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Identification of efficient inbred testers to strengthen established heterotic groups in pearl millet (*Pennisetum glaucum* [L.] R. Br)

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Abstract

Pearl millet has two major heterotic groups, HGB (Heterotic Group B) and HGR (Heterotic Group R), each with unique genetic backgrounds and traits. Leveraging appropriate genetic resources is crucial for enhancing the potential of these heterotic groups in hybrid breeding programmes. Testers are essential in this context, determining the combining ability of new breeding lines and accurately assessing the performance and potential of parental lines in hybrid combinations. Two sets of test crosses were produced using line × tester mating design: Set 1 with six HGB testers crossed with new restorer lines and Set 2 with six HGR testers crossed with new seed parental lines, evaluated at multiple locations in India. Testers were evaluated for their effectiveness using multiple criteria, such as rank correlation analysis for line performance in hybrid combinations, discrimination ability, general combining ability, per se performance and Biplot analysis. These assessments determined their relative ranking, with HGB1-T3, HGB2-T3, HGR1-T1 and HGR2-T1 identified as efficient testers. The genetic analysis helps identify efficient testers for selecting superior genotypes, thereby enhancing heterotic group performance by incorporating appropriate new breeding material.

KEYWORDS
combining ability, discriminating ability, GGE Biplot, heterotic groups, rank correlation, tester efficiency

1 | INTRODUCTION

Pearl millet (*Pennisetum glaucum* [L.] R. Br., 2n = 2x = 14) is a vital staple crop grown in arid and semi-arid regions of Africa and Asia. It ranks as the sixth most significant cereal crop globally, occupying 32.11 million ha with a production of 30.46 million metric tons, mainly in Africa (19.72 million ha) and Asia (11.63 million ha) (FAO, 2020). India ranks first in the world in terms of area and production of pearl millet. This crop holds significant value due to its climate resilience and nutrient-rich grain, serving as human food and livestock fodder. Its grain features a balanced essential amino acid profile and is rich in vital micronutrients like iron, zinc, carbohydrates, proteins, lipids, fibre, vitamins, antioxidants and resistant starch. This nutritional profile makes pearl millet a promising candidate for addressing malnutrition and ensuring food and nutritional security. The commercial feasibility of hybrid pearl millet has been enabled by the cross-pollination breeding system, enhanced heterosis and the stable cytoplasmic-nuclear male sterility (CMS) along with its fertility restorers. Hybrid breeding significantly improved pearl millet cultivars, enhancing yield, disease resistance and overall productivity. Successful hybrid implementation in India elevated average productivity from 305 kg ha^{-1} in the 1950s to 1,132 kg ha^{-1} (Yadav & Rai, 2013), which is currently around

1,391 kg ha^{-1} (Directorate of Millets Development, 2021). Through collaboration with Indian public and private breeding programmes and ICRISAT-Asia's pearl millet breeding, the genetic diversity of hybrid parents was enhanced using potential breeding material. Currently, single-cross hybrids are extensively cultivated, covering more than 70% (about 6 million ha) of the total pearl millet production area in India. The utilization of pearl millet hybrids is on the rise in various parts of the world, including Eastern and Western African countries, Central Asian countries, Brazil and other regions.

In pearl millet hybrid breeding programmes, selecting suitable hybrid parental lines is a pivotal step. These lines contribute desired traits to offspring, and the success of the programme depends on choosing lines with complementary traits that result in superior hybrids. These lines should also belong to compatible heterotic groups to maximize hybrid performance. Genetic diversity and heterotic group information facilitate efficient inbred line development, enabling breeders to leverage complementary lines consistently to maximize hybrid breeding outcomes. Various studies have examined the molecular genetic diversity in pearl millet and have categorized breeding lines into genetic groups (Gupta et al., 2015; Kapila et al., 2008; Nepolean et al., 2012; Ramya et al., 2018; Singh et al., 2013, 2018; Stich et al., 2010). These investigations also suggested the presence of two primary pools in hybrid parents, corresponding to B-lines (seed parents) and R-lines (restorer parents). Gupta et al. (2020) assessed 320 R-lines and 260 B-lines from six major Indian breeding programmes. Based on heterotic performance and combining ability, they identified B-line heterotic groups (HGB-1 and HGB-2) and corresponding R-line groups (HGR-1 and HGR-2). To enhance heterotic groups, it is necessary to identify genotypes with good combining ability with the opposite heterotic group testers. When the established heterotic groups are available, selected elite genotypes from them can be used as testers to evaluate new breeding lines for their integration into heterotic groups (Melchinger & Gumber, 1998). The 'line × tester' analysis can be a useful approach in this context. In this process, testers play a pivotal role in elucidating the heterotic relationships of new inbred lines and assessing genotypic breeding values to enhance population improvement (Hallauer et al., 2010). Developing hybrid-oriented heterotic populations and enhancing parental line-combining ability are integral to pearl millet hybrid breeding. Investigations on identifying efficient inbred testers from heterotic groups are essential to enhance the selection efficiency and genetic gain in the pearl millet hybrid breeding programme.

The selection of the tester may encompass various options (Castellanos et al., 1998). These alternatives could include a wide genetic base (OPVs or Synthetics) versus a narrow genetic diversity (inbred line), a prevalence of high allele frequency versus low allele frequency, the consideration of general combining ability versus specific combining ability, prioritizing high yield versus low yield and the utilization of multiple testers versus a single tester. A plethora of maize-specific research has produced subtle delineations of the best or most convenient tester (Allison & Curnow, 1966; Guimarães et al., 2012; Hallauer, 1975; Hallauer et al., 1988; Hallauer & Miranda Filho, 1988; Matzinger, 1953; Pinto et al., 2004; Rawlings & Thompson, 1962; Russell, 1961; Smith, 1986). Zambezi et al. (1986) demonstrated the efficacy of inbred lines as testers, enhancing both the general combining ability (GCA) and specific combining ability (SCA) in maize breeding. Matzinger (1953) and Guimarães et al. (2012) suggested testers showing maximal genetic variances among testcrosses for evaluating inbred lines. Russell (1961) emphasized that greater genetic differences among testcrosses characterize an ideal tester parent. Smith (1986) emphasized the identification of lines with higher frequencies of favourable alleles by using testers that exhibit low allele frequencies or the absence of favourable alleles in test crosses. Rawlings and Thompson (1962) defined a proficient tester as efficiently differentiating among lines and accurately classifying them based on their hybrid performance, noting low-yielding testers with low frequency of dominant alleles as better discriminators of combining ability among maize inbred lines. Hallauer and Miranda Filho (1988) indicated that a homozygous recessive line or low allele frequency population for important traits can effectively serve as testers in hybrid breeding. Conversely, Hallauer and Carena (2009) recommended testers with high frequencies of favourable alleles to identify lines with superior specific combining ability. In recent years, tools such as the GGE biplot have proven valuable for evaluating combining ability effects and identifying proficient testers in line × tester studies. Akinwale et al. (2014), Yan (2014) and Annor et al. (2020) evaluated tester effectiveness by examining tester relationships and their discrimination ability in Maize.

Despite significant advancements in comprehending heterotic groups, testers, and their relevance in crop enhancement, especially in maize breeding, research addressing these aspects in pearl millet remains limited. Our study represents an initiative in this regard, with a primary focus on the identification of efficient inbred testers from the heterotic groups in pearl millet. In an exercise to enhance the existing heterotic groups in pearl millet, representative testers were identified from HGB and HGR and were systematically examined for their ability to access the combining ability of new breeding lines. The efficient tester for accessing the combining ability of new breeding lines was based on two main criteria for a good tester, that is, an effective tester should be able to rank inbred lines correctly for performance in hybrid combinations and increase the differences between test crosses for efficient discrimination (Rawlings & Thompson, 1962). This assessment of tester efficiency was based on several evaluative parameters, including the ability to accurately rank entries based on their relative performance in hybrid combinations via rank correlation analysis. Additionally, the discriminating capability of testers was quantified through the variance of testcross means, providing insights into their ability to distinguish poor combiners from good combiners. Moreover, other performance evaluations were conducted, encompassing parameters such as GCA, per se performance and the strategic employment of Genotype Main Effect plus Genotype × Environment Interaction (GGE) Biplot for line × tester data. Through genetic analyses of different sets of test crosses, this study strategically investigated efficient inbred testers to strengthen established heterotic groups in pearl millet. These evaluations collectively informed the ranking of testers based on their relative merit.

2 | MATERIAL AND METHODS

2.1 | Genetic material

The genetic material employed in this study comprised 24 newly developed inbred lines, divided into two categories: 12 seed parents (B-lines: B-L1 to B-L12) and 12 restorer parents (R-lines: R-L1 to R-L12), of diverse pedigrees, selected from the pearl millet breeding programme of ICRISAT Patancheru (Table 1). Concurrently, a set of 12 representative hybrid parental lines was chosen to act as testers. Among these testers, three were selected from each of the pearl millet heterotic groups, namely, HGB-1, HGB-2, HGR-1 and HGR-2. The selection of these candidate testers for the present study was based on their alignment with the established heterotic group, their combining ability/hybrid performance as representatives of their respective heterotic groups (Gupta et al., 2020) and their diverse pedigree (see Table S1).

2.2 | Development of testcross hybrids and their evaluation

In the rainy season of 2019, a total of 72 single crosses were produced using a line × tester design at ICRISAT, Patancheru. The experimental material included Set 1, formed by crossing six Heterotic Group B (HGB) testers with 12 Restorer lines (new R-lines), and Set 2, generated by crossing 12 new B-lines (B-L1 to B-L12) with six Heterotic Group R (HGR) testers. Subsequently, during the rainy season of 2020, an evaluation of these test crosses and their parental lines was conducted at four distinct locations in India. The majority of pearl millet hybrid cultivars in India are cultivated in better-endowed environments, covering about 4.5 to 5 million ha in northern and peninsular India during the rainy season, which extends from June to September. These locations were chosen to represent the major pearl millet cultivating regions in India. The evaluation sites included Jaipur and Alwar in Rajasthan, characterized by sandy loam soils with an annual total rainfall between 400 and 600 mm. The other two sites were Aurangabad and Pachora in Maharashtra, which featured heavy soils and experienced milder temperature conditions, with an annual rainfall of 400–700 mm.

To prevent competition among taller and vigorous hybrid genotypes against the parent lines, randomization processes were implemented for both the hybrids and parental genotypes. Subsequently, these groups were evaluated separately in adjacent blocks. The experimental design involved planting hybrid genotypes from Sets 1 and 2 in an alpha lattice design with two replications, while parental genotypes of Sets 1 and 2 parents followed a Randomized Block Design (RBD) with two replications (as described in Table 2). Each entry was planted with specific dimensions: two rows, each measuring 4 m in long, with a spacing of 50 cm between rows and 15 cm between plants.

TABLE 1 Restorer (Set 1) and seed parent (Set 2) of pearl millet lines and testers used in the study.

Set 1		Set 2	
Lines: Restorer (R) lines		Lines: Seed parental (B) lines	
Line code	Genotype name	Line code	Genotype name
R-L1	ICMR 14222	B-L1	ICMB 100693
R-L2	ICMR 15999	B-L2	ICMB 100694
R-L3	ICMR 101096	B-L3	ICMB 101925
R-L4	ICMR 101083	B-L4	ICMB 100128
R-L5	ICMR 100294	B-L5	ICMB 100713
R-L6	ICMR 101087	B-L6	ICMB 101926
R-L7	ICMR 101089	B-L7	ICMB 100551
R-L8	ICMR 101093	B-L8	ICMB 100524
R-L9	ICMR 13777	B-L9	ICMB 100741
R-L10	ICMR 100390	B-L10	ICMB 100743
R-L11	ICMR 101094	B-L11	ICMB 12444
R-L12	ICMR 101129	B-L12	ICMB 14111
Heterotic Group B testers		Heterotic Group R testers	
HGB1-T1		HGR1-T1	
HGB1-T2		HGR1-T2	
HGB1-T3		HGR1-T3	
HGB2-T1		HGR2-T1	
HGB2-T2		HGR2-T2	
HGB2-T3		HGR2-T3	

TABLE 2 Evaluation of parental lines and their testcross hybrids.

Set and description	Name or designation	Experimental design
Set 1 parents:	12 R-lines (R-L1 to R-L12) and 6 HGB inbred testers (HGB1-T1, HGB1-T2, HGB1-T3, HGB2-T1, HGB2-T2 & HGB2-T3)	Randomized block design
Set 1 testcrosses:	6 HGB testers (HGB1-T1, HGB1-T2, HGB1-T3, HGB2-T1, HGB2-T2 & HGB2-T3) × 12 R-lines (R-L1 to R-L12)	Alpha lattice design with 15 blocks and 5 entries in each block (including 3 checks)
Set 2 parents:	12 B-lines (B-L1 to B-L12) and 6 HGR inbred testers (HGR1-T1, HGR1-T2, HGR1-T3, HGR2-T1, HGR2-T2 & HGR2-T3)	Randomized block design
Set 2 testcrosses:	12 B-lines (B-L1 to B-L12) × 6 HGR-line testers (HGR1-T1, HGR1-T2, HGR1-T3, HGR2-T1, HGR2-T2 & HGR2-T3)	Alpha lattice design with 15 blocks and 5 entries in each block (including 3 checks)

The lines and the testers chosen were the advanced breeding lines that underwent rigorous screening for tolerance to major biotic stresses like downey mildew and blast during generation advancement and designation into hybrid parental lines, which is a regular step in line development in pearl millet breeding. All the genetic material investigated belongs to a market segment/product profile that requires medium to late-maturing hybrid parental lines, constituting a major market segment in India. Hence, our study focused on grain yield, an important economic trait.

2.3 | Agronomic management practices

Standard agronomic practices (Yadav et al., 2012) were followed across all locations to ensure optimal crop growth. Initial field preparation included applying 100 kg of Diammonium Phosphate (DAP) containing 18% nitrogen (N) and 46% phosphorus (P). This was supplemented by a top dressing of 100 kg urea with 46% N, meeting recommended N and P levels. Irrigation was provided after sowing and as needed throughout the season. Seedling thinning occurred 15 days after sowing to maintain uniform spacing at 15 cm intervals. Cultural practices, including weeding, pest and disease control, were consistently applied. Harvesting involved collecting all panicles per plot. Harvested material was sun-dried for 10 to 15 days, then threshed and quantified for grain yield in kilogrammes and eventually converted to yield per hectare (kg ha^{-1}).

2.4 | Mating design, crosses and genetic analysis

The selected new inbred lines were derived from B × B and R × R bi-parental crosses using a trait-based breeding approach at ICRISAT. Preliminary information suggests the existence of B-lines and R-lines as two separate hybrid parental pools in pearl millet (Gupta et al., 2015, 2020; Nepolean et al., 2012; Ramya et al., 2018; Singh et al., 2013, 2018). Elite genotypes from established heterotic groups were used as testers to evaluate the combining ability of new breeding lines. The line × tester mating design was employed, with new inbred lines directly crossed with their opposite heterotic group testers. Lines exhibiting high general combining ability (GCA) were considered for heterotic group enhancement. High GCA indicates optimal performance of a new line in hybrid combinations with diverse inbred testers belonging to the opposite heterotic group. If a new B line shows high GCA with a set of heterotic group R testers, it represents HGB, and vice versa for new R lines, indicating HGR. The relative efficiency of HGB and HGR testers was systematically examined for their ability to assess the combining ability of new breeding lines, based on various evaluative parameters, including the ability to accurately rank entries based on their relative performance in hybrid combinations via rank correlation analysis. Other criteria include discrimination ability, general combining ability, per se performance and GGE Biplot analysis of line × tester data.

2.5 | Statistical analyses

Combined analysis of variance was carried out using PROC MIXED (SAS v9.4, SAS Institute Inc., 2018), considering location, genotypes and replication as fixed and block as random factor. In order to pool the data across locations and to make the error variance homogeneous, individual location variances were estimated and modelled to error distribution using the residual maximum likelihood (REML) procedure. The procedure of the line × tester analysis according to Kempthorne (1957) was used for estimating general and specific combining ability effects. The variance due to general combining ability (σ^2GCA) and variance due to specific combining ability (σ^2SCA) were estimated as described by Singh and Chaudhary (1977). The predictability ratio was computed following Baker (1978) to estimate the relative importance of GCA in explaining hybrid performance. The variance of the testcross mean was calculated as the average of the squared differences between the individual cross and the mean value of the testcrosses for each of the testers. It is a measure of the variation among the testcross progenies (F_1's; half-sibs) of a tester. The coefficient of concordance (W), a rank correlation technique introduced by Kendall and Smith (1939), was used to assess the degree of agreement in ranking among the testers. This coefficient, varying between 0 and 1, quantifies the level of agreement among tester's rankings. A value of 0 indicates an absence of similarity in ranking, while a value of 1 signifies complete agreement among testers. Spearman's rank correlation coefficients (Spearman, 1987) were used to assess the correlation between the rankings of inbred lines based on their testcross performance for grain yield (kg ha^{-1}). This analysis involved calculating these coefficients for all pairs of testers and comparing them to the GCA ranking. The efficiency assessment of testers also involved a (GGE) biplot analysis of mean grain yield values across different locations. This analytical framework, outlined by Yan and Hunt (2002) and as elucidated by Yan (2014), Akinwale et al. (2014), Badu-Apraku and Akinwale (2019) and Annor et al. (2020), was utilized to gauge tester efficiency.

3 | RESULTS

3.1 | Analysis of variance for test crosses of HGB and HGR testers

This study involved the comprehensive analysis of two sets of test crosses and their corresponding parental lines to identify efficient inbred testers from heterotic groups. The ANOVA conducted for grain yield (kg ha^{-1}) in the test crosses of Heterotic Group B (HGB) and Heterotic Group R (HGR) is presented in Table 3. Combined ANOVA for combining ability effects across two testcross sets showed significant variance ($p < .05$) attributed to location, suggesting materials were evaluated across diverse environments. Utilizing data from diverse locations enhances statistical power, strengthens reliability and aids in identifying good combiners across varied

TABLE 3 Analysis of variance for grain yield (kg ha^{-1}) of heterotic group-B (HGB) and heterotic group-R (HGR) test crosses and their parents.

Source of variation	DF	HGB (Set 1)		HGR (Set 2)	
		F value	*P* value	*F* value	*P* value
Parents					
Environment	3	42.43	<.0001	26.57	<.0001
Replication (Loc.)	4	21.87	<.0001	2.46	.0724
Genotype	17	10.93	<.0001	9.57	<.0001
Location × genotype	51	3.88	.0015	3.95	.0006
Hybrids					
Loc	3	17.39	<.0001	9.29	.0003
REP (Loc)	4	10	.0003	3.51	.0235
TRT	74	2.42	<.0001	3.16	<.0001
Hybrids	71	2.46	<.0001	3.07	<.0001
Hybrid-line	11	2.45	.0144	4.91	<.0001
Hybrid-tester	5	2.98	.0189	3.57	.0072
Hybrid-line × tester	55	1.76	.0034	1.75	.0034
Checks	2	1.85	.1611	4.54	.0118
Orthogonal contrasts for tester comparison					
[HG(B/R)1-T1 vs. HG(B/R)1-T2][a]	1	6.4	.0123	9.83	.002
[HG(B/R)1-T1 vs. HG(B/R)1-T3]	1	2.53	.1134	9.13	.0028
[HG(B/R)1-T2 vs. HG(B/R)1-T3]	1	1	.3175	0.03	.8742
[HG(B/R)2-T1 vs. HG(B/R)1-T1]	1	0.87	.3533	9.16	.0028
[HG(B/R)2-T1 vs. HG(B/R)1-T2]	1	2.6	.1088	0.01	.9407
[HG(B/R)2-T1 vs. HG(B/R)1-T3]	1	0.42	.5202	0.01	.9357
[HG(B/R)2-T1 vs. HG(B/R)2-T2]	1	9.41	.0025	13.18	.0004
[HG(B/R)2-T1 vs. HG(B/R)2-T3]	1	0.37	.5451	0.004	.9519
[HG(B/R)2-T2 vs. HG(B/R)1-T1]	1	4.4	.0372	0.39	.5351
[HG(B/R)2-T2 vs. HG(B/R)1-T2]	1	22.29	<.0001	13.92	.0002
[HG(B/R)2-T2 vs. HG(B/R)1-T3]	1	14.53	.0002	13.26	.0003
[HG(B/R)2-T2 vs. HG(B/R)2-T3]	1	6.24	.0133	14.6	.0002
[HG(B/R)2-T3 vs. HG(B/R)1-T1]	1	0.12	.7336	10.24	.0016
[HG(B/R)2-T3 vs. HG(B/R)1-T2]	1	5.02	.0262	0.001	.9873
[HG(B/R)2-T3 vs. HG(B/R)1-T3]	1	1.64	.2015	0.02	.8827
Variance component					
VAR_GCA		25,789.13		43,320.91	
VAR_SCA		58,553.71		51,421.4	
Predictability ratio		0.46833		0.62755	
CV %		18.07		18.24	

Abbreviations: CV, coefficient of variation; DF, degrees of freedom; Loc., location; REP, replication; TRT, treatment; VAR_GCA, variance of general combining ability; VAR_SCA, variance of specific combining ability.

[a]The notation B/R in 'HG(B/R)1-T1 versus HG(B/R)1-T2' is used to represent comparisons involving testers HGB1-T1 versus HGB1-T2 and for HGR1-T1 versus HGR1-T2.

growing conditions. Significant interactions were found among line × environment, tester × environment, and line × tester × environment for grain yield. The presence of significant genetic variation in both sets of testcrosses, demonstrated by the high significance ($p < .05$) of genotypic variation due to hybrids, lines and testers, underlined the substantial genetic diversity within parents and hybrids for grain yield productivity. The variance attributed to both GCA and SCA effects was highly significant within the test crosses, emphasizing the importance of both additive and non-additive genetic effects in determining grain yield productivity. Furthermore, the orthogonal comparisons conducted in the ANOVA for HGB and HGR tester pairs demonstrated a strong statistical significance. This highlights significant differences between the pairs of testers within both heterotic groups.

The variation in test-cross means for testers belonging to heterotic group B (HGB) and heterotic group R (HGR), evaluated for grain yield, is depicted graphically in Figure 1a,b, respectively. Tables 4 and 5 present a comprehensive summary of the extracted data to identify suitable testers from heterotic groups B and R for grain yield. The estimation of variances of the test crosses mean for the Heterotic Group B (HGB) testers indicated that HGB1-T3 and HGB2-T1 exhibited the highest variances of the testcross mean. HGB2-T3, HGB2-T2, HGB1-T1 and HGB1-T2 closely followed these. Similarly, within Heterotic Group R (HGR), HGR2-T1 and HGR1-T1 showed the highest variances of test cross mean. Subsequently, HGR-2 T3, HGR-1 T2, HGR-2 T2 and HGR-1 T3 followed suit in terms of their variances of testcross mean. The yield variations of test crosses indicate the difference between the highest and lowest observed grain yield values among the test crosses. The range of grain yield values among the test crosses was wide. This indicates significant variability in the test lines' performance in crosses with appropriate testers. A broader range suggests that certain lines exhibited the highest yields in their test crosses, while others yielded the lowest. This variation can be attributed to genetic differences among the test lines, enabling them to transmit positive favourable alleles to their resulting test crosses with an appropriate tester. This, in turn, indicates the tester's ability to

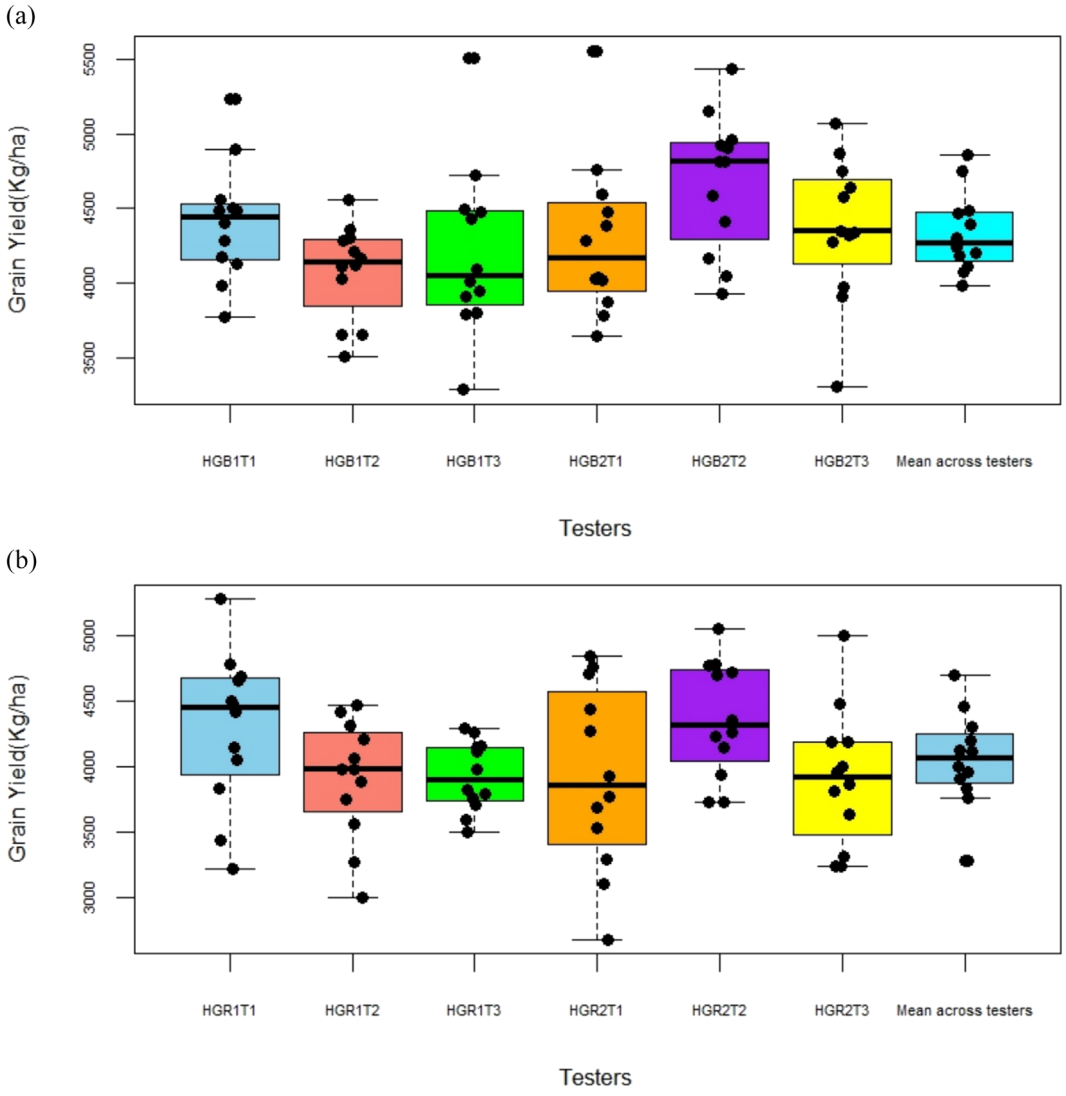


FIGURE 1 (a) Graphical representation depicting the variation in testcross means for six heterotic group B (HGB) testers evaluated for grain yield. Abbreviations: HGB1-T1, heterotic group B1 tester 1; HGB1-T2, heterotic group B1 tester 2; HGB1-T3, heterotic group B1 tester 3; HGB2-T1, heterotic group B2 tester 1; HGB2-T2, heterotic group B2 tester 2; HGB2-T3, heterotic group B2 tester 3. *Note*: The black dots in the figure represent the relative performance of restorer parental lines in test crosses with heterotic group B (HGB) testers for grain yield. The mean across testers represent the average performance of restorer line across six heterotic group B (HGB) testers for grain yield. (b) Graphical representation depicting the variation in testcross means for six heterotic group R (HGR) testers evaluated for grain yield. Abbreviations: HGR1-T1, heterotic group R1 tester 1; HGR1-T2, heterotic group R1 tester 2; HGR1-T3, heterotic group R1 tester 3; HGR2-T1, heterotic group R2 tester 1; HGR2-T2, heterotic group R2 tester 2; HGR2-T3, heterotic group R2 tester 3. *Note*: The black dots in the figure represent the relative performance of seed parental lines in test crosses with heterotic group R (HGR) testers for grain yield. The mean across testers represents the average performance of seed parental line across six heterotic group R (HGR) testers for grain yield.

TABLE 4 Relative ranks of test crosses, per se performance, variance of test cross means, correlation coefficients and combining ability effect estimates for identifying efficient inbred testers from heterotic group B (HGB) for grain yield (GY) (kg ha^{-1}).

		Across 6 tester			HGB1 T1				HGB1 T2			
		Testcross			Testcross				Testcross			
New R line	Per se grain yield (kg ha^{-1})	Mean GY	GCA^{L}	Rank	GY	SCA	ts gca	Rank	GY	SCA	ts gca	Rank
R_L1	2,980	4,749	410.87*	**2**	5,236	415.4	69	**1**	4,209	−281.44	11	**5**
R_L2	4,413	4,398	59.62	**5**	4,490	20.27	7	**5**	4,358	219.17	23	**2**
R_L3	3,311	4,070	−268.15*	**11**	4,507	365.78	8	**4**	3,507	−304.13	−48	**12**
R_L4	2,782	3,983	−355.19*	**12**	4,561	506.48	13	**3**	4,032	308.44	−4	**9**
R_L5	3,000	4,486	147.67	**3**	4,896	338.5	41	**2**	3,650	−576.51*	−36	**11**
R_L6	2,068	4,186	−151.67	**9**	4,177	−80.94	−19	**9**	4,282	354.34	17	**4**
R_L7	3,006	4,471	132.77	**4**	4,283	−259.61	−11	**8**	4,305	92.63	19	**3**
R_L8	2,242	4,202	−136.03	**8**	3,983	−291.03	−36	**11**	4,112	168.83	3	**8**
R_L9	3,640	4,302	−35.97	**6**	3,770	−603.43*	−53	**12**	3,655	−388.45	−35	**10**
R_L10	2,620	4,864	525.72*	**1**	4,485	−451.02	6	**6**	4,560	−44.71	40	**1**
R_L11	3,274	4,234	−103.46	**7**	4,402	95.95	−1	**7**	4,116	140.41	3	**7**
R_L12	3,433	4,112	−226.20*	**10**	4,127	−56.34	−24	**10**	4,164	311.43	7	**6**
Tester per se grain yield (kg ha^{-1})						1,562				2,509		
Mean of testcrosses (kg ha^{-1})						4,410				4,079		
Range of testcrosses (kg ha^{-1})						3,370–5,236				3,507–4,560		
Variance of testcross mean						154,979				101,924		
GCA^{T} effect						71.89				−258.77*		
Spearman's correlation coefficient (for ranks of GCA)						.238				.476		

Note: ts gca is tester-specific GCA calculated as the deviation of an individual testcross grain yield from the overall mean of the 12 test crosses belonging to a particular tester.
Abbreviations: GCA^{L}, general combining ability effect for lines; GCA^{T}, general combining ability effect for testers; GY, grain yield (kg ha^{-1}); SCA, specific combining ability effect; ts gca, tester-specific general combining ability effect.
*Significant at .05 level of probability.

TABLE 4 (Continued)

New R line	HGB1 T3				HGB2 T1				HGB2 T2				HGB2 T3			
	Testcross				Testcross				Testcross				Testcross			
	GY	SCA	ts gca	Rank	GY	SCA	ts gca	Rank	GY	SCA	ts gca	Rank	GY	SCA	ts gca	Rank
R_L1	4,728	110.8	44	**2**	4,015	−684.07*	−23	**9**	5,437	346.98	63	**1**	4,869	92.32	42	**2**
R_L2	4,491	225.6	24	**3**	4,481	133.8	16	**4**	3,924	−814.86*	−63	**12**	4,641	216.02	23	**4**
R_L3	3,792	−145.87	−35	**11**	3,875	−145.01	−34	**10**	4,417	6.56	−22	**9**	4,320	222.68	−4	**8**
R_L4	3,797	−53.49	−34	**10**	4,031	98.45	−21	**8**	4,167	−156.3	−43	**10**	3,307	−703.57*	−88	**12**
R_L5	4,479	125.6	23	**4**	4,388	−47.57	8	**5**	5,156	330.03	40	**2**	4,343	−17.05	−2	**7**
R_L6	3,287	−767.28*	−77	**12**	4,041	−94.83	−21	**7**	4,582	55.39	−8	**8**	4,747	533.31	32	**3**
R_L7	4,092	−247.12	−10	**6**	4,758	337.18	39	**2**	4,811	−.15	11	**7**	4,576	77.07	18	**5**
R_L8	4,435	364.72	19	**5**	4,285	132.75	0	**6**	4,047	−496.07	−53	**11**	4,351	120.8	−1	**6**
R_L9	4,009	−160.65	−16	**7**	5,558	1,306.08*	106	**1**	4,907	264.23	19	**5**	3,912	−417.77	−38	**11**
R_L10	5,508	776.64*	109	**1**	4,600	−213.31	26	**3**	4,959	−245.94	23	**3**	5,070	178.34	59	**1**
R_L11	3,911	−191.31	−25	**9**	3,778	−406.16	−43	**11**	4,921	345.28	20	**4**	4,278	15.83	−7	**9**
R_L12	3,942	−37.64	−22	**8**	3,644	−417.31	−54	**12**	4,817	364.84	12	**6**	3,975	−164.98	−33	**10**
Tester per se grain yield (kg ha^{-1})	2,890				2,621				2,257				2,443			
Mean of testcrosses (kg ha^{-1})	4,206				4,288				4,679				4,366			
Range of testcrosses (kg ha^{-1})	3,287–5,508				3,644–5,558				3,924–5,437				3,307–5,070			
Variance of testcross mean	324,342				274,989				212,497				227,723			
GCA^{T} effect	−131.86				−49.94				340.82*				27.86			
Spearman's correlation coefficient (for ranks of GCA)	.860*				.538				.622*				.664*			

Note: ts gca is tester-specific GCA calculated as the deviation of an individual testcross grain yield from the overall mean of the 12 test crosses belonging to a particular tester.

Abbreviations: GCA^{L}, general combining ability effect for lines; GCA^{T}, general combining ability effect for testers; GY, grain yield (kg ha^{-1}); SCA, specific combining ability effect; ts gca, tester-specific general combining ability effect.

*Significant at .05 level of probability.

TABLE 5 Relative ranks of test crosses, per se performance, variance of test cross means, correlation coefficients and combining ability effect estimates for identifying efficient inbred testers from heterotic group R (HGR) for grain yield (GY) (kg ha^{-1}).

		Across 6 testers			HGR1 T1				HGR1 T2			
		Testcross			Testcross				Testcross			
New B line	Per se grain yield (kg ha^{-1})	Mean GY	GCA^{L}	Rank	Mean GY	SCA	ts gca	Rank	Mean GY	SCA	ts gca	Rank
B_L1	2,091	4,695	642.46*	**1**	5,277	346.29	82	**1**	4,467	−84.13	47	**1**
B_L2	2,593	4,120	66.71	**5**	4,410	54.47	10	**7**	4,205	229.5	25	**4**
B_L3	1,086	3,765	−287.39*	**11**	4,143	141.74	−12	**8**	3,982	360.99	6	**6**
B_L4	2,422	3,910	−142.44	**9**	4,472	326.16	15	**6**	4,066	300.26	13	**5**
B_L5	2,107	4,004	−49.26	**7**	4,494	255.09	17	**5**	3,890	30.96	−2	**8**
B_L6	2,475	4,192	139.54	**4**	4,053	−375.41	−20	**9**	4,416	367.6	42	**2**
B_L7	2,596	4,299	246.00*	**3**	4,686	151.55	33	**3**	4,306	151.39	33	**3**
B_L8	1,891	4,454	401.67*	**2**	4,778	87.72	41	**2**	3,746	−564.24*	−14	**9**
B_L9	1,459	4,116	63.53	**6**	4,653	301.19	30	**4**	3,559	−412.53	−29	**10**
B_L10	2,294	3,835	−217.60*	**10**	3,831	−239.78	−38	**10**	3,981	290.56	6	**7**
B_L11	1,674	3,281	−771.85*	**12**	3,440	−77.04	−71	**11**	3,005	−131.61	−75	**12**
B_L12	2,208	3,961	−91.39	**8**	3,225	−972.00*	−89	**12**	3,278	−538.76*	−53	**11**
Tester per se grain yield (kg ha^{-1})						2,386				3,844		
Mean of testcrosses (kg ha^{-1})						4,289				3,908		
Range of testcrosses (kg ha^{-1})						3,225–5,277				3,005–4,467		
Variance of testcross mean						339,680				201,103		
GCA^{T} effect						235.82*				−144.42		
Spearman's correlation coefficient (for ranks of GCA)						.748*				.545		

Note: ts gca is tester-specific GCA calculated as the deviation of an individual testcross grain yield from the overall mean of the 12 test crosses belonging to a particular tester.
Abbreviations: GCA^{L}, general combining ability effect for lines; GCA^{T}, general combining ability effect for testers; GY, grain yield (kg ha^{-1}); SCA, specific combining ability effect; ts gca, tester-specific general combining ability effect.
*Significant at .05 level of probability.

TABLE 5 (Continued)

New B line	HGR1 T3 Testcross Mean GY	HGR1 T3 Testcross SCA	HGR1 T3 Testcross ts gca	HGR1 T3 Testcross Rank	HGR2 T1 Testcross Mean GY	HGR2 T1 Testcross SCA	HGR2 T1 Testcross ts gca	HGR2 T1 Testcross Rank	HGR2 T2 Testcross Mean GY	HGR2 T2 Testcross SCA	HGR2 T2 Testcross ts gca	HGR2 T2 Testcross Rank	HGR2 T3 Testcross Mean GY	HGR2 T3 Testcross SCA	HGR2 T3 Testcross ts gca	HGR2 T3 Testcross Rank
B_L1	3,977	−592.77*	4	**6**	4,760	20.05	70	**2**	4,694	−313.18	27	**5**	4,996	443.74	91	**1**
B_L2	3,599	−394.98	−27	**11**	3,932	−52.58	1	**6**	4,764	332.26	33	**3**	3,808	−168.68	−9	**8**
B_L3	3,708	68.03	−18	**10**	3,290	−339.68	−52	**10**	4,227	149.23	−12	**8**	3,243	−380.31	−56	**12**
B_L4	3,789	3.89	−12	**8**	3,769	−6.28	−12	**7**	3,727	−495.63	−53	**12**	3,639	−128.41	−23	**9**
B_L5	4,145	267.17	18	**4**	3,531	−337.57	−32	**9**	4,716	400.63	29	**4**	3,245	−616.28*	−55	**11**
B_L6	4,152	85.26	19	**3**	4,272	215.45	30	**5**	4,263	−240.96	−9	**7**	3,998	−51.94	7	**5**
B_L7	4,294	120.19	31	**1**	4,702	538.10*	65	**3**	3,936	−674.40*	−36	**10**	3,869	−286.84	−3	**7**
B_L8	4,116	−212.87	16	**5**	4,838	518.79*	77	**1**	4,777	10.34	34	**2**	4,472	160.25	47	**2**
B_L9	4,255	263.98	27	**2**	3,692	−288.84	−19	**8**	4,349	−79.63	−1	**6**	4,190	215.83	23	**3**
B_L10	3,764	54.68	−14	**9**	3,105	−594.85*	−68	**11**	4,145	−2.27	−18	**9**	4,184	491.65	23	**4**
B_L11	3,507	351.47	−35	**12**	2,683	−462.21	−103	**12**	3,733	139.95	−53	**11**	3,318	179.43	−49	**10**
B_L12	3,822	−14.06	−9	**7**	4,436	609.61*	43	**4**	5,047	773.66*	57	**1**	3,960	141.55	4	**6**
Tester per se grain yield (kg ha^{-1})		2,250				1,797				3,480				2,297		
Mean of testcrosses (kg ha^{-1})		3,927				3,917				4,365				3,910		
Range of testcrosses (kg ha^{-1})		3,507–4,294				2,683–4,838				3,727–5,047				3,243–4,996		
Variance of testcross mean		69,722				487,759				190,382				271,279		
GCA^{T} effect		−125.44				−135.31				311.89*				−142.54		
Spearman's correlation coefficient (for ranks of GCA)		.636*				.881*				.455				.664*		

Note: ts gca is tester-specific GCA calculated as the deviation of an individual testcross grain yield from the overall mean of the 12 test crosses belonging to a particular tester.

Abbreviations: GCA^{L}, general combining ability effect for lines; GCA^{T}, general combining ability effect for testers; GY, grain yield (kg ha^{-1}); SCA, specific combining ability effect; ts gca, tester-specific general combining ability effect.

*Significant at .05 level of probability.

differentiate line performance in its test crosses. The variance of test crosses increased in tandem with the increasing range of grain yield (GY). This information is also important for making decisions regarding tester selection and for understanding the impact of genetic factors on trait expression.

3.2 | Testcross mean and combining ability estimates of heterotic group B (HGB) and heterotic group R (HGR) testers

Testcross mean grain yield ranged from 3,287 to 5,236 kg ha^{-1} for Heterotic Group B (HGB) and 2,683 to 5,277 kg ha^{-1} for Heterotic Group R (HGR) across environments, reflecting genotypic differences. Among HGB testers, the highest mean testcross grain yield was observed in HGB2-T2 (4,679 kg ha^{-1}) and HGB1-T1 (4,410 kg ha^{-1}), followed by HGB2-T3 (4,366 kg ha^{-1}), HGB2-T1 (4,288 kg ha^{-1}), HGB1-T3 (4,206 kg ha^{-1}) and HGB1-T2 (4,079 kg ha^{-1}). In HGR test crosses, the highest mean grain yield was recorded for HGR2-T2 (4,365 kg ha^{-1}) and HGR1-T1 (4,289 kg ha^{-1}), followed by HGR1-T3 (3,927 kg ha^{-1}), HGR2-T1 (3,917 kg ha^{-1}), HGR2-T3 (3910 kg ha^{-1}), and HGR2-T2 (3,908 kg ha^{-1}). The SCA estimates ranged from −972.00 (B-L12 × HGR1-T1) to 773.66 (B-L12 × HGR2-T2) for test crosses of HGR, with B-L8 × HGR2-T1 (518.79*), B-L7 × HGR2-T1 (538.10*), B-L7 × HGR2-T1 (538.10*) and B-L12 × HGR2-T2 (773.66*) exhibiting the highest positive and significant SCA effects. For HGB, the SCA effect ranged from −814.86 (HGB2-T2 × R-L2) to 1,306.08 (HGB2-T1 × R-L9), with HGB1-T3 × R-L10 (776.64*) and HGB2-T1 × R-L9 (1,306.08*) having the highest and positive significant SCA effects. GCA estimates for HGB ranged from −258.77* (HGB1-T2) to 340.82* (HGB2-T2), with positive GCA observed in HGB1-T1 (71.89) and HGB2-T3 (27.86). In HGR, GCA ranged from −144.42 (HGR1-T2) to 311.89 (HGR2-T2), with significant positive GCA observed in HGR2-T2 (311.89*) and HGR1-T1 (235.82*). Good combiner lines with high GCA effects identified in the study for incorporating into HGB are B-L1 (642.46), B-L8 (401.67), B-L7 (246.00), B-L6 (139.54), B-L2 (66.71) and B-L9 (63.53), and for HGR are R-L10 (525.72), R-L1 (41.87), R-L5 (147.67), R-L7 (132.77) and R-L2 (59.62).

3.3 | Correlation analysis for the relative performance of lines in its test crosses

This study aimed to find the most suitable tester for ranking a set of lines based on grain yield response. The effective tester should accurately rank the lines based on how they perform in their respective testcrosses, as outlined by Hallauer (1975). The rankings of the 12 R-lines by the 6 HGB testers and the rankings of the 12 B-lines by the 6 HGR testers are presented in Tables 4 and 5. These rankings were used to compute the coefficient of concordance (denoted as W), a measure introduced by Kendall and Smith (1939). This coefficient helps assess the degree of agreement in rankings among the testers. Notably significant coefficients of concordance were found for the grain yield ranks of the R-lines (W = 0.37, $p = .011$) when assessed by HGB testers and the B-lines (W = 0.46, $p = .001$) when evaluated by HGR testers.

Spearman's rank correlation among pairs of testers for testcrosses exhibited a range of −.22 to .86 for HGB (Figure 2a) and −.15 to .88 for HGR (Figure 2b). Testers serve to select lines with superior combining ability, that is, those with above-average combining ability effects or testcross performance. Building on this concept and considering the mean across six testers or GCA as a baseline, testers HGB1-T3 (.86) and HGB2-T3 (.66) displayed higher correlations with GCA ranks than other HGB testers. Similarly, within the HGR testers employed in the study, the testcrosses of HGR1-T1 (.75) and HGR2-T1 (.88) demonstrated superior rank correlation coefficients and exhibited rankings in line with the GCA across six testers.

Figure 3a illustrates a comparison of correlation coefficients (r) related to grain yield. It examines the testcross means of individual testers versus those derived from combinations of testers from both HGB-1 and HGB-2. These combinations were correlated to the mean calculated across all testers, essentially representing General Combining Ability (GCA) for grain yield. Similarly, Figure 3b presents correlation coefficients between individual testers and combinations of testers originating from both HGR-1 and HGR-2, also in relation to a mean calculated across all testers. Among individual HGB testers, significant correlations were found for HGB1-T3 (.84), HGB2-T3 (.76) and HGB2-T2 (.58). Likewise, all HGR testers exhibited significant correlations, except for HGR2-T2. Combinations of tester pairs between HGB1 and HGB2 displayed overall significant positive correlations, except HGB1-T2 + HGB2-T1 (.55). Among the combinations of testers between HGB-1 and HGB-2, HGB1-T3 + HGB2-T3 (.92) and HGB1-T3 + HGB2-T2 (.9) showed the highest correlations compared to the mean performance of the six HGB testers. These combinations outperformed individual testers, enhancing the probability of identification of good combiners. In the case of HGR, all tester combinations exhibited significant positive correlation coefficients. Particularly, combinations like HGR1-T1 + HGR2-T1 (.96) and HGR1-T2 + HGR2-T1 (.92) showed the highest correlations and improved performance in selecting good combiners.

3.4 | Association between performance per se, GCA and variance of testcross mean for grain yield

The study examined the relationship between per se performance and the variance of testcross means, focusing on testcrosses involving HGB and HGR testers. The findings revealed an absence of a definitive trend in this relationship for HGB (Figure 4a) and HGR testers (Figure 4b). For HGB testers, the tester per se exhibited a positive correlation ($r = .58$) with the variance of the testcross meanwhile displaying a negative correlation with its GCA effects ($r = -.46$). Conversely, for HGR testers, the tester's performance per se showed a negative correlation ($r = -.47$) with the variance of the testcross mean, and a positive correlation ($r = .28$) with GCA effects. The study's analysis revealed a lack of a consistent trend in the association between per se performance and variance of testcross means and GCA effects for the testcrosses of

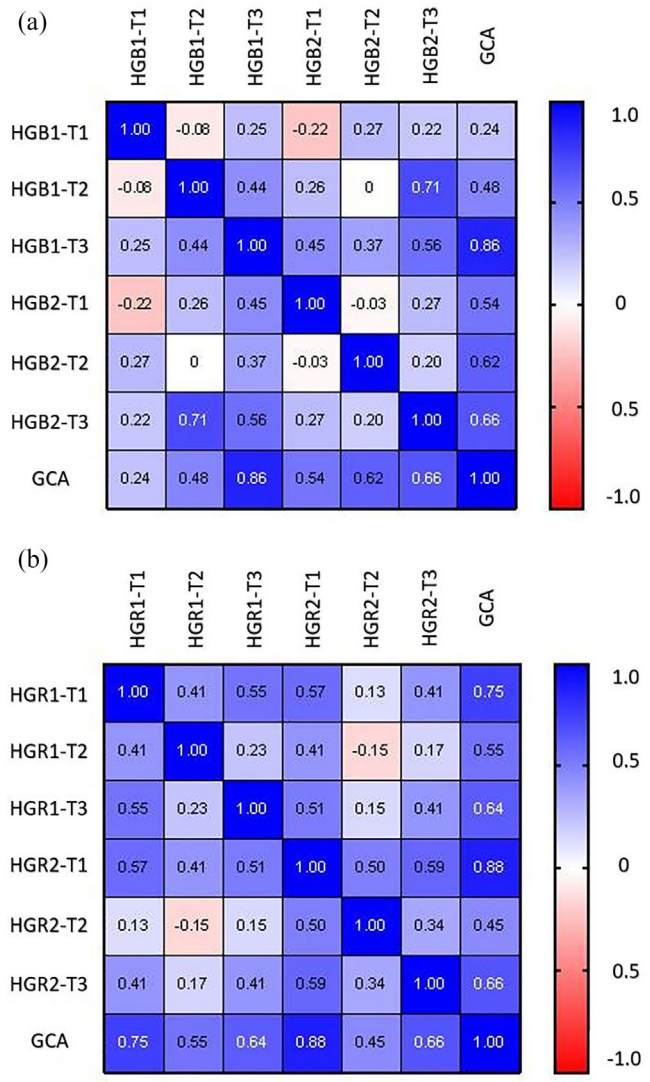


FIGURE 2 (a) Spearman rank correlation coefficients for the relative ranking of inbred lines across the heterotic group B (HGB) testers for grain yield. Abbreviations: HGB1-T1, heterotic group B1 tester 1; HGB1-T2, heterotic group B1 tester 2; HGB1-T3, heterotic group B1 tester 3; HGB2-T1, heterotic group B2 tester 1; HGB2-T2, heterotic group B2 tester 2; HGB2-T3, heterotic group B2 tester 3; GCA, general combining ability effect. (b) Spearman rank correlation coefficients for the relative ranking of inbred lines across the heterotic group R (HGR) testers for grain yield. Abbreviations: HGR1-T1, heterotic group R1 tester 1; HGR1-T2, heterotic group R1 tester 2; HGR1-T3, heterotic group R1 tester 3; HGR2-T1, heterotic group R2 tester 1; HGR2-T2, heterotic group R2 tester 2; HGR2-T3, heterotic group R2 tester 3; GCA, general combining ability effect.

HGB and HGR testers. These correlations underscore the complex interactions between these factors within the study's context.

3.5 | Biplot analysis of the line × tester data for graphical interpretation of tester efficiency

The GGE biplot analysis results for line × tester data from Sets 1 and 2 are presented in Figure 5a,b respectively. The biplot model explained a substantial portion of the yield variation for both HGB and HGR testcross hybrids. Specifically, in the case of HGB, the model accounted for 65.5% of the total variation, with PC1 and PC2 contributing 40.72% and 24.84%, respectively. Similarly, for HGR, the biplot model explained 77.21% of the yield variation, with PC1 and PC2 contributing 59.11% and 18.11%, respectively. Within the context of HGB testers, the biplot analysis revealed that HGB2-T2, HGB1-T2, HGB2-T3 and HGB1-T3 exhibited acute angles with average tester axis, indicating strong positive correlations. Based on the vector lengths, the discriminating power of testers could be ranked as follows: HGB1-T3 > HGB2-T1 > HGB2-T3 > HGB1-T1 > HGB2-T2 > HGB1-T2. Likewise, in the case of HGR testers, the presence of acute angles between each of the tester vectors and the average tester axis indicated high positive correlations. The hierarchy of testers' effectiveness, as determined by vector lengths, was as follows: HGR2-T1 > HGR1-T1 > HGR2-T3 > HGR1-T2 > HGR2-T2 > HGR1-T3. This ranking delineates the relative discriminating power of HGR testers in evaluating the combining ability.

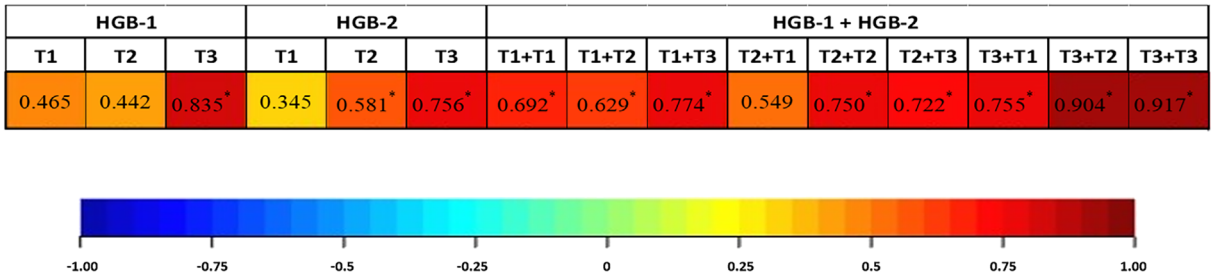
4 | DISCUSSION

The present study was carried out to determine the relative performance of the heterotic group inbred testers in evaluating the combining ability of new inbred lines. The genetic analysis allowed identification of efficient inbred testers from opposite heterotic groups for selection of inbred lines with good combining ability effect for grain yield, to strengthen the existing heterotic groups. This study integrates insights from previous research that considered various factors for selecting optimal testers in hybrid breeding (Allison & Curnow, 1966; Castellanos et al., 1998; Guimarães et al., 2012; Hallauer, 1975, 1988; Hallauer & Lopez-Perez, 1979; Matzinger, 1953; Pinto et al., 2004; Rawlings & Thompson, 1962, etc.). The relative performance of inbred lines in test crosses with appropriate testers has proven useful in selecting inbred lines with good combining abilities. The results were analysed to test the two main criteria for a good tester; that is, the tester must correctly classify the entries under consideration based on their relative performance in hybrid combinations (for GCA), and the tester must discriminate efficiently among the materials under test for grain yield.

4.1 | Variance for testcross means for HGB and HGR testers

The ANOVA for grain yield due to GCA and SCA effects showed a highly significant differences in test crosses, demonstrating that parental lines varied greatly in their general combining ability effect. Notably, testers exhibited significant differences ($p < .05$), indicative of their effectiveness in eliciting significant genetic variability in the grain yield of their testcrosses. The tester's ability to differentiate among the lines being assessed is crucial, and this ability is reflected in the variance of their testcross mean. This variance indicates the tester's effectiveness in distinguishing between lines with good or poor

(a)



(b)

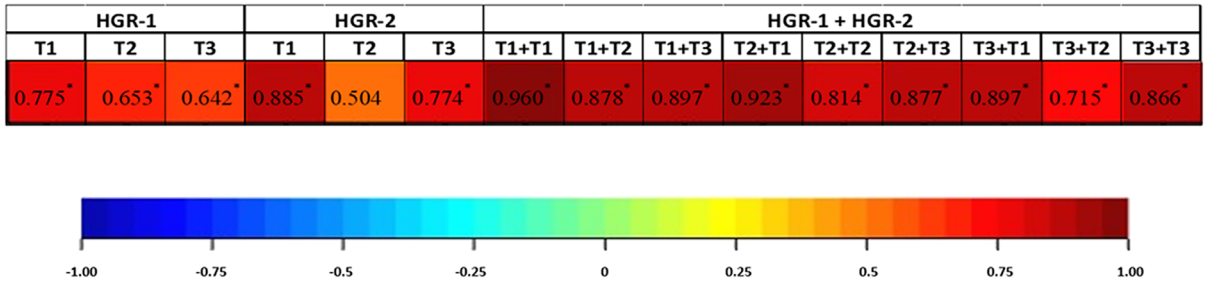


FIGURE 3 (a) Comparison of correlation coefficients between individual testers and combinations of testers from both heterotic group B1 (HGB-1) and heterotic group B2 (HGB-2), with a mean calculated across all testers, for grain yield. Abbreviations: individual testers: HGB1-T1, heterotic group B1 tester 1; HGB1-T2, heterotic group B1 tester 2; HGB1-T3, heterotic group B1 tester 3; HGB2-T1, heterotic group B2 tester 1; HGB2-T2, heterotic group B2 tester 2; HGB2-T3, heterotic group B2 tester 3; combinations of testers: HGB1-T1 + HGB2-T1; HGB1-T1 + HGB2-T2; HGB1-T1 + HGB2-T3; HGB1-T2 + HGB2-T1; HGB1-T2 + HGB2-T2; HGB1-T2 + HGB2-T3; HGB1-T3 + HGB2-T1; HGB1-T3 + HGB2-T2; HGB1-T3 + HGB2-T3. (b) Comparison of correlation coefficients between individual testers and combinations of testers from both heterotic group R1 (HGR-1) and heterotic group R2 (HGR-2) with a mean calculated across all testers, for grain yield. Abbreviations: individual testers: HGR1-T1, heterotic group R1 tester 1; HGR1-T2, heterotic group R1 tester 2; HGR1-T3, heterotic group R1 tester 3; HGR2-T1, heterotic group R2 tester 1; HGR2-T2, heterotic group R2 tester 2; HGR2-T3, heterotic group R2 tester 3; combinations of testers: HGR1-T1 + HGR2-T1; HGR1-T1 + HGR2-T2; HGR1-T1 + HGR2-T3; HGR1-T2 + HGR2-T1; HGR1-T2 + HGR2-T2; HGR1-T2 + HGR2-T3; HGR1-T3 + HGR2-T1; HGR1-T3 + HGR2-T2; HGR1-T3 + HGR2-T3.

combining abilities for grain yield. These criteria ensure that the chosen tester is reliable in assessing the potential of new breeding lines and can discern their performance differences in hybrid combinations. The variation in test-cross means among six HGB testers and six HGR testers varied greatly for grain yield (Figure 1a,b). In the context of HGB testers, the testers HGB1-T3 and HGB2-T1 exhibited the highest variances of testcross mean (Table 4), followed sequentially by HGB2-T3, HGB2-T2, HGB1-T1 and HGB1-T2. For the HGR scenario, the highest variances of the testcross mean were associated with the tester pairs HGR2-T1 and HGR1-T1 (Table 5). Subsequently, this was followed by HGR2-T3, HGR1-T2, HGR2-T2 and HGR1-T3. The statistical significance of differences among tester pairs was ascertained through orthogonal comparisons within the framework of ANOVA. Moreover, the significant differences in the variance of testcross means, seen when contrasting testcrosses that involve testers from HGB and HGR, indicate the influence of distinct genetic factors in distinguishing between inter-line variations regarding their relative yields in testcrosses. The selection of an appropriate tester is also contingent upon the relative ranges in mean trait values, as proposed by Lopez-Perez (1979). In the current study, the variation of testcrosses increased in tandem with the increasing range of grain yield (GY).

4.2 | Testcross mean and combining ability estimates of heterotic group B (HGB) and heterotic group R (HGR) testers

The testcross mean grain yield across environments varied from 3,287 to 5,236 kg ha^{-1} for testcrosses of HGB and from 2,683 to 5,277 kg ha^{-1} for testcrosses of HGR, illustrating the substantial differences in grain yield among the genotypes. The significant SCA effects implied the potential for developing promising hybrids by crossing lines from complementary heterotic groups, thereby optimizing heterosis expression (Hallauer et al., 2010). The significant GCA effects for both lines and testers suggested the successful accumulation of alleles with additive effects for the trait, aligning with the breeding strategy. GCA represents the overall breeding potential of a genotype, indicating its consistent contribution of positive genetic factors to hybrid populations. A positive SCA ensures that the desired traits are reliably expressed in the hybrids. Based on the performance of testcross mean and GCA estimates for grain yield, the testers could be ranked in descending order of their superiority as follows: HGB2-T2 > HGB1-T1 > HGB2-T3 > HGB2-T1 > HGB1-T3 > HGB1-T2 for HGB testers and HGR2-T2 > HGR1-T1 > HGR1-T3 > HGR2-T1 > HGR2-T3 > HGR1-T2 for HGR testers. However, the chosen testers

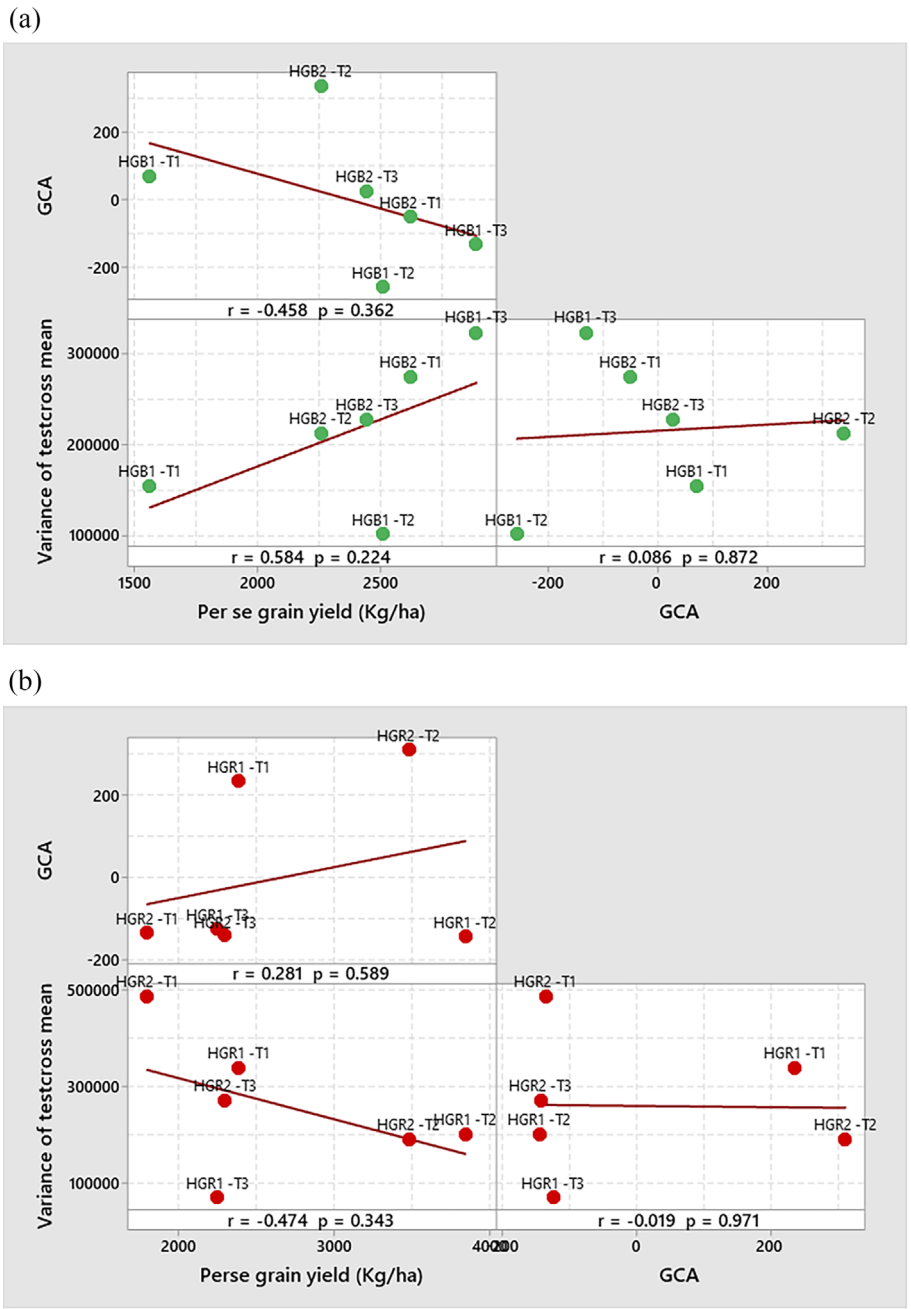


FIGURE 4 (a) Relationship between the per se performance, general combining ability effect (GCA) and the variance of testcross means for heterotic group B (HGB) testers evaluated for grain yield. Abbreviations: HGB1-T1, heterotic group B1 tester 1; HGB1-T2, heterotic group B1 tester 2; HGB1-T3, heterotic group B1 tester 3; HGB2-T1, heterotic group B2 tester 1; HGB2-T2, heterotic group B2 tester 2; HGB2-T3, heterotic group B2 tester 3; GCA, general combining ability effect. (b) Relationship between the per se performance, general combining ability effect (GCA) and the variance of testcross means for heterotic group R (HGR) testers evaluated for grain yield. Abbreviations: HGR1-T1, heterotic group R1 tester 1; HGR1-T2, heterotic group R1 tester 2; HGR1-T3, heterotic group R1 tester 3; HGR2-T1, heterotic group R2 tester 1; HGR2-T2, heterotic group R2 tester 2; HGR2-T3, heterotic group R2 tester 3; GCA, general combining ability effect.

represent the top-performing heterotic groups/clusters, and the genotypes representing these groups were expected to be good combiners with opposite heterotic groups; as a result, other metrics are given more weight when evaluating their efficiency.

4.3 | Relative ranking of inbred lines across testers

Concordance coefficient estimates indicate consistency of line rankings among testers. Nevertheless, certain lines received consistent rankings from all six testers, while others displayed variable testcross yields across different testers. This variability could be attributed to potential gene interactions between the tester parent and inbreds during crosses, potentially obscuring the accurate genotype determination of the studied lines through testcross performance (Castellanos et al., 1998; Genter, 1963). Spearman's rank correlation coefficients between tester pairs, assessing the ranking of lines based on relative yields in crosses for HGB (Figure 2a) and HGR testers (Figure 2b), revealed greater differences in their ranking ability. Guided by the principle of using testers to eliminate weak combiners and considering GCA as a reference, certain testers demonstrated superior rank correlation coefficients. Specifically, testers HGB1-T3 (.86), HGB2-T3 (.66), HGR1-T1 (.75) and HGR2-T1 (.88) exhibited stronger correlations and aligned line rankings more closely with across-tester GCA evaluations.

Following Hallauer (1975), a suitable tester is one that accurately ranks the relative merits of tested lines. Building upon this premise, the ranking of testers can be established based on the magnitude of

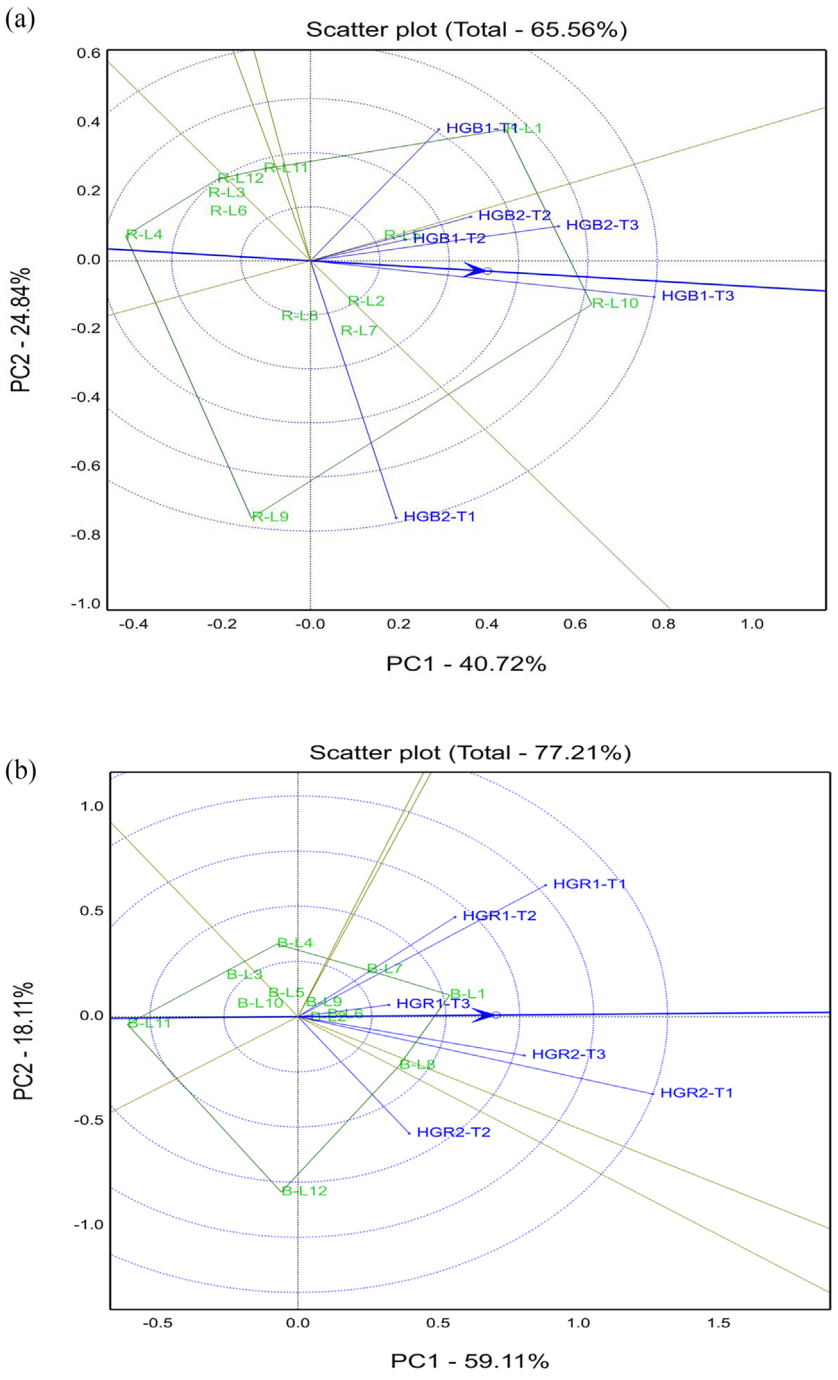


FIGURE 5 (a) Genotype main effect plus genotype × environment interaction (GGE) biplot for line × tester data showing the efficient testers from heterotic group B (HGB), based on the discriminating power and representativeness of the testers for grain yield. Abbreviations: HGB1-T1, heterotic group B1 tester 1; HGB1-T2, heterotic group B1 tester 2; HGB1-T3, heterotic group B1 tester 3; HGB2-T1; heterotic group B2 tester 1; HGB2-T2, heterotic group B2 tester 2; HGB2-T3, heterotic group B2 tester 3; R-L1 to R-L12, restorer line 1 to restorer line 12; PC1, principal component 1; PC2: principal component 2. (b) Genotype main effect plus genotype × environment interaction (GGE) biplot for line × tester data showing the efficient testers from heterotic group R (HGR), based on the discriminating power and representativeness of the testers for grain yield. Abbreviations: HGR1-T1, heterotic group R1 tester 1; HGR1-T2, heterotic group R1 tester 2; HGR1-T3, heterotic group R1 tester 3; HGR2-T1; heterotic group R2 tester 1; HGR2-T2, heterotic group R2 tester 2; HGR2-T3, heterotic group R2 tester 3; B-L1 to B-L12, seed parental line 1 to seed parental line 12; PC1, principal component 1; PC2: principal component 2.

correlation coefficients that determine the alignment of line rankings by testers (tester specific gca or testcross mean) with those derived from across-tester GCA evaluations. Within the context of HGB testers, their hierarchical superiority can be delineated in descending order as follows: HGB1-T3 > HGB2-T3 > HGB2-T2 > HGB2-T1 > HGB1-T2 > HGB1-T1. Similarly, within the purview of HGR testers, their ranking unfolds as HGR2-T1 > HGR1-T1 > HGR2-T3 > HGR1-T3 > HGR1-T2 > HGR2-T2. This methodology underscores the importance of testers' consistency in reflecting across-testers GCA rankings when evaluating line performance. Notably, certain testers demonstrated higher correlation values compared to others in this regard. The underlying rationale behind this analysis revolved around the concept of utilizing tester-specific testcross mean or tester-specific gca (ts gca) to select individuals, aiming to achieve gains akin to those anticipated in the context of across-tester GCA evaluations, and vice versa (Eduardo, 2020).

The correlation coefficients between combinations of testers, as depicted in Figure 3a for HGB and Figure 3b for HGR, in relation to the across-testers GCA for grain yield (kg ha^{-1}) revealed notable insights. Particularly, the tester pair HGB1-T3 + HGB2-T3 (.92**) and HGB1-T3 + HGB2-T2 (.9**) exhibited the highest anticipated correlations compared to individual testers. This observation suggests that the utilization of an optimal combination of tester pairs originating from distinct heterotic subgroups, namely, HGB-1 and HGB-2, can offer an enhanced evaluation of the general combining ability of new breeding lines. In the context of commercial seed industry breeding

programmes, the practice of utilizing restorers from their premier hybrids to assess the combining ability of seed parents, and vice versa, is widespread. This approach, conducted in parallel, essentially contributes to the improvement of specific combining ability (SCA). However, this strategy followed by seed industry finds its effectiveness when targeting the development of parental lines of hybrids tailored to a specific ecoregion, whereas institutions like ICRISAT, with a global mandate and public research organizations entrusted with the creation of diverse breeding materials adaptable to various ecoregions, face challenges. In such cases, the reliable selection of lines exhibiting high GCA, suitable for multiple ecoregions, necessitates the use of distinct testers for the assessment of combining ability, both in the context of seed parent pool (HGB) and restorer parent pool (HGR).

4.4 | Association between per se performance and the variance of testcross means, gene action and selection strategies

The significant variation expressed among testers and lines suggests significant differences in the genetic makeup of the lines and testers included. Investigating the relationship between the tester's performance per se and the variation among their testcrosses, this study's results do not establish a distinct and conclusive pattern for this relationship within both HGB and HGR testers, as indicated by the absence of statistically significant associations in Figure 4a,b. Nonetheless, in the case of HGB testers, tester per se was positively correlated ($r = .58$) with the variance of the testcross mean. The variance of testcross means increased with an increase in tester per se performance. A tester with a larger testcross variance could discriminate groups of inbred lines and identify the best lines among testcrosses (Rawlings & Thompson, 1962). The test crosses of the high-yielding testers HGB1-T3 and HGB1-T1 had the largest variance for grain yield, possibly due to these testers might carry relatively higher frequency of allele at yield influencing loci with predominantly overdominant and/epistatic gene effects that induced the larger genetic differences among testcrosses for grain yield. In general, the negative correlation of the tester per se with its GCA effects in HGB ($r = -.46$) (Figure 4a) and the ratio of GCA/SCA variance of .47 (Table 3) support the role of non-additive gene effects. Testers with a high frequency of favourable alleles can also be used to identify the best lines with the highest specific combining ability (Hallauer & Carena, 2009). So the suitable HGB tester is the one that is high yielding, has good discriminating ability among lines and forms productive hybrid combinations. High yield, however, is achieved in combination with other agronomic and farmer's preferred traits.

In contrast to HGB, the tester per se performance of HGR was positively correlated ($r = .281$) with GCA effects (Figure 4b), and also, the ratio of GCA/SCA variance was relatively higher (.63) (Table 3), indicating that the tester exhibits relatively higher of additive gene effects. The tester's performance per se was negatively correlated ($r = -.47$) with the variance of testcross means and the low per se tester, HGR2-T1 and HGR1-T1, had the largest testcross variance for grain yield. Opting for a HGR tester that exhibits lower per se performance can be strategic. Such a tester may have better discriminatory ability, helping to identify promising B-lines (female parents) that excel in combining ability while maintaining high per se performance. This is particularly important in hybrid seed production, where selecting B-lines that are good combiners and have high individual performance is essential. The primary requirement in the restorer line is its yield potential in hybrid combinations followed by strong and stable fertility restoration with profuse pollen production.

4.5 | Biplot analysis of the line × tester data for graphical interpretation of tester efficiency

The study utilized biplot analysis on testcross (line × tester) data to identify and validate the ideal inbred testers. The efficiency of testers was evaluated based on the principles of GGE biplot analysis (Akinwale et al., 2014; Annor et al., 2020; Badu-Apraku & Akinwale, 2019; Yan, 2014; Yan & Hunt, 2002). The study assessed tester efficiency using two primary criteria: the angle formed by a tester's vector concerning the average tester axis and the length of the tester's vector. Angle proximity indicated correlation coefficient similarity, while vector length approximated standard deviation and discriminating power. An effective tester is one that possesses the longest vector among all testers, indicating high discrimination capability, and also exhibits no or low projection onto the average tester axis, demonstrating a strong correlation to GCA estimates of the tester group. In this study, efficient testers were identified for HGB-1 and HGB-2 as HGB1-T3 and HGB2-T3, respectively (Figure 5a). Similarly, for HGR1 and HGR2, efficient testers were recognized as HGR1-T1 and HGR2-T1 (Figure 5b). Biplot analysis of line-tester data is a useful technique for visually interpreting the efficiency of testers in pearl millet hybrid breeding programmes.

This study systematically evaluated the relative performance of HGB and HGR inbred testers in assessing the combining ability of new breeding lines. A comprehensive analysis, including rank correlation, variance of testcross means and parameters such as GCA and individual performance, was conducted to identify the most suitable testers, and these findings were consistent with the results obtained from GGE Biplot analysis. Among the HGB testers, HGB1-T3 and HGB2-T3 consistently demonstrated their ability to effectively rank entries by their performance in hybrid combinations. These testers exhibited strong discriminating ability, as reflected in the variance of testcross means. In the case of HGR testers, HGR1-T1 and HGR2-T1 emerged as top performers, showcasing their potential for identifying good combiner lines for enhancing the performance of existing heterotic groups.

5 | CONCLUSION

In pearl millet breeding, inbred lines are considered promising when they exhibit high yield potential and good combining ability, enhancing the likelihood of yielding high-performing hybrids derived from opposite heterotic groups. Evaluating combining ability using opposite heterotic group testers is crucial in this context, and it is proposed

that assessing GCA be integrated into the process of strengthening these heterotic groups in pearl millet. Strategically chosen efficient testers allow accurate evaluation of combining ability and prediction of hybrid performance, optimizing parental selection, resource conservation and trial consistency. This study focused on identifying efficient inbred testers to strengthen existing heterotic groups of pearl millet. The choice of suitable testers presented in this study is based on multiple factors, including their performance in test crosses, their ability to discriminate between inbred lines, their correlation with GCA estimates and GGE biplot analysis. The identified testers, such as HGB1-T3, HGB2-T3, HGR1-T1 and HGR2-T1, showed considerable performance in various aspects, making them strong candidates for further breeding efforts.

AUTHOR CONTRIBUTIONS

Conception and design of the study: Rakshith Papanna and Shashi Kumar Gupta. *Conductance of experiments*: Rakshith Papanna and Shashi Kumar Gupta. *Formal analysis and investigation*: Rakshith Papanna and Shashi Kumar Gupta. *Writing—original draft preparation*: Rakshith Papanna and Shashi Kumar Gupta. *Writing—review and editing*: Rakshith Papanna and Shashi Kumar Gupta. *Contribution to experimental materials*: Shashi Kumar Gupta. *Reading and approval of the final manuscript*: All authors.

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CONFLICT OF INTEREST STATEMENT

The authors state that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request. Interested researchers can access the discussed genetic materials by contacting the corresponding author, facilitating collaborative scientific advancement.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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