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Genotype-by-environment interaction effects on blast disease severity and genetic diversity of advanced blast-resistant rice lines based on quantitative traits

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Introduction: Among the rice diseases, rice blast caused by the pathogen *Magnaporthe oryzae* is a major threat to the global rice cultivation. This experiment was aimed at investigating the genotype by environment interaction effects on the severity of blast disease and variability of the advanced blast resistant rice lines using quantitative characters.

Materials and methods: The experiment was laid out in randomized complete block design conducted at three locations. Data were collected on 21 traits which included vegetative, physiological, yield and yield components and were subjected to analysis of variance and variance component analysis. Cluster analysis was authenticated using principal component analysis for genotypes' classification.

Results and discussion: All vegetative and yield traits showed highly significant variation among the advanced lines and the check. Seberang Prai showed the highest average yield (5.62t/ha), followed by Tanjung Karang (5.39t/ha) and UPM (4.97t/ha). All the advanced lines showed high resistance to blast disease. Evaluation across the three environments indicated that genotype G3, from MR219 based population, had the highest yield and resistance to blast infection. Genotype G21, from MR263 based population, performed best across the three

environments studied and were selected for further breeding programme. The two selected lines, three and four clusters derived from MR219 and MR263 based populations, respectively, were recommended as new lines for further breeding programmes.

KEYWORDS

G×E, genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), heritability, genetic advance, *Oryza sativa* L., *Magnaporthe oryzae*

1 Introduction

Among many leading cereal crops in the world, rice is considered a staple food for more than 3.5 billion of the world population particularly in the Asian continent (Chukwu et al., 2019a; Oladosu et al., 2020). Due to the continuous increase in rice demands, it was forecast that current global rice production must increase by 25% by 2025 in order to cope with the growing population rate (Maclean et al., 2002; Oladosu et al., 2019). Therefore, it is a matter of great challenge to meet the increasing rice demand with diminishing natural resources. In Malaysia, rice is regarded as a staple food, and it is important to the Malaysian culture. It is the third most significant crop after palm oil and rubber in terms of production. Farmers in Malaysia currently produce 2.6 million tons of paddy grain on a yearly basis (Siwar et al., 2014), which account for only about 70% of total consumption, while the remaining 30% shortfall is compensated for by importation from neighboring countries.

Rice production in Malaysia began a long time ago and now the country proves that it is capable of producing different types of rice that are mainly grown in 12 major granary areas in Malaysia: 10 in Peninsular Malaysia and 1 each in Sabah and Sarawak. According to Chukwu et al. (2019b), diseases are the most important limiting factors affecting rice production in Malaysia and anywhere in the world. The major diseases affecting rice include rice blast, bacterial leaf blight, and sheath blight. Among these diseases, rice blast has the most serious constraints on high productivity (Chukwu et al., 2019c). Between 1988 and 1994, a severe outbreak of blast disease was reported in the states of Perak, Penang, Selangor, and Kedah in Malaysia, which affected over 40% of the planted areas, causing an estimated yield loss of about 10%–50%. Disease management can be accomplished through chemical protection, host plant resistance, and biological control (Chukwu et al., 2022b). Chemical controls are not always effective and some are injurious to the rice plants, coupled with the fact that these chemicals are not eco-friendly. The use of biocontrol agents to control bacterial blast remains to be explored in detail. Therefore, an efficacious, cost-effective, and eco-friendly

bacterial blast management strategy is crucial for sustainable rice production not only for Malaysia but also for the world at large. The most effective way of controlling blast disease is through the development of a resistant variety, which eventually minimizes yield loss (Akos et al., 2019; Akos et al., 2021).

The major step in plant breeding towards the development of improved varieties is to evaluate interactions of genotypes by environment (G×E). When genotypes or varieties are evaluated across a series of different location, their yield performance usually differs. This, however, makes it difficult for breeders to demonstrate the significance of any superior variety. This significant interaction between genotype and environment is usually present whether the varieties are developed through conventional or non-conventional methods. Statistically, the effect of large G×E interactions was reported to affect the progress of selection (Comstock and Moll, 1963). Over the years, environmental stratification has been effectively used to reduce the G×E interaction. The region for which a breeder is developing improved varieties can often be so subdivided that all environments in the subregion are somewhat similar. This stratification is usually based on macro-environmental differences such as arid soil types, rainfall distribution, and temperature gradients. However, even with this refinement of technique, the interaction of genotypes with locations in a subregion, and with environments encountered at the same location in different years, frequently remains too large. Allard and Bradshaw (1964) classified as unpredictable the environmental variation for which stratification is not effective. Since little additional progress can be expected in reducing G×E interactions by the stratification of environments, other methods need to be investigated. One such method was to select a genotype that showed less interaction with the environments in which they are cultivated. If the genotype ability to show a minimum interaction with the environment or stability performance is greatly controlled by the genetics, then there is a need to conduct a preliminary evaluation to select the stable genotype before presenting to the final stage for the breeder to select the superior genotype.

In the crop improvement programs, the ultimate goal of plant breeders is to develop high-yielding cultivars with broad

adaptability (Okporie et al., 2013), although it became more challenging when dealing with G×E interactions. Minimally, two genotypes (cultivars) and two environments are needed for genotype-by-environment (G×E) evaluation. Statistically, there are different methods used in G×E analysis comprising parametric and non-parametric techniques. Study objectives and data variability evaluation play an important role in the decision of the biological statistical model combination that will be used. Thus, an efficient statistical technique is needed to discover morphological and physiological traits that are related to environmental effects. The linear regression approach has been used to evaluate the magnitude of G×E interaction. Later, this method was modified by Finlay and Wilkinson (1963) in examining the yield stability of barley genotype and by Eberhart and Russell (1966). Other methods for estimating G×E interaction include cluster analysis, pattern analysis, additive main effects and multiplicative interaction (AMMI), genotype main effects, and genotype and G×E interaction effects (GGE). A suitable statistical analysis depends on the experimental data, the number of environments involved, and the accuracy of the information. The objective of this particular experiment was to study the genotype-by-environment interaction (GEI) effects on the severity of blast disease and the genetic variation of the advanced blast-resistant rice lines using quantitative traits.

2 Materials and methods

2.1 Plant materials

Thirteen lines of BC₂F₂ generation from an advance-backcross of MR219 × Pongsu Seribu-1 and 26 lines from an advance backcross of MR263 × Pongsu Seribu-1 obtained from previous studies (Miah et al., 2015; Chukwu et al., 2020a; Chukwu et al., 2020b) were evaluated, in addition to two check materials from both populations. A total of 41 lines were used for the study. Pongsu Seribu-1 (PS1), which was developed by the Malaysian Rice Research Centre, Malaysian Agricultural Research and Development Institute (MARDI) possesses broad-spectrum resistance against blast fungal isolates. MR219 and MR263 have high-yielding potentials with a suitable grain quality and good eating quality. Unfortunately, these varieties are very susceptible to blast (Hasan et al., 2016).

2.2 Research location

The field evaluation was performed repeatedly in three locations: first, at MARDI station in Tanjung Karang from October 2014 to January 2015; second, at MARDI research station in Seberang Perai from September 2015 to December 2015; and, third, at Universiti Putra Malaysia (UPM), Field 10, from September 2016 to January 2017. The climate could be described as hot humid tropic, with high humidity and adequate rainfall. The weather details of the locations are provided in Table 1.

1 2.3 Agronomic practices

Thirty grams of each rice accession was placed into plastic Petri dishes and oven dried at 50°C for 24 h to deactivate seed dormancy. Later, the seeds were soaked with water for 24 h, and each Petri dish was covered and allowed to germinate for 3 days. To avoid drying out, water was added to each Petri dish on a daily basis. For easier establishment of each sprouted seed, a nursery of 41 compartments was made in the soil-filled tray, to which excess water was added. Three-day-old seedlings were transferred from Petri dishes to plastic trays that were later transplanted to the field after a period of 21 days in the nursery. In this experiment, a randomized complete block design (RCBD) with three replications was adopted. A planting distance of 25 cm within and between rows was applied. Other management practices, such as irrigation, weeding, fertilization, and application of pesticides and insecticides, were done following standard procedures (Azmi et al., 2008). The physicochemical properties of the soil were determined before and after planting (Table 2).

2.4 Blast screening under natural and artificial conditions

The advance lines were grown at a rice field at Mardi Station in Tanjung Karang and Seberang Perai where the infection of blast naturally occurred. All the advanced lines were grown under the glasshouse condition where the infection of blast was

TABLE 1 Weather information of the research locations.

S/N	Location	Altitude	Av. temp. Min–Max	Av. Hum.	Rainfall (monthly mean)
1	3°25'0N 101°10'E	3 m	23°C to 31°C	83	782.4 (195.6)
2	05°25'N 100°15'E	3 m	22°C to 30°C	88	934.7 (233.7)
3	3° 02'N 101°42'E	32 m	24°C to 38°C	67	623.4 (115.9)

1, MARDI station Tanjung Karang; 2, MARDI station Seberang Perai; 3, UPM Field 10.

TABLE 2 Physicochemical properties of the soil before and after planting.

Minerals element	Site 1(B)	Site 1(A)	Site 2(B)	Site 2(A)
N %	0.133	0.124	0.154	0.170
P %	0.059	0.057	0.054	0.081
K %	1.098	1.030	0.833	0.881
Mg %	0.101	0.116	0.133	0.140
Ca %	0.002	0.002	0.002	0.002
Na %	0.212	0.196	0.136	0.146
Cu mg/L	20	24	16	20
Zn mg/L	88	96	108	160
Mn mg/L	116	104	72	100
Fe mg/L	14452	14280	13116	13932
pH	5.3	5.5	6.1	5.8
% sand	55.90	57.07	56.02	56.31
% clay	22.21	20.60	22.21	23.28
% silt	20.50	22.21	20.60	20.17

(B) Before planting, (A) After harvesting.

introduced to the plant *via* the spraying technique. Inoculum was prepared by introducing the spores of *M. oryzae* from 10-day colonies on complete media and suspended in sterilized water to 2×10^4 conidia/ml dilution (Koutroubas et al., 2009; Tanweer et al., 2015a; Tanweer et al., 2015b). The inoculation was performed during the evening hours at six to seven leaf stages by spraying 3 ml of the conidial suspension on each rice plant using a fine air sprayer. Water was sprinkled on the leaves three times a day between 11 a.m. and 4 p.m. in order to facilitate blast development (Koutroubas et al., 2009). The individual plant was assessed on day 80 after inoculation (DAI) using a standard evaluation system introduced by the International Rice Research Institute, IRRI (IRRI, 2014). The symptoms of blast in rice crop are shown in Figure 1.

2.5 Agro-morphological data collection

The morphological and agronomic traits of the evaluated lines were measured based on 21 parameters adapted from Oladosu et al. (2018) and IRRI (2014). Five representative plants for each genotype in each replication were randomly selected to record observations. The parameters assessed were panicle length, filled grains per panicle, unfilled grains per panicle, total grain per panicle, grain weight per panicle, tillers per hill, panicles per hill, thousand grain weight, total grain weight per plant, percentage effective tiller, percentage filled grain, plant height, days to flowering, days to maturity, flag leaf length-to-width ratio, and yield in t/ha. The SPAD-502 instrument was used to determine the chlorophyll content of

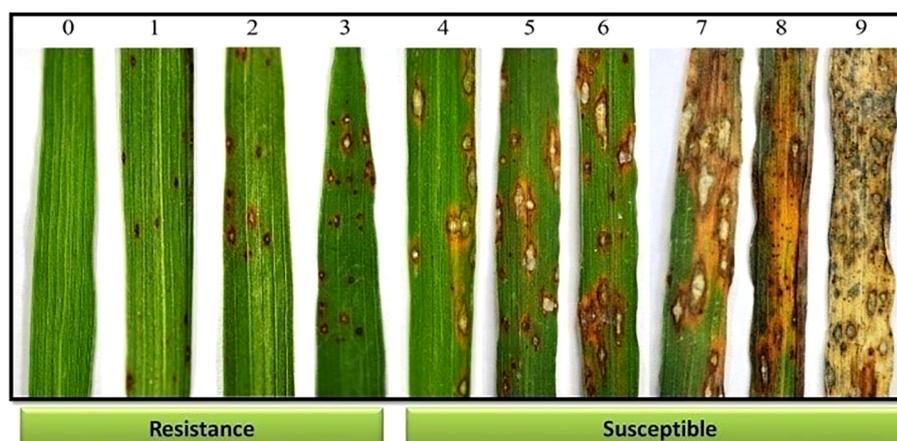


FIGURE 1
Symptoms of blast disease in rice.

fully matured leaf from the top of the plants at day 72 and 86 after transplant. An average value per plot was derived from five plants per lines and three leaves per individual plant.

2.6 Statistical analysis

Descriptive statistics such as the mean, range, standard deviation, and coefficient of variation (CV) were calculated for each trait. Phenotypic correlation coefficient, cluster analysis (CA), and principal component analysis (PCA) were run with the aid of SAS software version 9.4. Analysis of variance (ANOVA) was calculated for all of the traits to determine variation among the genotypes, populations, and locations. The data were first analyzed individually on the basis of the three sites and two populations. Where there were no significant differences found among the genotypes, the data were pooled over sites. Mean comparisons were performed using LSD. The association and relationship of the various characteristics were worked out at the phenotypic level using Pearson correlation coefficients. The ANOVA table and expected mean squares for combined sites and population are as shown in Table 3. The GGE biplot was used to graphically analyze the multivariate stability in order to provide an interpretation of the relationship between genotype and environment. R studio is a streamlined version of the R statistical software, which was utilized in the computation of the GGE biplots. The GUI package was utilized for the creation of GGE biplots (RStudio, 2014). The GGE biplots were utilized for the purposes of visualizing the presence of GEI and ranking genotypes according to stability and mean. The created graph is based on the Mega environment (i.e., which-won-where pattern of GGE) and genotype evaluation.

2.7 Mega-environment analysis (which-won-where)

Plotting of the GGE biplot graph was constructed in such a way that the first principal component (PC1) of genotype and

environment scores is plotted against the second principal component (PC2) that resulted from singular value decomposition (SVD) of environment standardization or environment center of genotype–environment data (GED). The mega-environment graph consists of an irregular polygon containing scattered genotypic and environmental markers. The polygon is constructed in such a way that it connects all genotypes that are far away from the biplot origin. Lines that originated from the center of the biplot that perpendicularly intersect the polygon divide the polygon into sectors. Hence, genotype at the vertex of the polygon is stable for all the environments in that sector. A single genotype is said to perform best if all environmental markers fall into one sector. In contrast, if the environmental markers fall into different sectors, the genotype at the vertex of each sector won in the environments in each sector, hence revealing the “which-won-where” pattern (Ebem et al., 2021).

2.8 Variance components

Genetic parameters were estimated with the use of SAS software (version 9.4) to determine genetic variation among genotypes and to assess genetic and environmental effects on various traits. The phenotypic and genotypic correlations were estimated by the method of Singh (1985) and genetic advance was calculated using the method of Assefa et al. (1999). Also, heritability estimates were determined by the procedure by Falconer (1989).

3 Results

3.1 Genotype-by-environment interaction effects

Blast disease severity: The results in Table 4 show the blast disease severity for combined site and population. Sources of

TABLE 3 ANOVA table for combined sites and population.

Source of variation	df	EMS
Replications (S)	$s(r-1)$	$\sigma^2_e + gs\sigma^2_r$
Sites (S)	$s-1$	$\sigma^2_e + r\sigma^2_{gs} + rg\sigma^2_s$
Genotypes (G)	$g-1$	$\sigma^2_e + r\sigma^2_{gs} + rs\sigma^2_g$
Populations (P)	$P-1$	$\sigma^2_e + r\sigma^2_{g/s(p)} + gr\sigma^2_{ps} + rs\sigma^2_{g(p)} + grs\sigma^2_p$
G(P)	$p(g-1)$	$\sigma^2_e + r\sigma^2_{g/s(p)} + gr\sigma^2_{ps} + rs\sigma^2_{g(p)}$
G×S	$(g-1)(s-1)$	$\sigma^2_e + r\sigma^2_{gs}$
P×S	$(p-1)(s-1)$	$\sigma^2_e + r\sigma^2_{g/s(p)} + gr\sigma^2_{ps}$
G(P)×S	$(g-1)p(s-1)$	$\sigma^2_e + r\sigma^2_{g/s(p)}$
Error	$(r-1)(gps-1)$	σ^2_e

R, blocks; G, genotypes; P, population; e, error; df, degree of freedom; MS, mean squares; EMS, expected mean squares.

TABLE 4 Blast disease severity by combined site and populations.

Source of variation	df	Disease severity
Sites (S)	2	4.54**
Genotypes (G)	40	3.86**
Populations (P)	(1)	30.19**
G(P)	(39)	3.18**
G×S	80	0.29 ^{ns}
P×S	(2)	1.37*
G×S(P)	(78)	0.26 ^{ns}
Error	240	0.35

*Significant at the 0.05 level, **Highly significant at the 0.01 level; ns, non-significant; S.O.V., source of variation; df, degree of freedom; Ds, disease severity.

variation such as sites, replication within site, genotype, population, genotype within population, and population by sites showed a significant difference while there was no significant difference observed in genotype by site and genotype by site within population. The nonsignificant difference observed among the genotype by site within the population indicated the absence of environmental effect on the blast disease severity.

3.1.1 Vegetative and physiological traits

The pooled ANOVA for vegetative and physiological traits based on sites and populations is presented in Table 5. From the result obtained, all the traits showed significant variation among the sites, genotypes, population, and genotype within population. In addition, only number of tillers and number of panicles had no significant difference among the replication within sites while the others varied significantly ($p \leq 0.01$). Days to flowering and days to maturity showed no significant differences among the population by sites while a significant difference at $p \leq 0.05$ was observed in the plant height. Other traits including flag leaf ratio, number of panicle, and percentage effective tillers showed highly

significant differences between the genotypes by sites within the population.

3.1.2 Yield and yield components

The results obtained on 10 traits regarding yield and yield components are presented in Table 6. From the results, all the traits varied significantly among the sites, genotypes, and genotypes within the population. All the traits except for unfilled grain, total grain weight per plant, and yield per hectare showed significant differences in replication within sites. In addition, only flag leaf trait recorded a nonsignificant difference by the population while the other nine traits showed highly significant differences among the population. Grain dimension, total grain weight per plant, 1,000 grain weight, and yield (t/ha) were significantly affected by the population by sites, while only two traits, grain dimension and 1,000 grain weight, were influenced significantly by the genotype by site within population.

3.2 Phenotypic and genetic coefficient of variation and heritability across locations

3.2.1 Blast disease severity

From the result presented in Table 7, blast disease severity showed a high value of phenotypic coefficient variation and genotypic coefficient variation (45.42% and 33.43%, respectively). In addition, this trait also recorded moderate broad sense heritability (54.16%) and high value of genetic advance (50.68%).

3.3 Relationships among agronomic traits

Correlation coefficients among the morphological traits and yield and its components for population MR219 and MR263 are

TABLE 5 Vegetative and physiological traits by combined site and populations.

Source of variation	DF	PH	DF	DM	FLR	PLL	NTLR	NPL	PET	72 CC	86 CC
Sites (S)	2	280.73**	805.24**	1,149.10**	1,479.64**	74.67**	6,428.69**	2,954.38**	220.88**	1,408.27**	1,435.47**
Genotypes (G)	40	137.59**	63.34**	63.02**	42.75**	3.57**	193.72**	127.01**	94.77**	74.64**	62.64**
Populations (P)	(1)	3,272.28**	1,162.55**	1,176.84**	978.20**	68.07**	6,474.83**	3,634.34**	1,515.31**	373.63**	122.41**
G(P)	(39)	57.22**	35.16**	34.46**	18.77**	1.92**	32.66**	37.08**	58.35**	66.97**	61.11**
G×S	80	3.18 ^{ns}	13.36**	13.78**	7.24 ^{ns}	1.04**	39.16**	23.39**	28.77 ^{ns}	4.57**	5.83**
P×S	(2)	37.98*	1.11 ^{ns}	0.87 ^{ns}	46.26**	10.48**	852.16**	416.89**	397.48**	56.77**	139.89**
G×S(P)	(78)	2.29 ^{ns}	13.67**	14.11**	6.24 ^{ns}	0.80*	18.31**	13.30 ^{ns}	19.32 ^{ns}	3.23**	2.40**
Error	240	9.43	8.62	8.62	5.44	0.53	16.01	12.66	24.56	1.16	1.68

*Significant at the 0.05 level, **Highly significant at the 0.01 level; ns, non-significant; S.O.V., source of variation; df, degree of freedom; Ph, plant height; Df, day to flowering; Dm, day to maturity; Flr, flag leaf length-to-width ratio; PLL, panicle length; NTLr, number of tiller; NPL, number of panicle; Pet, percentage effective tillers; 72Cc, 72 days of chlorophyll content; 86Cc, 86 days of chlorophyll content.

TABLE 6 Yield and yield components by combined site and populations.

Source of variation	df	FG	UFG	PFG	TG/PL	GD	GW/PL	TGW/PT	1,000 GW	Y/T(ha)
Sites (S)	2	1,181.12*	6,116.45**	202.54**	25,836.21**	0.73**	0.80*	1,011.53**	530.31**	25.88**
Genotypes (G)	40	722.26**	2,144.67**	418.61**	2,462.46**	0.21**	0.86**	836.79**	27.96**	21.43**
Populations (P)	(1)	132.50 ^{ns}	15,802.14**	2,775.66**	11,557.78**	6.37**	17.51**	27,873.33**	789.47**	713.78**
G(P)	(39)	737.38**	1,794.48**	358.17**	2,229.25**	0.06**	0.43**	143.54*	8.44**	3.68*
G×S	80	388.78 ^{ns}	362.33 ^{ns}	90.08 ^{ns}	1,032.54 ^{ns}	0.04**	0.25 ^{ns}	115.86 ^{ns}	7.65**	16.88**
P×S	(2)	301.77 ^{ns}	51.40 ^{ns}	75.02 ^{ns}	158.48 ^{ns}	1.14**	0.57 ^{ns}	1,484.91**	72.57**	38.01**
G×S(P)	(78)	391.01 ^{ns}	370.31 ^{ns}	90.47 ^{ns}	1054.95 ^{ns}	0.02**	0.24 ^{ns}	80.75 ^{ns}	5.98**	2.07 ^{ns}
Error	240	312.7	471.05	84.88	808.51	0.02	0.21	89.56	3.17	2.29

*Significant at the 0.05 level, **Highly significant at the 0.01 level; ns, nonsignificant; S.O.V., source of variation; df, degree of freedom; Fg, filled grain; Ufg, unfilled grain; Pfg, percentage filled grain; Tg/pl, total grain per panicle; Gd, grain dimension; Gw/pl, grain weight per panicle; Tgw/pt, total grain weight per plant; 1,000 GW, thousand grain weight; Y/T(ha), yield in ton per hectare.

shown in Table 8. The grain yield (t/ha) in both populations demonstrated a significantly positive correlation with panicle length, filled grain, total grain per panicle, grain weight per panicle, total grain weight per plant, percentage effective tillers, and percentage filled grain, except for 1,000 grain weight and flag leaf ratio, which only showed a significantly positive correlation in the MR219-based population, and for number of tillers and number of panicle, which only showed a significantly positive correlation in the MR263-based population. A few characteristics in the MR219 population, such as unfilled grain, 72 days of chlorophyll, 86 days of chlorophyll, and plant height, and in the MR263 population, such as days to flowering and days to maturity, showed a significantly negative correlation with grain yield. Equally important, disease score exhibited a significantly positive correlation only with total grain per panicle. Unlike MR219, MR263 had few characteristics such as the number of tillers, number of panicles, percentage effective tillers, grain dimension, and 86 days of chlorophyll that correlated positively with disease score. A significantly negative correlation was detected between disease score and plant height for MR219, while panicle length, 1,000 grain weight, days to

flowering, days to maturity, and flag leaf ratio negatively correlated to disease score.

3.4 Cluster analysis and principal component analysis

The standardized morphological data of two populations, MR219-based (13 advanced lines) and MR263-based (26 advanced lines) populations, were subjected to cluster analysis. Three MR219 and four MR263 groups based on 21 morphological traits were derived from the analysis performed following the Euclidian distance method (Figures 2, 3). In the dendrogram, the 13 genotypes plus one check variety were grouped into three clusters based on 21 traits. Among the three clusters, cluster I had the largest number of genotypes (12). Clusters II and III had only one genotype each. The genotype in cluster III is the check variety. The MR263 population had four clusters with the largest number of genotypes (17) grouped in cluster II. In addition, cluster I had five lines, followed by cluster VI with three genotypes and only one genotype in cluster III (Figure 3). The patterns of cluster analysis were also authenticated by the principal component analysis (Figures 4, 5).

TABLE 7 Phenotypic and genetic coefficient of variation and heritability for blast disease severity across locations.

Traits	Disease severity
Mean DS	1.87
σ^2_p	0.72
σ^2_g	0.39
σ^2_e	0.33
PCV (%)	45.42
GCV (%)	33.43
h^2_b (%)	54.16
GA (%)	50.68

DS, disease score; σ^2_p , phenotypic variance; σ^2_g , genotypic variance; σ^2_e , error variance; PCV, phenotypic coefficient of variation; GCV, genotypic coefficient of variation; h^2_b , broad sense heritability; GA, genetic advance.

3.5 Genotype evaluation

The average-environment axis (AEA) view of the GGE biplot, also known as the average-environment coordination (AEC) view, is utilized for ranking genotypes in accordance with the stabilities and their average mean performance (Figure 6). The AEC ordinate (horizontal line) and the AEC abscissa (vertical line) are the two lines that make up this graph. The abscissa of the AEC is the single arrowed line that runs through the hypothetical average environment as well as through the origin of the biplot, which is defined by the average scores of PC1 and PC2 across all environments. This origin is indicated by the small circle at the

TABLE 8 Correlation between all traits for MR219 (below orthogonal matrix) and MR263 (above orthogonal matrix) populations.

	PIL	Fg	Ufg	Tgpl	Gwpl	NTr	NPI	1,000gw	Tgwpt	Ds	Pet	Pfg	Gd	72Cc	86Cc	PH	DF	DM	Flr	Tha
PIL	1	0.07	-0.21**	0.12	0.27**	-0.36**	-0.25**	0.45**	0.16*	-0.16*	0.04	0.17**	-0.32**	-0.30**	-0.30**	-0.17**	0.03	-0.07	0.35**	0.16*
Fg	0.16	1	0.02	0.45**	0.77**	0.06	0.11	-0.16*	0.36**	0.07	0.19**	0.11	0.08	-0.03	0.05	0.00	-0.20**	-0.19**	0	0.36**
Ufg	-0.54**	-0.28**	1	0.49**	-0.23**	0.21**	0.19**	-0.39**	-0.06	0.1	0.04	-0.69**	0.1	-0.07	0.15*	0.09	0.02	0.06	-0.08	-0.06
Tgpl	0.40**	0.56**	-0.09	1	0.24**	-0.17**	-0.03	-0.15*	0.18**	0.02	0.19**	-0.49**	-0.18**	-0.35**	-0.14*	-0.06	-0.18**	-0.25**	0.27**	0.18**
Gwpl	0.02	0.72**	-0.23**	0.30**	1	-0.1	-0.07	0.21**	0.26**	-0.06	0.08	0.29**	-0.04	-0.08	-0.13*	-0.04	-0.05	-0.06	0.05	0.26**
NTr	-0.50**	0.09	0.16	-0.29**	-0.03	1	0.93**	-0.55**	0.23**	0.27**	0.05	-0.14*	0.48**	0.55**	0.58**	0.29**	-0.08	0.1	-0.55**	0.23**
NPI	-0.39**	0.11	0.06	-0.20*	-0.04	0.96**	1	-0.50**	0.39**	0.32**	0.31**	-0.15*	0.34**	0.46**	0.50**	0.25**	-0.21**	-0.08	-0.39**	0.39**
1,000gw	0.34	-0.12	-0.27**	0.14	0.23*	-0.50**	-0.45**	1	0.07	-0.19**	-0.15*	0.45**	-0.33**	-0.33**	-0.45**	-0.22**	0.07	-0.05	0.37**	0.07
Tgwpt	0.22*	0.30**	-0.21*	0.33**	0.36**	-0.03	0.06	0.47**	1	0.12	0.38**	0.18**	-0.05	0.08	0.07	-0.08	-0.31**	-0.31**	0.08	1.00**
Ds	0.04	0.12	0.08	0.27**	0.07	-0.07	-0.08	0.01	-0.05	1	0.13*	-0.12	0.14*	0.06	0.28**	0.08	-0.23**	-0.19**	-0.16*	0.12
Pet	0.21*	-0.05	-0.18*	0.19*	0	-0.36**	-0.13	0.23**	0.24**	-0.05	1	-0.04	-0.05	0.01	0.01	0.02	-0.25**	-0.25**	0.08	0.38**
Pfg	0.19*	0.37**	-0.56**	0.07	0.25**	0.19*	0.24**	0.04	0.36**	-0.06	-0.02	1	-0.07	0.13*	0	-0.09	-0.03	-0.05	0.08	0.18**
Gd	0.04	0.07	-0.06	0.12	-0.03	-0.07	-0.05	-0.07	-0.16	0.04	0.01	0.05	1	0.30**	0.35**	0.25**	0.06	0.19**	-0.50**	-0.05
72Cc	-0.49**	0.01	0.32**	-0.34**	0.02	0.68**	0.60**	-0.46**	-0.27**	0.05	-0.34**	-0.04	-0.02	1	0.56**	0.21**	-0.23**	-0.09	-0.41**	0.09
86Cc	-0.46	0.06	0.29**	-0.26**	0.05	0.62**	0.56**	-0.46**	-0.24**	0.04	-0.29**	0.01	0.04	0.76**	1	0.29**	-0.15*	-0.02	-0.38**	0.07
PH	-0.17	-0.12	0.07	-0.32**	-0.09	0.29	0.20*	-0.25**	-0.2	-0.20*	-0.37**	-0.01	-0.07	0.21*	0.25**	1	0.05	0.11	-0.29**	-0.08
DF	-0.08	0.1	0.06	0.04	0.15	-0.14	-0.16	0.09	0.14	0.04	0.06	0.03	-0.15	-0.26**	-0.15	0.06	1	0.98**	-0.06	-0.31**
DM	-0.22*	0.09	0.15	-0.07	0.16	-0.01	-0.06	0	0.08	0.02	0	0.02	-0.17	-0.12	-0.03	0.11	0.98*	1	-0.21**	-0.31**
Flr	0.66**	0.13	-0.26**	0.56**	0	-0.58**	-0.48**	0.39**	0.23**	0.14	0.22*	-0.02	0.11	-0.54**	-0.46**	-0.42**	-0.14	-0.30**	1	0.08
Tha	0.22*	0.30**	-0.21*	0.33**	0.36**	-0.03	0.06	0.47**	1**	-0.05	0.24**	0.36**	-0.16	-0.27**	-0.24**	-0.19*	0.14	0.08	0.23**	1

*Significant at the 0.05 level, **Highly significant at the 0.01 level; ns, non-significant; S.O.V., source of variation; df, degree of freedom; PIL, panicle length; Fg, filled grain; Ufg, unfilled grain; Tgpl, total grain per panicle; Gwpl, grain weight per panicle; NTr, number of tiller; NPI, number of panicles; 1000gw, thousand grain weight; Tgwpt, total grain weight per plant; GS, grain dimension; Ds, disease score; Pet, percentage effective tillers; Pfg, percentage filled grain; Gd, grain dimension; 72Cc, 72 days of chlorophyll content; 86Cc, 86 days of chlorophyll content; PH, plant height; DF, days to flowering; DM, day to maturity; Flr, flag leaf length-to-width ratio; Tha, yield in ton per hectare.

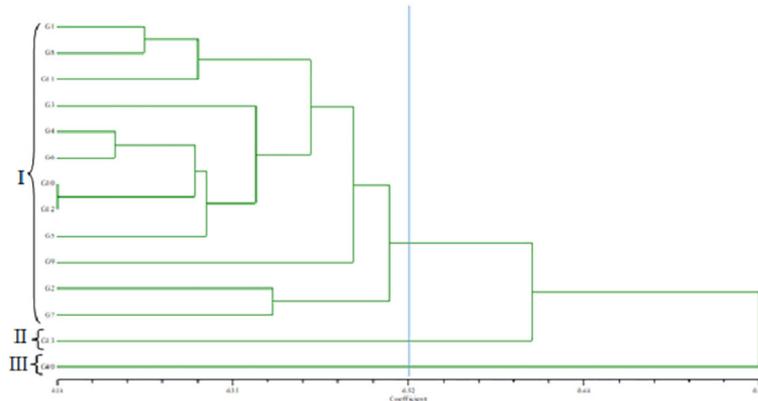


FIGURE 2 Dendrogram grouping the MR219-based population.

very end of the arrowhead (Figure 6). On the AEA abscissa, the direction of the arrowhead points in the direction of greater mean values for yield performance. In this study, the yield per hectare that was obtained in G14 was the highest, while the yield that was recorded in G29 was the lowest. The stability of the genotypes is shown by the line that cuts through the middle of the biplot and is drawn as an ordinate of the AEC. Greater variability or instability in either direction is indicative of genotype vectors that are further from the AEC. Therefore, the performance of the genotype is less variable or more stable across the studied contexts the shorter the distance or projection is from the AEA, and *vice versa*. Genotypes are then ranked based on their contact from the positive side of the line. The genotype that falls on the line is said to be most stable while the genotype with the longest contact with the AEC abscissa is considered to be unstable. An ideal genotype is the one having both high mean performance and perhaps high stability in a mega-

environment representing a target location. Therefore, genotype 14 is considered as the ideal genotype based on high mean and short vector (Figure 6).

4 Discussion

Rice cultivation in an open field is greatly exposed to blast disease, which hinders the possibility of obtaining high yield during disease infestation. Blast disease resistance plays a significant role in enhancing yield performance because the blast lesions that infected the paddy especially the leaves will reduce the photosynthesis rate of individual leaves. There would be an increase in crop yield where this process is contributing more than 90% of crop biomass (Makino, 2011). Titone et al. (2015) discovered that blast disease had a negative correlation

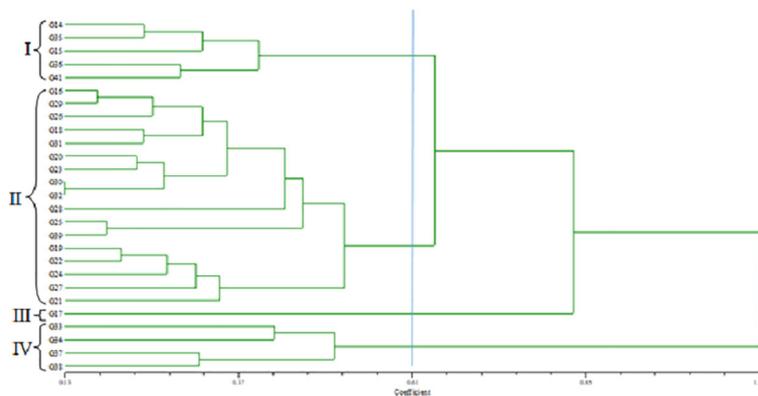


FIGURE 3 Dendrogram grouping the MR263-based population.

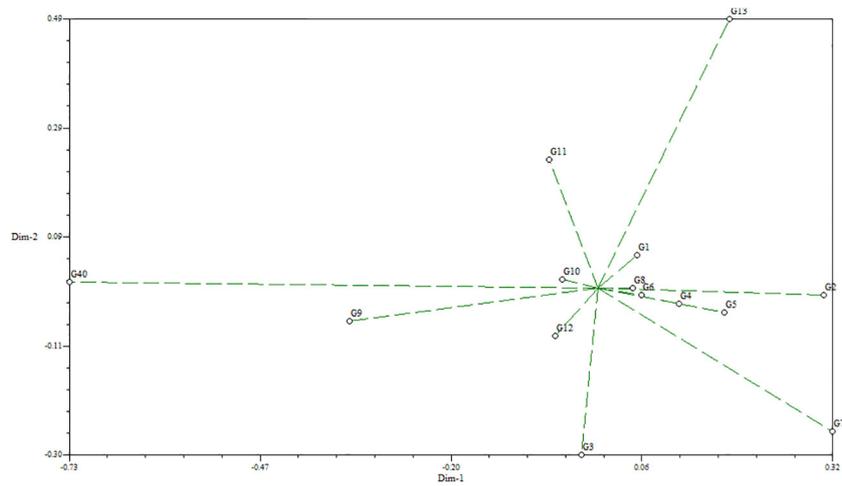


FIGURE 4
Principal component analysis for the MR219-based population.

with grain yield. This is because when the rice is severely affected by the blast, both grain yield and quality decreased significantly. In this study, all the 39 advance lines showed a score of 1–2, which indicates that all of them are resistant to blast disease. However, there is low correlation and no significant correlation between the disease resistance and yield. This is because the plant yield is also influenced by other factors such as the availability of nutrient for grain filling, water requirement, and many more. Significant differences were observed among the traits assessed in the 41 rice accessions, indicating the existence of variation in the population. In this regard, several reports have

been published concerning the phenotypic variation among rice genotypes (Halim et al., 2021). Similarly, Pandey et al. (2009) reported highly significant differences among 40 rice accessions with the use of 12 quantitative characteristics. Similarly, Rao (1991) discovered 95% differences among five rice populations using 20 morphological characteristics. Conforming to Acuña and Wade (2012), the environment influenced the actual performance of genotype under varying soil types. Similarly, Krisnawati and Adie (2018) also reported that genotype was unstable in yield performance when evaluated across different locations because the high-yielding genotypes are adapted to a

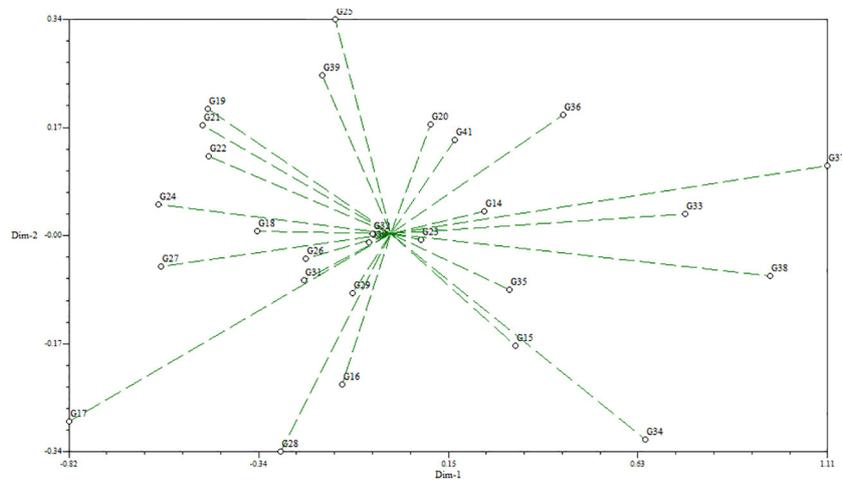
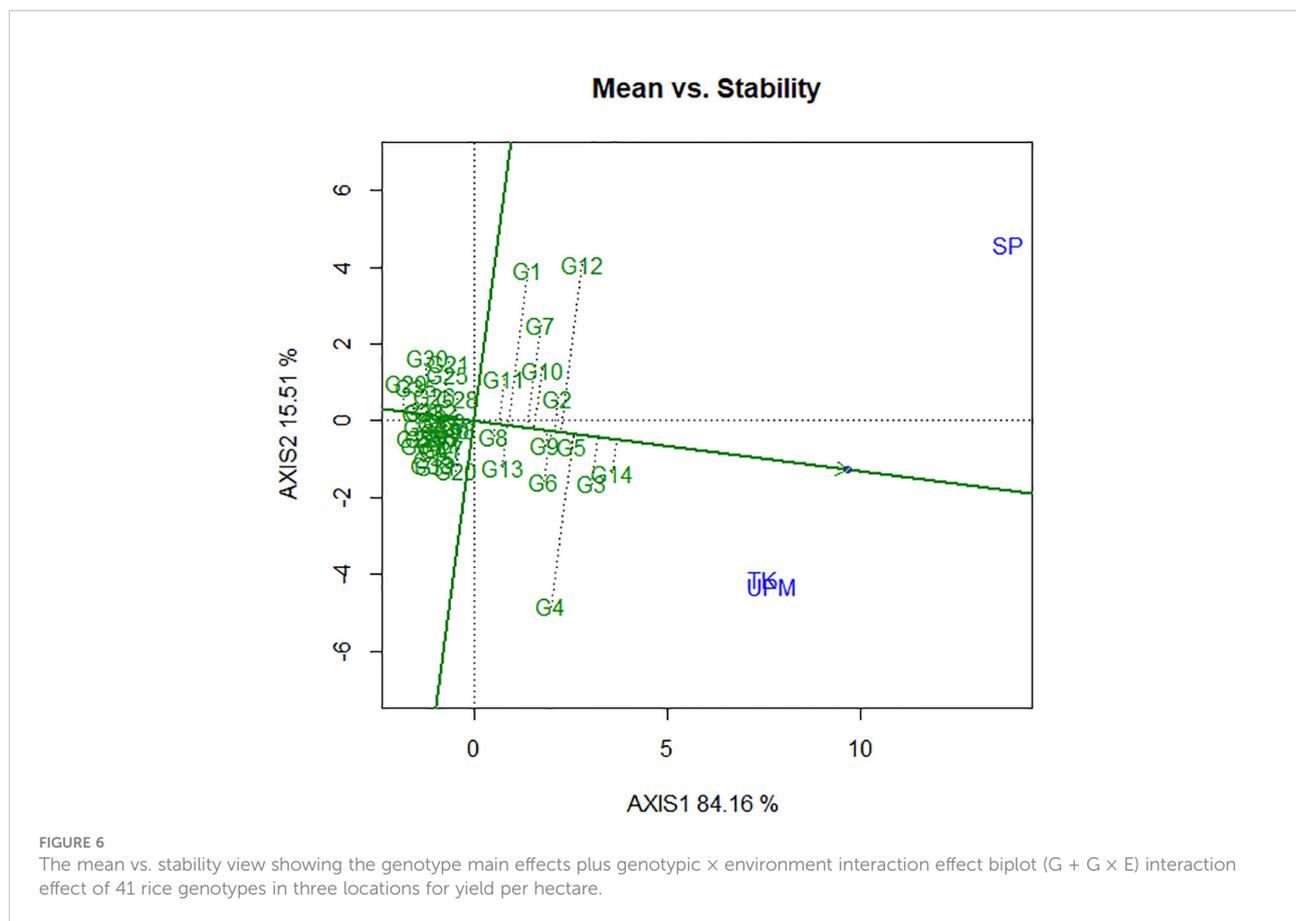


FIGURE 5
Principal component analysis for the MR263-based population.



specific environment. Furthermore, [Oladosu et al. \(2017\)](#) proved that the changes in environment significantly influenced the variation in grain yield of rice.

Significant difference was observed among vegetative traits, which include plant height, days to flowering, days to maturity, flag leaf ratio, panicle length, number of tillers, number of panicle, and percentage effective tillers. It was observed that all genotypes had intermediate height. This feature was as a result of a short internode. The importance of intermediate height could be attributed to effective assimilate partitioning at the expense of vegetative growth. Thus, instead of having tall plants, increase in yield compensates for the vegetative deficiency. This trait is also advantageous in protection against lodging. Although plant height is primarily governed by the genetic makeup, going by the pedigree of the advance breeding lines used in the study, both recurring parents had moderate height. Therefore, height in this regard is highly heritable. While height trait is highly influenced by environmental factors, as indirectly noted earlier, rice yield is indirectly related to its height because of sink competition for the limited photosynthates produced by delimited sources. Thus, what will be used for yield increase will be unnecessarily used for somatic cell enlargement, resulting in luxuriant vegetative growth and enhanced height. In this experiment, all of the

high-yielding varieties were found to be of intermediate height, suggesting that a moderate plant height is desirable when breeding for high-yielding varieties. Another essential factor for enhancing the yield of rice grain is flag leaves. This trait can increase about 41%–43% of the grain weight, which later leads to the yield increment ([Al-Tahir, 2014](#)). In this experiment, MR219 showed greater mean value in flag leaf ratio (21.55 cm) and higher yield (7.26 t/ha) compared to MR263 (flag leaf ratio, 18.12 cm; yield, 4.32 t/ha). Flag leaves play important roles in improving rice yield because these leaves are the source of assimilate production for the filling spikelets during the grain filling stage ([Wang et al., 2006](#); [Chukwu et al., 2022a](#); [Ahmed et al., 2022](#)). The larger the area of a flag leaf, the higher the yield because it intercepts the solar rays from the sun to manufacture food for the plant, and in addition, it is the last leaf to undergo senescence. Therefore, the flag leaf area was directly related to all vegetative traits such as plant height, days to flowering, days to maturity, flag leaf ratio, panicle length, number of tillers, number of panicle, and percentage effective tillers. Furthermore, the flag leaf has been found to be metabolically active to support higher grain yield. Corroborating our findings in this work, [Ashrafuzzaman et al. \(2009\)](#) clearly stated that yield components such as number of grains per panicle, 1000 grain

weight, total grain weight per hill, and yield per hectare positively correlated to the flag leaf area.

The number of tillers plays an important role in defining the yield of the rice grain because it has a direct relationship with the number of panicles. Therefore, fewer tillers produced fewer panicles, while excessive tillers cause high tiller abortions, small panicles, poor grain filling, and reduction in grain yield. The leaf area index and plant nitrogen status are the two primary factors that affect tiller production in rice crops. When an adequate nutrient supply exists, mitotic cell division is enhanced, and the growth of tillers and plant general vegetative life increases. In this work, the tiller production was between moderate and low levels. Thus, tiller abortion was not a problem during the production period. Percentage effective tiller is one of the important traits that contribute to the high yield in rice because this trait is precisely related to number of tillers that produced the panicle per unit ground area. Dutta et al. (2013) clearly stated that high yields in rice can be obtained when the genotypes manufacture a higher number of effective tillers per plant. However, this trait is highly affected by the environment in which two primary factors that influence its production are leaf area index and plant nitrogen status. The growth of tillers and vegetative life will increase if an adequate nutrient supply exists. In this study, percentage effective tillers in the MR219 population recorded a lower value (77%–90%) compared to the MR263 population (85%–93%); however, its production for both populations was at high levels. Thus, the number of effective tillers is dependent on the number of tillers produced, and this number is directly proportional to the panicles produced per unit area and, finally, depends on the variety (Hossain et al., 2008).

The panicle number is another major factor that has a direct influence on the yield. Therefore, yield could be increased when agronomic manipulation is used to increase the number of panicles produced per unit area. The panicle length is among the yield-contributing characteristics. The yield is proportional to the number of potential spikelets to be filled during the grain filling stage. Varieties with long panicle length, high number of total grains per panicle, and high percentage filled grain will contribute to the increase in rice yields. Ranawake et al. (2013) clearly reported that panicle length and number of spikelets per panicle have a positive and strong correlation between them, which means that the longer the panicle, the more rice grain can be accommodated during the grain filling stage. Days to flowering is one of the yield attribute traits in determining the final grain yield of rice. Adaptation of rice to different agro-climatologically zones such as temperature fluctuation, light day intensity, and short day condition results in variation in days to flowering. Ranawake et al. (2014) reported that the effect of days to flowering to the rice yield is positively correlated and maximum started from 80 days up to 90 days and becomes negative when exceeding 90 days. Another explanation to this phenomenon is the fact that higher sinking productivity was

exhibited by a higher score in filled grain percentage of those that start flowering earlier compared to late flowering, which reduced the dry matter accumulation in grain. Variation in days to flowering can be clearly seen in this study as the shortest days to flowering was recorded in Tanjung Karang (73 days) followed by UPM (77 days) and Seberang Perai (78 days). Seberang Perai (5.62 t/ha) recorded the highest value of yield in tons per hectare followed by the Tanjung Karang (5.39 t/ha) and UPM (4.97), and these data were supported by Ranawake et al. (2014) findings as 78 days is closer to the range of the maximum positive effects to the rice yield. Days to maturity is closely related to days to flowering. A variety that has a shorter flowering day will mature earlier than that which flowered late. Areas with minimal rainfall are encouraged to use a variety that matured earlier because they grow faster during the vegetative phase (Sabri et al., 2020; Sarif et al., 2020).

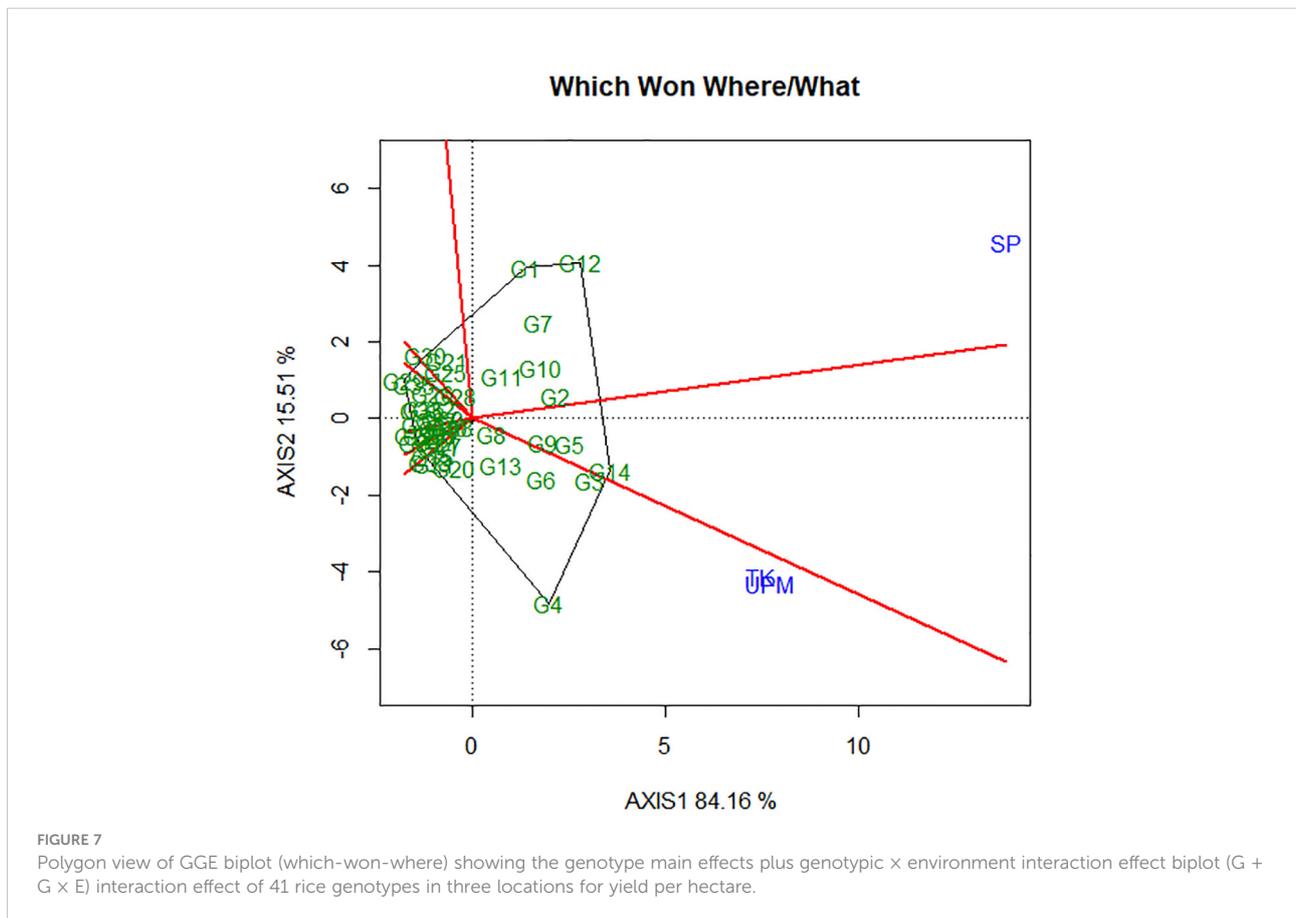
The grain filling rate among the varieties ranged from high (210) for G37 in Tanjung Karang to low (98) in G26 for UPM. An increase in the number of filled grains could be attributed to the efficient translocation of carbohydrates from the sources to the spikelets (sinks), consequently increasing the grain yield (Xu and Zhou, 2007). The varietal yield in this work was between high and low. Yield differences among different rice varieties have been reported any time a comparison is made between different varieties of rice in both field and glasshouse trials (Sabri et al., 2020). These differences are genetically based, although the environment greatly contributes to the manifestation of the inherent potential. In this work, the genotypes with higher numbers of effective tillers and higher numbers of grains per panicle also had higher yields. This result is consistent with the observation of Dutta et al. (2002). The result of the present study demonstrated that the 1,000 grain weight varied significantly among the tested varieties. Similar reports have been published by Ashrafuzzaman et al. (2009). The panicle length determines how many spikelets can be found in a panicle and, therefore, the number of filled spikelets and the final grain yield. Longer panicles result in more spikelets and filled grains if the other environmental conditions are not limiting. As found in this study, the panicle length positively correlated with the final yield. Agreement with this research finding can be found in the work of Chakraborty and Chakraborty (2010), who found a significant positive association between the panicle length and grain yield per hill.

The existence of genetic diversity is due to the inequality in the genetic structure of the individual in the population and distinct environment in which it is grown. The genetic variability found in plant germplasm and its estimates is an important factor for enlightening the gene pool and requires reliable heritability estimates in the effort to establish an effective breeding program. Tuhina-Khatun et al. (2015) stated that the appropriate selection and the magnitude of genetic improvement through the selection of the successive nature of the generation can be predicted with the knowledge of

heritability. The effective selection can be accomplished with the character having high heritability, and it can be done at the beginning of the generation in order to obtain more dominant genetic factors in the plant genetic appearance. In this study, disease score had a higher value for the genotypic coefficient of variation, heritability, and genetic advance for the MR219 population, while for the MR263 population, percentage effective tillers had a higher value. Similar to the analysis by population, the characteristic that recorded a high value for genotypic coefficient variation, heritability, and genetic advance in Tanjung Karang, Seberang Perai, and UPM was also disease score. Therefore, selection for these traits is likely to assemble extra additive genes leading to further advancement of their performance. The positive association between the yield component and vegetative characteristics could be very effective to perform simultaneous selection to develop a new variety. The positive correlation between final yield and filled grain, total grain per panicle, grain weight per panicle, number of tillers, number of panicles, total grain weight per plant, percentage effective tillers, days to flowering, and days to maturity implies that better exploration of these characteristics could be used to establish desired genotypes. [Chukwu et al.](#)

(2013) emphasized that the product of correlation is a tremendous value in the appraisal of the most effective procedures for selection of superior genotypes.

This study revealed the effectiveness of quantitative traits in grouping rice genotypes. Genetic divergence analysis among rice genotypes based on morphological traits can be used to classify and differentiate different genotypes in a population ([Franco et al., 2001](#)). This genetic divergence analysis also plays a vital role in selecting diverse genotypes for further improving rice varieties through breeding ([Shahidullah et al., 2010](#); [Oladosu et al., 2022](#)). Clustering analysis based on qualitative and quantitative traits grouped 13 advance lines with the check variety in the MR219 population and 26 advance lines plus the check variety in the MR263 population into three and four different groups, respectively. Similarly, [Ahmadikhah et al. \(2008\)](#) clustered 58 rice varieties into four groups using 18 morphological traits, whereas [Mazid et al. \(2013\)](#) had his 41 rice genotypes clustered into 6 groups based on 13 morphological traits while [Chukwu et al. \(2015\)](#) also utilized cluster analysis in characterizing germplasm. To obtain greater heterosis, genotypes having distant clusters could be used as parents for the next hybridization program.



The significant differences observed in yield across the environment or location demonstrate the importance of conducting research on rice varieties in several environments. This also demonstrates the challenges that rice breeders encounter when choosing which types of rice should be commercially available. According to the findings of [Oladosu et al. \(2017\)](#), ANOVA does not provide a comprehensive explanation of the GEI. In light of this, further statistical analyses, such as multivariate and univariate, are more useful in characterizing and comprehending the GEI. According to [Oladosu et al. \(2017\)](#), the evaluation of stability and adaptability is the primary consideration to make when assessing genotypes across a broad spectrum of environmental conditions based on mega-environment analysis and genotype evaluation. A polygonal representation of the 41 rice accessions that were investigated for this study in three distinct environments is presented in [Figure 7](#). In theory, the winning cultivar can be found at the vertex of the polygon, which is formed by the intersection of two sides. The perpendicular lines of the polygon create the boundary of the sector ([Figure 7](#)). In addition, [Yan et al. \(2000\)](#) observed that the genotype located at the sector's vertices had the maximum yield in the environment that corresponds to that particular sector. According to the findings of [Oladosu et al. \(2017\)](#) and [Hashim et al. \(2021\)](#), genotypes that are located inside the polygon and are closer to the origin are resistant to the effects of environmental variability. Hence, if all of the environmental markers cluster together in one area, this suggests that a single genotype is optimal for all environments. However, if the environmental indicators were distributed across the sectors, this suggests that various genotypes prevailed in various environments. For the purpose of this investigation, the GGE biplot was produced based on the yield performance of 41 rice accessions across three different environments. It was revealed that genotypes G4 and G14 have the most yield and the most stable performance in TK and UPM, while genotype G12 has the highest yield per hectare in the SP environment.

5 Conclusions

The variability observed in this study shows that there is ample scope for selection of superior rice genotypes. In addition, the significant and positive correlations observed in some yield and yield component traits indicated that these traits could be useful as selection criteria for simultaneous improvement towards high yield. The high values of heritability and genetic advance together with genotypic coefficient of variation for some important agronomic traits could also be utilized as selection criteria in rice improvement programs. Seberang Perai was the environment (location) that produced the highest average yield (5.62 t/ha), closely followed by Tanjung Karang (5.39 t/ha) and UPM (4.97 t/ha). Evaluation across the environments revealed

that from the MR219-based population, genotype G3 had the highest yield and resistance to blast. The genotype also performed well in other agro-morphological traits studied. On the other hand, from the MR263-based population, G21 performed best across the three environments investigated. The selected genotypes also showed better performance as compared to their respective parents with higher yield and more resistance to the blast disease. Future breeding programs could be designed using the selected genotypes as well as the three plus four clusters derived from this study as new lines for further breeding programs.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

Conceptualization, SS and MYR; methodology, SS and MYR; software, SS, OY, and MYR; validation, SS, MYR, and SC; formal analysis, SS and MYR; investigation, SS and MYR; resources, SS, MYR, MI, AR, SC, OY, and N'AH; data curation, SS and MYR; writing—original draft preparation, SS and SC; writing—review and editing, SS, MYR, MI, SC, and OY; visualization, SS and MYR; supervision, MYR, MI, and AR; project administration, SS and MYR; funding acquisition, SS and MYR. All authors have read and agreed to the published version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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