlo* genes (Dreiseitl, 2017).

The recessive *B. graminis* resistance gene in accession VIR-23787 is distinct from the *mlo11* and not associated with negative pleiotropic effects which are characteristic of the *mlo* alleles induced by chemical mutagenesis. In addition, unlike the accessions carrying recessive *mlo* alleles, no symptoms of fungal damage were detected on plants of accession VIR-23787. Therefore, we assume that this accession is protected by a new pathogen resistance gene.

Recently, a novel recessive gene conferring broad-spectrum resistance against *Blumeria graminis* f. sp. *hordei* was found in a spring barley line selected from a Moroccan landrace at the Polish Plant Breeding and Acclimatization Institute (Piechota et al., 2020). The gene designated *mlmr* was mapped at the long arm of chromosome 6H. In the other study performed with the use of phytopathological testing, a new resistance allele *MLLu* was identified among 16 winter barley accessions originating from four gene banks (Dreiseitl, 2019). Thus, identification of novel genes in barley landraces can facilitate

**Table 5. Segregation for resistance to *B. graminis* of the F₂ hybrids obtained from crossing resistant barley accessions with IL Ingrid **

| Cross combination | Total number of plants | The ratio of phenotypes (R:S) | \( \chi^2 \) | \( p \) |
|-------------------|------------------------|------------------------------|----------|-----|
| VIR-30225 × VIR-28212 | 363 | 363:0 | - | - |
| VIR-30225 × VIR-17554 | 203 | 203:0 | - | - |
| VIR-30225 × VIR-23787 | 582 | 254:328 | 7.9 | 0.00 | 0.995 |

Molecular marker-based assessment of powdery mildew resistant barley plants with the use of primer pairs ADUP7-Mlo6 (a) and Mlo6-Mlo10 (b). a – the 1.2 kb fragment is specific for the mlo11 allele; b – the 380 bp fragment is amplified in the genotypes with the wild-type Mlo allele and a fragment of approx. 440 bp size is amplified in the genotypes carrying the mlo11 allele. 1 – susceptible control VIR-22089 (cultivar Belogorsky); 2 – line VIR-30225 with the mlo11 allele; 3 – VIR-28212; 4 – VIR-17554; 5 – VIR-23787. M – molecular weight marker.
the broadening of the available powdery mildew resistance germplasm. Moreover, knowledge of resistance phenotypes can assist in determining accessions authenticity and their genotype purity in gene banks (Dreiseitl, Zavřelová, 2018).

Conclusion
The cultivation of barley varieties carrying effective genes for resistance against B. graminis f. sp. hordei can significantly limit the harmfulness of the pathogen. The specificity in the interaction between the fungus and its host plant requires a continuous search for new resistance donors. Barley landraces are traditionally considered as sources of novel genes for pathogen resistance. The present study performed under field and laboratory conditions has revealed rather low genetic diversity for effective resistance against powdery mildew within the examined set of 264 barley accessions from Dagestan. Only two accessions, VIR-23787 and VIR-28212, were resistant to the Dagestan population of B. graminis at the adult stage and to the St. Petersburg population of the pathogen at the seedling stage. Accession VIR-28212 is protected by the effective resistance gene mloII, which was probably introgressed from accession VIR-17554 (Ethiopia). Accession VIR-23787 has another recessive B. graminis resistance gene which is distinct from mloII and does not have negative pleotropic effects typical for other mlo alleles obtained by chemical mutagenesis.

References
Abdullaev R.A., Lebedeva T.V., Alpatieva N.V., Yakovleva O.V., Kovalova O.N., Radchenko E.E., Batasheva B.A., Karabitsina Yu.I., Kuznetsova E.B. Genetic diversity of barley accessions from Ethiopia for powdery mildew resistance. Russ. Agric. Sci. 2019;45(2):232-235. DOI 10.3103/S1068367419030029.
Balkema-Boomstra A.G., Masterbroek H.D. Effect of powdery mildew (Erysiphe graminis f. sp. hordei) on photosynthesis and grain yield of partially resistant genotypes of spring barley (Hordeum vulgare L.). Plant Breed. 1995;114(2):126-130. DOI 10.1111/j.1439-0523.1995.tb00776.x.
Bonnam J.M., Bockelman H.E., Jackson L.F., Steffenson B.J. Disease and insect resistance in cultivated barley accessions from the USDA National Small Grains Collections. Crop Sci. 2005;45(4):1271-1289. DOI 10.2135/cropsci2004.0546.
Dorokhov D.B., Kloke E. Rapid and economical technology of RAPD analysis of plant genes. Genetika = Genetics (Moscow). 1997;33(4):443-450. (in Russian)
Dreiseitl A. Genes for resistance to powdery mildew in European barley cultivars registered in the Czech Republic from 2011 to 2015. Plant Breed. 2017;136(3):351-356. DOI 10.1111/pbr.12471.

Dreiseitl A. A novel resistance against powdery mildew found in winter barley cultivars. Plant Breed. 2019;138(6):840-845. DOI 10.1111/pbr.12730.

Dreiseitl A., Zavřelová M. Identification of barley powdery mildew resistance genes in gene bank accessions and the use of gene diversity for verifying seed purity and authenticity. PLoS One. 2018;13(12):e0208719. DOI 10.1371/journal.pone.0208719.

Ge X.T., Deng W.W., Lee Z.Z., Lopez-Ruiz F.J., Schweizer P., Ellwood S.R. Tempered mlo broadband-spectrum resistance to barley powdery mildew in an Ethiopian landrace. Sci. Rep. 2016;6:29558. DOI 10.1038/srep29558.
Gong X., Li C., Zhang G., Yan G., Lance R., Sun D. Novel genes from wild barley Hordeum spontaneum for barley improvement. In: Advance in barley Sciences. Proc. 11th Int. barley Genetic Symp. Zhang G., Li C., Liu X. (Ed.). Dordrecht Heidelberg; New York; London: Zhejiang University Press, Springer, 2013;69-89. DOI 10.1007/2F978-94-007-4682-4_6.pdf.

Jørgensen J.H. Discovery, characterization and exploitation of Mlo powdery mildew resistance in barley. Euphytica. 1992;63(1-2):141-152. DOI 10.1007/BF00023919.

Jørgensen J.H. Genotypes of powdery mildew resistance in barley. Crit. Rev. Plant Sci. 1994;13(1):97-119. DOI 10.1080/713608055.
Kusch S., Panstruga R. mlo-based resistance: an apparently universal “weapon” to defeat powdery mildew disease. Mol. Plant Microbe Interact. 2017;30(3):179-189. DOI 10.1094/MPMI-12-16-0255-CR.

Loskutov I.G., Kovalova O.N., Blinova E.V. Methodological Guidelines for Studying and Maintaining the Global Collection of barley and oat. St. Petersburg: VIR, 2012. (in Russian)

Mains E.B., Dietz S.M. Physiologic forms of barley Erysiphe graminis hordei Marchal. Phytopathology. 1930;20:229-239.
Piechota U., Slowacki P., Czembor P.C. Identification of a novel recessive gene for resistance to powdery mildew (Blumeria graminis f. sp. hordei) in barley (Hordeum vulgare). Plant Breed. 2020;139:730-742. DOI 10.1111/pbr.12819.

Piennelli P., Ramsay L., Waugh R., Benabdelmouna A., D’Hont A., Hollricher K., Jørgensen J.H., Schulze-Leiert P., Panstruga R. A barley cultivation-associated polymorphism conveys resistance to powdery mildew. Nature. 2004;43(7002):887-891. DOI 10.1038/nature02781.

Reinstädler A., Müller J., Jerzy H., Czembor J.H., Piffanelli P., Panstruga R. Novel induced mlo mutant alleles in combination with site-directed mutagenesis reveal functionally important domains in the heptahelical barley Mlo protein. BMC Plant Biol. 2010;10:31. DOI 10.1186/1471-2229-10-31.

Scheholzer S. Isolation and Characterization of New R-protein Variants Encoded at the Barley Mlo Locus that Specify Resistance against the Fusarium Powdery Mildew. University of Zurich, Faculty of Science, 2009;131. DOI 10.5167/uzh-31283.

Skou J.P., Jørgensen J.H., Linhold U. Comparative studies on callus formation in powdery mildew compatible and incompatible barley. Phytopathol. Z. 1984;109(2):147-168. DOI 10.1111/j.1439-0434.1984.tb00702.x.