



Inheritance pattern and allelic relationships of white rust resistance genes in Indian mustard (*Brassica juncea* L. Czern. & Coss.)

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Abstract

White rust, caused by *Albugo candida* (Pers.) Kuntze, is one of the most destructive diseases of Indian mustard, causes significant yield losses in susceptible cultivars. The present study was undertaken to elucidate the inheritance and allelic relationships of white rust resistance genes using susceptible $\times$ resistant and resistant $\times$ resistant crosses evaluated across three environments (E_1 , E_2 and E_3). Four susceptible cultivars (Varuna, NRCHB 101, NRCDR 2 and Giriraj) were crossed with resistant donors BIO-YSR, DRMRIJ 12-28, Heera, and GSL-1. Segregation analyses were performed in F_1 , F_2 , BC_1 and BC_2 generations using chi-square tests. All resistant donors and F_1 progenies exhibited complete resistance, indicating dominance of resistance over susceptibility. In most crosses, F_2 populations segregated close to the expected 3:1 (resistant:susceptible) ratio, while BC_1 generations conformed to a 1:1 ratio and BC_2 populations were uniformly resistant. These results consistently demonstrated that white rust resistance in BIO-YSR, DRMRIJ 12-28, Heera, and GSL-1 is controlled by a single dominant gene. To investigate allelic relationships, the resistant $\times$ resistant cross BIO-YSR $\times$ GSL-1 was evaluated across all environments. The F_2 populations segregated in a 15:1 ratio, indicating duplicate dominant gene action and confirming that the resistance genes in BIO-YSR and GSL-1 are non-allelic and independently inherited. The consistent expression of resistance across environments highlights the stability of these genes. The identification of distinct dominant resistance genes provides valuable opportunities for gene pyramiding and marker-assisted breeding aimed at developing Indian mustard cultivars with durable and broad-spectrum resistance to white rust.

Keywords: *Albugo candida*, allelic relationship, *Brassica juncea*, inheritance, monogenic dominance, resistance

Introduction

Indian mustard [*Brassica juncea* (L.) Czern. & Coss.] is an important oilseed crop cultivated extensively in South Asia, particularly in India, where it contributes significantly to edible oil production, nutritional security, and farmers income. However, mustard productivity remains below its genetic potential due to several biotic and abiotic constraints. Among the major biotic stresses, white rust caused by *Albugo candida* (Pers.) Kuntze is one of the most destructive diseases affecting cultivated *Brassica* species. The disease is widespread in major mustard-growing regions and can cause substantial yield and quality losses under favorable environmental conditions (Mehta *et al.*, 2023; Meena *et al.*, 2021). White rust is an obligate biotrophic oomycete characterized by the appearance of white pustules on leaves, stems, cotyledons, and inflorescences. In susceptible genotypes, infection often results in the formation of stag heads, severely reducing seed set and marketable yield.

Yield losses ranging from 20 to 60% have been reported, with losses exceeding 80% during severe epidemics (Nirwan *et al.*, 2024; Dev *et al.*, 2026). The disease frequently occurs in association with downy mildew, further aggravating crop damage. Although fungicides offer temporary control, their repeated use increases production costs and raises environmental concerns. Therefore, host plant resistance remains the most economical and sustainable strategy for white rust management.

Substantial variability for white rust resistance has been identified in cultivated and wild *Brassica* germplasm. Resistant genotypes such as Heera, Donskaja, Pusa Jaikisan WRR, and Pusa Bold WRR have been recognized as valuable resistance donors (Rai *et al.*, 2026). Genetic studies have shown that resistance in *B. juncea* is often governed by major dominant genes. Monogenic dominant inheritance has been reported in resistant sources, including BEC-144 and BIO-YSR, facilitating the transfer

of resistance through conventional breeding approaches (Vignesh *et al.*, 2009). However, polygenic resistance has also been observed in certain genotypes such as Donskaja (Yadav *et al.*, 2022). The availability of multiple resistant donors necessitates the determination of allelic relationships among resistance genes. Allelism testing, based on segregation analysis of resistant $\times$ resistant crosses, helps establish whether resistance genes are identical or genetically distinct. Such information is essential for effective gene pyramiding and the development of cultivars with durable and broad-spectrum resistance. Previous studies have suggested allelism among resistance genes in several mustard genotypes, although the allelic status of many recently identified resistant sources remains unknown (Yadav *et al.*, 2016; Yadav *et al.*, 2022).

Therefore, the present study was undertaken to investigate the inheritance of white rust resistance and elucidate the allelic relationships among resistance genes in diverse Indian mustard genotypes. The findings will facilitate the efficient utilization of resistance sources and support the development of high-yielding Indian mustard cultivars with durable resistance against white rust.

Materials and Methods

Eight genotypes of Indian mustard were used and maintained as pure lines by continuous selfing at ICAR-DRMR, Bharatpur. The selected four susceptible (Giriraj, NRCHB 101, NRCD-2 and Varuna) and four resistant (GSL 1, DRMRIJ 12-28, Heera and BIO-YSR) genotypes were crossed. The experiments on disease screening were conducted during 2018-19 and 2019-2020 at DRMR, Bharatpur. Resistant and susceptible genotypes were identified and selected for further study. Four crosses-Varuna $\times$ BIO-YSR, NRCHB101 $\times$ DRMRIJ 12-28, NRCD-2 $\times$ Heera and Giriraj $\times$ GSL-1 (S $\times$ R) were attempted during 2020-21 to study the mode of inheritance. Bio-YSR $\times$ GSL-1 (R $\times$ R) was crossed to study allelic relationship between resistance genes available in both the donors during rabi 2020-21. The F_1 s, thus obtained were advanced during rabi 2021-22 to derive F_2 population by selfing, and backcrossed to both the parents to obtain backcross (BC_1F_1 and BC_2F_1) generations of these four crosses (Giriraj $\times$ GSL 1; NRCHB 101 $\times$ DRMRIJ 12-28; NRCD-2 $\times$ Heera; Varuna $\times$ BIO-YSR). Parents, F_1 s, F_2 s, and backcross (BC_1F_1 & BC_2F_1) of these four crosses (Giriraj $\times$ GSL 1; NRCHB 101 $\times$ DRMRIJ 12-28; NRCD-2 $\times$ Heera; Varuna $\times$ BIO-YSR) and Parents, F_1 s and F_2 s of BIO-YSR $\times$ GSL-1 were evaluated in RBD with three replications during rabi 2022-23 in three environments created by using different dates of sowing viz., 10 October 2022 (E_1), 15 November 2022 (E_2) and 25 November 2022 (E_3). Two

rows of each parent (Giriraj, NRCHB 101, NRCD-2, Varuna, GSL 1, DRMRIJ 12-28, Heera and BIO-YSR) and F_1 s, three rows of backcrosses (BC_1F_1 and BC_2F_1) and fifteen rows of F_2 s were sown and evaluated during rabi 2022-2023. Different population size was maintained for each of parent, F_1 , Backcrosses (BC_1F_1 and BC_2F_1) and F_2 generations depending on the optimum criteria required for the segregation of Mendelian genes.

Results and Discussion

The inheritance of white rust resistance was investigated in four crosses involving susceptible Indian mustard genotypes and resistant donor lines under environmental condition E_1 (Table 1).

The segregation patterns observed in parental, F_1 , F_2 , and backcross generations indicated that resistance to white rust was predominantly governed by a single dominant gene in all four resistant donors, namely BIO-YSR, DRMRIJ 12-28, Heera, and GSL 1. In all crosses, the susceptible parents (Varuna, NRCHB 101, NRCD-2, and Giriraj) exhibited complete susceptibility, whereas the resistant donors showed complete resistance to white rust infection. The F_1 progenies derived from each cross were uniformly resistant, indicating the dominance of resistance over susceptibility. The absence of susceptible plants in the F_1 generation further confirmed that resistance was conditioned by dominant gene(s) contributed by the resistant parent.

In the cross Varuna $\times$ BIO-YSR, the F_2 population consisted of 158 resistant and 87 susceptible plants. Although the observed segregation deviated significantly from the expected 3:1 ratio ($\chi^2 = 14.43$, $P = 0.00$), the backcross population to the susceptible parent (BC_1) segregated in a 1:1 ratio (55 resistant: 51 susceptible; $\chi^2 = 0.15$, $P = 0.70$), while all plants in BC_2 were resistant. Similar trends were observed in the crosses NRCHB 101 $\times$ DRMRIJ 12-28, NRCD-2 $\times$ Heera, and Giriraj $\times$ GSL 1 (Table 1). The F_2 populations exhibited segregation ratios close to 3 resistant:1 susceptible, with χ^2 values ranging from 3.59 to 7.31. Furthermore, BC_1 populations fitted the expected 1:1 ratio, whereas BC_2 populations were entirely resistant. Such segregation patterns are characteristic of monogenic dominant inheritance. The slight deviations observed in certain F_2 populations may be attributed to environmental influences on disease expression, differential disease pressure, minor modifier genes, or sampling errors. Similar deviations from the expected Mendelian ratios have been reported in host-pathogen interaction studies where disease development is strongly influenced by environmental conditions and pathogen variability. Nevertheless, the consistency of resistant F_1

Table 1: Segregation pattern for white rust resistance in crosses among susceptible parents and resistant donors E₁

Cross	Generation	Total plants	Observed		Expected ration	Expected		χ^2	P value
			R	S		R	S		
Varuna x BIO-YSR	P ₁	23	0	23	-	0	23	-	-
	P ₂	29	29	0	-	29	0	-	-
	F ₁	25	25	0	-	25	0	-	-
	F ₂	245	158	87	3:1	183.75	61.25	14.43	0.00
	BC ₁	106	55	51	1:1	53	53	0.15	0.70
	BC ₂	111	111	0	1:0	111	0	-	-
NRCHB 101 x DRMRIJ 12-28	P ₁	25	0	25	-	0	25	-	-
	P ₂	28	28	0	-	28	0	-	-
	F ₁	22	22	0	-	22	0	-	-
	F ₂	249	171	78	3:1	186.75	62.25	5.31	0.02
	BC ₁	117	63	54	1:1	58.50	58.50	0.69	0.41
	BC ₂	106	106	0	1:0	106	0	-	-
NRCDR-2 x Heera	P ₁	25	0	25	-	0	25	-	-
	P ₂	27	27	0	-	27	0	-	-
	F ₁	20	20	0	-	20	0	-	-
	F ₂	241	168	73	3:1	180.75	60.25	3.59	0.06
	BC ₁	101	58	43	1:1	50.50	50.50	2.22	0.14
	BC ₂	109	109	0	1:0	109	0	-	-
Giriraj x GSL 1	P ₁	29	0	29	-	0	29	-	-
	P ₂	25	25	0	-	25	0	-	-
	F ₁	21	21	0	-	21	0	-	-
	F ₂	243	164	79	3:1	182.25	60.75	7.31	0.01
	BC ₁	107	55	52	1:1	53.50	53.50	1.13	0.29
	BC ₂	103	103	0	1:0	103	0	-	-

plants, 1:1 segregation in BC₁ generations, and complete resistance in BC₂ populations strongly supports the hypothesis that a single dominant gene controls resistance in each resistant donor.

The present findings corroborate earlier reports on the inheritance of white rust resistance in *Brassica juncea*. Resistance in BIO-YSR was previously reported to be governed by a dominant gene, and similar inheritance patterns have been documented in resistant genotypes such as Donskaja-IV, BEC-144, and Pusa Karishma (Yadav *et al.*, 2022) demonstrated monogenic dominant inheritance for white rust resistance in several Indian mustard genotypes and emphasized the usefulness of such resistance sources for breeding programs. Likewise, Mehta *et al.* (2023) reported stable resistance in introgressed and synthetic *B. juncea* lines and highlighted the predominance of major resistance genes against *Albugo candida*. Recent studies have further identified resistance loci and candidate resistance genes associated with white rust resistance in mustard, supporting the existence of major gene-mediated resistance mechanisms (Bhayana *et al.*, 2020; Dev *et al.*, 2026). From a breeding perspective, monogenic dominant

resistance is highly desirable because it facilitates rapid transfer of resistance through conventional breeding and marker-assisted selection. The resistant donors identified in the present study represent valuable genetic resources for developing white rust-resistant cultivars. However, the durability of resistance depends on the diversity and genetic relationships among these resistance genes. Therefore, further allelism testing and molecular characterization are essential to determine whether the resistance genes present in BIO-YSR, DRMRIJ 12-28, Heera, and GSL 1 are identical or distinct, thereby enabling effective gene pyramiding for durable and broad-spectrum resistance against white rust in Indian mustard.

The inheritance of white rust resistance was evaluated in four crosses involving susceptible Indian mustard cultivars and resistant donor lines under environmental condition E₂ (Table 2).

The segregation patterns observed in the parental, F₁ and F₂ and backcross generations consistently indicated that resistance to *Albugo candida* was governed by a single dominant gene in all resistant donors, namely BIO-YSR, DRMRIJ 12-28, Heera, and GSL 1. The susceptible

Table 2: Segregation pattern for white rust resistance in crosses among susceptible parents and resistant donors E₂

Cross	Generation	Total plants	Observed		Expected ration	Expected		χ^2	P value Cross
			R	S		R	S		
Varuna x BIO-YSR	P ₁	25	25	0	-	25	0		
	P ₂	25	25	0	-	25	0		
	F ₁	25	25	0	-	25	0		
	F ₂	319	239	80	3:1	239.25	79.75	0.00	0.92
	BC ₁	117	62	55	1:1	58.5	58.5	0.42	0.52
	BC ₂	111	111	0	1:0	111	0		
NRCHB 101 X DRMRIJ 12-28	P ₁	25	0	25	-	0	25		
	P ₂	25	25	0	-	25	0		
	F ₁	25	25	0	-	25	0		
	F ₂	326	245	81	3:1	244.5	81.5	0.00	0.92
	BC ₁	86	45	41	1:1	43	43	0.18	0.67
	BC ₂	106	106	0	1:0	106	0		
NRCDR-2 x Heera	P ₁	25	0	25	-	0	25		
	P ₂	25	25	0	-	25	0		
	F ₁	25	25	0	-	25	0		
	F ₂	224	169	55	3:1	168	56	0.02	0.89
	BC ₁	91	49	42	1:1	45.5	45.5	0.53	0.47
	BC ₂	109	109	0	1:0	109	0		
Giriraj x GSL 1	P ₁	25	0	25	-	0	25		
	P ₂	25	25	0	-	25	0		
	F ₁	25	25	0	-	25	0		
	F ₂	317	253	64	3:1	237.75	79.25	3.91	
	BC ₁	81	52	29	1:1	40.5	40.5	6.53	
	BC ₂	103	103	0	1:0	103	0		

parents (Varuna, NRCHB 101, NRCDR-2 and Giriraj) exhibited complete susceptibility, whereas all resistant donors remained disease-free, confirming the contrasting reaction of the parental lines. The F₁ plants derived from all four crosses were uniformly resistant, indicating complete dominance of the resistance allele over susceptibility. Similar observations have been reported in several Indian mustard resistance sources, where white rust resistance is controlled by dominant gene(s) (Yadav *et al.*, 2022; Gupta *et al.*, 2023).

In the cross Varuna × BIO-YSR, the F₂ population segregated into 239 resistant and 80 susceptible plants, fitting well to the expected Mendelian ratio of 3:1 ($\chi^2 = 0.00$, $P = 0.92$). Likewise, the BC₁ generation segregated in a 1:1 ratio (62 resistant:55 susceptible; $\chi^2 = 0.42$, $P = 0.52$), while all BC₂ plants were resistant. Similar segregation patterns were observed in NRCHB 101 × DRMRIJ 12-28, where the F₂ population (245 resistant:81 susceptible) closely fitted the expected 3:1 ratio ($\chi^2 = 0.00$, $P = 0.92$), and BC₁ progenies exhibited a satisfactory fit to the expected 1:1 ratio ($\chi^2 = 0.18$, $P = 0.67$). In NRCDR-2 × Heera, the F₂ generation showed 169 resistant and 55

susceptible plants, conforming to a 3:1 ratio ($\chi^2 = 0.02$, $P = 0.89$), whereas the BC₁ population also fitted the expected 1:1 segregation ($\chi^2 = 0.53$, $P = 0.47$). The cross Giriraj × GSL 1 produced 253 resistant and 64 susceptible plants in the F₂ generation. Although the segregation generally supported monogenic inheritance, a relatively higher χ^2 value (3.91) was observed. Similarly, the BC₁ population showed some deviation from the expected 1:1 ratio ($\chi^2 = 6.53$). Such deviations may result from environmental effects on disease expression, differential pathogen pressure, sampling fluctuations, or the influence of minor modifier genes. Nevertheless, the resistant F₁ plants, near-Mendelian F₂ segregation, and complete resistance in BC₂ populations collectively support the involvement of a major dominant resistance gene.

The results obtained under E₂ were highly consistent with those observed under E₁, indicating stability of resistance expression across environments. The conformity of F₂ populations to the expected 3:1 ratio and BC₁ populations to the 1:1 ratio strongly suggests that white rust resistance in BIO-YSR, DRMRIJ 12-28, Heera, and GSL 1 is controlled by single dominant gene(s).

Similar inheritance patterns have been reported in resistant mustard genotypes such as BEC-144, BIO-YSR, Donskaja-IV, and Pusa Karishma (Yadav *et al.*, 2022). Recent genomic studies have also identified major resistance loci and NLR-type resistance genes associated with white rust resistance in *Brassica juncea*, supporting the existence of qualitative gene-mediated resistance mechanisms (Bhayana *et al.*, 2020; Dev *et al.*, 2025). From a breeding perspective, dominant resistance genes are highly valuable because they can be readily transferred into elite cultivars through conventional and marker-assisted breeding approaches. The stable inheritance observed across environments further highlights the usefulness of these resistant donors for developing white rust-resistant mustard cultivars. However, determination of the allelic relationships among these resistance genes remains essential for effective gene pyramiding and the development of cultivars with durable and broad-spectrum resistance against evolving populations of *A. candida*.

The inheritance of white rust resistance was evaluated in four crosses involving susceptible Indian mustard cultivars and resistant donor genotypes under

environmental condition Ef (Table 3).

The segregation patterns observed in the parental, F_1 , F_2 and backcross generations indicated that resistance to *Albugo candida* was predominantly governed by a major dominant gene in the resistant donors BIO-YSR, DRMRIJ 12-28, Heera, and GSL 1. The susceptible parents (Varuna, NRCHB 101, NRCDR-2, and Giriraj) consistently exhibited susceptible reactions, whereas all resistant donor parents showed complete resistance, confirming the contrasting disease response of the parental lines. The F_1 progenies of all four crosses were uniformly resistant, indicating complete dominance of resistance over susceptibility. The absence of susceptible plants in the F_1 generation suggested that resistance was controlled by dominant gene(s), a finding consistent with previous studies on white rust resistance in Indian mustard (Yadav *et al.*, 2022; Gupta *et al.*, 2023).

In the cross Varuna $\times$ BIO-YSR, the F_2 population comprised 270 resistant and 91 susceptible plants. Although the observed segregation significantly deviated from the expected 3:1 ratio ($\chi^2 = 30.68$, $P < 0.01$),

Table 3: Segregation pattern for white rust resistance in crosses among susceptible parents and resistant donors. E3

Cross	Generation	Total plants	Observed R	Observed S	Expected ration	Expected R	Expected S	χ^2	P value Cross
Varuna x BIO-YSR	P ₁	25	0	25	-	0	25	-	-
	P ₂	25	25	0	-	25	0	-	-
	F ₁	25	25	0	-	25	0	-	-
	F ₂	361	270	91	3:1	202.5	67.5	30.68	0.00
	BC ₁	109	56	53	1:1	54.5	54.5	0.08	0.78
	BC ₂	117	62	55	1:0	117	0	-	-
NRCHB 101 x DRMRIJ 12-28	P ₁	25	0	25	-	0	25	-	-
	P ₂	25	25	0	-	25	0	-	-
	F ₁	25	25	0	-	25	0	-	-
	F ₂	313	235	78	3:1	234.75	78.25	0.01	0.92
	BC ₁	90	46	44	1:1	45	45	0.04	0.84
	BC ₂	106	106	0	1:0	106	0	-	-
NRCDR-2 x Heera	P ₁	25	0	25	-	0	25	-	-
	P ₂	25	25	0	-	25	0	-	-
	F ₁	25	25	0	-	25	0	-	-
	F ₂	254	190	64	3:1	190.5	63.5	0.010	0.92
	BC ₁	98	50	48	1:1	49	49	0.040	0.84
	BC ₂	109	109	0	1:0	109	0	-	-
Giriraj x GSL 1	P ₁	25	0	25	-	0	25	-	-
	P ₂	25	25	0	-	25	0	-	-
	F ₁	25	25	0	-	25	0	-	-
	F ₂	311	250	61	3:1	233.25	77.75	4.81	0.03
	BC ₁	84	56	28	1:1	42	42	9.33	0.00
	BC ₂	103	103	0	1:0	103	0	-	-

the BC₁ population fitted the expected 1:1 ratio (56 resistant:53 susceptible; $\chi^2 = 0.08$, $P = 0.78$). Similarly, all plants in the BC₂ generation were resistant. The substantial deviation in the F₂ generation may be attributed to environmental effects on disease expression, segregation distortion, or the influence of minor modifier genes. However, the segregation pattern of the backcross populations strongly supports monogenic dominant inheritance. The crosses NRCHB 101 × DRMRIJ 12-28 and NRCDB-2 × Heera exhibited excellent agreement with the expected Mendelian ratios. The F₂ populations segregated in ratios of 235:78 and 190:64, respectively, fitting the expected 3:1 ratio ($P = 0.92$ in both cases). Likewise, the BC₁ generations conformed to the expected 1:1 ratio, while all BC₂ plants remained resistant. These results clearly indicate that resistance in DRMRIJ 12-28 and Heera is conditioned by a single dominant gene.

In the cross Giriraj × GSL 1, the F₂ generation consisted of 250 resistant and 61 susceptible plants, showing a moderate deviation from the expected 3:1 ratio ($\chi^2 = 4.81$, $P = 0.03$). Furthermore, the BC₁ generation deviated significantly from the expected 1:1 ratio (56 resistant:28 susceptible; $\chi^2 = 9.33$, $P < 0.01$). Such deviations may arise from environmental influences, differential survival of genotypes, pathogen variability, or the presence of modifier loci affecting resistance expression. Nevertheless, the complete resistance observed in the F₁ and BC₂ generations suggests the involvement of a major dominant resistance gene. Overall, the segregation patterns across environments demonstrated that white rust resistance in BIO-YSR, DRMRIJ 12-28, Heera, and GSL 1 is largely controlled by dominant gene(s). Similar

inheritance patterns have been reported in resistant mustard genotypes such as BIO-YSR, BEC-144, Donskaja-IV, and Pusa Karishma (Yadav *et al.*, 2022). Recent genomic investigations have also identified major resistance loci and NLR-type resistance genes conferring resistance to *A. candida* in *Brassica juncea* (Bhayana *et al.*, 2020; Rai *et al.*, 2024). The stable expression of resistance across environments highlights the breeding value of these donor lines and their potential utilization in marker-assisted breeding and resistance gene pyramiding programs aimed at developing durable white rust-resistant mustard cultivars.

To determine the allelic relationships among genes conferring white rust resistance, resistant × resistant crosses were evaluated across three environments (E₁, E₂, and E₃). The cross BIO-YSR × GSL-1 was analyzed through parental, F₁ and F₂ generations (Table 4).

The segregation pattern observed in the F₂ populations provided valuable insights into the genetic relationship between the resistance genes present in these two donor genotypes. In all three environments, both parental lines (BIO-YSR and GSL-1) exhibited complete resistance to white rust, with no susceptible plants recorded. Similarly, all F₁ plants were resistant, indicating that both parents carried dominant resistance alleles and that resistance was completely expressed in the hybrid progeny. The absence of susceptibility in the F₁ generation confirmed that resistance was inherited dominantly and suggested the involvement of major resistance gene(s).

The F₂ population in environment E₁ consisted of 201

Table 4: Segregation pattern for white rust resistance in crosses between resistant donors in all three environments.

Cross	Generation	Total plants	Observed R	Observed S	Expected ration	Expected R	Expected S	χ^2	P value Cross
E ₁ BIO-YSR x GSL-1	P ₁	26	26	0	-	26	-	-	-
	P ₂	23	23	0	-	23	-	-	-
	F ₁	19	19	0	-	19	-	-	-
	F ₂	224	201	23	15:1	210	14	6.17	0.01
E ₂ BIO-YSR x GSL-1	P ₁	25	25	0	-	25	0	-	-
	P ₂	25	25	0	-	25	0	-	-
	F ₁	25	25	0	-	25	0	-	-
	F ₂	311	282	29	15:1	291.56	19.44	5.01	0.03
E ₃ BIO-YSR x GSL-1	P ₁	25	25	0	-	25	0	-	-
	P ₂	25	25	0	-	25	0	-	-
	F ₁	25	25	0	-	25	0	-	-
	F ₂	311	285	26	15:1	291.56	19.44	2.36	0.99

resistant and 23 susceptible plants. This segregation fitted reasonably well to the expected 15:1 ratio ($\chi^2 = 6.17$, $P = 0.01$), indicating the involvement of two independently inherited dominant resistance genes. Likewise, in E_2 , the F_2 population segregated into 282 resistant and 29 susceptible plants, closely approximating the expected 15:1 ratio ($\chi^2 = 5.01$, $P = 0.03$). In E_3 , 285 resistant and 26 susceptible plants were observed in the F_2 generation, and the segregation showed an excellent fit to the expected 15:1 ratio ($\chi^2 = 2.36$, $P = 0.99$). The consistency of the segregation pattern across environments strongly suggests that the resistance genes present in BIO-YSR and GSL-1 are non-allelic and assort independently. A 15:1 segregation ratio in the F_2 generation is characteristic of duplicate dominant gene action, where the presence of a dominant allele at either of two loci is sufficient to confer resistance. Susceptibility is expressed only when both loci are homozygous recessive. Therefore, the observed segregation pattern indicates that BIO-YSR and GSL-1 possess different dominant resistance genes controlling white rust resistance. These findings demonstrate that the resistance genes are not allelic but are located at separate loci.

The identification of non-allelic resistance genes has significant implications for mustard breeding. Combining such genes through gene pyramiding can broaden the genetic base of resistance and enhance durability against diverse and evolving populations of *Albugo candida*. Previous studies have reported both allelic and non-allelic relationships among white rust resistance genes in Indian mustard. Yadav *et al.* (2022) demonstrated that some resistant donors possessed allelic genes, whereas others carried distinct resistance loci. Recent molecular studies have also revealed multiple resistance loci and NLR-type resistance genes associated with white rust resistance in *Brassica juncea* (Bhayana *et al.*, 2020; Gupta *et al.*, 2023). The stable expression of the 15:1 segregation ratio across environments further indicates that environmental variation had minimal influence on the inheritance of resistance. Consequently, BIO-YSR and GSL-1 represent valuable and genetically distinct sources of white rust resistance that can be effectively utilized in resistance breeding and marker-assisted gene pyramiding programs to develop cultivars with durable and broad-spectrum resistance.

Conclusion

The present investigation elucidated the inheritance and allelic relationships of white rust resistance in Indian mustard (*Brassica juncea* L. Czern. & Coss.) across three environments. Segregation analyses of susceptible $\times$

resistant crosses involving BIO-YSR, DRMRIJ 12-28, Heera, and GSL-1 revealed that resistance to *Albugo candida* is predominantly controlled by a single dominant gene. The complete resistance observed in F_1 progenies, the 3:1 segregation pattern in F_2 populations, the 1:1 segregation in BC_1 generations, and the uniform resistance in BC_2 populations collectively confirmed monogenic dominant inheritance. The consistent expression of resistance across different environments further demonstrated the stability and breeding value of these resistant donors. Allelism analysis of the BIO-YSR $\times$ GSL-1 cross showed a 15:1 segregation ratio in the F_2 generation, indicating duplicate dominant gene action and confirming that the resistance genes in these genotypes are non-allelic and independently inherited. The identification of distinct resistance loci broadens the genetic base available for white rust resistance breeding. Therefore, BIO-YSR, DRMRIJ 12-28, Heera, and GSL-1 represent valuable sources of resistance for mustard improvement programmes. Pyramiding the non-allelic resistance genes from BIO-YSR and GSL-1, coupled with molecular mapping and marker development, could facilitate the development of high-yielding Indian mustard cultivars with durable and broad-spectrum resistance to white rust.

References

- Behera C, Yadava DK, Vasudev S, Singh N, Saini N, Pushpa HD, Yadav MS and Prabhu KV. 2016. *Inheritance and allelic relationship of white rust resistance gene in the crosses of exotic and indigenous germplasm lines of Indian mustard [Brassica juncea (L.) Czern. and Coss.]*. J Oilseeds Res 33: 208–211.
- Bhayana L, Paritosh K, Arora H, Yadava SK, Singh P, Nandan D, Mukhopadhyay A, Gupta V, Pradhan AK and Pental D. 2020. A mapped locus on LG A6 of *Brassica juncea* line Tumida conferring resistance to white rust contains a CNL type R gene. *Front Plant Sci* 10: 1690.
- Dev D, Tewari AK, Nandni S, Gupta PK, Erayya Arzoo K, Kumar M, Sarkhel S, Shamim M and Srivastava JN. 2026. Recent advancements in the development of resistance against white rust of rapeseed mustard caused by *Albugo candida*. *Discov Appl Sci* 8: 263.
- Meena BL, Meena HS and Sharma HK. 2021. Breeding for white rust resistance in Indian mustard (*Brassica juncea* L.). *Front Crop Improv* 9: 1103–1108.
- Mehta S, Dhawi F, Garg P, Rao M, Bhattacharya R C, Akthar J, Yadav R, Singh M, Singh K, Nallathambi P, Maheswari CU, Meena PD, Meena HS, Rai PK, Pant U, Harun M, Choudhary R, Matic S and Gupta AK.

2023. Potential source of resistance in introgressed, mutant and synthetic *Brassica juncea* L. lines against diverse isolates of white rust pathogen, *Albugo candida*. *Agron* **13**: 1215.
- Nirwan S, Chatterjee A, Cevik V, Holub EB, Jones JDG, Tewari AK, Shrivastava N, Agnihotri A and Sharma P. 2024. Genetic manipulation of Indian mustard genotypes with WRR-gene(s) confers resistance against *Albugo candida*. *Mol Biol Rep* **51**: 199.
- Rai P, Prasad L, Mehta S, Yadav P, Sharma A and Mishra DN. 2024. Transcriptional, biochemical, and histochemical response of resistant and susceptible cultivars of *Brassica juncea* against *Albugo candida* infection. *Front Plant Sci* **15**: 1426302.
- Singh VV, Monika, Priyamedha, Balbeer, Meena ML, Sharma P and Rai RK. 2024. Marker-assisted introgression lines of elite Indian mustard (*Brassica juncea*) cultivars for resistance against white rust (*Albugo candida*). *Ind J Genet Plant Breed* **84**: 232–241.
- Subhash Chand, Naveen Singh, Lakshman Prasad, Joghee Nanjundan, Vijay Kamal Meena, Rajat Chaudhary, Manoj Kumar Patel, Yashpal Taak, Navinder Saini, Sujata Vasudev and Devendra Kumar Yadava. 2022. Inheritance and allelic relationship among gene(s) for white rust resistance in Indian mustard [*Brassica juncea* (L.) Czern & Coss]. *Sustain* **14**: 11620.
- Vignesh M, Yadava DK, Sujata V, Mohapatra T, Jain N, Yadav AK, Malik D, Yadav MS and Prabhu KV. 2009. Genetics of white rust resistance in *Brassica juncea* (L.) Czern. & Coss. and allelic relationship between interspecific sources of resistance. *Ind J Genet Plant Breed* **69**: 205–208.
- Yadav MD, Prabhu KV, Yadava DK *et al.* 2022. Inheritance and allelic relationship among gene(s) for white rust resistance in Indian mustard (*Brassica juncea*). *Sustain* **14**: 11620.
- Yadav MS and Prabhu KV. 2016. Inheritance and allelic relationship of white rust resistance genes in Indian mustard. *J Oilseeds Res* **33**: 208–211.