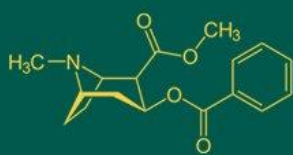


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Unveiling gene effects and yield determinants in CMS-based rice hybrids through heterosis and Genotype by Yield* Trait (GYT) biplot

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Abstract

The primary challenge for nations in developing countries across Asia and Africa, where large populations depend on a rice-based diet, is achieving sustainable development to feed growing populations. To address this equation, a research trial was conducted to exploit heterosis using three WA-CMS lines of rice. Analysis of variance revealed significant variation for all studied traits, indicating that selection and crossing of superior parental genotypes were promising. A high SCA value and dominance variance were recorded. The presence of non-additive gene action emphasizes the potential of genotypes to exploit heterosis within the genetic material to develop hybrids. Parents viz. Kasturi, HPU 2216, and Naggardhan were the top performers for significant GCA contribution, while the hybrids IR 79156A×Naggardhan, IR 68897A×Kasturi, IR 58025A×HPU 1156, IR 68897A×HPU 2216, and IR 58025A×HPU 2866 ranked as the top five performing hybrids for grain yield plant⁻¹, based on SCA effects and standard check variety heterosis. Grain yield plant⁻¹ depicted a significant positive correlation with total tillers plant⁻¹ (0.79***), effective tillers plant⁻¹ (0.80***), and plant height (0.22*), while showing a significant negative correlation with pollen fertility (-0.36***). The GYT biplot revealed G46, G52, G64, G67, G1, G25, and others were superior.

Keywords: Heterosis, combining ability, correlation, GYT, rice and yield

Introduction

Rice (*Oryza sativa* L.) is a self-pollinated, annual grass from the genus *Oryza* of the *Poaceae* family, having 2n = 24 chromosomes. It originated in Southeast Asia, where it exhibits significant genetic diversity (Chang, 1976) [7]. It is a widely consumed crop prized for its high content of protein, carbohydrates, vitamins, and minerals, along with low-fat content (Ullah Zaid *et al.*, 2019; El-Mowafi *et al.*, 2021; Abd El-Aty *et al.*, 2022; Rezvi *et al.*, 2022) [38, 12, 1, 34]. The projected global population will rise from 7.7 billion to 9 billion by 2035, so rice demand will be expected to increase from 763 million tonnes to 850 million tonnes. However, rice yield has only increased by about 1% annually over the past decade, despite being the highest among producing nations (Gaballah *et al.*, 2022) [16]. Rice breeders are having a hard time improving rice production because of more environmental problems and a growing population (Chen *et al.*, 2020) [8]. To cope with this yield penalty, exploiting heterosis using superior genotypes is a potential solution to develop hybrids through crossing genetically distinct parents (Khush, 2013; Huang *et al.*, 2015; Vaz Mondo *et al.*, 2016) [22, 19, 39]. Heterosis has notably contributed to food security and environmental benefits (Duvick, 1999) [11]. CMS-based hybrid rice varieties offer yield gains of 20–25% over pure lines, making rice a commercially viable crop (Rather *et al.*, 2001; Abebe *et al.*, 2017; El-Namaky, 2018; Liao *et al.*, 2021) [33, 2, 13, 25]. The Genotype by Yield*Trait (GYT) biplot denotes a novel, comprehensive, and emphatic method for genotype evaluation across multiple traits. It graphically ranks genotypes by their combined yield and target trait strata, elucidating their strengths and weaknesses. Selection results depend merely on the traits analyzed; therefore, only indispensable traits for cultivar success should be included in GYT biplot analysis (Yan & Fregeau-Reid, 2018) [40].

Material and methods

Experimental materials, site, and experimental design

In this experiment, three WA-CMS rice lines were crossed with twenty testers in a modified line $\times$ tester (MLT) mating design (Arunachalam 1974) at the Rice and Wheat Research Centre (RWRC), Malan, Himachal Pradesh, during kharif-2022. Next year, in kharif-2023, 60 F_1 crosses, 20 testers, and three CMS lines were transplanted along with maintainer lines in a Randomized Block Design (RBD) with three replications. The RWRC Malan is situated between 32°01'N latitude and 76°01'E longitude at an altitude of 950 m above mean sea level (AMSL). The soil has a silty clay loam texture with a p^H range of 5.8 to 6.0, which is well suited to cultivating rice in the Himalayan region.

Observations recorded

The study examined several phenological and agronomic key traits, including days to 50% flowering (DTF), days to maturity (DM), plant height (PH), total tillers plant⁻¹ (TTPP), effective tillers plant⁻¹ (ETPP), panicle length (PL),

spikelets panicle⁻¹ (SPP), grains panicle⁻¹ (GPP), pollen fertility (PF), spikelet fertility (SF), grain yield plant⁻¹ (GYPP), 1000-grains weight (TGW), grain length (GL), grain breadth (GB) and to breadth ratio (LBR). The detailed information of the studied material is depicted below in Tables 1 and 2.

Statistical analysis

Analysis of variance (ANOVA) was performed using Panse & Sukhatme, (1985) [31]; narrow-sense heritability was calculated using Singh & Chaudhary, (1977) [37], while combining ability (Arunachalam, 1974) [5] and relative and standard check variety heterosis were studied using Singh and Chaudhary's (1977) [37] methods. For data analysis, TNAU STAT software (version 2014) [26] was used, whereas GYT biplots, corplot, heatmap, and dendrogram were generated using RStudio (version R 4.5.3 (March, 2026)) [9], and a violin plot was created using the Data Tab online tool at <https://datatab.net/statistics-calculator/charts/create-boxplot>.

Table 1: Name, code, parentage and type of the parental genotype used in the study

Code	Genotype	Parentage	Type
CMS lines			
L1	IR 58025 A	Wild Abortive (WA) - IRRI Philippines	Indica
L2	IR 79156 A	Wild Abortive (WA) - IRRI Philippines	Indica
L3	IR 68897 A	Wild Abortive (WA) - IRRI Philippines	Indica
Restorers			
T1	Kasturi	Basmati 370/CRR 88-17-1-5	Indica
T2	HPR 2866	HPR 2143/AC 19146/VL 30424	Indica
T3	HPR 2749	Hasansarai/T 23/IR 66295-36-2	Indica
T4	HPU2216	IR 8/IR 2033-521-1-1/IR 36	Indica
T5	China 988	Secondary selection from China 988	Indica
T6	HPR 1156	IR 32429-122-3-1-2/IR 31868-64-2-3-3-3	Indica
T7	Himalaya II	Sabarmati/Ratana	Indica
T8	HPR 2143	HPR 9020-2-2-2-1-1-1Phul Patas/HUP 741	Indica
T9	Naggardhan	Ching Shi 15(Acc.36852)	Japonica
T10	HPR 2612	Hassan serai/T 23/IR-66295-36-2	Indica
T11	Varundhan	Kunjen 4 (HPR K 2001) IET 16020	Japonica
T12	VL 221	IR 2053-521-1-1-1/China 1039	Indica
T13	HPR 1068	IR 42015-83-3-2-2/IR9758-K2	Indica
T14	HPU 741	CR 126-42-5/IR 2061-213	Indica
T15	Himalaya I	IR 8/Tadukan	Indica
T16	HPR 2880	HPU 2216/Tetep	Indica
T17	HPR 2703	RP 2421/VL 221	Indica
T18	HPR 2720	Selection from Begmi	Indica
T19	HPR 2795	Selection from IC 3131180 germplasm	Indica
T20	HPR 2840	Kalizini/HPR2143//HPR2143	Indica

Table 2: Details of genotypic code of parents and crosses for GYT biplot

GC	Parent/Cross	GC	Parent/Cross	GC	Parent/Cross
G1	IR 58025A	G29	IR 58025A×HPR 1156	G57	IR 79156A×HPU 741
G2	IR 79156A	G30	IR 58025A×Himalaya II	G58	IR 79156A×Himalaya I
G3	IR 68897A	G31	IR 58025A×HPR 2143	G59	IR 79156A×HPR 2880
G4	Kasturi	G32	IR 58025A×Naggardhan	G60	IR 79156A×HPR 2703
G5	HPR 2866	G33	IR 58025A×HPR 2612	G61	IR 79156A×HPR 2720
G6	HPR 2749	G34	IR 58025A ×Varundhan	G62	IR 79156A×HPR 2795
G7	HPU 2216	G35	IR 58025A×VL 221	G63	IR 79156A×HPR 2840
G8	China 988	G36	IR 58025A×HPR 1068	G64	IR 68897A×Kasturi
G9	HPR 1156	G37	IR 58025A×HPU 741	G65	IR 68897A×HPR 2866
G10	Himalaya II	G38	IR 58025A×Himalaya I	G66	IR 68897A×HPR 2749
G11	HPR 2143	G39	IR 58025A×HPR 2880	G67	IR 68897A×HPU 2216
G12	Naggardhan	G40	IR 58025A×HPR 2703	G68	IR 68897A×China 988
G13	HPR 2612	G41	IR 58025A×HPR 2720	G69	IR 68897A×HPR 1156
G14	Varundhan	G42	IR 58025A×HPR 2795	G70	IR 68897A×Himalaya II
G15	VL 221	G43	IR 58025A×HPR 2840	G71	IR 68897A×HPR 2143

G26	HPR 1068	G44	IR 79156A×Kasturi	G72	IR 68897A×Naggardhan
G17	HPU 741	G45	IR 79156A×HPR 2866	G73	IR 68897A×HPR 2612
G18	Himalaya I	G46	IR 79156A×HPR 2749	G74	IR 68897A×Varundhan
G19	HPR 2880	G47	IR 79156A×HPU 2216	G75	IR 68897A×VL 221
G20	HPR 2703	G48	IR 79156A×China 988	G76	IR 68897A×HPR 1068
G21	HPR 2720	G49	IR 79156A×HPR 1156	G77	IR 68897A×HPU 741
G22	HPR 2795	G50	IR 79156A×Himalaya II	G78	IR 68897A×Himalaya I
G23	HPR 2840	G51	IR 79156A×HPR 2143	G79	IR 68897A×HPR 2880
G24	IR 58025A×Kasturi	G52	IR 79156A×Naggardhan	G80	IR 68897A×HPR 2703
G25	IR 58025A×HPR 2866	G53	IR 79156A×HPR 2612	G81	IR 68897A×HPR 2720
G26	IR 58025A×HPR 2749	G54	IR 79156A×Varundhan	G82	IR 68897A×HPR 2795
G27	IR 58025A×HPU 2216	G55	IR 79156A×VL 221	G83	IR 68897A×HPR 2840
G28	IR 58025A×China 988	G56	IR 79156A×HPR 1068		

Results

Analysis of variance and per se performance

Findings of ANOVA marked significant variations ($*p<0.05$) across all traits, with notable differences observed among lines, testers, line × tester, and crosses. Significant differences were also found among parents and parents vs. crosses for most of the traits, except for grains panicle⁻¹ and pollen viability. To depict the data, a violin plot was created based on the mean and range performances of the studied traits. Flowering and maturity periods of assorted parents and hybrids were examined, revealing that the average days to 50% flowering and maturity time ranged from 91.36 to 120.61 days. Hybrids IR 79156A×VL 221 and IR 58025A×HPR 1156 (80 days), were the earliest flowering hybrids, followed by IR 79156A×Naggardhan (83 days) and IR 68897A×Himalaya II (84 days), respectively. The average plant height was recorded 109.62 cm, with the shortest parent being Himalaya I at 83.67 cm and the shortest hybrid, IR 68897A×HPR 1068 (84.33 cm), followed by IR 68897A×HPR 2840 (87.13 cm) and IR 68897A×Himalaya I (87.33 cm). The mean of total and effective tillers plant⁻¹ was 9.26 and 8.76, respectively, with hybrids depicting a higher average of effective tillers. The average panicle length general mean was 25.18 cm, generally longer in hybrids, with the parent Kasturi having the longest panicle at 29.67 cm. Among hybrids, IR

79156A×HPR 2720 had the longest panicle of 29.40 cm, followed by IR 79156A×Kasturi (29.10 cm) and IR 79156A×HPR 2866 (28.65 cm). The parent genotype HPR 2795 (188.07) had the highest spikelets panicle⁻¹ and grains panicle⁻¹, while the hybrid IR 58025A×HPR 2720 (208.67) had the highest spikelets panicle⁻¹. Pollen viability for parents ranged from 81.91% to 99.29%, while spikelet fertility varied from 48.98% to 94.34%. Hybrids showed average pollen viability of 79.08% and spikelet fertility of 60.44%. The parent, China 988 (99.29%), had the highest pollen viability, and the highest spikelet fertility was observed in Naggardhan (94.34%). Maximum grain yield plant⁻¹ was observed in the hybrid, IR 79156A×Naggardhan (19.46 g), and the parent, IR 79156A (17.70 g). The general mean value for 1000-grain weight was 22.96 g, while the weight for parents was 23.78 g and 22.64 g for hybrids. Grain length varied from 5.12 mm to 7.69 mm in parents and 5.58 mm to 7.67 mm in hybrids. The best-performing hybrids for grain breadth were IR 58025A×HPR 2840 (2.39) followed by IR 58025A×HPR 2795 (2.26), IR 79156A×Varundhan (2.20), IR 68897A×HPR 2143 (2.18), and IR 68897A×HPU 741(2.18). The average L: B ratio for parents was 3.44 mm, and the best-performing hybrids for grain length were IR 58025A×HPR 2720 (4.74) (Table 3 and Figure 1).

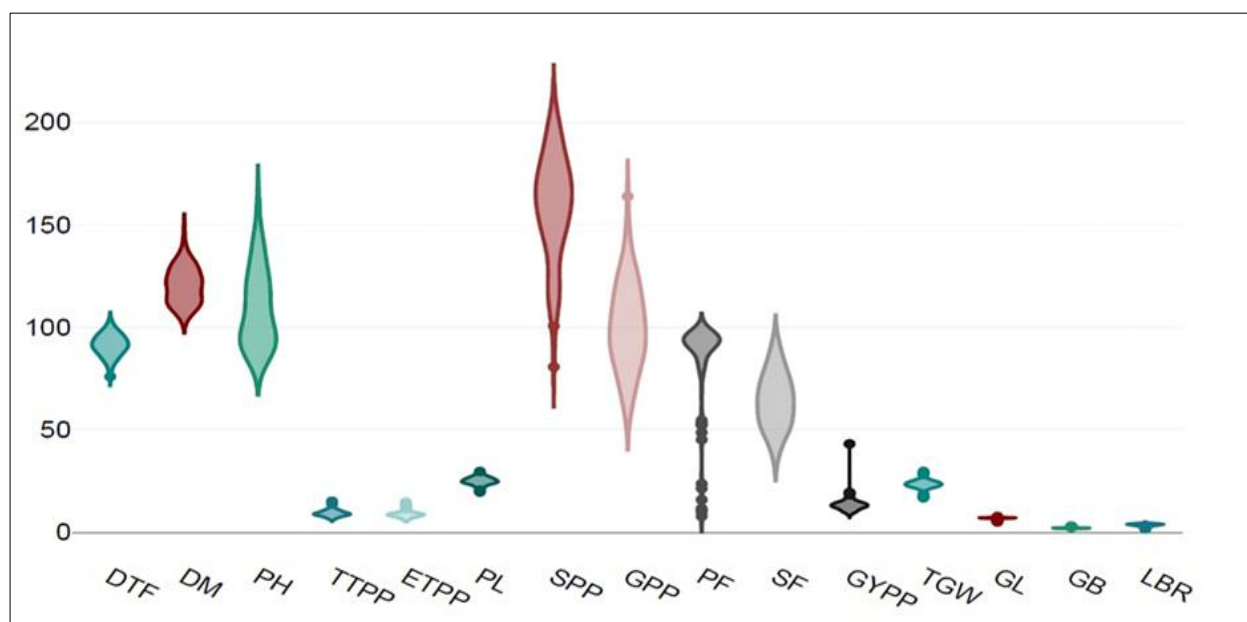


Fig 1: Violin plot of studied traits

Table 3: Grand mean (GM), mean, and range for studied traits in parents and F1 in rice

Traits	GM	Parents		Crosses	
		Mean	Range	Mean	Range
Days to 50 % flowering	91.36	90.04	76.00 – 103.00	91.87	80.00 – 102.00
Days to maturity	120.61	120.87	105.00 – 137.33	120.51	105.33 – 147.67
Plant height at maturity (cm)	109.62	113.31	83.67 – 162.53	108.20	84.33 – 144.40
Total tillers plant ⁻¹	09.26	09.30	06.47 – 13.83	09.24	06.40 – 15.130
Effective tillers plant ⁻¹	08.76	08.72	06.00 – 13.17	08.77	06.03 – 14.60
Panicle length (cm)	25.18	24.05	19.67 – 29.67	25.62	23.17 – 29.40
Spikelets panicle ⁻¹	158.81	138.59	80.73 – 188.07	166.56	113.80 – 208.67
Grains panicle ⁻¹	100.69	101.57	70.87 - 163.97	100.36	57.93 – 145.23
Pollen viability (%)	83.35	94.47	81.91 – 99.29	79.08	07.84 – 96.62
Spikelet fertility (%)	64.42	74.82	48.98 – 94.34	60.44	36.95 – 84.49
Grain yield plant ⁻¹ (g)	12.96	12.54	08.22 – 17.7	13.12	08.58 – 19.46
1000-grain weight (g)	22.96	23.78	18.66 – 29.63	22.64	16.74 – 28.61
Grain length (mm)	06.84	06.66	05.12 – 07.69	06.91	05.58 – 07.67
Grain breadth (mm)	01.91	02.01	01.62 – 03.02	01.87	01.44 – 02.39
L: B ratio	03.65	03.44	01.81 – 04.47	03.73	02.59 – 04.74

Genetic analysis

The study revealed that additive variance in traits was lower than dominance variance. Spikelet fertility (15.31) had maximum additive variance, followed by L:B ratio (10.49), spikelets panicle⁻¹ (8.51), grain yield plant⁻¹ (8.25), plant height at maturity (7.58), and spikelets panicle⁻¹ (4.22), respectively. For grain breadth (0.001), L:B ratio (0.001), grain length (0.02), total tillers plant⁻¹ (0.04), effective tillers plant⁻¹ (0.04), panicle length (0.02), days to 50% flowering

(0.76), spikelet fertility (0.48), grain yield plant⁻¹ (0.06), and thousand grain weight (0.18), there was the lowest additive variance. The highest GAM was found in pollen viability (57.72), which was significantly high (>20%), followed by spikelet fertility (31.25), grains panicle⁻¹ (30.60), grain yield plant⁻¹ (30.54), spikelets panicle⁻¹ (28.75), effective tillers plant⁻¹ (27.03), total tillers plant⁻¹ (25.52), plant height at maturity (24.24), L:B ratio (20.34), 1000-grain weight (20.24), and grain breadth (20.06), respectively (Table 4).

Table 4: Estimates of genetic components of variance, average degree of dominance, narrow-sense heritability, genetic advance as a percentage of mean, and per cent contribution of lines, testers, and their interaction for different traits in rice

Traits	(σ^2A) F=1	(σ^2D) F=1	$\sqrt{\sigma^2D/2\sigma^2A}$	(h^2ns) (%)	GAM (%)	Contributions		
						Lines	Testers	Lines × Testers
Days to 50 % flowering	0.76	05.11	2.59	2.47	1.85	00.20	72.74	27.06
Days to maturity	2.38	36.42	3.91	4.66	11.80	00.61	68.82	30.58
Plant height at maturity	7.58	174.41	4.80	3.28	24.24	39.85	21.57	38.58
Total tillers plant ⁻¹	0.04	01.48	6.08	2.33	25.52	09.51	45.73	44.76
Effective tillers plant ⁻¹	0.04	01.43	5.98	2.28	27.03	09.19	44.84	45.97
Panicle length	0.02	01.17	7.65	1.10	5.63	22.78	27.79	49.43
Spikelets panicle ⁻¹	4.22	305.91	8.51	0.62	28.75	03.02	43.91	53.07
Grains panicle ⁻¹	8.54	302.93	5.96	3.08	30.60	16.94	39.45	43.61
Pollen viability	11.48	420.79	6.05	1.72	57.72	16.37	39.29	44.34
Spikelet fertility	0.48	112.46	15.31	0.46	31.25	15.82	24.16	60.02
Grain yield plant ⁻¹	0.06	04.08	8.25	1.43	30.54	06.63	40.27	53.10
1000-grain weight	0.18	03.62	4.48	2.36	20.24	10.01	52.63	37.36
Grain length	0.02	00.11	2.35	10.24	6.00	02.09	45.40	52.50
Grain breadth	0.001	00.03	5.48	3.36	20.06	05.74	33.73	60.53
L: B ratio	0.001	00.11	10.49	0.23	20.34	07.49	25.43	67.08

(σ^2A) = Additive variance, (σ^2D) = Dominance variance, $\sqrt{\sigma^2D/2\sigma^2A}$ = Average degree of dominance, (h^2ns) (%) = Narrow sense heritability, GAM (%) = Genetic advance as percentage of mean

Traits like days to 50% flowering (1.85), panicle length (5.63), and grain length (6.0) showed low (<10%) GAM, indicating a mix of additive and non-additive gene effects. It is evident from the table that female parents played an important role in plant height at maturity (39.85%), indicating a predominant maternal influence for this trait. Male parents contributed a larger proportion for some important traits, viz., days to 50 percent flowering (72.74%), days to maturity (68.82%), 1000-grain weight (52.63%), and total tillers plant⁻¹ (45.73%), revealing the predominant paternal influence for these traits. For the remaining traits, viz., effective tillers plant⁻¹ (45.97%), panicle length (49.43%), pollen viability (44.34%), spikelets panicle⁻¹ (53.07%), grains panicle⁻¹ (43.61%), spikelet fertility (60.02%), grain yield plant⁻¹ (53.10%), grain length

(52.50%), grain breadth (60.53%), and L:B ratio (67.08%), the contribution of maternal and paternal interaction (female × male) was observed to be highest in proportion, indicating that the concerned characters were influenced by non-additive gene action. The line × tester interactions revealed that days to maturity (68.82%) had the greatest effect due to the paternal effect, and the L:B ratio (67.08%) again due to line × tester interactions (Table 4).

Combining Ability

The analysis of variance (ANOVA) for combining ability across studied traits revealed significant differences among lines, testers, and interactions, with specific combining ability variances exceeding general combining ability variances, indicating non-additive gene action. Negative

combining ability is better for the days to flowering trait, with no significant negative effects observed among the CMS lines. The highest negative GCA effect was observed in the Himalaya II (-6.87) parent, followed by VL 221 (-5.98) and HPR 1156 (-4.98). Five hybrids early flowered and displayed significant negative SCA effects, with the highest being IR 79156A×VL 221 (-5.67). The CMS line IR 68897A (-0.64) was the best general combiner for early maturity. The highest negative GCA effect was observed in HPR 1156 (-11.39), followed by HPR 2880 (-10.62) and Himalaya II (-9.51). The highest negative GCA effect was observed in IR 79156A×HPR 2749 (-10.94), followed by IR 58025A×HPR 2720 (-10.47). The study found that CMS lines, such as IR 68897A (12.08) and IR 58025A (-3.04), had a significant negative GCA effect on plant height, and among testers, HPR 1068 (-16.20) showed the highest negative GCA effect. The highest negative SCA effect was observed in IR 58025A×HPR 2720 (-28.57), followed by IR 79156A×VL 221 (-22.21) and Himalaya I (-20.08). CMS line IR 79156A (0.61) for TTPP and (0.58) for ETPP had a significant positive GCA effect, while tester HPR 2749 (2.79) for TTPP and (2.82) for ETPP had the highest positive GCA effect, followed by Kasturi and HPU 2216. Hybrid IR 79156A×HPR 2749 depicted a maximum SCA effect (2.49) for TTPP and (2.44) for ETPP. The study identified seven hybrids with significant positive GCA effects for panicle length, with the highest effect observed in IR 58025A×HPR 2795 (2.12), followed by IR 79156A×Kasturi (2.00). CMS line IR 58025A (2.87) was identified as a significant contributor to the GCA effect for spikelets panicle-1. Among the seven testers, HPR 2720 (30.65) depicted the highest significant positive GCA effect. Ten hybrids revealed significant positive SCA effects for spikelets panicle-1, maximum in IR 79156A×HPR 2866 (33.04), followed by IR 58025A×HPR 2703 (29.63), IR 79156A×Himalaya I (26.57), IR 68897A×Varundhan (23.84), and IR 58025A×HPR 2143 (16.54). For the trait GPP, a significant positive GCA effect was observed in the female parents IR 58025A (4.78) and IR 79156A (7.45) and in the male parent HPR 2720 (31.58). Significant SCA effect was noted in twenty-two hybrids, with the highest desirable SCA effect in IR 68897A×HPR 2720 (25.53), followed by IR 68897A×HPU 2216 (24.62), IR 68897A×VL 221 (23.81), IR 68897A×Naggardhan (21.4), and IR 58025A×HPR 2703 (20.5). The female parent IR 68897A (13.05) showed a significant positive GCA effect for pollen viability, while the male parent HPR 2840 (14.99) exhibited the highest GCA value. Notably, the hybrid IR 68897A×Varundhan (42.69) demonstrated the maximum specific combining ability (SCA) effect for pollen viability, followed by IR 68897A×Naggardhan (39.97), IR 68897A×VL 221 (28.97), IR 79156A×HPR 1068 (25.31), and IR 79156A×HPR 2795 (24.54). For spikelet fertility, female parents IR 58025A (2.27) and IR 79156A (3.86) depicted significant positive GCA effects. Among the male parents, nine revealed significant positive GCA effects, with HPU 2216 having the highest (11.28), followed by HPR 2866 (8.48) and HPR 2720 (6.56). Twenty-three hybrids showed significant positive SCA effects for spikelet fertility, with maximum in IR 58025A×Varundhan (25.21), followed by IR 58025A×HPR 2866 (13.3), IR 68897A×HPR 2720 (11.99), IR 79156A×HPR 2143 (10.71), and IR 79156A×HPR 2795 (10.48). The CMS lines IR 79156A (0.43) and IR 58025A (0.38), along with testers Kasturi

(3.24) and HPU 2216 (2.42), were identified as significant positive contributors to GCA. For specific combining ability effects, twenty-two hybrids were recognized as effective combiners for grain yield plant⁻¹, and the hybrid IR 79156A×Naggardhan (4.17) was identified with highest positive SCA effect, followed by IR 68897A×Kasturi (3.60), IR 58025A×HPR 1156 (2.67), IR 58025A×Varundhan (2.59), and IR 68897A×HPU 2216 (2.43). For 1000-grain weight, CMS line IR 79156A (0.48) and IR 68897A (0.53) showed significant positive GCA effects. Among the male parents, HPR 2880 showed the highest positive GCA effect (13.96), followed by HPR 2866 (2.81) and HPR 2749 (1.78). Twelve hybrids depicted significant positive SCA effects, with the highest recorded by IR 58025A×Himalaya I (3.48), followed by IR 68897A×HPR 2749 (3.28), IR 58025A×Varundhan (2.74), IR 68897A×Naggardhan (2.47), and IR 79156A×Kasturi (2.41). Research results revealed that the positive general combining ability (GCA) effect for grain length was significant only among male parents, with the highest effect in parent HPR 2749 (0.40). The maximum specific combining ability (SCA) effect was observed in nine hybrids, peaking with IR 58025A×HPR 2720 (0.7), followed by IR 79156A×HPR 2840 (0.63), IR 79156A×HPU 2216 (0.59), IR 58025A×HPR 2143 (0.51), and IR 68897A×China 988 (0.46). Among female parents, IR 58025A (-0.4) and IR 68897A (-0.1) depicted significant negative GCA effects for grain breadth. Among male parents, nine showed significant negative GCA effects, with HPR 2720 (-0.19) followed by HPR 2703 (-0.14), HPR 1068 (-0.11), and VL 221 (-0.11). A total of 28 hybrids displayed significant negative SCA effects, with the most significant negative found in IR 68897A×Varundhan (-0.26), followed by IR 68897A×HPR 2840 (-0.24), IR 79156A×HPR 2840 (-0.24), and IR 68897A×HPR 2795 (-0.22), respectively. The CMS line IR 58025A (0.13) exhibited a significant positive general combining ability (GCA) effect for the L: B ratio, with seven male parents demonstrating notable positive GCA effects. Additionally, fifteen hybrids displayed significant specific combining ability (SCA) effects. Parent Kasturi (0.34) recorded the highest GCA effect for the L:B ratio, while the hybrid IR 58025A×HPR 2720 (0.88) had the greatest SCA effect, followed by IR 79156A×HPR 2840 (0.87), IR 68897A×Varundhan (0.76), IR 79156A×Naggardhan (0.49), and IR 58025A×VL 221 (0.46).

Heterosis

Heterosis for days to 50 percent flowering in F₁s varied from -7.89 (IR 58025A×HPR 1156) to 13.73% (IR 79156A×Himalaya I) for midparents and from -8.05 (IR 79156A×VL 221) to 17.24% (IR 58025A×HPR 2840) compared to the standard check variety HPR 2880 (Table 5). No hybrids exhibited significant negative mid-parent heterosis, though IR 79156A×VL 221(-8.01%) showed a notably significant negative heterosis compared to the standard check. The hybrid IR 79156A×VL 221 (-14.76%) exhibited the highest significant negative mid-parent heterosis for early maturity, followed by IR 58025A×HPR 2143 (-12.57%), IR 79156A×HPR 2703 (-12.42%), IR 79156A×Himalaya II, and IR 58025A×HPR 1156 (-11.82%). Additionally, IR 68897A×HPR 2840 (-9.52%) showed significant negative standard check variety heterosis, followed by IR 79156A×Himalaya II (-5.95%)

and IR 58025A×HPR 1156 (-5.65%). The heterotic responses of F₁ hybrids for plant height ranged from -31.27 to 32.65% for the mid-parent and -26.5 to 25.86% over the standard check variety (Table 5). The hybrid IR

68897A×HPR 2703 exhibited the maximum significant negative mid-parent heterosis at -31.27%, followed by IR 68897A×HPR 2795 (-26.44%), IR 79156A×VL 221 (-25.99%), and IR 58025A×HPR 2720 (-24.77%).

Table 5: Mean and range of mid-parent heterosis (MP) and standard check variety heterosis (SV) of studied traits in rice

Traits	MP (Percent)		SV (Percent)	
	Mean	Range	Mean	Range
DTF	00.77	-07.89 – 13.73	-05.59	-08.05 – 17.24
DM	-02.82	-14.76 – 20.71	07.59	-05.95 – 31.85
PH	-02.18	-31.27 – 32.65	-05.69	-26.50 – 25.86
TTPP	-09.17	-45.50 – 47.40	-03.75	-33.33 – 57.64
ETPP	-08.02	-43.02 – 51.56	-05.00	-34.66 – 58.12
PL	04.40	-14.07 – 17.08	10.28	04.67 – 32.83
SPP	12.48	-29.62 – 42.47	57.18	07.39 – 96.92
GPP	-02.10	-49.89 – 84.59	08.18	-37.55 – 56.56
PV	-16.32	-91.67 – 03.33	-18.78	-91.95 – -00.77
SF	-13.48	-53.13 – 46.76	-30.82	-57.70 – -03.39
GYPP	-00.21	-34.98 – 58.38	-07.01	-39.21 – 37.91
TGW	-04.61	-33.29 – 19.44	-10.93	-34.15 – 12.55
GL	02.72	-14.54 – 21.95	11.11	-10.24 – 23.32
GB	-03.81	-28.62 – 22.53	-02.59	-24.96 – 24.44
LBR	06.90	-30.44 – 57.12	15.26	-19.88 – 46.45

The highest standard check variety heterosis was noted in IR 68897A×HPR 1068 (-26.5%), followed by IR 68897A×HPR 2840 (-24.06%), IR 68897A×Himalaya I (-23.88%), IR 68897A×HPR 2703 (-23.77%), and IR 58025A×Himalaya II (-23.53%). Heterosis over mid-parent for total tillers plant⁻¹ ranged from -45.5 to 47.4%, with an average of -9.17% (Table 5). Heterosis for the standard check variety showed a range from -33.33 to 57.64%. For effective tillers plant⁻¹, eight hybrids displayed significant heterosis for the standard check variety, which ranged from -34.66 to 58.12% (Table 5). The highest significant positive heterosis for the standard check was seen in IR 79156A×HPR 2749 (58.12%), followed by IR 79156A×Naggardhan (33.21%), IR 68897A×Kasturi (25.99%), IR 68897A×HPU 2216 (21.66%), and IR 58025A×HPR 1156 (19.89%), respectively. Panicle length heterosis ranged from -14.07 to 17.08% over the mid-parent and 4.67 to 32.83% over the standard check variety (Table 5). Significant heterotic hybrids identified included 20 for mid-parent and 55 for standard check varieties. The hybrids IR 79156A×HPR 2720 (17.08%) for mid-parent and IR 79156A×HPR 2720 (32.83%) exhibited the highest heterosis in their categories. Top-performing hybrids for the standard check variety were IR 79156A×Kasturi (31.48%), IR 79156A×HPR 2866 (29.43%), IR 79156A×HPR 2703 (26.05%), IR 58025A×HPR 2840 (25.9%), and IR 58025A×HPR 2143 (25.06%). Mid-parent heterosis for spikelets panicle⁻¹ varied from -29.62 to 42.47%, while standard check variety heterosis spanned 7.39 to 96.92% (Table 5). Significant positive mid-parent heterosis was observed in thirty-five hybrids, with the highest magnitude in IR 68897A × Naggardhan (42.47%). Fifty-eight hybrids exhibited significant positive standard check variety heterosis, with the highest magnitude found in IR 58025A×HPR 2720 (96.92%). The highest significant mid-parent heterosis for grains panicle⁻¹ was observed in the hybrid IR 68897A×HPR 2720 (84.59%), followed by IR 68897A×HPU 2216 (48.89%), IR 79156A×HPU 741 (26.87%), and IR 68897A×HPU 741 (23.25%). Thirty hybrids exhibited significant positive heterosis over the standard check variety, with the highest heterosis found in IR 68897A×HPR 2720, followed by IR 58025A×HPR 2840

(55.95%), IR 79156A×HPR 2143 (51.96%), IR 79156A×HPR 2866 (42.01%), and IR 79156A×HPU 741 (40.56%). Significant positive direction of heterosis for pollen fertility varied from -91.67 to 3.33% for mid-parent heterosis and -91.95 to 0.77% over standard check variety heterosis. None of the cross combinations recorded a significant positive value of heterosis over the standard check variety heterosis. Spikelet fertility heterosis for mid-parent ranged from -53.13 to 46.76% and -57.7 to -3.39% over standard check variety heterosis. Grain yield plant⁻¹ heterosis ranged from -34.98 to 58.38% for the mid-parent and -39.21 to 37.91% for the standard check variety. The hybrid IR 68897A×Kasturi (58.38%) showed the highest mid-parent heterosis (58.38%). The hybrid IR 79156A×Naggardhan exhibited the highest heterosis over the standard check variety (37.91%). Top hybrids for mid-parent heterosis in grain yield plant⁻¹ included IR 79156A×Naggardhan (41.71%), IR 58025A×HPR 1156 (38.39%), IR 68897A×HPR 2749 (37.91%), and IR 58025A×VL 221 (29.50%). The hybrids excelling over the standard check variety were IR 68897A×Kasturi (35.71%), IR 68897A×HPU 2216 (21.61%), IR 58025A×HPR 1156 (18.99%), IR 58025A×HPR 2866 (17.62%), and IR 58025A×Kasturi (16.67%). Eight hybrids exhibited significant positive mid-parent heterosis for 1000-grain weight, with the highest recorded in hybrid IR 79156A×HPR 2703 (19.44%), followed by IR 58025A×Himalaya I (19.32%), IR 79156A×Kasturi (17.72%), IR 58025A×HPR 2866 (16.77%), and IR 68897A×HPR 2749 (16.55%). The highest significant positive standard check variety heterosis was observed in hybrid IR 79156A×HPR 2866 (12.55%). Grain length heterosis ranged from -14.54 to 21.95% for mid-parent and -10.24 to 23.32% for the standard check variety. Fifteen hybrids exhibited significant positive mid-parent heterosis, with the highest observed in hybrid IR 79156A×Naggardhan (21.95%), followed by IR 79156A×HPU 2216 (14.79%), IR 68897A×Varundhan (13.24%), IR 68897A×Naggardhan (12.95%), and IR 58025A×VL 221 (12.31%). The hybrid IR 58025A×HPR 2143 (23.32%) had the highest standard check variety heterosis, followed by IR 79156A×HPU 2216 (21.93%), IR 68897A×HPR 2749 (21.23%), IR

68897A×HPR 1156 (20%), and IR 58025A×VL 221 (19.62%). In accordance with the GCA/SCA effect, per se performance and standard check variety heterosis for the top

3 economic parents and top 5 economic hybrids for grain yield plant⁻¹ are depicted in Table 6.

Table 6: Top 3 economic parents and top 5 economic hybrids for grain yield plant⁻¹

Parents/Hybrids	GCA/SCA effect	Per se performance (g)	Standard check variety heterosis (%)	GCA effect of the parents	Significant GCA/SCA effect for other related traits
Kasturi	3.24*	13.36	---	---	TTPP, ETTP, SPPP, PV, TGW, GL, GB, LBR
HPU 2216	2.42*	15.59	---	---	DTF, TTPP, ETTP, GPP, PV, SF, GB, LBR
Naggardhan	1.74*	09.77	---	---	DTF, DM, PH, TTPP, ETTP
IR 79156A×Naggardhan	4.17*	19.46	37.91*	Good × Good	DTF, TTPP, ETTP, SF, GL, LBR,
IR 68897A×Kasturi	3.60*	19.15	35.71*	Poor × Good	DTF, TTPP, ETTP, SPPP, GPP
IR 58025A×HPR 1156	2.67*	16.79	18.99*	Good × Good	DTF, DM, TTPP, ETTP, GPP, SF
IR 68897A×HPU 2216	2.43*	17.16	21.61*	Poor × Good	DTF, TTPP, ETTP, SF, TGW
IR 58025A×HPR 2866	1.86*	16.60	17.62*	Good × Poor	PH, SF, GPP, TTPP, ETTP, TGW

Negative mid-parent heterosis for grain breadth was significant in thirty-seven hybrids, with the lowest value in hybrid IR 68897A×Varundhan (-28.62%), followed by IR 79156A×Naggardhan (-25.65%), IR 58025A×HPR 1068 (-21.13%), IR 58025A×China 988 (-20.61%), and IR 79156A×HPR 1068 (-17.99%). Thirty-eight hybrids displayed significant negative standard check variety heterosis, with IR 58025A×HPR 2720 (-24.96%), followed by IR 58025A×HPR 2880 (-19.24%), IR 58025A×VL 221 (-16.12%), IR 68897A×Varundhan (-15.08%), and IR 58025A×HPR 2703 (-15.08%). The range of L: B ratio for mid-parent heterosis varied from -30.44 to 57.12%, and standard check variety heterosis from -19.88 to 46.45%. The hybrid IR 79156A×Naggardhan (57.12%) exhibited the highest significant positive mid-parent heterosis, followed by IR 68897A×Varundhan (45.96%), IR 58025A×VL 221 (33.37%), IR 79156A×HPR 1068 (30.89%), and IR 79156A×HPR 2840 (29.57%). A total of forty-one hybrids

were identified as significant heterotic hybrids for standard check variety heterosis, with IR 58025A×HPR 2720 (46.45%).

Correlation analysis: Correlation analysis of the traits was done using Pearson's correlation in RStudio software version 4.3.2 2024. The scatter plot in Figure 2 illustrates the correlations among the studied variables. constitutes the main source of primary healthcare in most rural populations, especially in many African countries, due to its affordability and availability. However, as the usage of these medicinal plants becomes more widespread around the world, there are questions and misgivings about the quality, efficacy, and safety of the products utilized in the health sector [2, 3, 4]. These concerns have hampered the sensible use and validation of bio-products derived from these herbs for the treatment and management of disorders [5]. The validation and quality assurance of medicinal plant products has been hampered by a lack of or incorrect plant identification.

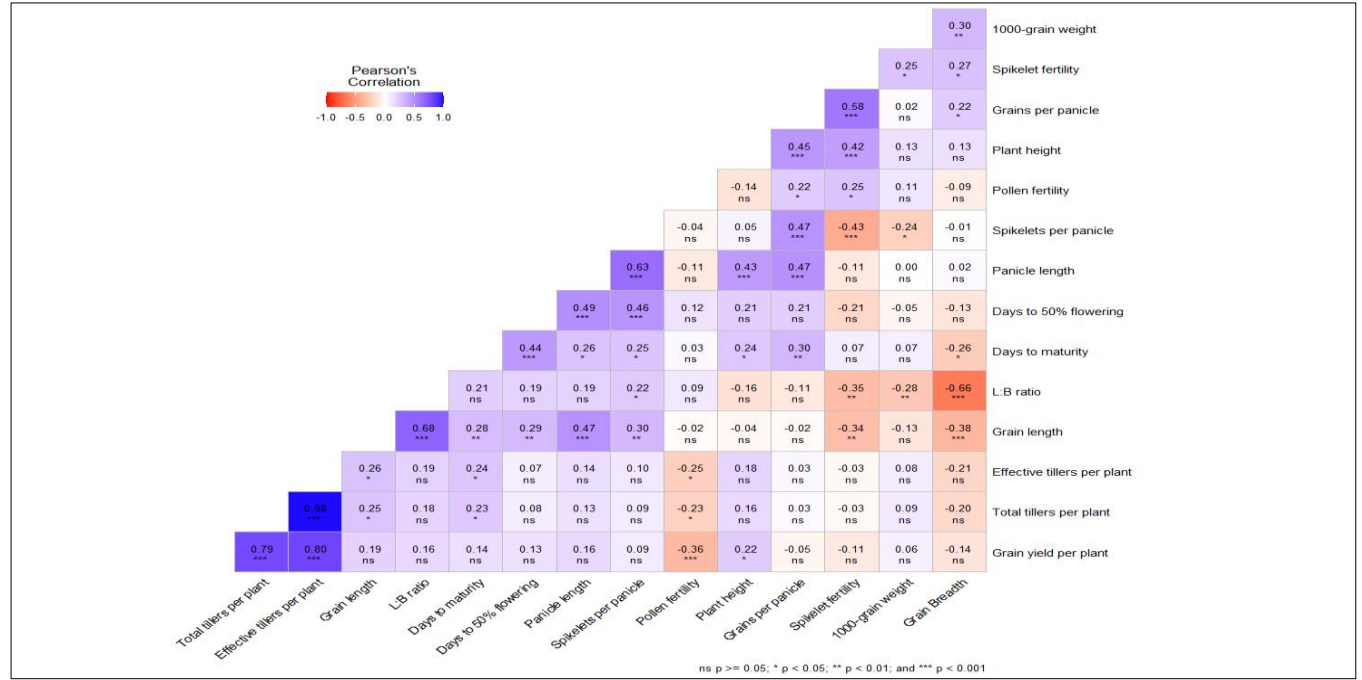


Fig 2: Corplot of the studied traits

ETPP showed a highly significant positive correlation with TTPP (0.98***), DM (0.24*), and GL(0.26*). LBR was significantly negatively correlated with GB (-0.66***) and positively correlated with GL (0.68***). GYPP exhibited a

significant positive correlation with TTPP (0.79***), ETPP (0.80***), and PH (0.22*), while showing a significant negative correlation with PF (-0.36***). PL positively correlated with GPP (0.47***), PH (0.43***), and SPP

(0.63***). PH was positively correlated with GPP (0.45***) and SF (0.42***). GPP was positively correlated with GB (0.22*) and SF (0.58***). PF was positively correlated with SF (0.25*) and GPP (0.22*). SPP correlated with TGW (0.24*), SF (0.43***), and GPP (0.47***). DM correlated positively with GPP (0.30**), PH (0.24*), SPP (0.25*), PL (0.26*), and DTF (0.44***), while negatively correlating with GB (-0.26*) (Figure 2).

Cluster analysis: Cluster analysis was conducted using Euclidean distance and Ward's algorithm in RStudio software version 4.3.2 2024 to group the genotypes (parents and hybrids). As shown in Figure 3, all genotypes were classified into four clusters. Additionally, a heatmap was created to illustrate the relationship between the genotypes (parents and hybrids) and the studied traits (Figure 4)

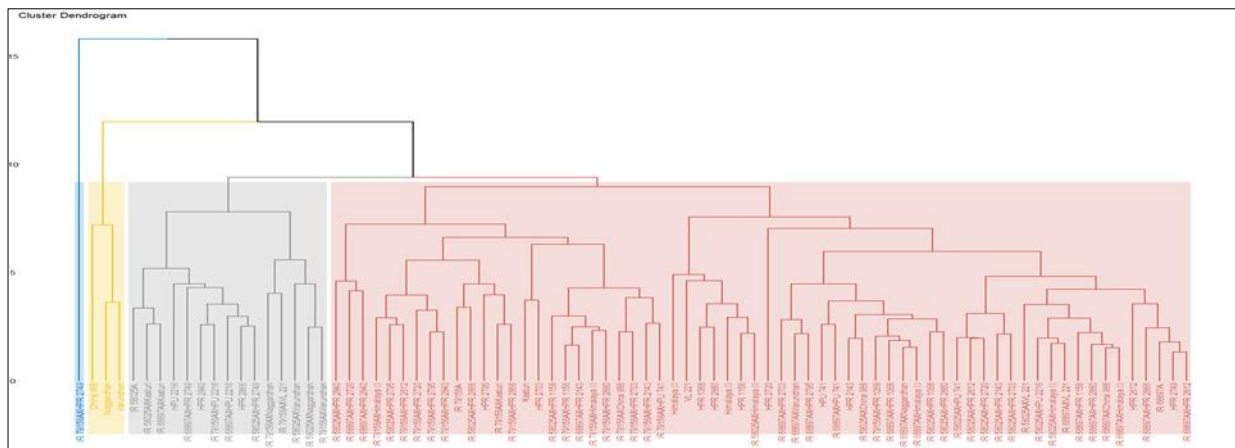


Fig 3: A tangle gram showing results of cluster analysis based on Euclidean coefficient and Ward method

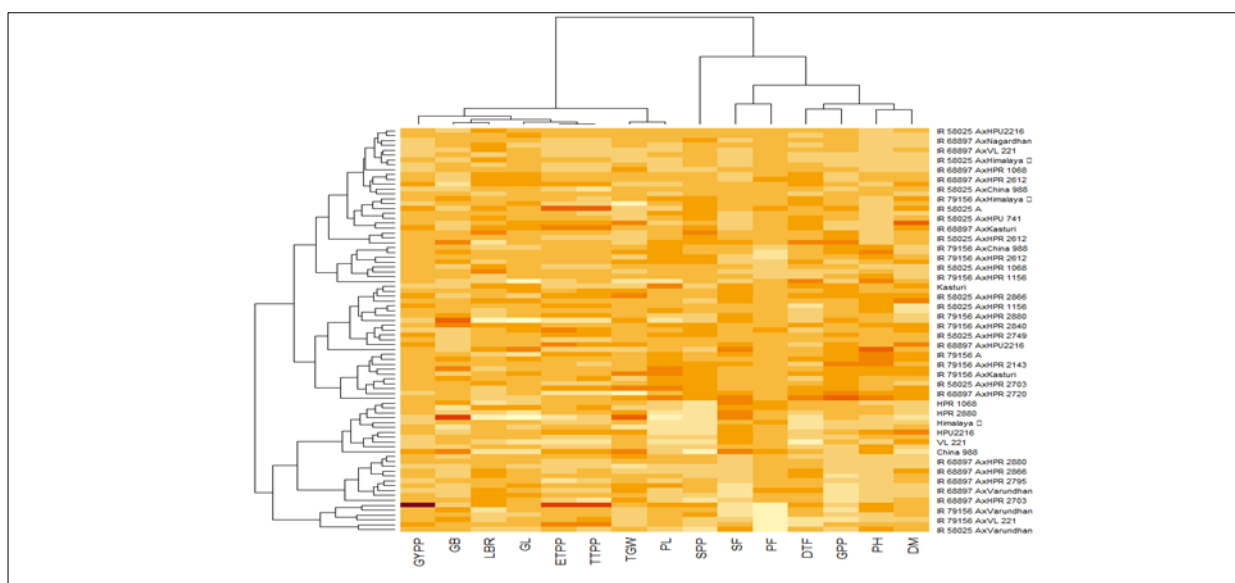


Fig 4: Heatmap of the relationship between genotypes and the studied traits

Genotype by yield*trait (GYT) biplot analysis

The genotype by yield-trait (GYT) biplot ranks genotypes by their ability to combine yield with various breeding objectives, such as agronomic traits, grain quality, processing quality, nutritional quality, or disease resistance. It also displays their trait profiles, highlighting strengths and weaknesses. Figure 5 shows that all combinations of yield traits positively correlate with one another, as they share yield components and form acute angles between the vectors. The average tester coordinate (ATC) showed that hybrids G46, G52, G64, G67, G1, G25, and others were

superior, while hybrids G55, G32, G62, G36, G12 and several more were inferior (Figure 6). To rank the genotypes by performance, a line was drawn through the biplot origin. Using the superiority index, the hybrids were ranked by yield trait combinations from top-performing hybrids to poor performers: G46 > G52 > G64 > G1 > G67 > G25 > G29 > G8 > G47, with others similarly ranked as shown in the figure. The worst-performing hybrids were G14 > G15 > G82 > G12 > G39 > G77 > G78, and others ranked similarly (Figure 7).

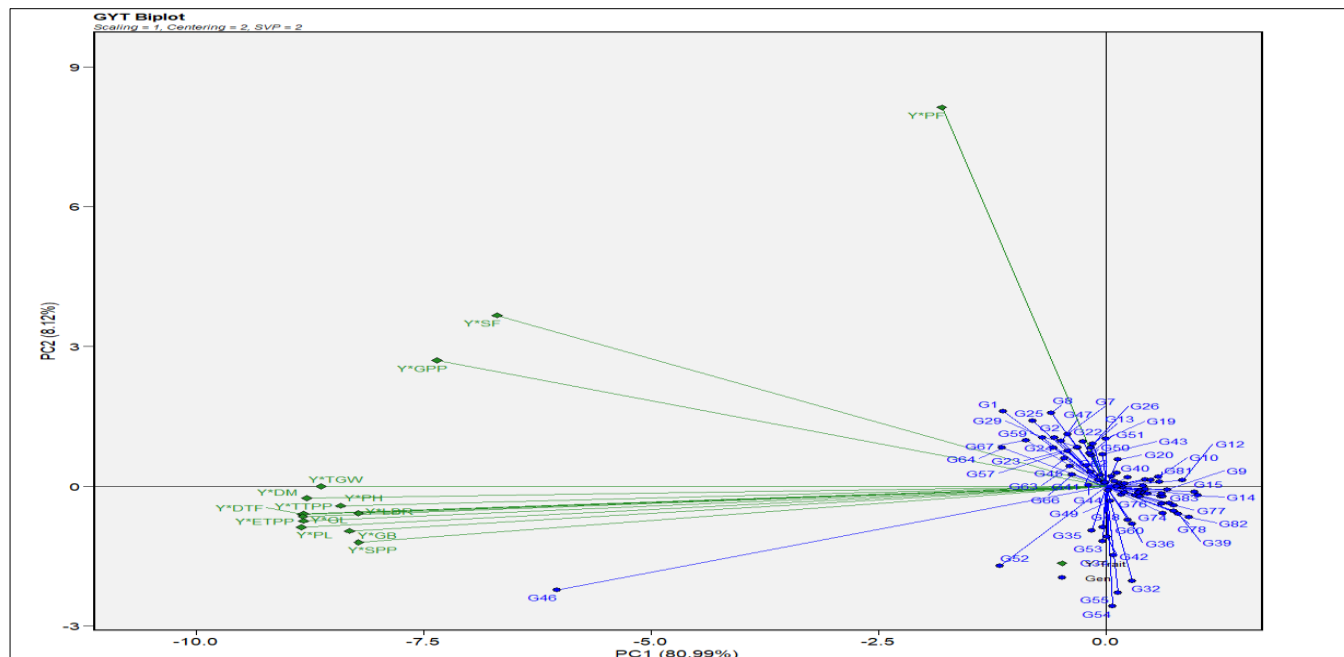


Fig 5: Genotype by yield trait (GYT) biplot based on trait data (Table 3). The GYT biplot was based on singular value decomposition of trait-standardized data ("Scaling=1, Centering=2") and trait-focused singular value partition ("SVP=2")

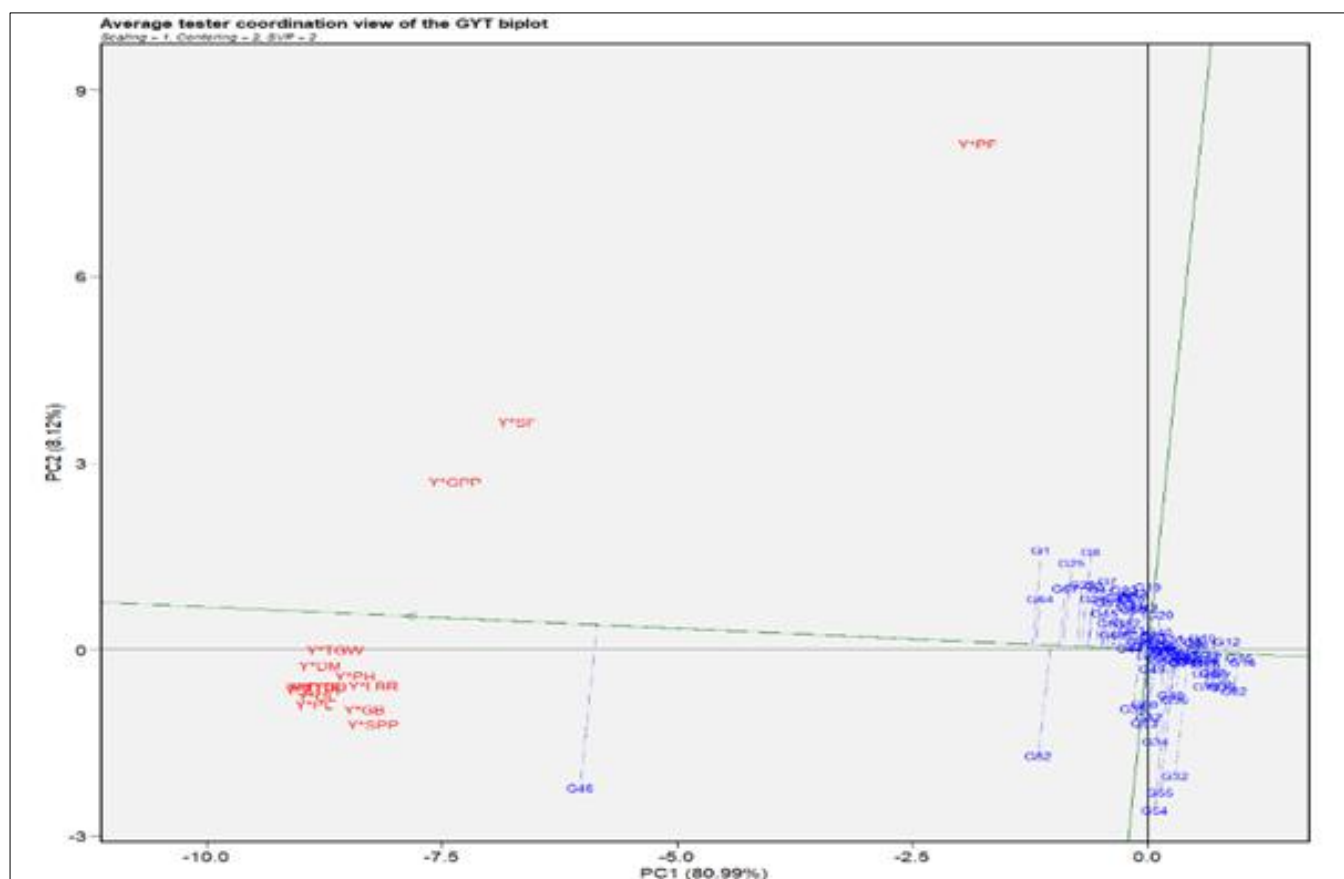


Fig 6: Average Tester Coordinate (ATC) view of the genotypes by GYT biplot based on overall superiority and their strength and weaknesses based on trait data (Table 3). The GYT biplot was based on singular value decomposition of trait-standardized data ("Scaling=1, Centering=2") and trait-focused singular value partition ("SVP=2")

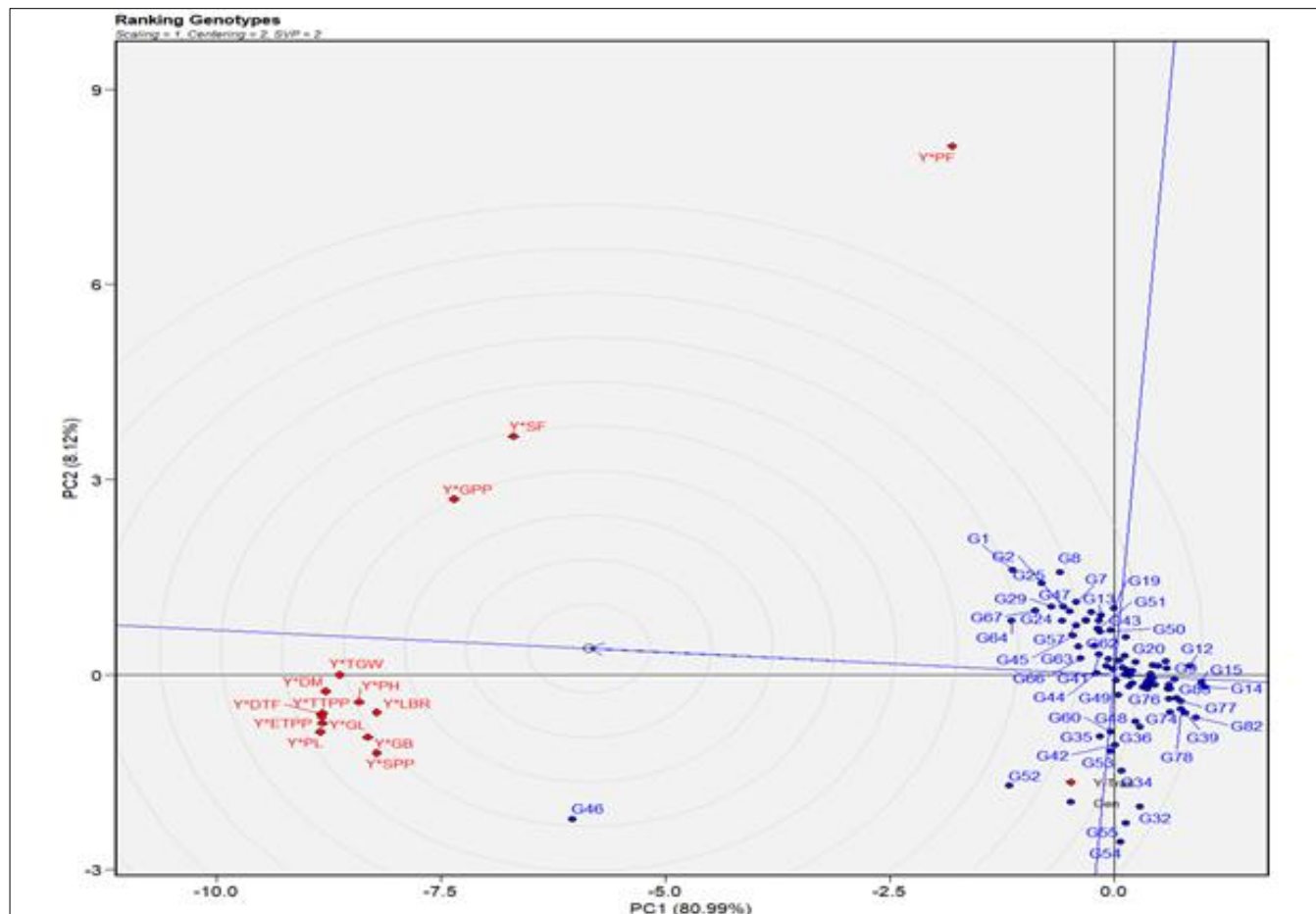


Fig 7: Ranking of genotypes using Average Tester Coordinate (ATC) view of the genotypes by GYT biplot based on overall superiority and inferiority based on trait data (Table 3). The GYT biplot was based on singular value decomposition of trait- standardized data (“Scaling=1, Centering=2”) and trait-focused singular value partition (“SVP=2”)

Significant variations among the traits evince improvement through both selection and hybridization (Adhikari *et al.*, 2018) [3]. The *per se* performance of parental lines frequently influences the performance of the resulting hybrids (Gilbert, 1958) [18]. Maternal parent effect (39.85%) on plant height was in sync with Faiz *et al.*, (2007) [14]. Traits like DTF (72.74%), DM (68.82%), TGW (52.63%), and TTPP (45.73%) influenced the paternal parent, consistent with findings of Ghorbani *et al.*, (2014) [17] and Montazeri *et al.*, (2014) [28]. σ^2 SCA exceeded σ^2 GCA for all the studied traits, indicating non-additive gene effects, where dominance variance outweighs additive variance, which was consistent with findings of Sari *et al.*, (2020) [36]. In this study, GCA effects of the lines showed variability, with the tester Kasturi exhibiting significant positive effects on GYPP. These effects were further enhanced by factors such as ETPP, TTPP, GL, and L:B ratio. In contrast, CMS lines IR 79156A (0.43) and IR 58025A (0.38) also demonstrated significant positive GCA effects on GYPP. This study, consistent with Yuga, (2018) [41], found no single parent exhibiting optimal GCA for all traits examined. CMS line IR 79156A exhibited the highest GCA for TTPP (0.61), ETPP (0.58), PL (0.93), GPP (7.45), TGW (0.48), and SF (3.86). The hybrid IR 79156A×Naggardhan (4.17) displayed the highest SCA effect for GYPP, coupled with superior *per se* performance (19.46) and standard check variety heterosis (37.91). PH, TTPP, ETPP, SPP, GPP, SF, GB, and L:B ratio exhibited high GAM (>20%), suggesting a combination of additive and non-additive gene effects in governing their inheritance. Roy & Shil, (2020) [35] observed similar results

for PL, and Prasad *et al.*, (2017) [32] for and. DTF, PL, and GL showed moderate GAM (10%- 20%), aligning with Ajmera *et al.*, (2017) [4]. Most traits exhibited low narrow-sense heritability (h^2 (ns) < 10%), except for GL (10.24%), which was medium (10-20%). The dominance of non-additive gene effects counsels to enhance yield by maintaining heterozygosity. Cross combinations with high SCA effects from poor × poor GCA parents may stem from dominance × dominance non-allelic gene interactions, resulting in non-fixable overdominance. In such cases, biparental mating or reciprocal recurrent selection will be plummy (Latha *et al.*, 2013) [24].

Negative heterosis for DTF promotes earlier flowering in hybrid IR 58025A×HPR 1156 (-10.99) than in the standard check variety (Deepika *et al.*, 2023; Nivedha *et al.*, 2024) [10, 30]. Similarly, negative heterosis for days to maturity is desirable to achieve early maturity that impels multiple cropping systems, and its maximum magnitude depicted by hybrid IR 79156A×VL 221 exhibited the highest significant negative mid-parent heterosis (-14.76), while IR 68897A×HPR 2840 showed the highest negative heterosis over the standard check (-9.52) that was familiar with prior researchers' findings with Deepika *et al.*, (2023) [10] and Nivedha *et al.*, (2024) [30]. Semi-dwarfing is associated with lodging resistance, making negative heterosis for plant height desirable. The most significant negative mid-parent heterosis was observed in IR 68897A×HPR 2703 (-31.27), and the highest negative standard check heterosis was in IR 68897A×HPR 1068 (-26.5), with similar patterns in rice using CMS lines (Kiruba *et al.*, 2023; Negm *et al.*, 2023) [23,

^{29]}. A higher number of tillers per plant is correlated with increased grain yield. Most hybrids displayed significant negative heterosis over mid-parent and standard check varieties. Hussein *et al.*, (2021) ^[20], Mohan *et al.*, (2021) ^[27], and Arunkumar & Narayanan, (2024) ^[6] also observed both positive and negative standard check variety heterosis for TTPP. For maximum grain yield, the relationship between grain yield and its governing traits, including number of ETTP, PH, SF, SPP, and HI, plays a key role (Faysal *et al.*, 2022) ^[15].

Cluster analysis, a statistical tool, uncovers genetic relationships and diversity in rice genotypes, facilitating their use in breeding programs. Dendrogram cluster analysis groups similar genotypes, assisting breeders in selecting suitable genotypes for yield improvement. G*YT index-based selection ensures consistently high-yielding genotypes. This method provides a robust and comprehensive approach and visually highlights each genotype's strengths and weaknesses based on combined traits with yield (Kendal, 2019) ^[21]. Acute angles between vectors in the GYT biplot indicate positive correlations among yield-trait combinations (Figure 5). This key feature allows meaningful graphical ranking of genotypes based on their yield*trait combinations.

Conclusion

Heterosis exploitation serves to cope with formidable rice challenges. CMS-based hybrid rice production is a highly efficient technique. Hybrids showing positive specific combining ability (SCA) effects for yield and related attributes can be utilized in hybrid rice breeding programs. Correlation analysis helped to determine key yield-attributing traits identified with significant association ship, while cluster analysis revealed significant genetic diversity among the genotypes for future breeding programmes for yield improvement. The GYT technique depicted a strong and restricted (often positive) relationship between combinations and highlighted the top-performing genotype among all genotypes in terms of grain yield* and other traits.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this manuscript. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

1. Abd El-Aty MS, Abo-Youssef MI, Galal AA, Salama AM, Salama AA, El-Shehawi AM, *et al.* Genetic behavior of earliness and yield traits of some rice (*Oryza sativa* L.) genotypes. Saudi J Biol Sci. 2022;29(4):2691-2697.
2. Abebe T, Alamerew S, Tulu L. Genetic variability, heritability and genetic advance for yield and its related traits in rainfed lowland rice (*Oryza sativa* L.) genotypes at Fogera and Pawe, Ethiopia. Adv Crop Sci Technol. 2017;5(2):272.
3. Adhikari BN, Joshi BP, Shrestha J, Bhatta NR. Genetic variability, heritability, genetic advance and correlation among yield and yield components of rice (*Oryza sativa* L.). J Agric Nat Resour. 2018;1(1):149-160.
4. Ajmera S, Kumar SS, Ravindra Babu V. Evaluation of genetic variability, heritability and genetic advance for yield and yield components in rice genotypes. Int J Curr Microbiol Appl Sci. 2017;6(10):1657-1664.
5. Arunachalam V. The fallacy behind the use of a modified line $\times$ tester design. Indian J Genet Plant Breed. 1974;34(2):280-287.
6. Arunkumar P, Narayanan R. Combining ability and gene action for productivity traits in rice (*Oryza sativa* L.) under saline conditions. Mysore J Agric Sci. 2024;58(1):40-47.
7. Chang TT. The rice cultures. Biol Sci. 1976;275(936):143-157.
8. Chen C, Van Groenigen KJ, Yang H, Hungate BA, Yang B, Tian Y, *et al.* Global warming and shifts in cropping systems together reduce China's rice production. Glob Food Sec. 2020;24:100359.
9. De Mendiburu F. Agricolae tutorial. Version 1.3-5. La Molina, Peru: Universidad Nacional Agraria; 2021.
10. Deepika K, Manimaran R, Pushpa R, Bama KS, Umamageswari C, Suresh R. Study on combining ability and heterosis for yield and nutritional traits in rice (*Oryza sativa* L.). Electron J Plant Breed. 2023;14(3):1135-1146.
11. Duvick DN. Heterosis: feeding people and protecting natural resources. In: Coors JG, Pandey S, editors. Genetics and exploitation of heterosis in crops. Madison (WI): American Society of Agronomy; 1999. p. 19-29.
12. El-Mowafi HF, AlKahtani MD, Abdallah RM, Reda AM, Attia KA, El-Hity MA, *et al.* Combining ability and gene action for yield characteristics in novel aromatic cytoplasmic male sterile hybrid rice under water-stress conditions. Agriculture. 2021;11(3):226.
13. El-Namaky R. The genetic variability of floral and agronomic characteristics of newly-bred cytoplasmic male sterile rice. Agriculture. 2018;8(5):68.
14. Faiz FA, Ijaz M, Awan TH, Manzoor Z, Ahmad M, Waraich NM, *et al.* Effect of wild abortive cytoplasm inducing male sterility on resistance/tolerance against brown plant hopper and white backed plant hopper in Basmati rice hybrids. J Anim Plant Sci. 2007;17(1-2):16-20.
15. Faysal ASM, Ali L, Azam MG, Sarker U, Ercisli S, Golokhvast KS, *et al.* Genetic variability, character association, and path coefficient analysis in transplant Aman rice genotypes. Plants. 2022;11(21):2952.
16. Gaballah MM, Attia KA, Ghoneim AM, Khan N, El-Ezz AF, Yang B, *et al.* Assessment of genetic parameters and gene action associated with heterosis for enhancing yield characters in novel hybrid rice parental lines. Plants. 2022;11(3):266.
17. Ghorbani HR, Lahiji HS, Rabiei B, Gholipour MA. Line $\times$ tester analysis for yield and yield components in rice lines. Iran J Field Crop Sci. 2014;44(4):124-132.

18. Gilbert NEG. Diallel cross in plant breeding. *Heredity*. 1958;12:477-498. doi:10.1038/hdy.1958.48.
19. Huang M, Chen LY, Chen ZQ. Diallel analysis of combining ability and heterosis for yield and yield components in rice by using positive *loci*. *Euphytica*. 2015;205(1):37-50.
20. Hussein FA. Heterosis and combining ability of some colored rice genotypes for yield characteristics and grain micronutrient content using line $\times$ tester analysis. *J Plant Prod*. 2021;12(6):635-643.
21. Kendal E. Comparing durum wheat cultivars by genotype $\times$ yield $\times$ trait and genotype $\times$ trait biplot method. *Chil J Agric Res*. 2019;79:512-522.
22. Khush GS. Strategies for increasing the yield potential of cereals: case of rice as an example. *Plant Breed*. 2013;132(5):433-436.
23. Kiruba G, Geetha S, Saraswathi R, Santhi R, Uma D, Pushpa R. Heterosis, character association and path analysis for grain protein content in rice (*Oryza sativa* L.). *Electron J Plant Breed*. 2023;14(3):876-883.
24. Latha S, Sharma D, Sanghera GS. Combining ability and heterosis for grain yield and its component traits in rice (*Oryza sativa* L.). *Not Sci Biol*. 2013;5(1):90-97.
25. Liao C, Yan W, Chen Z, Xie G, Deng XW, Tang X. Innovation and development of the third-generation hybrid rice technology. *Crop J*. 2021;9(3):693-701.
26. Manivannan N. TNAU STAT: statistical package. 2014. Available from: <https://sites.google.com/site/tnaustat>
27. Mohan YC, Krishna L, Singh TV, Raju CD, Babu TK, Ramana NV. Combining ability and heterosis studies for grain yield in rice (*Oryza sativa* L.). *J Crop Weed*. 2021;17(2):245-254.
28. Montazeri Z, Babaeian JN, Bagheri N. Genetic dissection of some important agronomic traits in rice using line $\times$ tester method. *Int J Adv Biol Biomed Res*. 2014;2(1):181-191.
29. Negm ME, Abo-Marzoka EA, Abdelhameed MM, Ghidan WF. Inheritance of some biochemical, morpho-physiological and yield attributes trait of some rice genotypes under salinity condition. *Egypt J Agric Res*. 2023;101(2):552-568.
30. Nivedha R, Manonmani S, Kalaimagal T, Raveendran M, Kavitha S. Comprehensive assessment of combining ability and heterosis for the development of superior three-line hybrids in rice (*Oryza sativa* L.). *Electron J Plant Breed*. 2024;15(1):31-41.
31. Panse VG, Sukhatme PV. Statistical methods for agricultural workers. New Delhi, India: Indian Council of Agricultural Research; 1985. p. 87-89.
32. Prasad KR, Radha-Krishna KV, Bhavane MHV, Subba-Rao LV. Genetic variability, heritability and genetic advance in boro rice (*Oryza sativa* L.) germplasm. *Int J Curr Microbiol Appl Sci*. 2017;6(4):1261-1266.
33. Rather AG, Zargar MA, Sheikh FA. Genetic divergence in rice (*Oryza sativa*) under temperate conditions. *Indian J Agric Sci*. 2001;71(5):344-345.
34. Rezvi HUA, Tahjib-Ul-Arif M, Azim MA, Tumpa TA, Tipu MMH, Najnine F, *et al*. Rice and food security: climate change implications and the future prospects for nutritional security. *Food Energy Secur*. 2023;12(1):e430.
35. Roy SC, Shil P. Assessment of genetic heritability in rice breeding lines based on morphological traits and caryopsis ultrastructure. *Sci Rep*. 2020;10(1):7830.
36. Sari WK, Nualsri C, Junsawang N, Soonsuwon W. Combining ability and heritability for yield and its related traits in Thai upland rice (*Oryza sativa* L.). *Agric Nat Resour*. 2019;54(3):229-236.
37. Singh RK, Chaudhary BD. Biometrical methods in quantitative genetic analysis. New Delhi, India: Kalyani Publishers; 1981.
38. Ullah Zaid I, Tang W, He J, Ullah Khan S, Hong D. Association analysis uncovers the genetic basis of general combining ability of 11 yield-related traits in parents of hybrid rice. *AoB Plants*. 2019;11(1):ply077.
39. Vaz Mondo VH, Nascente AS, Neves PDCF, Taillebois JE, Neto MOAC. Flowering synchronization in hybrid rice parental lines. *Aust J Crop Sci*. 2016;10(8):1213-1221.
40. Yan W, Frégeau-Reid J. Genotype by yield $\times$ trait (GYT) biplot: a novel approach for genotype selection based on multiple traits. *Sci Rep*. 2018;8(1):8242.
41. Yuga M, Kimani P, Kimani JM, Nzuve FM, Olubayo MF, Muthomi JW. Combining ability and heterosis for agronomic and yield traits in *indica* and *japonica* rice crosses. *J Agric Sci*. 2018;10(12):92-103.