

Identification of high-yielding and stable resistance donors for yellow mosaic disease in blackgram (*Vigna mungo* L. Hepper)

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Abstract: Yellow mosaic disease (YMD) in blackgram (*Vigna mungo* L. Hepper) is caused by whitefly-transmitted begomoviruses, particularly *Mungbean yellow mosaic virus* (MYMV) and *Mungbean yellow mosaic India virus* (MYMIV), which cause substantial economic losses across South and Southeast Asia. Exploitation of host plant resistance to develop resistant cultivars remains the most effective, economically feasible and sustainable management strategy. In northern India, MYMIV is a major viral disease affecting blackgram crop. The investigations were carried out to identify potential donors carrying genes imparting resistance against MYMIV-associated YMD in blackgram through large-scale field-based phenotyping using a standardised 1–9 disease rating scale. A diverse panel of 216 blackgram genotypes comprising released varieties, advanced breeding and experimental lines were evaluated under natural epiphytotic conditions at a MYMIV hotspot (Jhansi, India) during Kharif 2023 and Kharif 2024. Disease severity was recorded at the pod-filling stage, and the percent disease index (PDI) was calculated to classify genotypes into various disease reaction levels. Out of 216 genotypes, 51 genotypes were classified as resistant (PDI < 5%), 81 as moderately resistant (PDI = 5–10%), 58 as moderately susceptible, 25 as susceptible and only one accession as highly susceptible. Presence of the MYMIV-specific amplicon in plants exhibiting YMD symptoms confirmed MYMIV infection at the molecular level and complemented the PDI-based resistance classification. A highly significant negative correlation ($r = -0.88^{***}$) was observed between PDI and SYPP, indicating that MYMIV-associated YMD severity accounts for approximately 77% of yield variation. Several released varieties, such as IC-236718, IPU-2K-99-221, KU-302 and elite breeding lines RLBU-L1-33 and RLBU-L2-15, showed stable resistance across both Kharif 2023/24 seasons. These genotypes may represent useful allelic diversity for MYMIV-associated YMD resistance and can serve as potential donors in future breeding programmes aimed at developing high-yielding, YMD-resistant blackgram varieties.

Keywords: begomovirus; disease resistance; donor identification; field phenotyping; *Mungbean yellow mosaic India virus* (MYMIV); urdbean

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Blackgram (*Vigna mungo* L. Hepper) is an important short-duration grain legume widely cultivated in the Indian subcontinent and Southeast Asia. It serves as a major source of dietary protein and contributes to sustainable agriculture through biological nitrogen fixation. During the year 2023 to 2024, blackgram was grown in 3.53 million hectares area with a total production of 2.31 million tonnes with an average productivity of 656 kg/ha in India (<https://upag.gov.in/>). Despite its considerable agronomic and nutritional value, a wide gap between realised and potential yield was observed in blackgram. This limitation is mainly attributed to a limited genetic diversity and the poor resilience of existing cultivars against key abiotic and biotic stresses. Among the biotic stresses, yellow mosaic disease (YMD) remains a major factor contributing to the low harvest index of present-day cultivars (Anjum et al. 2010).

YMD is a major disease of blackgram, characterised by yellow speckling, mosaic mottling, leaf distortion, stunted growth, and impaired pod set, which can cause yield losses ranging from 10% to complete crop failure under epidemic conditions (Mandal et al. 1997; Biswas et al. 2009; Parihar et al. 2017; Pratap et al. 2018). YMD is caused by whitefly-transmitted begomoviruses (WTV, family Geminiviridae), collectively known as Legume yellow mosaic viruses (LYMVs) (Qazi et al. 2007; Malathi & John 2008). In pulses, these viruses mainly comprise of four species; *Mungbean yellow mosaic virus* (MYMV), *Mungbean yellow mosaic India virus* (MYMIV), *Dolichos yellow mosaic virus* (DoYMV), and *Horsegram yellow mosaic virus* (HgYMV), with a restricted natural host range largely confined to leguminous crops.

In repeated studies over consecutive years in India, it is now confirmed that two viral strains, i.e. MYMV and MYMIV species, causing YMD are prevalent in the Indian subcontinent. Out of which, MYMIV is considered to be more predominant in northern, central and eastern India and MYMV in the western and southern parts of India (Usharani et al. 2004; Dikshit et al. 2020; Mishra et al. 2020). Since the present study was conducted in central India (Jhansi, 25°26'11"N and 78°34'2"E), where MYMIV is frequently reported as the predominant virus associated with yellow mosaic disease, the disease observed in the present investigation is referred to as MYMIV-associated YMD. YMD is transmitted by *Bemisia tabaci* in a persistent-circulative manner (Whitfield et al. 2015). Temperature, humidity and

rainfall can influence whitefly survival, movement, feeding, and population build-up, thereby affecting virus spread. Warm and humid conditions generally favour virus transmission, whereas heavy rainfall may suppress vector activity and population buildup (Kataria et al. 2019).

Chemical control of the vector is often costly, environmentally hazardous, and unreliable, largely because *Bemisia tabaci* populations can rapidly develop resistance to several classes of insecticides (Palumbo et al. 2001; Aktar et al. 2009; Horowitz et al. 2020). Therefore, deployment of genetically resistant cultivars is considered the most reliable, economical and eco-friendly strategy for YMD management (Mishra et al. 2020). Screening germplasm for disease resistance is a key prerequisite for identifying resistant sources and further deployment of these sources in future breeding programmes. Field-based phenotyping under natural epiphytotic conditions in hotspots using susceptible spreader genotypes at regular intervals remains the most practical approach for screening large germplasm collections and identifying resistant genetic resources (Nene 1973; Kumar et al. 2016).

Several recent studies have reported the screening of blackgram genotypes for resistance to YMD, based primarily on field evaluation under natural disease incidence (Iqbal et al. 2011; Obaiah et al. 2013; Mohan et al. 2014; Subedi et al. 2016; Bandi et al. 2018; Pavishna et al. 2019; Tamilzharasi et al. 2020). Although, many resistant varieties of blackgram against LYMVs have been developed through conventional breeding (Singh et al. 2015; Pandiyan et al. 2018; Geetha et al. 2020). However, the durability of resistance does not sustain for a long time due to the limited genetic diversity within cultivars as well as the rapid emergence of new strains of begomoviruses (Varma et al. 2011). Hence, the search for new resistant lines, is a continuing process (Akhtar et al. 2011), necessitates regular screening of available germplasm.

In view of the above limitations and the limited availability of region-specific information on resistant sources against MYMIV-associated YMD in blackgram, the present study was undertaken in the Bundelkhand region of Uttar Pradesh. The study aimed to: (1) assess genetic variability for MYMIV-associated YMD resistance in a diverse panel of 216 blackgram genotypes, and (2) identify superior donors that combine stable resistance with high yield potential under natural epiphytotic conditions.

MATERIAL AND METHODS

Plant material and experimental site. A diverse panel of 216 blackgram genotypes comprising released varieties, advanced breeding and experimental lines along with 4 checks (IPU-13-1, Pant U-8, Pant U-9 and Pratap Urd-1) were screened during the two consecutive years i.e. Kharif 2023 and Kharif 2024, respectively at the Research Farm of Rani Lakshmi Bai Central Agricultural University (RLBCAU), Jhansi, Uttar Pradesh which is located at 25.51°N latitude, 78.56°E longitude, and 227 m above mean sea level (MSL).

Experimental layout. An augmented randomised complete block design (RCBD) (Federer 1956) was employed due to the large number of genotypes and limited seed availability. The experimental plot was divided into 5 blocks in which each block consisted of approximately 52 rows having row length of 3 m, with row-to-row spacing of 30 cm and plant to plant spacing of 10 cm, respectively. Within each block the four checks (IPU-13-1, Pant U-8, Pant U-9, and Pratap Urd-1) and test entries were randomised according to the augmented RCBD. Highly susceptible spreader genotype CO-5 was also planted after every 10 rows to ensure adequate disease pressure build-up among test genotypes. Although the whitefly population was not recorded quantitatively, natural vector-mediated disease pressure was considered adequate for field screening. For each test genotype, the most susceptible ten plants within a line were tagged and scored four weeks after planting, when approximately 90% of CO-5 spreader-row plants showed typical MYMIV-associated yellow mosaic disease symptoms. Standard agronomic practices were followed during the growing season to raise healthy

plant stand. No insecticide was applied to facilitate the natural build-up of whitefly population (Nene 1973; Mandal et al. 1997).

Observations recorded. Observations were recorded for the percent disease severity (PDI) and seed yield per plant (SYPP) during the investigation. For each genotype, the ten tagged plants within each row were individually scored for disease severity using the modified 1–9 disease rating scale as described by Alice and Nadarajan (2007) (Table 1). Further, the recorded scores were used to calculate the PDI.

The PDI was calculated using the formula by Wheeler (1969):

$$PDI = \frac{\sum \text{Disease ratings}}{\text{Number of plants} \times \text{Maximum scale}} \times 100$$

Based on the PDI scores, the blackgram genotypes were divided into six disease reaction levels i.e., highly resistant (HR), resistant (R), moderately resistant (MR), moderately susceptible (MS), susceptible (S) and highly susceptible (HS) as shown in Table 2. Yield parameter was recorded as SYPP, ten plants per row/genotype were previously tagged for disease scoring were harvested in bulk at physiological maturity. The total seed weight of these ten plants was recorded and subsequently divided by 10 to obtain the seed yield per plant (g). The complete phenotypic dataset, including disease reaction, pooled mean PDI, and SYPP for all 216 blackgram genotypes evaluated during Kharif 2023 and Kharif 2024, is provided in Table S1 in Electronic Supplementary Material (ESM).

DNA isolation and PCR-based detection of MYMIV. Plants classified as resistant, moderately resistant, and susceptible based on their phenotypic reac-

Table 1. Disease rating scale for yellow mosaic disease severity in blackgram on the basis of visual assessment

Rating scale	Description
1	no visible symptoms on leaves or very minute yellow specks on leaves
2	small yellow specks with restricted spread covering 1–5% leaf area
3	yellow mottling of leaves covering 5–10% leaf area
4	yellow mottling of leaves covering leaf area 10–15%
5	yellow mottling and discolouration of 15–30% leaf area
6	yellow discolouration of 30–50% leaf area
7	pronounced yellow mottling and discolouration of leaves and pods, reduction in leaf size and stunting of plants covering 50–75% foliage
8	severe yellow discolouration of leaves covering 75–90% foliage, stunting of plants and reduction in pod size
9	severe yellow discolouration of entries covering above 90% foliage, stunting of plants and no pod formation

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Table 2. Categorisation of disease reaction levels based on the percent disease index (PDI) for yellow mosaic disease

Reaction	PDI (%)
Highly resistant (HR)	0
Resistant (R)	< 5
Moderately resistant (MR)	5–10
Moderately susceptible (MS)	11–25
Susceptible (S)	26–50
Highly susceptible (HS)	> 50

tion to yellow mosaic disease were selected for molecular confirmation, with the susceptible check CO-5 included as a positive control. Young leaf samples from the selected plants were collected and stored at -80°C until DNA isolation. Total genomic DNA was isolated from the leaf tissues using the cetyltrimethylammonium bromide (CTAB) method (Doyle & Doyle 1987). The isolated genomic DNA was used as the template for PCR amplification of the intergenic region of MYMIV using the primer pair RepVI/RepCI as reported by Biswas et al. (2009). The forward primer RepVI had the sequence 5'-AATG-TAAAAGGCGACTCATA-3', whereas the reverse primer RepCI had the sequence 5'-GAGAATTCAC-CGGTCGCGGGGGCA-3'. Each PCR reaction was performed in a final volume of 10 μL containing 3.5 μL PCR master mix, 0.5 μL each of forward and reverse primers (10 μM), 2.0 μL template DNA, and 3.5 μL sterile molecular grade water. PCR amplification was performed in Bio-Rad thermal cycler (C1000 Touch Thermal Cycler, Bio-Rad Laboratories, Inc., USA) following conditions: an initial denaturation at 92°C for 2 min, followed by 35 cycles of denaturation at 92°C , annealing at 55°C for 1 min and extension at 72°C for 30 s, and a final extension at 72°C for 10 min. The amplified products were resolved by electrophoresis on a 3.0% agarose gel and visualised using a gel documentation system.

Statistical analysis. The experimental data of PDI and SYPP were subjected to multivariate analysis. The scoring of two-year data (Kharif 2023 and Kharif 2024) was subjected to Bartlett's test, and non-significant results of both PDI and SYPP ($P > 0.05$) led to pooling of both seasons' data. Analysis of variance (ANOVA) was performed using the augmented RCBD package in R software (Ver. 4.4.1) (Aravind et al. 2020), following the model:

$$Y_{ij} = \mu + B_i + T_j + e_{ij}$$

where:

Y_{ij} – observation of the j^{th} genotype in the i^{th} block;

μ – overall mean;

B_i – effect of the i^{th} block;

T_j – effect of the j^{th} treatment;

e_{ij} – error.

Genotype effects, including test genotypes and checks, were treated as fixed, whereas block effects were treated as random. The repeated checks were used to estimate block effects and adjust the performance of unreplicated test entries. Descriptive statistics including mean, range, standard deviation, coefficient of variation (CV%), genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) (Burton & De Vane 1953) was calculated from package “variability”, entry mean heritability in broad sense was calculated by following Cullis method (Cullis et al. 2006) to account for the unbalanced nature of augmented design within “heritable” package in R environment following the equation:

$$h_{\text{cullis}}^2 = 1 - \frac{v_{\Delta}^{\text{BLUP}}}{2\sigma_g^2}$$

where:

v_{Δ}^{BLUP} – average standard error of genotypic BLUPs;

$2\sigma_g^2$ – variance due to genotypes.

Genetic advance (GA) as a percentage of the mean (GAM) (Johnson et al. 1955) was calculated at 5% selection intensity ($k = 2.06$) as follows:

$$\text{GA} = k \times \sigma_p \times h_{\text{bs}}^2$$

$$\text{GAM\%} = \frac{\bar{X}}{\text{GA}} \times 100$$

where:

GA – genetic advance;

k – the selection intensity;

σ_p – the phenotypic standard deviation;

h_{bs}^2 – broad-sense heritability;

$\bar{X}$ – the trait mean.

GAM expresses the expected genetic gain following selection as a percentage of the population mean and, when interpreted together with broad-sense heritability, provides insight into the likely effectiveness of selection. GCV and PCV were estimated to quantify genotypic and phenotypic variability, respectively,

while their relative magnitude was used to infer the extent of environmental influence on trait expression (Burton 1952; Falconer & Mackay 1996).

Principal component analysis (PCA) was performed using the “FactoMineR” and “factoextra” packages in R to assess phenotypic variation and inter-relationships among the 216 genotypes based on PDI and SYPP. The proportion of variance explained by each principal component and the distribution of genotypes and traits were visualised using a scree plot and PCA biplot, respectively. Hierarchical cluster analysis was performed using Ward’s minimum variance method based on Euclidean distance to group the 216 genotypes according to their phenotypic similarity for PDI and SYPP and to identify phenotypically divergent resistant sources. The relationship between block adjusted YMD severity (PDI) and yield (SYPP) was quantified using the Pearson correlation coefficient. The coefficient of determination (R^2) was calculated as the square of the correlation coefficient to determine the proportion of variation in SYPP statistically associated with variation in PDI.

RESULTS

Screening efficiency and ANOVA. Typical YMD symptoms, including yellow specks, mosaic mottling, leaf deformation and stunting, were observed in the susceptible check CO-5. The consistent expression of characteristic symptoms in the susceptible check indicated adequate natural disease pressure for effective phenotypic screening. The analysis of variance (ANOVA) revealed highly significant differences ($P < 0.05$) among treatments for both PDI and SYPP, indicating the presence of substantial genetic variability for yellow mosaic disease response and yield traits in the evaluated blackgram genotypes. (Table 3).

The adjusted mean squares due to treatments were highly significant ($P \leq 0.01$) for both PDI and SYPP, confirming that the genotypes differed markedly in their response to MYMIV-associated YMD infection and yield performance. Overall, the significant genotype effects observed in the ANOVA provide a strong statistical basis for further genetic analyses, including estimation of variability parameters, principal component analysis, and identification of promising genotypes for YMD resistance and yield improvement in blackgram.

Categorisation of MYMIV resistance. Based on the field evaluation and PDI scores, the 216 blackgram genotypes were categorised into five distinct disease reaction classes. Out of 216 genotypes, fifty-one (23.6%) were classified as resistant (PDI $< 5\%$), while the largest group, comprising of eighty-one genotypes (37.5%), were identified as moderately resistant (PDI 5–10%). Furthermore, 58 genotypes fell into the moderately susceptible category, 25 were susceptible, and only a single genotype, RLBU-L3-21, was found to be highly susceptible (PDI $> 50\%$) as depicted in Table 4. Representative phenotypic differences between resistant and susceptible genotypes under natural MYMIV-associated YMD infection are shown in Figure S1 in the ESM. The percentage distribution of 216 blackgram genotypes based on their reaction to MYMIV associate YMD is depicted in Figure 1. PCR amplification using the MYMIV-specific RepVI/RepCI primer pair produced a ~ 600-bp amplicon in CO-5 and in representative susceptible and moderately resistant plants. In contrast, no corresponding amplification was detected in the resistant genotype RLBU-L1-33 (Figure 2). These results provided molecular confirmation of the association of MYMIV with YMD in the experimental material and were consistent with the phenotypic classification of the tested genotypes.

Table 3. ANOVA for percent disease index (PDI) and seed yield per plant (SYPP) among blackgram genotypes

Source of variation	df	Mean square	
		PDI	SYPP
Blocks	4	12.45	1.15
Treatment	215	412.35**	42.18**
Treatment: check	3	156.40**	18.25*
Treatment: test	211	388.12**	35.40**
Treatment: test vs. check	1	1 245.80**	154.62**
Residuals	12	6.82	1.96

df – degree of freedom

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Table 4. List of blackgram genotypes showing variable disease reactions to *Mungbean yellow mosaic India virus* (MYMIV)

Scale	Reaction	PDI (%)	Genotypes
0	highly resistant (HR)	0	none of the genotypes
1	resistant (R) (51)	< 5	IC-236718, KU-302, IC-11668, IPU-2K-99-221, IPU-6-20, IPU-99-177, NP-3, IPU-99-236, IC-277045, IPU-9-18, Palampur-1, IPU-91-7, KUG-502, IPU-1004, RLBUL-1-13, RLBUL-1-31, RLBUL-1-115, RLBUL-1-16, RLBUL-1-33, RLBUL-1-22, RLBUL-1-4, RLBUL-2-43, RLBUL-2-52, RLBUL-2-50, RLBUL-2-26, RLBUL-2-31, RLBUL-2-19, RLBUL-2-15, RLBUL-2-54, RLBUL-2-13, RLBUL-2-17, RLBUL-2-5, RLBUL-2-6, RLBUL-2-18, RLBUL-3-11, RLBUL-3-13, RLBUL-3-7, RLBUL-3-16, RLBUL-3-20, RLBUL-3-9, IPU-13-1, PANT-U8, PANT-U9, PRATAP URD-1, Palampur-3, KUG-500, IC-519910, Palampur-2, IC-274045, IC-236702, RLBUL-1-5
3	moderately resistant (MR) (81)	5–10	IPU-99-112, IPU-19, IPU-35, GU-91-20, IPU-96-1, IC-250240, IC-519911, IPU-99-178, IPU-01-392, KU-96-3, IC-9928, IPU-94-2, IPU-10-04, IPU-10-15, IPU-99-235, IC-385720, IPU-10-19, IPU-99-218, IPU-99-60, IPU-99-244, IPU-10-10, IC-380892, IPU-10-17, IPU-99-217, GAU-4, IPU-99-229, IC-436620, IPU-99-220, IC-381010, KUG-489, IPU-99-221, IPU-120, IPU-99-231, IC-346276, IC-119020, UT-14, MASH-391, RLBUL-1-30, RLBUL-1-6, RLBUL-1-21, RLBUL-1-44, RLBUL-1-37, RLBUL-1-35, RLBUL-1-27, RLBUL-1-18, RLBUL-1-14, RLBUL-1-25, RLBUL-1-24, RLBUL-1-2, RLBUL-1-15, RLBUL-1-17, RLBUL-2-12, RLBUL-2-4, RLBUL-2-3, RLBUL-2-7, RLBUL-2-24, RLBUL-2-44, RLBUL-2-39, RLBUL-2-8, RLBUL-2-55, RLBUL-2-10, RLBUL-2-29, RLBUL-2-41, RLBUL-1-36, RLBUL-2-42, RLBUL-2-22, RLBUL-2-37, RLBUL-2-2, RLBUL-2-30, RLBUL-3-6, RLBUL-3-8, RLBUL-3-5, RLBUL-3-14, RLBUL-3-18, RLBUL-3-20, RLBUL-3-35, RLBUL-3-38, RLBUL-3-40, IPU-99-61, IC-250242, IC-385721
5	moderately susceptible (MS) (58)	11–25	IPU-99-45, IC-33-1242, Azad-2, IPU-2k-997, IPU-2k-226, IC-330852, IC-99-245, IPU-2-43, IC-519909, IPU-10-12, IC-250238, IC-14520, MASH-11, IPU-99-126, KU-219, KU-15, IPU-10-20, IPU-24-21, IPU-99-224, IPU-01-390, IPU-10-16, IPU-10-09, IPU-99-16, T-9, IPU-180, MASH-114, IPU-10-05, KUG-479, IC-16-511, DUS-34, IC-27264, IC-261178, IC-343967, IPU-01-415, IC-3945-51, IPU-247, IPU-99-79, IPU-2000-1, IPU-99-294, PANT-U-12, RLBUL-1-23, RLBUL-1-42, RLBUL-1-3, RLBUL-1-11, RLBUL-1-39, RLBUL-1-20, RLBUL-2-11, RLBUL-2-32, RLBUL-2-25, RLBUL-2-35, RLBUL-2-46, RLBUL-2-47, RLBUL-3-17, RLBUL-3-3, RLBUL-3-4, RLBUL-3-1, RLBUL-3-19, RLBUL-3-15
7	susceptible (S) (25)	26–50	IPU-20-226, IC-345623, IPU-01-427, IPU-99-115, KU-9905, IPU-99-239, IPU-10-18, IPU-14, PANT-4, MASH-479, RLBUL-1-40, RLBUL-1-8, RLBUL-1-32, RLBUL-1-28, RLBUL-1-29, RLBUL-1-26, RLBUL-1-38, RLBUL-1-34, RLBUL-2-45, RLBUL-2-27, RLBUL-2-9, RLBUL-2-33, RLBUL-2-21, RLBUL-2-23, RLBUL-3-10
9	highly susceptible (HS) (1)	> 50	RLBUL-3-21

Impact of MYMIV on seed yield (correlation).

A strong, negative Pearson correlation coefficient ($r = -0.88^{***}$) was observed between PDI and SYPP, indicating that MYMIV-associated YMD severity is the major source for reduction in blackgram yield. The coefficient of determination ($R^2 = 0.77$) suggested that approximately 77% of the yield variation in this panel was directly attributable to disease severity. The yield distribution showed a significant decline

in productivity across disease reaction levels, with resistant genotypes yielding an average of 19.97 g compared to just 2.2 g in the highly susceptible line, as depicted in Figure 3. The distribution of mean percent disease intensity among disease reaction levels are shown in Figure 4.

Genetic variability, heritability, and genetic advance. Estimates of genetic parameters (Table 5) revealed high GCV and PCV for both PDI and SYPP,

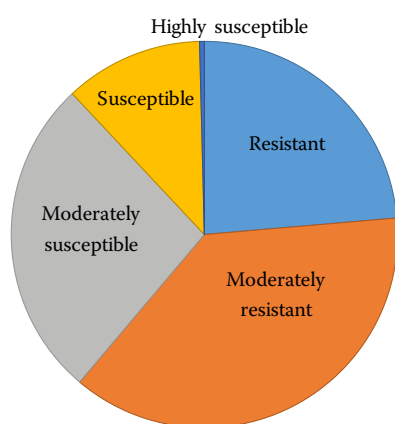


Figure 1. Percentage distribution of 216 blackgram genotypes based on their reaction to *Mungbean yellow mosaic India virus* (MYMIV)-associated yellow mosaic disease (YMD)

with a narrow difference between them, indicating low environmental influence. The high broad-sense heritability ($h^2_{bs} > 94\%$) coupled with high genetic advance as a percentage of the mean ($GAM > 100\%$) for both traits suggests that both MYMIV-associated YMD resistance and seed yield are under direct genetic control and less influenced by the confounding effect of environment. Therefore, the direct selection for these traits would be highly effective for the genetic improvement of blackgram.

Principal component analysis (PCA) and scree plot. The PCA biplot based on PDI and SYPP effectively explained the variation among blackgram genotypes for MYMIV-associated YMD response and yield performance (Figure 5). The first two principal components accounted for nearly all of the total variability among genotypes, with PC1 and

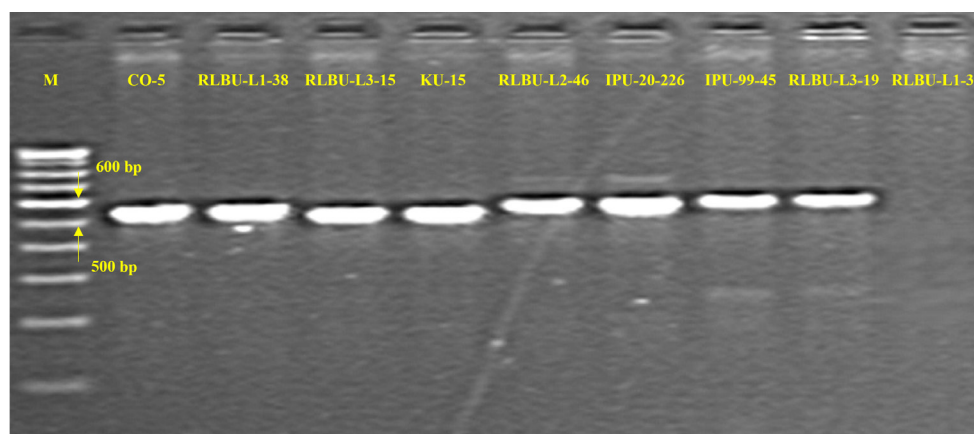


Figure 2. PCR amplification of the intergenic region of *Mungbean yellow mosaic India virus* (MYMIV) using the primer pair RepVI/RepCI in blackgram genotypes exhibiting various phenotypic reactions to MYMIV

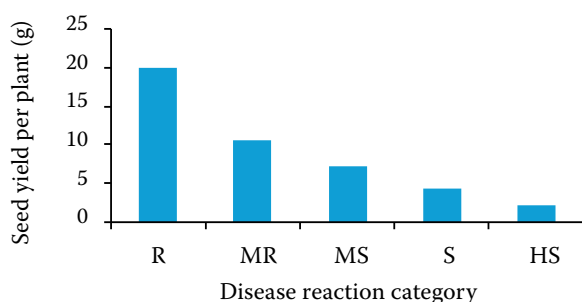


Figure 3. Impact of *Mungbean yellow mosaic India virus* (MYMIV)-associated yellow mosaic disease (YMD) severity on the average seed yield per plant (SYPP) (in g) in 216 blackgram genotypes

R – resistant; MR – moderately resistant; MS – moderately susceptible; S – susceptible; HS – highly susceptible

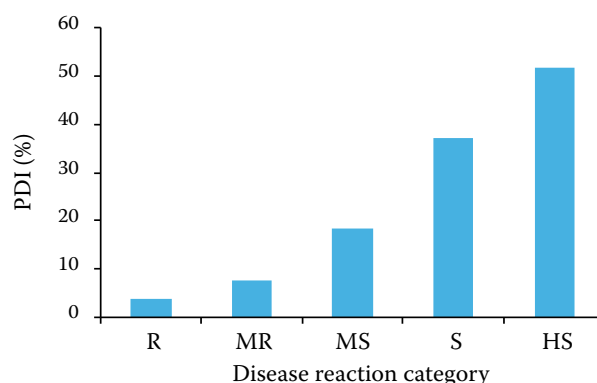


Figure 4. Average percent disease index (PDI, %) across different disease reaction levels in 216 blackgram genotypes R – resistant; MR – moderately resistant; MS – moderately susceptible; S – susceptible; HS – highly susceptible

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Table 5. Estimates of variability, heritability and genetic advance for percent disease index (PDI) and seed yield per plant (SYPP) in blackgram

Parameter	PDI	SYPP
Genotypic variance	126.11	30.82
Phenotypic variance	132.93	32.78
Genotypic coefficient of variation (%)	84.50	50.63
Phenotypic coefficient of variation (%)	86.76	52.22
Broad sense heritability	94.87	94.02
Genetic advance	22.53	11.09
Genetic advance as % of mean	169.55	101.13

PC2 explaining 85.98% and 14.01% of the variation, respectively with the PC1 having eigenvalue greater than 1 (1.31) is used for further analysis as depicted

in the scree plot (Figure 6). PC1 and PC2 denote the first and second principal components, accounting for the maximum and second-highest proportions

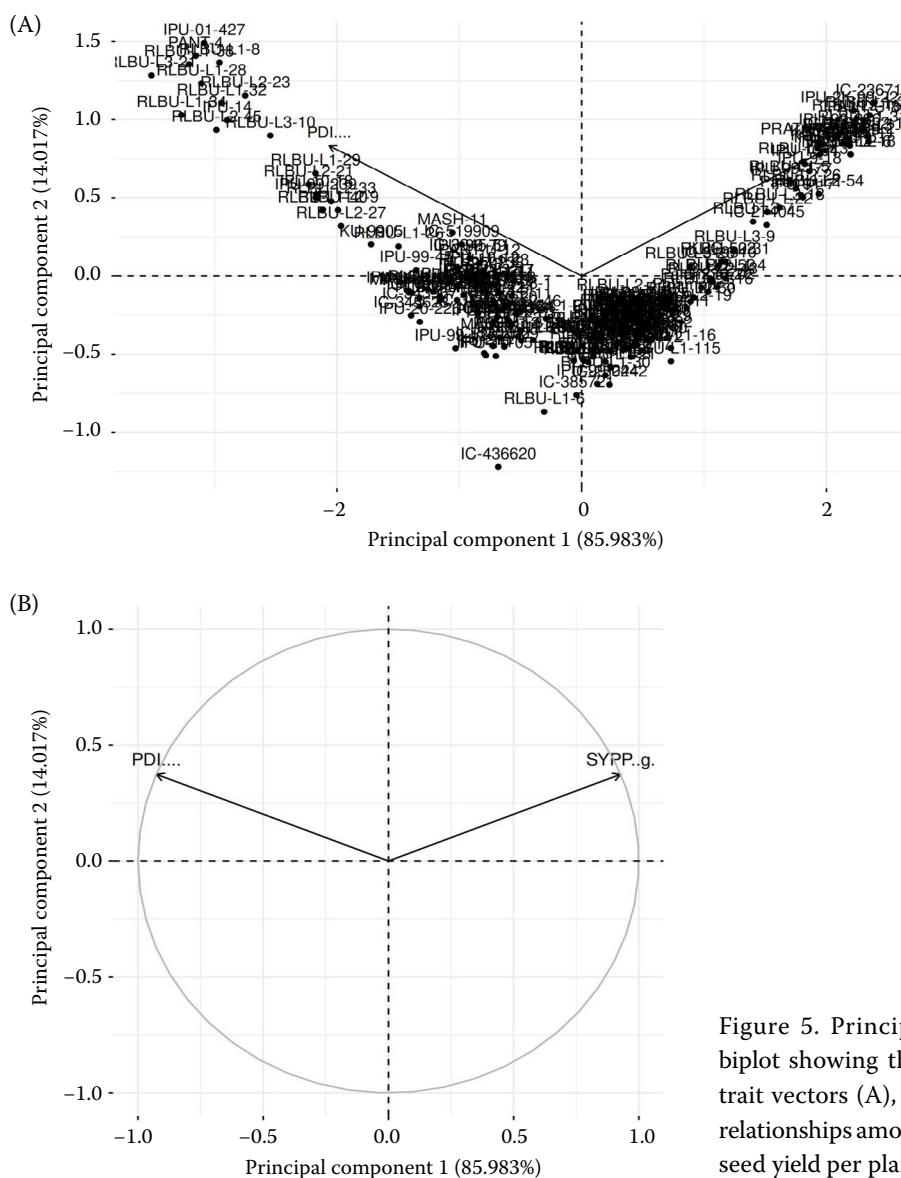


Figure 5. Principal component analysis (PCA): biplot showing the distribution of genotypes and trait vectors (A), and correlation plot showing the relationships among percent disease index (PDI) and seed yield per plant (SYPP)(B)

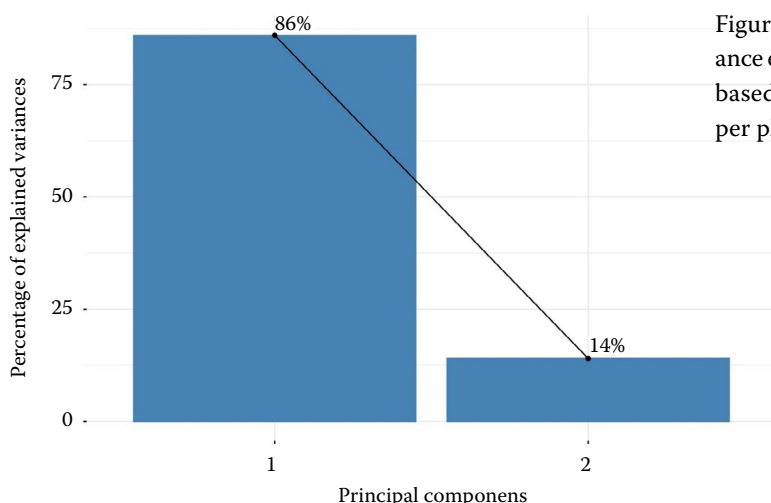


Figure 6. Scree plot showing the percentage of variance explained by the first two principal components based on percent disease index (PDI) and seed yield per plant (SYPP) in blackgram

of the total phenotypic variation, respectively. The principal component PC1 had positive correlation with SYPP ($r = 0.7071$), while negative correlation with PDI ($r = -0.7071$), indicating the adverse impact of YMD on productivity. Resistant and moderately resistant genotypes clustered on the negative side of PC1 near the SYPP vector, reflecting low PDI and higher yield potential. Genotypes such as IC-236718, RLBU-L1-33, IPU-2K-99-221, RLBU-L2-15, KU-302 and IPU-13-1 have the highest PC1 and PC2 scores, which were closely associated with superior yield

and resistance, highlighting their potential as donor parents. In contrast, susceptible and highly susceptible genotypes were grouped on the positive side of PC1 near the PDI vector, indicating higher disease severity and lower yield. Moderately susceptible genotypes occupied intermediate positions, suggesting partial resistance and variable yield response. Overall, PCA effectively discriminated genotypes for MYMIV-associated YMD resistance and yield, revealing genetically diverse and agronomically superior resistant genotypes for blackgram improvement.

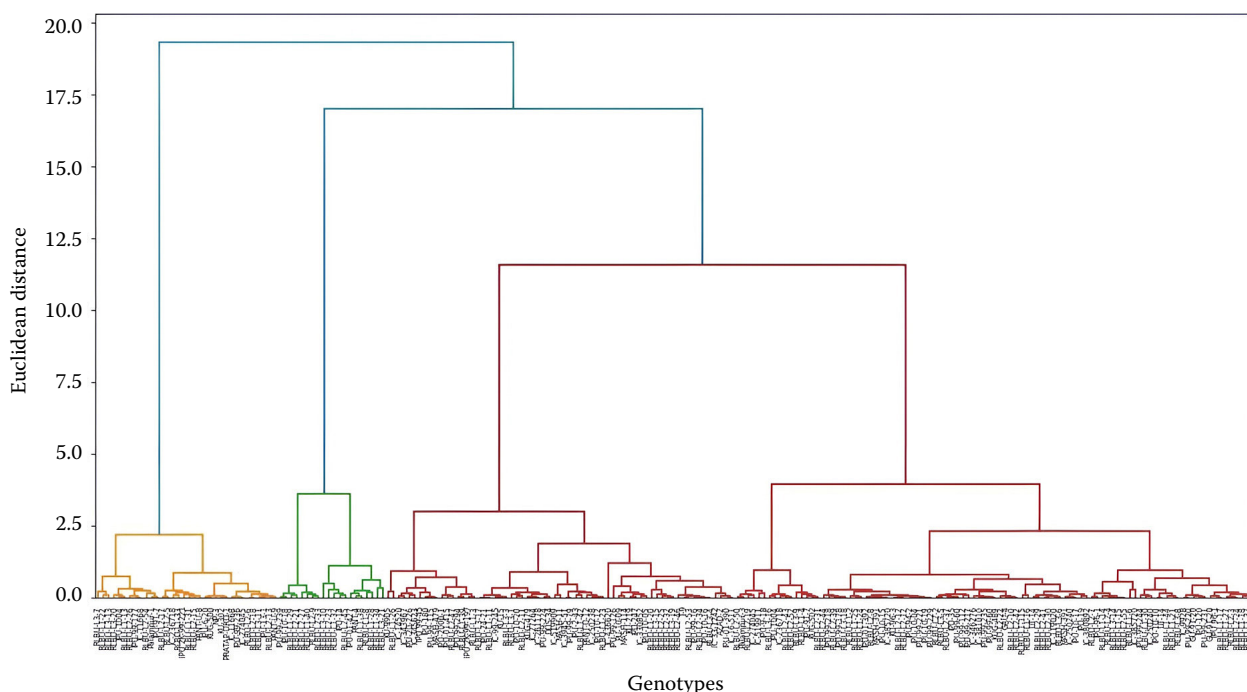


Figure 7. Hierarchical clustering dendrogram of blackgram genotypes based on adjusted mean values of percent disease index (PDI) and seed yield per plant (SYPP) using Euclidean distance and Ward's method

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Table 6. Grouping of genotypes into clusters based on percent disease index (PDI) and seed yield per plant (SYPP)

Cluster	No. of genotypes	Mean PDI (%)	Mean SYPP (g)	Reaction type
I	51	3.84	19.97	resistant (R)
III	81	7.75	10.58	moderately resistant (MR)
IV	58	18.35	7.11	Moderately susceptible (MS)
V	25	37.26	4.36	susceptible (S)
II	1	51.55	2.2	highly susceptible (HS)

The individual principal component scores (PC1 and PC2) for all 216 blackgram genotypes are provided in Table S2 in the ESM.

Diversity and hierarchical clustering. Hierarchical clustering using Ward's minimum variance method was employed to categorise the 216 blackgram genotypes into distinct groups based on their phenotypic response to MYMIV-associated YMD and yield performance. The resulting dendrogram (Figure 7) revealed five major clusters, representing varying levels of disease resistance and productivity. The genotypes were grouped as, Cluster I which comprise of 51 genotypes, including IC-236718, RLBU-L1-33, RLBU-L2-5, and IPU-13-1. This cluster was characterised by the lowest mean PDI (3.84) and the highest mean seed yield (19.97 g) (Table 6). Genotypes grouped within the same cluster exhibited high similarity, whereas those in different clusters showed considerable divergence, as evident from the larger linkage distances. The wide separation between clusters at higher Euclidean distances indicates that hybridisation between genotypes belonging to divergent clusters (e.g., resistant vs. susceptible groups) are likely to produce maximum heterosis and broader variability in segregating generations. The dendrogram effectively discriminates between genotypes with contrasting disease reactions. The significant Euclidean distance observed between Cluster I (Elite) and Cluster II (Susceptible) highlights the presence of substantial genetic diversity,

and this diversity is essential for identifying donor parents that can contribute unique alleles for YMD resistance.

Identification of superior donor genotypes.

The current study identified several released varieties, including IC-236718 (24.6 g), IPU-2K-99-221 (23.8 g), and KU-302 (21.7 g) and elite breeding lines RLBU-L1-33 (24.2 g) and RLBU-L2-15 (23.7 g), having high seed yield per plant as well as having stable and low PDI values across both environments. A summary of the top-performing donors based on both resistance and yield stability is presented in Table 7.

DISCUSSION

Field-based phenotyping under natural epiphytotic conditions provides a practical approach for large-scale germplasm screening as it enables resistance to be evaluated under natural vector-mediated infection and prevailing field conditions (Akhtar et al. 2009). The appearance of typical MYMIV-associated YMD symptoms, including yellow speckling, mosaic mottling, leaf deformation, and stunting in susceptible checks (CO-5) and spreader rows, confirmed adequate disease pressure for effective field screening. Weather conditions had a significant effect on whitefly survival, reproduction and dispersal. Warm, humid conditions, particularly 32–37 °C/21–29 °C Tmax/Tmin and light rainfall, favour population buildup by maintaining humidity, whereas heavy rainfall

Table 7. List of superior blackgram donors selected based on mean percent disease index (PDI) and seed yield per plant (SYPP) of both seasons i.e., Kharif 2023 and Kharif 2024

Genotype	Mean PDI (%)	Reaction	Mean SYPP (g)
IC-236718	3.2	resistant	24.6
RLBU-L1-33	2.8	resistant	24.2
IPU-2K-99-221	4.1	resistant	23.8
RLBU-L2-15	3.5	resistant	23.7
KU-302	4.5	resistant	21.7

> 85 mm suppresses populations through wash-off and mortality (Kataria et al. 2019). During the critical period from sowing to the initiation of YMD phenotyping (SMWs 28–32), the weather conditions in the present study (Figure S2 in the ESM) largely remained within favourable limits, indicating Kharif 2023/2024 environment was conducive for adequate whitefly activity and disease buildup. The highly significant treatment effects for PDI and SYPP further indicated the presence of substantial genetic variability among the evaluated blackgram genotypes for disease response and yield performance.

The classification of 216 blackgram genotypes into different disease-reaction groups; resistant, moderately resistant, moderately susceptible, susceptible and highly susceptible categories based on PDI scoring highlights a wide range of responses to MYMIV-associated YMD. Among them, fifty-one genotypes are resistant, eighty-one are moderately resistant, fifty-eight are moderately susceptible, twenty-five are susceptible, and only a single genotype, RLBU-L3-21, was classified as highly susceptible. Molecular analysis of representative genotypes further supported the association of MYMIV with the observed disease reactions, as the expected MYMIV-specific amplicon was detected in the susceptible check and representative susceptible and moderately resistant plants, whereas no detectable amplification was observed in the resistant genotype RLBU-L1-33. The absence of a detectable MYMIV-specific amplicon in the resistant genotype RLBU-L1-33 may be attributed to effective restriction of viral establishment and multiplication, resulting in viral DNA accumulation below the detection threshold of conventional PCR. The absence of completely immune genotypes (PDI = 0%) is consistent with previous studies in blackgram and mungbean, where resistance is generally partial but stable across environments (Mandal et al. 1997; Biswas et al. 2009). The absence of complete immunity and the range of resistance reactions observed in the present study may be attributed to the complex inheritance of YMD resistance in *Vigna* spp., where dominant, recessive, digenic, epistatic, and modifier-gene effects have been reported across different genetic backgrounds (Singh 1980; Gupta et al. 2005; Murugan & Nadarajan 2012; Thamodhram et al. 2016). In addition, variable blackgram MYMIV-associated YMD interactions and weather-driven fluctuations in whitefly activity may influence disease expression under natural field conditions (Sudha et al. 2013).

The identification of several resistant and moderately resistant genotypes indicates the presence of useful resistance donors within the germplasm panel that may be exploited in future MYMIV-associated YMD resistance breeding programs.

The strong negative correlation observed between PDI and SYPP ($r = -0.88^{***}$) shows the negative association between YMD severity and seed yield in blackgram. The coefficient of determination ($R^2 = 0.77$) indicated that approximately 77% of the variation in seed yield was statistically associated with disease severity. Further, mean yield decline from 19.97 g in the resistant class to 2.2 g in the highly susceptible genotype highlights the importance of combining disease resistance with yield potential during parent(s) selection. Earlier studies have also recognised YMD as a major production constraint in blackgram, causing severe yield reduction under favourable disease conditions (Bag et al. 2014; Reddy et al. 2015).

High GCV and PCV for PDI and SYPP indicated substantial variability among blackgram genotypes for disease response and yield performance, while a narrow difference between GCV and PCV suggested limited environmental influence under the present conditions. High broad-sense heritability coupled with high genetic advance as a percentage of the mean indicated that trait variation observed for both traits is largely under the control of genetic factors rather than the confounding effect of environment. The Hierarchical Clustering and PCA results provide necessary information for planning the controlled hybridisation among the genotypes present in diverse clusters for prospecting the diverse alleles for MYMIV-associated YMD present in the germplasm panel. The significant Euclidean distance between Cluster I (Elite) and the other clusters suggests that these genotypes possess diverse allelic combinations for resistance.

Among the evaluated genotypes, IC-236718, RLBU-L1-33, IPU-2K-99-221, RLBU-L2-15, and KU-302 were identified as promising donors; these genotypes combined low PDI (< 4%) with superior seed yield per plant, significantly higher than the population mean (11.2 g). By crossing these identified elite donors, breeders can prospect the allelic diversity present in the current germplasm panel into a single elite genetic background through multi-parent crossing schemes. This approach may contribute to breeding for stable resistance, which is less likely to be overcome by new viral strains or whitefly biotypes (Subramaniyan et al. 2021).

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CONCLUSION

The present study identified 51 resistant blackgram accessions under natural epiphytotic conditions, indicating the presence of useful field resistance against MYMIV-associated YMD in the evaluated panel. Among these genotypes, IC-236718, RLBU-L1-33, IPU-2K-99-221, RLBU-L2-15, and KU-302 combined low PDI with superior seed yield, making them promising donor parents for breeding MYMIV-associated YMD resistance in high-yielding blackgram cultivars. The RLBU lines are particularly valuable for the Bundelkhand agro-climatic zone because they were developed and evaluated under natural disease epiphytotic conditions at Jhansi. These resistant sources may also be considered for direct varietal use after multi-location testing for agronomic performance, adaptation, and yield stability. In addition, the identified donors can serve as useful genetic resources for future gene tagging and marker-assisted breeding efforts aimed at developing stable, high-yielding, and YMD-resistant blackgram cultivars.

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