Range Management and Agroforestry 46 (1) : 70-74, 2025
ISSN 0971-2070 (Print); 2249-5231 (Online)
https://doi.org/10.59515/rma.2025.v46.i1.10

Research article

Genetics of resistance against powdery mildew (*Blumeria graminis* f.sp. *avenae*) in oat (*Avena sativa*) under northwestern Himalayan conditions

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Received: 26th March, 2024 Accepted: 06th March, 2025

Abstract

The inheritance pattern of oat's resistance to powdery mildew (caused by *Blumeria graminis* f. sp. *avenae*), one of the most destructive foliar diseases, was investigated. The segregation pattern of resistance was studied in progenies of F_1, F_2 and BC_1 generations, derived from different cross combinations of three resistant oat genotypes *viz.*, JPO-46, Palampur-1 and KRR-AK-26 with susceptible genotype HJ-8. Progenies were grown under natural epiphytotic and controlled conditions in the humid, sub-tropical climate of Palampur, located in the northwestern Himalayas. The resistant reaction of the F_1 plants, derived from different cross combinations, suggested the dominance of resistance over susceptibility to powdery mildew in oat genotypes. F_2 segregation of each cross showed a close fit to a 3:1 (Resistant: Susceptible) ratio as determined by significant chi-square value, both under field and controlled conditions, representing true genetic segregation. Backcross combinations ($BC_{1)}$ of each cross further agreed with the dominant behavior of the resistance, as shown by the segregation pattern of a 1:1 ratio. Hence, this study confirmed the single dominant gene-governed resistance of three genotypes, *viz.*, JPO-46, Palampur-1, and KRR-AK-26, against powdery mildew. These lines can be utilized in breeding programs as valuable donors of resistance to powdery mildew for incorporation into the cultivated varieties of oats.

Keywords: *Avena sativa*, *Blumeria graminis* f. sp. *avenae*, Fodder oat, Inheritance, Powdery mildew, Resistance

Introduction

Oat (*Avena sativa* L., 2n = 6x = 42), a constituent of the family Poaceae, has been used as grain and fodder as it is a good source of protein, fiber, and minerals. It ranks sixth in world cereal production, following wheat, maize, rice, barley, and sorghum. It requires a long and cool season for its growth; therefore can be successfully grown in hilly areas of the country. It is used as a green crop, hay, and silage for animal feed. Oats have adequate soluble carbohydrates to make good silage. It has excellent growth habits, quick recovery after cutting and provides good quality herbage. Furthermore, the demand for oat for human consumption has increased, particularly because the beta-glucans, the water-soluble fibers present in oat bran, inhibit cholesterol, which helps in preventing heart disease. However, the productivity of this crop is severely affected by various diseases *viz.*, powdery mildew (*Blumeria graminis* f.sp. *avenae*), leaf blight (*Phaeosphaeria avenaria*) and loose smut (*Ustilago avenae*). Among these, powdery mildew causes serious qualitative as well as quantitative losses to fodder and seed yield of oats (Banyal *et al.*, 2016) and the annual yield losses are estimated from 10 to 40% in the world (Reilly *et al.*, 2024).

Powdery mildew, caused by *Blumeria graminis* f. sp. *avenae* is one of the major and most devastating foliar diseases of cultivated oat. The fungus is an obligate parasite appearing as patches of white fluffy mycelium on the lower leaves and leaf sheaths. As the disease progresses, the patches become powdery and turn grey or brown. To control this pathogen, breeding of resistant cultivars is one of the most economical and environmentally friendly methods. Multiple studies have been carried out to identify various resistance genes in oat lines (Malannavar *et al.*, 2022; Banyal *et al.*, 2021; Sindhu *et al.*, 2023). The possibility of using resistance genes in breeding programs depends on their effectiveness against the existing pathogen races. Based on the literature, 13 powdery mildew Resistance (R)-genes, denoted as Pm (*Pm 1- Pm13*), have been identified that confer resistance to powdery mildew in oat (Herrmann and Mohler, 2018; Ociepa *et al.*, 2020, Ociepa & Okoń, 2022; Schurack *et al.*, 2024) and only five of them *viz.*, *Pm2*, *Pm4*, *Pm5*, *Pm7* and *Pm12* genes provide resistance to the current *B. graminis f. sp. Avenae* pathotypes while new virulent strains have overcome others (Okon 2015; Okon and Ociepa 2017 and Ociepa & Okoń, 2022). Okon and Ociepa (2017) have demonstrated that *B. graminis f. sp. avenae* population occurring in Poland is constantly changing and new virulent pathotypes can appear. Moreover, the continuous use of the same set of resistant genes often results in the selection of pathotypes with the matching virulence genes, resulting in resistance breakdown (Czembor and Czembor 2001). Also, knowledge about the nature and number of the gene(s) controlling resistance is the prerequisite for the success of the powdery mildew resistance breeding program. Several sources with resistance to powdery mildew, including common oats (Jones 1983; Hsam *et al.*, 1997; Hsam and Zeller, 1998), have been reported. However, for the genetics of powdery mildew resistance in oat, there are only limited reports (Sebesta *et al.*, 1993; Das and Griffey, 1994; Yu and Herrmann, 2006 and Hsam *et al.*, 2014) clarifying the nature of inheritance of the disease, resistance. Therefore, the present investigation was undertaken to study the segregation pattern of resistance using three cultivars possessing resistance to powdery mildew.

Materials and Methods

***Experimental material*:** The experiment was carried out at the Fodder Section Farm of the Department of Crop Improvement, CSKHPKV, Palampur, Himachal Pradesh, for three years during *Rabi* 2016-2019. The genetics of resistance against powdery mildew was studied using F_2 and backcross mapping populations developed using three resistant genotypes: JPO-46, Palampur-1 and KRR-AK-26 and one susceptible genotype, HJ-8. The staggered sowing was done for the four parents at an interval of 15 days with row-to-row and plant-to-plant spacing of 25 and 5 cm, respectively. The genotypes were raised as per the package of practices under irrigated conditions.

***Development of progenies populations*:** The crosses were attempted between susceptible and resistance parents (HJ-8 × JPO-46, HJ-8 × Palampur-1, and HJ-8 × KRR-AK-26) during 2016-17 to generate sufficient F_1 seeds under natural epiphytotic conditions. The F_1's were selfed to get F_2 population and as well as backcrossed with parental lines grown in pots under artificial conditions at CSK HPKV, Palampur during rabi 2017-18. During 2018-19, F_1, F_2 and backcross population, along with parents, were screened for their reaction against *Blumeria graminis f. sp. avenae*.

***Evaluation of genotypes*:** The resistant behavior of the four parents, along with their progenies in F_1, F_2 and backcross generations of all the crosses, were screened in a field under natural epiphytotic conditions as well as in the greenhouse under artificial epiphytotic conditions. Under field conditions, the disease incidence was intensified by growing the highly susceptible parent, i.e., HJ-8, as an infector row after every test row and also as a border row around the plot. The disease pressure was artificially enhanced by dispersing spores through spray inoculation. The spore concentration used for inoculation typically ranged from 10^4 to 10^5 spores per mL of spore suspension.

For *in-vitro* evaluation, the inoculum of the pathogen was multiplied on the susceptible oat plants grown in plastic pots under control conditions in the greenhouse at 23 ± 2°C. For evaluation of powdery mildew resistance, the plants of each genotype were raised in plastic pots and kept for two months in the greenhouse and then after inoculated with powdery mildew pathogen by dusting conidial inoculum on them by using a camel hair brush. These inoculated plants were kept in the greenhouse for incubation (22 ± 2°C and 66 ± 10% RH) and observations were recorded as percent area infected on the basis of visual observations.

***Statistical analysis*:** The data on powdery mildew severity was recorded using the 0-9 scale as per Mayee and Datar (1986) (Table 1). Estimation of the chi-square values was worked out with respect to the inheritance of powdery mildew disease for testing the goodness of fit.

Chi-Square test for goodness of fit:

$$\chi^2 = \sum(O_i-E_i)^2/E_i$$

Where: O_i = Observed frequency in the i^{th} category (e.g., number of resistant or non-resistant offspring); E_i = Expected frequency in the i^{th} category based on the hypothesis; For segregation analysis, the plants with score 0–3 were grouped as resistant and 5–9 were summarised as susceptible.

Results and Discussion

The data on genetic segregation in the different populations derived from different crosses involving resistant (JPO-46, Palampur-1, and KRR-AK-26) and susceptible (HJ-8) parents after evaluating under natural epiphytotic and artificial conditions were recorded (Tables 2 and 3).

***Nature of powdery mildew resistance in F_1 plants*:** The inheritance of resistance in F_1 plants provides insight into the genetic control of the trait, where complete

Table 1. Scale used to evaluate oat genotypes for disease reaction to powdery mildew

Grade	Level of resistance	Disease reaction
0	Highly resistant	No symptoms on the leaf
1	Resistant	Small specks of whitish-grey dots covering 1% or less of the leaf area
3	Moderately resistant	White powdery patches covering 1–10% of the leaf area
5	Moderately susceptible	Powdery patches big, covering 11–25% of the leaf area
7	Susceptible	Powdery patches big, covering 26–50% of the leaf area
9	Highly susceptible	Powdery patches big, coalescing to cover 51% or more of the leaf area

resistance in all F_1 individuals indicates dominance, while susceptibility suggests a recessive mode of inheritance requiring both parental alleles for expression. The resistant response observed in the F_1 plants of different cross combinations suggested that resistance to powdery mildew in oat genotypes JPO-46, Palampur-1, and KRR-AK-26, used as donor parents, is governed by a dominant gene. A total of 28, 30, and 35 F_1 plants from the crosses HJ-8 × JPO-46, HJ-8 × Palampur-1, and HJ-8 × KRR-AK-26, respectively, exhibited resistance to powdery mildew (Table 3). Hence, the observed resistance in F_1 plants indicated that at least one dominant allele from the resistant parent is sufficient to confer resistance, suggesting monogenic or oligogenic control of the trait. To further elucidate whether a monogenic or oligogenic inheritance pattern controls resistance, the segregation ratios in F_2 and backcross populations was analyzed in detail, providing insights into the number of genes governing powdery mildew resistance.

Inheritance of powdery mildew resistance in F_2 and backcross populations: To further investigate the inheritance of resistance, F_2 and backcross populations of the three crosses—HJ-8 × JPO-46, HJ-8 × Palampur-1, and HJ-8 × KRR-AK-26 were evaluated. F_2 seeds from each cross were sown under both field and greenhouse conditions to assess their response to powdery mildew. The observed data were categorized into discrete class frequencies and analyzed using the chi-square test to determine the goodness of fit for expected segregation ratios (Tables 2 and 3).

In the first cross, HJ-8 × JPO-46, the F_2s showed a segregation pattern of 3:1 ratio with the $\chi 2$ value of 1.744 based upon a chi-square test of goodness of fit. The cross HJ-8 × Palampur-1 also demonstrated a 3:1 ratio as the chi-square value obtained was 3.277 and similarly for HJ-8 × KRR-AK-26 with 0.653 chi-square value using a chi-square test of significance. Thus indicating that in the F_2 population resistant to susceptible ratio, fitted very closely to the 3:1 ratio for each cross under natural epiphytotic conditions. The results obtained under natural conditions could not be considered apt due to the chances of human error or the absence of one of the factors necessary for disease establishment or disease development. One set of the F_2 population of each cross (HJ-8 × JPO-46, HJ-8 × Palampur-1, and HJ-8 × KRR-AK-26) was subjected to phenotyping under artificial conditions in the greenhouse also exhibited almost similar segregation pattern with chi-square values of 0.532, 2.311 and 1.409 in all three cross combinations studied. Evaluation of F_2 segregation of each cross showed a close fit to a 3:1 (R: S) ratio with significant chi-square value both under field and greenhouse conditions, thus representing true genetic segregation. Also, the backcross combinations of each cross confirmed the dominant behavior of the resistance by showing a segregation pattern of 1:1 with chi-square values of 0.948, 0.750 and 0.381 for cross HJ-8 × JPO-46, HJ-8 × Palampur-1 and HJ-8 × KRR-AK-26, respectively under artificial conditions. Hence, studies on the inheritance of resistance in three lines, viz., JPO-46, Palampur-1 and KRR-AK-26, showed that resistance is governed by a single dominant gene against oat powdery mildew caused by *B. graminis* f. sp. *avenae.* A similar result was reported by Yu and Herrmann (2006) where genetic analysis of F_1, F_2, F_3 and BC_1 populations from two powdery-mildew resistant introgressed lines revealed that the resistance is controlled by a single dominant gene, tentatively designated Eg-5.

The use of resistant cultivars carrying effective genes against pathogens is generally accepted as the best alternative to control the most deleterious diseases like powdery mildew in oats. Development and use of resistant cultivars against powdery mildew should be a continuous process, as the virulence evolution of the pathogens is continuous and resistance breakdown is common. There are 13 major powdery mildew resistance genes that have been described in oats (Herrmann and Mohler, 2018; Hsam *et al.,* 2014; Ociepa *et al.* 2020; Okoń and Ociepa 2018; Ociepa & Okoń, 2022; Schurack *et al.,* 2024). Seven of these genes (pm1, pm3, pm6, pm8, pm9, pm 10, and pm13) originated from cultivated oat (*A. sativa*), while the remaining genes were introgressed from wild oat species, such as *A. hirtula* (pm2), *A. barbata* (pm4), *A. macrostachya* (pm5), *A. eriantha* (pm7), and *A. sterilis* (pm1, pm3, pm11 and pm12; Aung *et al.* 1977; Hsam *et al.* 2014; Ociepa *et al.* 2020). Some of these powdery mildew resistance genes have been utilized in oat breeding programs (Hsam *et al.* 2014). Some types of oat germplasm

Table 2. Inheritance of resistance to powdery mildew in F_2 population of different crosses of oat genotypes under natural epiphytotic conditions

Generation	Total number of plants	No. of plants				Expected Ratio (R:S)	χ^2 value	*p-value*
		Resistant		Susceptible				
		Observed	Expected	Observed	Expected			
HJ-8 × JPO-46 (F_2)	195	138	146	57	49	3:1	1.744	3.841
HJ-8 × Palampur-1 (F_2)	418	298	314	120	104	3:1	3.277	3.841
HJ-8 × KRR-AK-26 (F_2)	204	148	153	56	51	3:1	0.653	3.841

Table 3. Inheritance of resistance to powdery mildew in parents, F_1, F_2 and BC_1 generations of different crosses of oat genotypes under laboratory conditions

Generation	Total number of plants	No. of plants				Expected Ratio (R:S)	χ^2 value	*p-value*
		Resistant		Susceptible				
		Observed	Expected	Observed	Expected			
JPO-46	20	20	20	0	0	-	-	
Palampur-1	25	25	25	0	0	-	-	
KRR-AK-26	20	20	20	0	0	-	-	
HJ-8	22	0	0	22	22	-	-	
HJ-8 × JPO-46 (F_1)	28	28	28	0	0	-	-	
HJ-8 × Palampur-1 (F_1)	30	30	30	0	0	-	-	
HJ-8 × KRR-AK-26 (F_1)	35	35	35	0	0	-	-	
HJ-8 × JPO-46 (F_2)	161	117	121	44	40	3:1	0.532	3.841
HJ-8 × Palampur-1 (F_2)	152	106	114	46	38	3:1	2.311	3.841
HJ-8 × KRR-AK-26 (F_2)	136	108	102	28	34	3:1	1.409	3.841
HJ-8 × JPO-46 (BC_1)	38	22	19	16	19	1:1	0.948	3.841
HJ-8 × Palampur-1 (BC_1)	48	27	24	21	24	1:1	0.750	3.841
HJ-8 × KRR-AK-26 (BC_1)	42	23	21	19	21	1:1	0.381	3.841

exist that are resistant to powdery mildew, but they are not well characterized in terms of genetic control. The three lines evaluated under diverse agroecological conditions of Himachal Pradesh provided evidence for the presence of resistant genes in cultivated oat (*Avena sativa*) germplasm. A valuable source of resistance can only be utilized in a breeding program after determining whether this resistance is controlled by a new single gene or a combination of several genes (Okon 2015). However, given the continuous evolution of pathogen virulence, breeding programs must focus on identifying and incorporating durable resistance genes. The three resistant genotypes evaluated in this study provide a valuable genetic resource for developing improved oat varieties. Further molecular characterization is necessary to determine whether the identified resistance is governed by a novel gene or a combination of known resistance loci, ensuring effective utilization in future breeding programs. Therefore, these lines can be further utilized as a source of resistance for breeding resistant varieties against oat powdery mildew.

Conclusion

To study the genetics of powdery mildew resistance, three parents (JPO-46, Palampur-1 and KRR-AK-26) were categorized as resistant, while HJ-8 was highly susceptible. The segregation pattern obtained in F_2 and back cross generation BC_1 of the three crosses indicated that a single dominant gene controls powdery mildew in oats. Hence, these lines can be utilized in future oat breeding programs to develop resistance against powdery mildew.

Acknowledgment

The authors are grateful to the Department of Science and Technology, Government of India, for financial support to carry out this work.

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