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Estimation of the Genetic Parameters Associated with High-yielding and Early Harvesting in Rice

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ABSTRACT

Background: Climate change is threatening global food security, particularly rice production. This makes it crucial to identify rice cultivars that are both high-yielding and suitable for early harvesting. This study evaluated combining ability and estimated genetic parameters of F1 seeds from crosses among nine rice genotypes.

Methods: The study was conducted at the Greenhouse of the Faculty of Agriculture, Universitas Gadjah Mada, Yogyakarta, Indonesia, from September 2022 to March 2024. The study employed a North Carolina II (NC II) mating design and was arranged in an augmented randomized block design (ARAB) with three rows and six columns. Genotype was the fixed effect and block was the random effect.

Result: The results showed that 100-seed weight exhibited considerable General Combining Ability (GCA) and rice female genotype G4 had the most beneficial additive effect. Estimation of genetic parameters revealed that most were influenced by non-additive gene action. 100-seed weight showed the most significant additive variation and narrow-sense heritability, making it a good candidate for early-generation selection. Assessment of Specific Combining Ability (SCA), genotype performance and hierarchical clustering indicated that G4/GB was the most advantageous rice line, combining high yield and early harvest. These findings establish a strong foundation for developing high-quality rice that is resilient to climate change.

Key words: Combining ability, Early harvesting, High yielding, Rice.

INTRODUCTION

Indonesia is the world's fourth-largest rice consumer, with an average annual per capita consumption of 93.79 kg (Ministry of Agriculture, 2023; USDA, 2023). Indonesia's population is predicted to increase by 27.04% in 2045. This is likely to increase rice demand by 14.99% (Zainul *et al.,* 2021). The future challenge is meeting rice demand due to climate change. Indonesian rice production is predicted to decline by up to 14% due to rising temperatures, changing rainfall patterns and an increase in extreme weather events (Ansari *et al.,* 2021; Octania, 2021). Therefore, new rice breeding methods are needed to maintain and increase rice production. One way to mitigate the negative impacts of climate change is to develop high-yielding and early-harvesting rice varieties. This will result in lower water requirements and a lower risk of mortality due to drought or heat stress and the ability to cultivate more than once a year. This aligns with the primary goal of plant breeding: producing varieties with high yield potential while ensuring food security and economic resilience (Wang *et al.,* 2021; Yun, 2023).

Methodically selecting progenitors and understanding the genetic pathways that govern desired traits are essential. This is useful for selecting offspring that carry information on the inheritance of agronomic traits (Muthoni and Shimelis, 2020). Combining ability analysis is one of the most effective genetic tools because it can assess the additive effects of genes through General Combining Ability (GCA) and non-additive effects or interactions through Specific Combining Ability (SCA) (Falconer and Mackay, 1996; Acquaah, 2012). This provides clearer information about how genes influence each plant trait. This knowledge is crucial for formulating effective breeding strategies, especially in determining whether to focus selection on early generations or exploit heterosis through hybrid variety development (Sztepanacz and Blows, 2015).

Studies combining capability analysis with multi-trait evaluation to simultaneously increase yield and early

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harvesting in rice are still rare in Indonesia. The purpose of the study was to evaluate combining ability and estimate the genetic parameters of F1 seeds from various parents produced through crossbreeding. The benefits of this research are expected to accelerate the development of superior rice varieties with high yields, early harvesting and adaptability to climate change.

MATERIALS AND METHODS

The plant material consisted of nine rice genotypes selected as parental lines (four superior genotypes and five genotypes with early harvesting traits). These genotypes were used as female and male parents, respectively, to produce F_1 seeds and served as controls for the experiment. The mating design used was the North Carolina II (NC II) design, which systematically combines female and male parents to produce 20 cross-pairs (Acquaah, 2012). Verification of the F_1 seeds from the crosses was validated using Simple Sequence Repeat (SSR) molecular markers to ensure that the seeds were of the F_1 genotype. In this study, only 18 F_1 genotypes were used, because the remaining two genotypes were suspected of selfing (Aisya *et al.,* 2024) (Table 1).

The study was located at the Greenhouse of the Faculty of Agriculture, Universitas Gadjah Mada, Yogyakarta, Indonesia, from September 2022 to March 2024. Artificial hybridization was performed using selected parental genotypes based on predicted flowering periods to ensure synchronized anthesis timing. Five groups of seeds from each parent were planted sequentially with a two-week interval between groups. Emasculation was performed in the afternoon before pollination to prevent self-pollination. A vacuum emasculation procedure was used to quickly and gently remove the anthers from the flowers. This process was carried out at different plant ages depending on the genotype: G2 at 90 days after sowing (DAS), G4 at 91 DAS, G7 at 101 DAS, G10 at 87 DAS, SR Super at 84 DAS, Inbrida M70D at 87 DAS, Trisakti at 89 DAS, MSP 17 Beras Merah at 90 DAS and Genjah Blora at 82 DAS (Aisya *et al.,* 2024). Pollination success was assessed on the fifth day after pollination and F1 seeds were collected 30 days later.

Evaluation of F_1 genotypes was conducted using an augmented randomized complete block design (ARCBD) with three rows and six columns. Genotype was the fixed effect and block was the random effect (Haines, 2021). Seedlings were first germinated in Petri dishes for seven days. Seedlings were transferred to soil treated with fungicide for 21 days. Finally, seedlings were transplanted into pots containing a 1:1 mixture of soil and organic fertilizer.

Table 1: List of genotypes.

Genotype	Types	Description	Pedigree
G2	Promising lines	Female parent (high yield)	Fatmawati/IR64//Memberamo/Ciherang
G4	Promising lines	Female parent (high yield)	Sintanur/IR64//Memberamo/Ciherang
G7	National variety	Female parent (high yield)	Mutant rajalele klaten
G10	Promising lines	Female parent (high yield)	Mutant lakatesan
SR super (SR)	Not yet released	Male parent (early harvesting)	Unknown
Inbrida M70D (M70D)	National variety	Male parent (early harvesting)	Unknown
Trisakti (TRI)	Not yet released	Male parent (early harvesting)	Unknown
MSP 17 beras merah (MSP17)	Not yet released	Male parent (early harvesting)	Unknown
Genjah blora (GB)	Local variety	Male parent (early harvesting)	Unknown
G4/M70D	Progenies	F_1	G4/Inbrida M70D
G10/M70D	Progenies	F_1	G10/Inbrida M70D
G2/SR	Progenies	F_1	G2/SR super
G4/GB	Progenies	F_1	G4/Genjah blora
G7/M70D	Progenies	F_1	G7/Inbrida M70D
G2/MSP17	Progenies	F_1	G2/MSP 17 beras merah
G4/SR	Progenies	F_1	G4/SR super
G4/MSP17	Progenies	F_1	G4/MSP 17 beras merah
G10/GB	Progenies	F_1	G10/Genjah blora
G7/TRI	Progenies	F_1	G7/Trisakti
G2/M70D	Progenies	F_1	G2/Inbrida M70D
G10/TRI	Progenies	F_1	G10/Trisakti
G7/GB	Progenies	F_1	G7/Genjah blora
G4/TRI	Progenies	F_1	G4/Trisakti
G10/SR	Progenies	F_1	G10/SR super
G2/GB	Progenies	F_1	G2/Genjah blora
G7/SR	Progenies	F_1	G7/SR super
G7/MSP17	Progenies	F_1	G7/MSP17 beras merah

The fertilizers used were Urea, Ammonium Sulfate (ZA), Single Superphosphate (SP-36) and Potassium Chloride (KCl) at rates of 300, 100, 150 and 150 kg ha^{-1}, corresponding to 1.88, 0.63, 0.94 and 0.94 g per pot, respectively. Urea was applied three times at 14, 28 and 42 days after transplanting (DAT). ZA, SP-36 and KCl were applied once at 14 DAT. Watering was carried out daily. Integrated pest and disease management practices were implemented to control pests and diseases. This includes insecticides, fungicides and bactericides containing pymetrozine, mancozeb and copper hydroxide, respectively (Aisya *et al.,* 2024).

The observations of agronomic traits were conducted based on the Standard Evaluation System for Rice (SES) including the number of productive tillers (panicles $clump^{-1}$), total tillers number, plant height (cm), flowering time (days after sowing/DAS), harvesting time (DAS), number of grains per panicle, grain fertility (%), 100-grain weight (g) and grain weight per plant (g $clump^{-1}$) (IRRI, 2013).

Data were analyzed using a generalized linear mixed model (GLMM) and Dunnett's test (p<0.05) was used to compare each genotype with predefined control parents with high-yield traits. All statistical analyses were performed in SAS OnDemand for Academics software (SAS Institute Inc, 2021). Additionally, correlation matrices and hierarchical heatmaps were generated in RStudio software to visualize trait relationships and clustering patterns using the pheatmap, tidyverse and ggplot2 packages (Welham *et al.,* 2015; Kassambara, 2017; R Core Team, 2017; Wijayanti *et al.,* 2023).

RESULTS AND DISCUSSION

General and specific combining ability

The combining ability analysis revealed three distinct sources of variation: General Combining Ability (GCA) from female parents, GCA from male parents and Specific Combining Ability (SCA) in F_1 seeds. GCA effects were significant only for 100-seed weight from female parents, whereas SCA effects were significant for all observed traits (Table 2).

Maternal-effect tests revealed that female parents had no significant effect on any of the measured traits (Table 3). The lack of maternal effects corroborates that the combining ability estimates were unbiased, fulfilling a crucial assumption for precise genetic interpretation using the NC II mating design (Muthoni and Shimelis, 2020). The findings of this study shed important light on the genetic regulation of rice traits associated with high-yielding and early-harvesting, which is essential for breeding strategies aimed at adapting to climate change. Focused breeding strategies are guided by analyses of general combining ability (GCA) and specific combining ability (SCA), which clarify the type and degree of gene action underlying these traits (Abdel-Aty *et al.,* 2022). All traits exhibit significant SCA effects, indicating that non-additive gene activity, particularly dominance effects, plays a significant role in their inheritance (Chen *et al.,* 2019).

GCA is the mean performance of a parent across all its hybrid combinations (Chen *et al*., 2019). Female genotypes G2, G4, G7 and G10 had a significant impact on GCA for 100-seed weight (Table 4). Traits with substantial GCA effects were further investigated to determine parental

Table 2: ANOVA of combining ability analysis based on north carolina II.

SV	DF	MS				
		FT	HT	PH	NPT	TNT
Block	7	306.66	363.31	107.35	51.73	51.89
Female	3	944.10	937.37	961.49	92.42	98.92
Male	4	473.06	466.65	339.91	51.78	49.41
F_1	10	623.18*	640.48*	433.12**	88.78**	95.90**
SV	**DF**	**PL**	**NGP**	**GF**	**GW100**	**GWP**
Block	7	1.62	230.61	111.93	0.009	27.83
Female	3	22.63	2316.23	2979.50	0.88*	346.46
Male	4	13.76	1182.32	3741.03	0.61	154.62
F_1	10	18.82**	1204.04**	9977.88**	0.94**	164.44**

Note: * and ** indicate significance at p<0.05 and p<0.01. FT= Flowering time; HT= Harvesting time; PH= Plant height; NPT= Number of productive tillers; TNT= Total number of tillers; PL= Panicle length; NGP= Number of grains per panicle; GF= Grain fertility; GW100= 100-Seed weight; GWP= Grain weight per plant.

Table 3: Maternal effect.

	FT	HT	PH	NPT	TNT	PL	NGP	GF	GW100	GWP
F_{value}	2.00 ^{ns}	2.01^{ns}	2.83 ^{ns}	1.78 ^{ns}	2.00 ^{ns}	1.65 ^{ns}	1.96 ^{ns}	0.80 ^{ns}	1.45 ^{ns}	2.24 ^{ns}

Note: ^{ns} indicates not significant at p<0.05. FT= Flowering time; HT= Harvesting time; PH= Plant height; NPT= Number of productive tillers; TNT= Total number of tillers; PL= Panicle length; NGP= Number of grains per panicle; GF= Grain fertility; GW100= 100-Seed weight; GWP= Grain weight per plant.

contributions. G4 had the most potent positive GCA effect on 100-seed weight. This is more likely to pass this trait on to its offspring. This makes it a good choice for breeding operations. A higher GCA effect value for 100-seed weight is considered more advantageous. Genotypes with high GCA effects indicate a strong ability to pass the target trait on to their offspring.

In contrast to GCA, SCA effects were significant for all evaluated traits, highlighting the predominance of non-additive gene action in the studied population. Negative SCA effects were considered favourable for flowering and harvesting time because shorter duration is preferred, whereas positive SCA effects were advantageous for yield components. G4/GB had the least favourable SCA effect on flowering (-14.56) and harvest time (-15.58). G4/MSP had the most positive SCA effect on plant height with a score of 17.07. G2/GB had the highest positive SCA for productive tillers (5.25) and total tillers (5.56). G4/GB had the longest panicles, the highest number of grains per panicle and the best grain filling with values of 2.85 cm, 23.38 and 11.51%, respectively. G7/GB had the highest SCA for 100-grain weight (0.10) and G4/GB had the highest grain weight per plant (GWP) (13.0) (Table 5).

Table 4: GCA effect of females on 100 seed weight.

Genotype	100-seed weight
G2	-0.11
G4	0.15
G7	-0.03
G10	-0.01

Variance component analysis revealed that dominance variance exceeded additive variance for all traits. The ratios of additive to dominance variance were all less than 1. The additive variance was not greater than dominance variance for any trait. Consequently, narrow-sense heritability estimates were predominantly low. Yadav and Yadav (2023) informed that the high heritability is more than 0.3, moderate heritability is between 0.1 and 0.3 and low heritability is less than 0.1. Twelve traits showed low heritability, seven traits showed moderate heritability and just one trait showed high heritability. The 100-seed weight was the only trait with high narrow-sense heritability (Table 6). This supports a significant GCA effect, indicating that additive genetic selection can lead to substantial improvements in performance. The wide genetic variability and high heritability of various rice yield and quality traits indicate significant opportunities for improvement through direct selection (Saravanan *et al.,* 2024). Furthermore, Chandramohan *et al.* (2016) also confirmed that genetic diversity among rice genotypes provides a strong basis for sustainable breeding and yield improvement programs.

The consistent dominant variance values were higher than the additive variances for all traits. This trend suggests that the right parental pairing has a greater impact on hybrid performance than the overall effectiveness of each parent. Only the 100-seed weight showed significant GCA for all traits analyzed, while G4 was identified as the effective parent for improving this trait. The importance of additive gene effects in trait expression is evident by the significant GCA effect. This indicates consistent parental contributions across all hybrid combinations (Fang *et al.,* 2019; Kadium and Svyantek, 2023). The high narrow-sense heritability

Table 5: SCA effect in agronomic traits.

F_1	FT	HT	PH	NPT	TNT	PL	NGP	GF	GW100	GWP
G2/GB	3.52	3.09	-5.27	5.25	5.56	-0.20	-7.41	-6.53	-0.03	-0.62
G4/GB	-14.6	-15.6	5.61	3.14	3.43	2.85	23.38	11.51	-0.12	13.00
G7/GB	0.94	0.90	-5.93	-0.4	-0.40	-0.20	-7.08	11.48	0.10	-1.95
G10/GB	-7.56	-8.46	-2.82	0.85	0.82	1.69	21.37	8.45	-0.02	4.84
G2/M70	0.59	0.65	1.64	-3.90	-4.40	0.25	3.00	5.90	-0.13	-2.19
G4/ M70	2.99	3.53	-2.99	-3.30	-3.30	-0.30	-8.41	1.74	0.15	-3.12
G7/ M70	-9.22	-9.67	3.16	3.62	4.94	0.39	1.78	10.21	-0.03	4.44
G10/ M70	-7.26	-7.39	7.28	-1.80	-1.80	0.50	-1.12	7.13	0.28	0.24
G2/MSP	3.27	4.38	-2.09	-6.40	-7.10	-0.90	-11.6	-40.9	-0.06	-5.85
G4/MSP	-6.14	-6.61	17.07	-0.80	-1.30	1.20	3.57	2.60	0.02	-0.27
G7/MSP	9.85	10.35	1.76	1.65	1.69	2.40	20.26	8.00	-0.04	6.82
G2/SR	6.45	6.70	-3.26	0.89	1.71	0.02	-0.88	5.34	0.08	0.54
G4/SR	4.49	4.77	5.76	2.77	3.11	0.54	12.72	-13.10	0.16	1.32
G7/SR	0.40	0.38	-6.89	4.56	4.81	-0.10	1.59	6.14	0.11	1.69
G10/SR	6.32	6.72	4.22	-0.80	-0.70	-4.9	-17.30	-16.70	-0.23	-7.35
G4/TRI	2.81	2.91	-20.70	-6.10	-7.00	-1.60	-15.30	-7.76	-0.03	-7.59
G7/TRI	-0.38	-0.36	3.32	-1.80	-2.30	-0.50	-8.47	-3.61	-0.17	-6.21
G10/TRI	3.47	3.68	0.08	2.55	2.38	-1.10	-10.10	10.06	-0.05	2.27

Note: FT= Flowering time; HT= Harvesting time; PH= Plant height; NPT= Number of productive tillers; TNT= Total number of tillers; PL= Panicle length; NGP= Number of grains per panicle; GF= Grain fertility; GW100= 100-Seed weight; GWP= Grain weight per plant.

(h^2 = 0.35) of the 100-seed weight indicates the suitability of the trait as a selection target in early breeding generations. It suggests that it can be reliably transmitted to offspring (Table 6). Traits with high narrow-sense heritability tend to yield higher expected genetic gains through selection (Fang *et al.,* 2019).

F_1 genotypes' performance compared to high-yielding parents

The LS-Means differences between each F_1 genotype and the mean of the control female parent (G2, G4, G7 and G10) were presented in Fig 1. The horizontal axis represents the F_1 genotypes resulting from the cross. In contrast, the vertical axis shows the LS-Means values compared to the control female parent. A rising histogram indicates a higher value than the mean of the control female parent, while a falling histogram indicates a lower value. The light blue area in the middle indicates the 95% confidence interval for the assessment. Histograms outside this area indicate a statistically significant difference.

The G4/GB cross showed the shortest flowering duration and highest yield compared to the control group, with an average LS-Means value of 34 days after planting (DAP) for flowering and 93 DAP for harvest. On the other hand, not all F_1 genotypes differed significantly from their female parent in terms of yield components. These results indicate that G4/GB has a significantly earlier harvest and has comparable yield potential to the superior parent. This makes it a suitable candidate for breeding programs aimed at developing high-yielding and early-harvesting varieties.

Correlation analysis revealed that the examined qualities were interrelated in various ways. A strong negative correlation was observed between flowering and harvesting time (r = -0.94***). On the other hand, the flowering time was negatively correlated with plant height (r = -0.47*) and grain weight per plant (r = -0.41*). Likewise, harvesting time showed negative associations with the plant height (r = -0.46*), grain weight per plant (r = -0.48*), panicle length (r = -0.39*) and number of grains per panicle (r = -0.43*) (Fig 2a). These associations suggest that earlier flowering and harvesting were typically associated with improvements in yield components. The correlation matrix revealed a strong positive correlation between flowering and harvesting times, whereas all yield components exhibited either significant or insignificant negative correlations with these times.

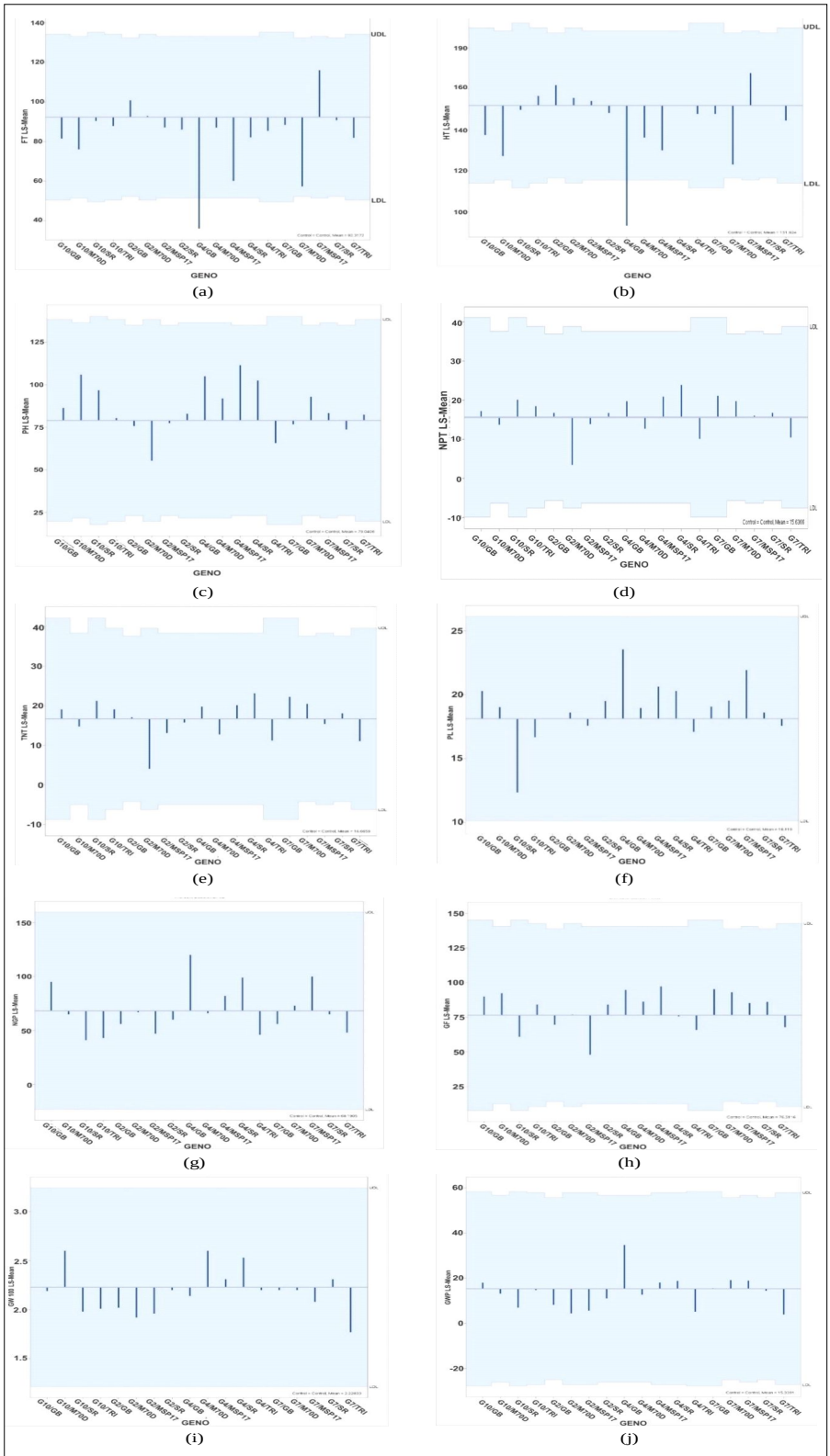
The cluster heatmap showed that the observed variables were grouped into two main clusters (Fig 2b). Cluster 1 consisted of flowering time and harvest time, while Cluster 2 encompassed all other observed traits. The cluster heatmap grouped the F_1 genotypes into two main clusters. The G4/GB genotype was the only one in cluster 1, distinguishing it from the others. G4/GB showed the earliest flowering and harvesting time, as well as relatively high yield component traits, especially grain weight per plant, panicle length and number of grains per panicle. The second cluster was divided into two subclusters. The first subcluster consisted of G7/TRI, G10/SR, G2/MSP17, G2/M70D and G4/TRI, which were generally characterized by relatively low yield components. In addition, the second sub-cluster includes G7/MSP17, G7/SR, G2/SR, G7/GB, G10/TRI, G2/GB, G4/SR, G4/M70D, G10/M70D, G7/M70D, G4/MSP17 and G10/GB, all of which were characterized by relatively high yield components.

A study found a negative correlation between specific yield components and harvest time. Variables such as panicle length and grain weight were significantly negatively correlated with flowering/harvest time. However, this can be explained by advances in rice genetics, where the *Ef-cd* locus has been shown to shorten the harvest period without sacrificing yield (Fang *et al.,* 2019). These results highlight the need for selection processes that consider both inter-trait correlations and combining ability. Furthermore, combining physiological trait modelling with genomic selection can accelerate the identification of new parental combinations with improved climate responsiveness. Our understanding of heterosis and trait inheritance in rice breeding efforts will be enhanced by examining the molecular mechanisms underlying the observed non-additive effects.

Table 6: Estimation of component genetic parameters.

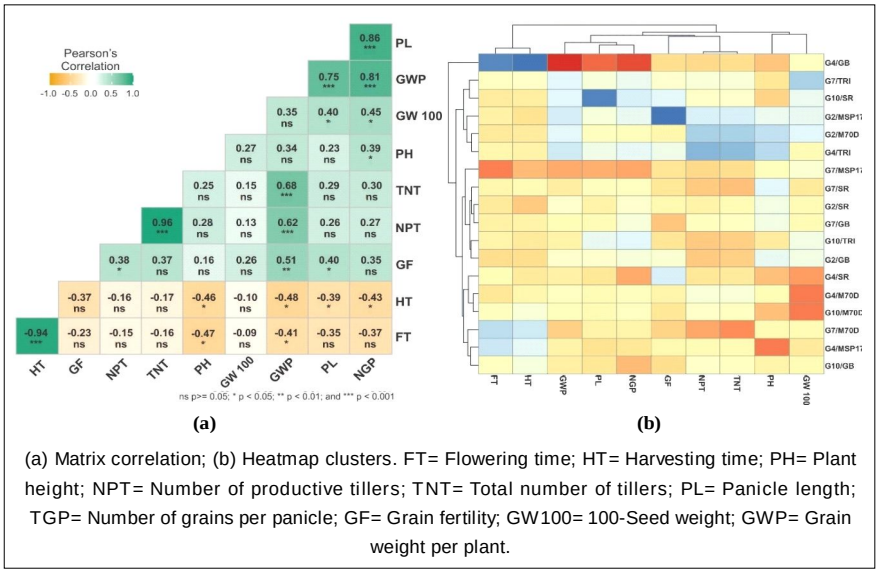
Traits	σ^2_A	σ^2_D	σ^2_A / σ^2_D	Gene action	h^2_{ns}	
FT	55.20	349.12	0.16	Dominant	0.08	(Low)
HT	48.33	372.59	0.13	Dominant	0.07	(Low)
PH	100.65	328.40	0.31	Dominant	0.18	(Moderate)
NPT	6.88	64.37	0.11	Dominant	0.07	(Low)
TNT	7.44	73.32	0.10	Dominant	0.07	(Low)
PL	0.96	15.67	0.06	Dominant	0.05	(Low)
NGP	263.77	907.12	0.29	Dominant	0.17	(Moderate)
GF	66.56	964.60	0.07	Dominant	0.06	(Low)
GW100	0.05	0.09	0.56	Dominant	0.35	(High)
GWP	41.42	142.08	0.29	Dominant	0.19	(Moderate)

Note: FT= Flowering time; HT= Harvesting time; PH= Plant height; NPT= Number of productive tillers; TNT= Total number of tillers; PL= Panicle length; NGP= Number of grains per panicle; GF= Grain fertility; GW100= 100-Seed weight; GWP= Grain weight per plant.



(a) Flowering time; (b) Harvesting time, (c) Plant height, (d) Number of productive tillers, (e) Total number of tillers, (f) Panicle length, (g) Number of grains per anicle, (h) Grain fertility, (i) 100-Seed weight, (j) Grain weight per plant.

Fig 1: Control differences between F_1 and female parents (G2, G4, G7 and G10) with Dunnett test (p<0.05).



(a) Matrix correlation; (b) Heatmap clusters. FT= Flowering time; HT= Harvesting time; PH= Plant height; NPT= Number of productive tillers; TNT= Total number of tillers; PL= Panicle length; TGP= Number of grains per panicle; GF= Grain fertility; GW100= 100-Seed weight; GWP= Grain weight per plant.

Fig 2: Evaluation of agronomic traits across genotypes.

CONCLUSION

G4 was selected as the parent with the most significant GCA effect on 100-seed weight. G4/GB demonstrated the best SCA effect on earlier flowering and harvesting, as well as improved performance in terms of total grains per panicle and grain weight per plant. G4/GB can be a good candidate for hybrid development.

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Informed consent

No animals are used in this research.

Conflict of interest

The authors declare that they have no conflict of interest.

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