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When the source of resistance can be considered effective - resistance to *Blumeria graminis* f. sp. *avenae* found in *Avena sterilis* L.

Sylwia Okoń · Aleksandra Nucia · Tomasz Ociepa · Andreas Börner · Krzysztof Kowalczyk

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Abstract Powdery mildew, caused by *Blumeria graminis* DC. f. sp. *avenae* Em. Marchal, is currently one of the most serious foliar diseases of common oats worldwide, leading to significant grain yield losses. So far, 13 resistance genes to powdery mildew have been identified and characterized in oats, but only a few of these genes are effective against the existing pathogen races. Therefore, there is a need to identify and characterize new and effective sources of resistance. *Avena sterilis* L. is identified as the most promising source of resistance genes against fungal diseases. However, identifying effective sources of resistance requires more extensive research using a larger group of differentiated isolates of *B. graminis* f. sp. *avenae*. This study aimed to characterize the effectiveness of resistance identified in *A. sterilis* genotypes. The research focused on 28 *A. sterilis* genotypes, from the IPK Genebank collection, which were known for their high level of resistance in screening tests. The effectiveness of resistance was evaluated in host–pathogen tests using 55 different *B. graminis* f. sp. *avenae* isolates collected from various regions of Europe. These isolates were known for their different infection patterns to known powdery mildew resistance genes. In the initial stage of the investigation, the 28 previously selected *A. sterilis* genotypes were tested against 5 different *B. graminis* f. sp. *avenae* isolates, resulting in the selection of seven resistant genotypes. Further tests using 50 different pathogen isolates revealed that only two of these genotypes showed very high effectiveness. These studies indicate that effective sources of resistance should be tested with a variety of pathogen isolates. Tests based on only 2–3 isolates are suitable only for preliminary screening.

Keywords *Avena sterilis* · *Blumeria graminis* f. sp. *avenae* · Resistance · Powdery mildew

Introduction

Genetically determined resistance is the most cost-effective and environmentally friendly strategy for reducing the incidence of fungal diseases in cereal crops (Dracatos et al., 2023; Dreiseitl, 2022). The ability of fungal pathogens to rapidly adapt to changing environmental conditions and overcome resistance genes necessitates the search for new and effective sources of resistance and their incorporation into

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S. Okoń · A. Nucia (✉) · T. Ociepa · K. Kowalczyk
Institute of Plant Genetics, Breeding and Biotechnology, University of Life Sciences, Lublin, Poland
e-mail: aleksandra.nucia@up.lublin.pl

A. Börner
Genebank Department, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Seeland, Gatersleben, OT, Germany

cultivated varieties (Hinterberger et al., 2022; McDonald & Linde, 2002; Menardo et al., 2016). Pietrusińska and Czembor (2015) suggest that incorporating resistant traits in a timely and spatial manner ensures the success of resistance breeding. Introducing a variety of resistance mechanisms is crucial for effective plant protection strategies, making it more difficult for pathogen populations to overcome them (Fabre et al., 2012; Hinterberger et al., 2022; Krattinger & Keller, 2016).

Powdery mildew, which is caused by the obligate biotroph *Blumeria graminis* f. sp. *avenae* (*Bga*), is one of the most common diseases affecting oat crops in temperate regions of the world. The disease is common in central and northwestern Europe and North America (Roderick et al., 2000; Schwarzbach & Smith, 1988). Moreover, due to climate changes, the disease has spread to areas where its symptoms had not been observed before. Literature sources report the occurrence of the disease, for example, in China or the northwestern Himalayan region (Banyal et al., 2016; Xue et al., 2017). Powdery mildew occurs with varying intensity each year, which contributes to a significant reduction in the size and quality of the obtained crops. Losses of oat grain yield caused by powdery mildew range from 5 to 10%, and in years favorable for infection can reach up to 39% (Clifford, 1995; Jones, 1977; Lawes & Hayes, 1965). The population of *B. graminis* f. sp. *avenae* is constantly evolving through migration, mutation, and recombination. The annual cycle of sexual reproduction leads to the formation of new allelic combinations, and subsequent cycles of asexual reproduction may result in an increase in the frequency of alleles determining greater virulence of the pathogen. In addition, climate change and associated extreme weather conditions facilitate the spread of *B. graminis* spores over long distances. These phenomena contribute to the formation of new and aggressive pathotypes (Cowger et al., 2016; Menardo et al., 2017). Reducing production losses caused by powdery mildew can be achieved by using appropriate agrotechnical treatments (Gacek, 2000). The use of fungicides and cultivation of resistant varieties are the most commonly used methods to reduce the occurrence of powdery mildew. The first method is ecologically undesirable and can lead to rapid adaptation of pathogens and, consequently, to increased resistance to the applied chemical compounds (Vielba-Fernández et al., 2020). Moreover, in many countries there are no fungicides available recommended for the protection of oats during the vegetation period. Because of this fact, the most effective method of controlling and limiting the effects of fungal disease infestationis to introduce varieties with genetically determined resistance (Stevens et al., 2004). Genetic sources of resistance are the main strategy for protecting oats against powdery mildew (Cieplak & Okoń, 2023; Herrmann & Mohler, 2018; Hsam et al., 1997, 1998; Okoń, 2012). According to the literature, 13genes have been identified that confer resistance to powdery mildew in oats (Herrmann & Mohler, 2018; Hsam et al., 2014; Ociepa & Okoń, 2022; Ociepa et al., 2020; Schurack et al., 2024). Recent research has shown that only the *Pm2, Pm4, Pm5*, and *Pm7* genes are the most effective against this disease (Cieplak et al., 2021; Okoń, 2015). This suggests the need to introduce more sources of resistance to ensure the sustainable cultivation of healthy plants under various environmental conditions. An excellent source of new genes, including resistance genes, comes from wild species related to cultivated forms (McIntosh et al., 1998; Pickering et al., 1995; Reader & Miller, 1991; Shi et al., 1998). In oats, one such species is *Avena sterilis* L., commonly known as sterile oat. It is a vital hexaploid wild relative of the cultivated oat and has a widespread global distribution (Bajwa et al., 2017; Mahajan & Chauhan, 2021; Thurston & Phillipson, 1976). Hybridisation with *A. sterilis* is relatively easy and can be used to increase oat genetic variability (Gupta et al., 1986; Lawrence & Frey, 1975). *A. sterilis* genotypes are a valuable source of diverse agronomically important traits, such as abundant tillering and leafage or good adaptation for grazing, which are very important in breeding oat varieties suited for sheep (Brown & Patterson, 1992). Sterile oats were also used as sources of high-yield potential genes for *A. sativa* varieties and genes conditioning better adaptation to different environmental conditions (Lawrence & Frey, 1975). *A. sterilis* also could be a donor of genes determining high protein and fat content (Thro & Frey, 1985). Effective resistance genes for oat crown rust and powdery mildew have been found in sterile oats (Herrmann & Roderick, 1996; Kiehn et al., 1976; Okoń et al., 2016; Roderick et al., 2000; Sowa, 2020).

The main objective of the conducted research was to identify sources of resistance among *A. sterilis* genotypes from the genebank collection of the

Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) in Gatersleben, Germany, and to determine the level of resistance of these genotypes based on multi-pathotype tests.

Materials and method

The subjects of this research were 28 *A. sterilis* genotypes, from the genebank collection of the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben (Germany). Our previous studies selected these genotypes as resistant to *Bga* infection (Okoń et al., 2024).

The effectiveness of the tested genotypes was assessed *in vitro* using host–pathogen tests. Each test was performed in two independent replicates.

Host–pathogen tests were carried out on the first leaves of 10-days-old seedlings according to the method described by Hsam et al. (1997). 10 leaf fragments from each of analyzed *A. sterilis* genotypes were placed on 12-well culture plates with benzimidazole agar (6 g of agar per 1 l of water and 35 mg/l of benzimidazole) in duplicate. Control genotypes with known *Pm* genes were put into the first and last wells of every dish. Plates with fragments of leaves were inoculated in an inoculation tower by placing about 500–700 spores of powdery mildew per 1 cm^2. Then the dishes were incubated in a phytotron at about 17 °C and illuminance of approximately 4 kLx. The effect on the leaves was determined 10 days after inoculation.

The tests were conducted in two stages. The first stage was based on 5 *Bga* isolates characterized by a different level of virulence and different origins. The second stage was based on 50 *Bga* isolates collected in different years (2014–2021) in different geographical regions of Europe (Poland, Germany, Ireland, Finland, Czech Republic).

Reaction type on each genotype was determined 10 days after inoculation and scored according to a 0–4 modified scale (Mains, 1934), where 0 = no infection, no visible symptoms; 1 = highly resistant, fungal development limited, no sporulation; 2 = moderately resistant, moderate mycelium with some sporulation; 3 = moderately susceptible, extensive mycelium, more sporulation; 4 = highly susceptible, large colonies, and abundant sporulation (Fig. 1). Reactions to the isolates were grouped into three classes: resistant – from 0 to 20% infection intermediate from 20 to 50% infection and susceptible – where the degree of infection exceeded 50% (Hsam et al., 1997). To confirm the reliability of the obtained results, every test was repeated twice.

The heatmap was created in R using the heatmap package. To create the heatmap, the average of the results obtained from all leaves of both replicates (20 leaves) for each genotype was taken into account. Isolates (rows) and genotypes (columns) were automatically grouped. Grouping the rows helps to estimate differences in virulence between isolates, while grouping the columns shows patterns of resistance within genotypes. A color gradient

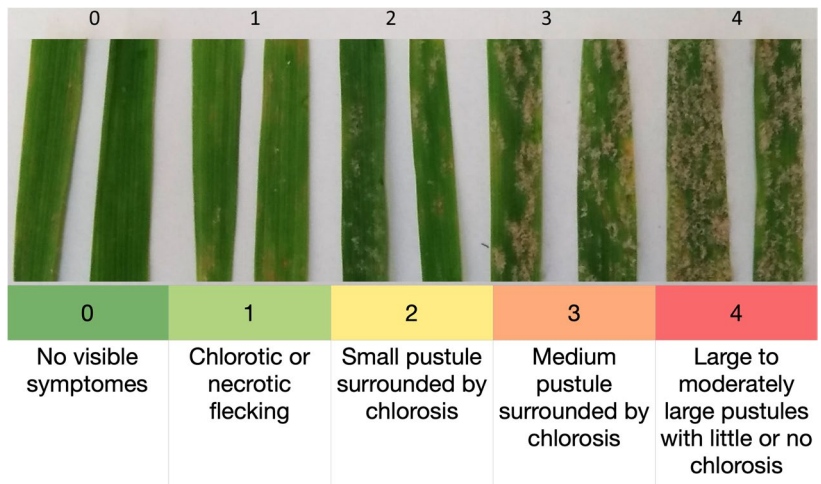


Fig. 1 Different types of plant response to *B. graminis* f. sp. *avenae* infection

according to Fig. 1 was used to visually represent the response to powdery mildew infection within genotypes.

Results

In the first test, 5 *Bga* isolates that varied in virulence compared to the control genotypes, aiding in the identification of a broad range of resistance, were examined (Fig. 2). The analyzed *A. sterilis* genotypes showed different levels of resistance to the isolates. All genotypes showed resistance to 2 of the selected isolates (Bga_Lb14 and Bga_Cz2). By using isolates Bga_Ch4 and Bga_St1, we were able to more rigorously evaluate the genotypes, with most showing a moderate level of resistance to two additional isolates. Utilizing the fifth isolate (Bga_Dn2) allowed us to effectively identify 7 genotypes with a very high level of resistance to *Bga*, as they were resistant to all 5 *Bga* isolates used in the host–pathogen tests.

In the second test, 50 *Bga* isolates collected from various locations between 2014 and 2020 were assessed (Supplementary Table 1). The tests were conducted on 7 genotypes of *A. sterilis* that were selected in the initial stage of the study. The genotypes AVE 446 and AVE 3183 displayed the lowest level of resistance. It showed a sensitive or moderate response to most of the isolates used and was completely resistant to only 4 and 5 of the isolates respectively. Genotypes AVE 5089, and AVE 4056 exhibited a moderate level of resistance to most of the isolates. A higher level of resistance was observed in genotypes AVE 2640 and AVE 3181 which were resistant or showed moderate resistance to the majority of the *Bga* isolates used in the tests. Genotype AVE 2640 were resistant to 15 *Bga* isolates and showed moderate response to net 15 isolates. The rest of the *Bga* isolates were virulent for this genotype. Whereas, genotype AVE 3181 displayed resistance to 23 of the 50 isolates, moderate resistance to 17, and sensitivity to the remaining 10 isolates.

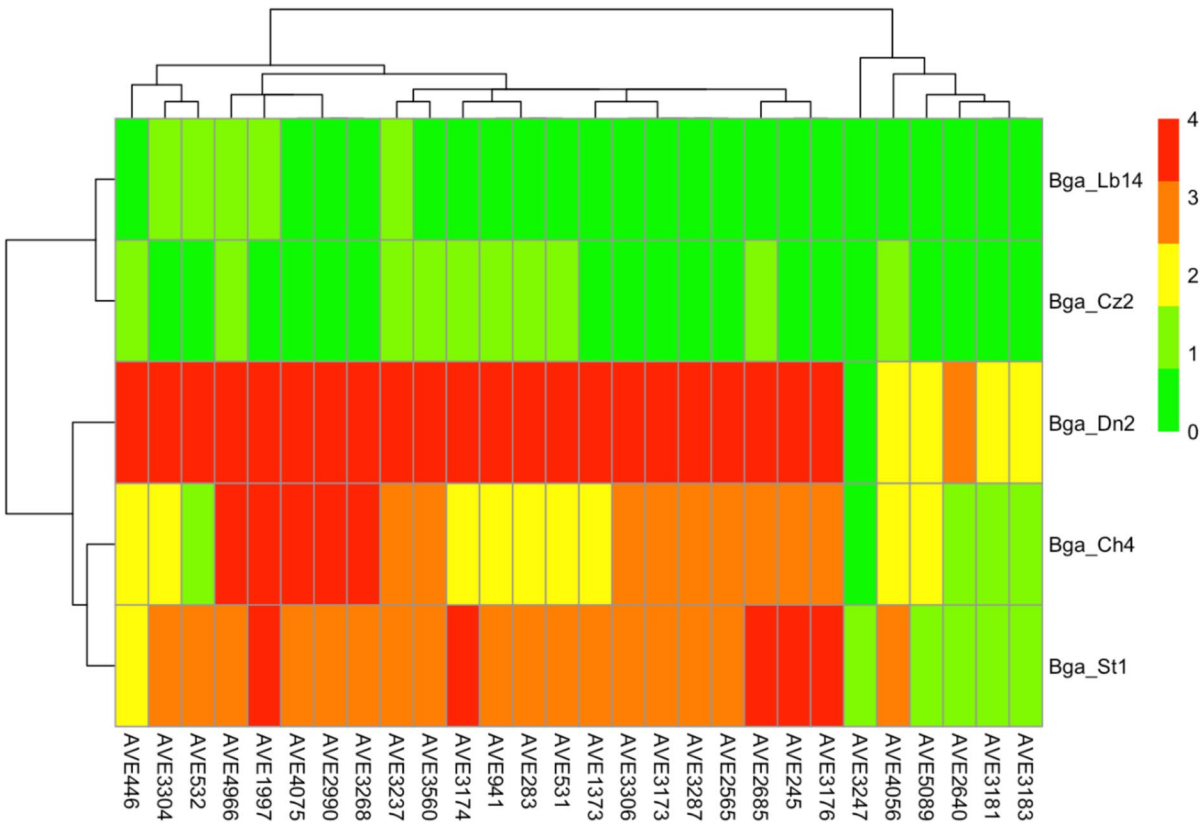


Fig. 2 Resistance of 28 *A. sterilis* genotypes in response to infections with 5 isolates of *B. graminis* f. sp. *avenae*

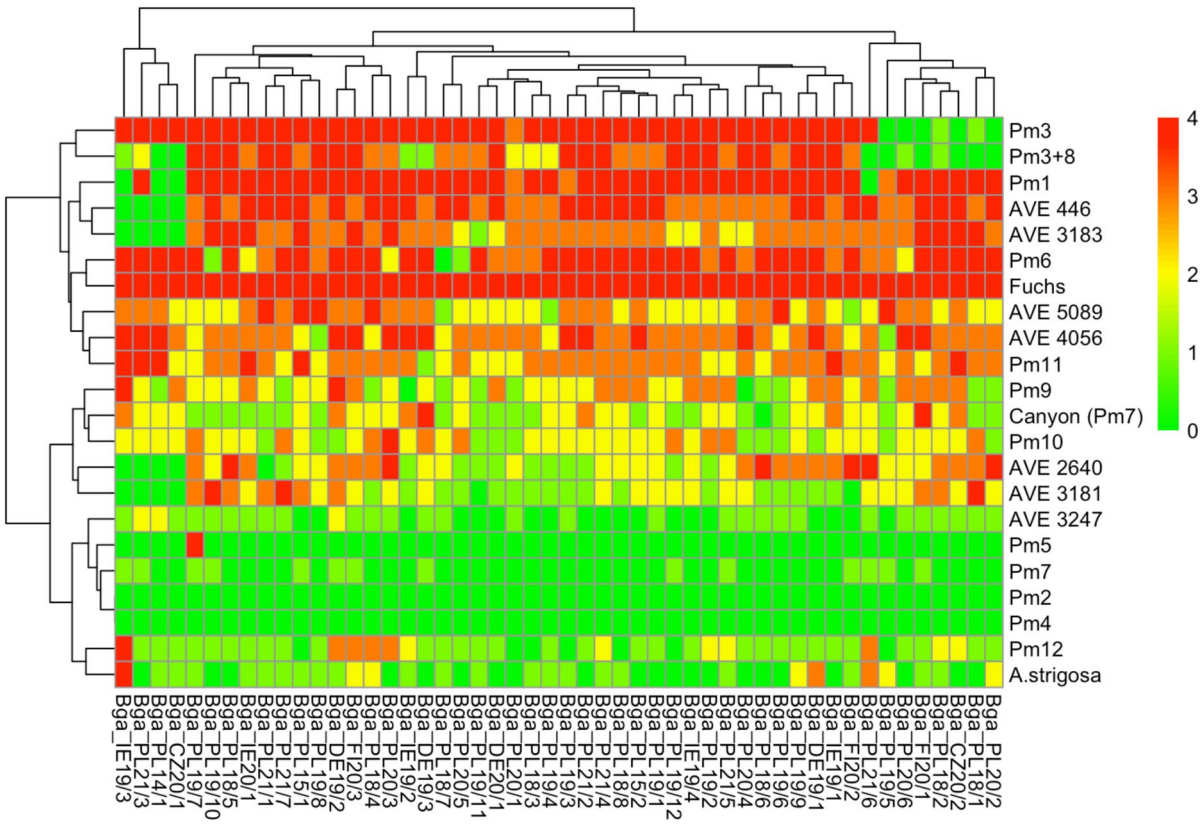


Fig. 3 Infection profiles of selected *A. sterilis* genotypes and control forms

Genotype AVE3247 demonstrated the higher level of effectiveness. This genotype was complete resistance to 47 *Bga* isolates and moderate resistance to the remaining 3 (Fig. 3, Supplementary Table 1). Infection profiles of the analyzed *A. sterilis* genotypes differed from the infection profiles of the control forms with known powdery mildew resistance genes. However, the infection profile of the AVE 446 and AVE 3183 genotypes was very similar to the profile of the control form with the Pm1 gene, which may indicate the presence of this gene in the mentioned forms. The differences in the other profiles indicate the presence of new, previously undescribed sources of resistance in the resistant genotypes.

Discussion

Resistance breeding aims to develop plant varieties that are resistant or tolerant to biotic and abiotic stress factors. Utilizing the achievements of resistance breeding in practical applications is considered one of the most effective and cost-efficient methods of plant protection. This approach offers numerous benefits, including unlocking the yield potential of the variety and minimizing the harmful effects of pesticides on the environment (Pietrusinska et al., 2019). The main challenge in resistance breeding is the development of new virulent pathotypes that can overcome previously resistant plant varieties. This is due to the high genetic variability of the fungus and its ability to rapidly generate new forms through mutations and DNA recombination (Bennett, 1984). In addition, the migration of spores carried by the wind over very long distances also promotes the emergence and spread of new genotypes of the pathogen (Limpert, 1999). Menardo et al. (2017) also suggested that hybridization between special forms of the fungus is a mechanism of adaptation to new crops introduced by agriculture. Moreover, long-term use of a set of several resistance genes in breeding carries the risk

of rapid overcoming of their potential by pathogens (Brodführer et al., 2023). Therefore, it is important to identify new sources of resistance to diversify the used resistance genes (Herrmann & Mohler, 2018; Ociepa et al., 2020; Okoń & Kowalczyk, 2020; Sánchez-Martín et al., 2012; Yu & Herrmann, 2006). The first step in resistance breeding is identifying a potential source of resistance. However, for the resistance source to be utilized in the breeding process, it must exhibit effective resistance in both time and space (Pietrusińska & Czembor, 2015). Therefore, it is important to precisely characterize the effectiveness of the identified resistance sources (Fahim et al., 2012; Harder and Legge 2000; Okoń et al., 2018). Identifying new resistance genes based on physiological tests using only 1 or 2 isolates of the pathogen may lead to low effectiveness in resisting various environmental conditions. Our studies have demonstrated the importance of testing newly identified resistance sources and determining their level of effectiveness. The first screening tests performed by Okoń et al. (2024) showed that out of the collection of 88 *A. sterilis* genotypes obtained from the IPK genebank collection, as many as 28 were selected as potential new sources of resistance to powdery mildew. The authors carried out tests based on 2 *Bga* isolates, which allowed the selection of resistant genotypes. The small number of isolates used allows the selection of genotypes with a relatively narrow resistance range. The isolates used by the authors came from Poland, so it should be assumed that the genotypes they selected will be effective in the regions from which the isolates came. Okoń and Ociepa (2018), analyzing the effectiveness of sources of resistance to powdery mildew, noted that conducting research based on one or two isolates may be insufficient to draw reliable conclusions. Therefore, in this work, broader studies were conducted on the genotypes selected by Okoń et al. (2023). Initially, we expanded the number of isolates to 5, which were characterized by a different level of virulence against control genotypes possessing the previously described genes for resistance to powdery mildew in oats. These tests showed that the resistance of some of the 28 tested genotypes was not as high as indicated by the tests conducted in our previous studies (Okoń et al., 2024). Therefore, we decided to conduct tests of selected genotypes on the entire collection of *Bga* isolates. The isolates were collected from various parts of Europe, including Poland, Germany, Ireland, the Czech Republic, and Finland. This suggests that the genotypes selected in this study will exhibit a wide spectrum of resistance in different regions. Identification of genotypes with a broad spectrum of resistance makes it possible to use them in breeding over a large area without losses caused by pathogen infections. Moreover, the isolates used in the study were gathered over 6 years (2014–2020). Studies conducted by Cieplak et al., (2021, 2022) and Okoń et al. (2021) on the dynamics of virulence changes in the *B. graminis* f. sp. *avenae* population have shown that the pathogen population is subject to continuous, albeit slow changes. However, an increase in the virulence of the pathogen can be observed in subsequent years of research. In our own studies, despite the use of isolates collected in the last few years in host–pathogen tests, no trend in the increase in pathogen virulence was observed against the analyzed genotypes. The resistance identified in genotypes AVE 3181 and AVE 3247 remained at a very high level against all isolates. The slow changes in virulence in the pathogen population described by Cieplak et al. (2022), Cieplak et al. (2021) and Okoń et al. (2021) may suggest that the rate of change will be maintained in the following years, and therefore it can be concluded that the resistance of genotypes will remain at a high level.

The genotype identified as effective source of resistance to powdery mildew originated from Libya (AVE3247). Several authors have emphasized that the Mediterranean region, given its high pathogen pressure, serves as an excellent hub for identifying genotypes that are resistant to fungal diseases (Carson, 2009, 2010; Loskutov, 2004; Okoń et al., 2016; Tan & Carson, 2013). This study has confirmed that genotypes from the Mediterranean region are an invaluable source of resistance to fungal diseases and should be considered in experiments searching for new resistance genes.

In summary, our studies have confirmed the thesis that identifying effective sources of resistance to powdery mildew at different times and locations requires the use of a large set of pathogen isolates with diverse levels of virulence and from diverse origins. The genotypes, identified in this study as resistant, require further investigation into the genetic basis of their

resistance and the mode of inheritance. Therefore, they can be integrated into breeding programs as new genes for resistance to powdery mildew. Due to their high efficiency, they can be utilized in breeding programs across almost all of Europe.

Data availability Data are available upon request from the corresponding authors.

Declarations The authors have no relevant financial or non-financial interests to disclose.

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