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Inheritance pattern of Qualitative traits, Genetic analysis and association of yield attributes in F_2 populations of Rice (*Oryza sativa*)

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F_2 segregants

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ABSTRACT

Understanding the extent of genetic variability within the segregating generations is crucial for identifying superior segregants with high yield and better market acceptability. Thus, the present study was carried out to quantify the extent of genetic variation available in the segregating population of rice. Three crosses, *viz*., CO 55 × IC 457996, CO 55 × IC 464685, and CO 55 × IC 115439 were evaluated using a non-randomized experimental design for six yield attributing and two physical grain quality traits in F_2 generation. The inheritance pattern of basal leaf sheath colour and grain colour in CO 55 × IC 115439 indicate digenic complementary gene interaction (9:7), whereas grain colour in CO 55 × IC 464685 exhibits inhibitory gene action (13:3). The positively skewed nature of productive tillers per plant and single-plant yield in the F_2 segregants emphasizes the need for intensive selection to facilitate rapid improvement due to the influence of complementary gene action. Moderate to high GCV with high heritability and GAM for traits such as plant height, productive tillers per plant, hundred seed weight, grain width, and single-plant yield in the F_2 segregants underscore the prevalence of additive gene action and thus provide the most effective condition for simple phenotypic selection. Moreover, productive tillers per plant and single-plant yield showed a strong positive association in all the crosses. Therefore, productive tillers per plant can be considered an indicator trait when selecting high-yielding segregants for grain yield improvement.

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1 Introduction

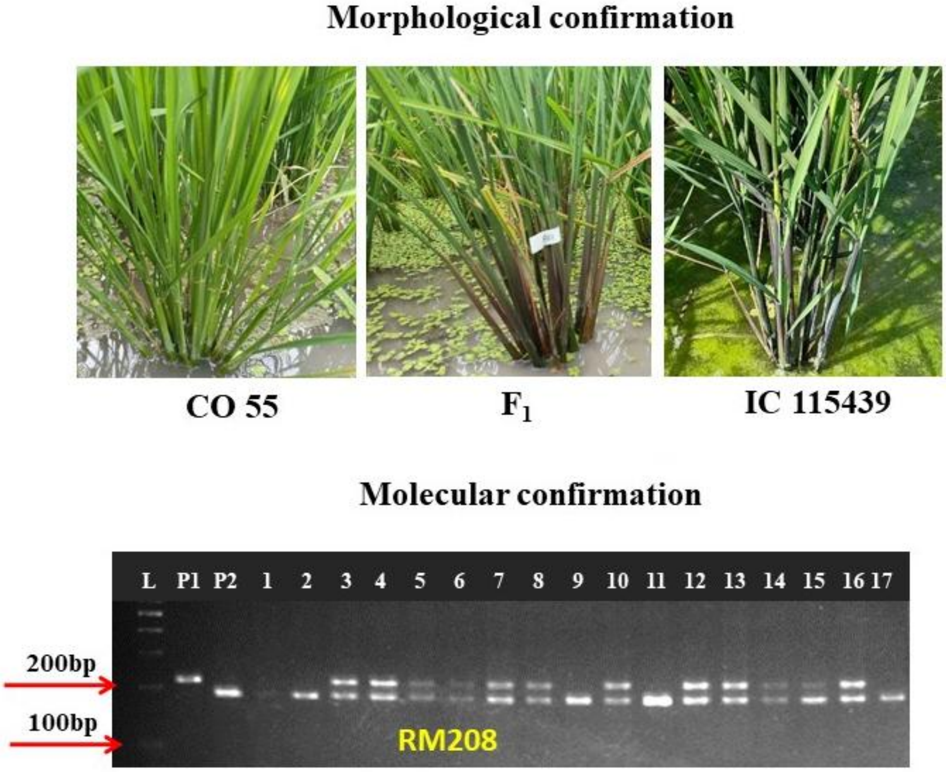
Rice (*Oryza sativa* L.) is a primary dietary food source that sustains half of the world's population. As the world's population is projected to reach approximately 9.7 billion in 2050, the demand for food is expected to surge by 70% (Bin Rahman and Zhang 2021). However, to keep pace with the growing population, the current annual rice production levels are expected to increase by approximately 5.8 million tons (Santhiya et al. 2024). Over the past decades, the annual growth rate of rice yield remained $\leq 1\%$, failing to keep pace with the escalating demand due to various constraints (Khush 2013). In the present era, the importance of quality parameters is increasingly recognized, particularly in areas where rice production is self-sustaining. This underscores the importance of developing rice cultivars that yield high and exhibit superior quality. In light of the presently recognized resource limitations and changing climatic conditions, boosting rice production through sustainable practices remains a significant challenge. Thus, creating new variability through hybridization is one among several genetic approaches aimed at overcoming the yield barrier and enhancing rice productivity.

Genetic variability is crucial for effectively selecting superior segregants from the segregating population (Thúy et al. 2022). The genetic variability parameters, such as genotypic and phenotypic coefficient of variation, provide an insight into the relative amount of variation present in the segregating generations. However, the knowledge of the degree of heritable proportion of variation from the parent to its progeny is of paramount importance in deciding the traits to be selected (Bassuony et al. 2022). Third and fourth-degree statistics, specifically skewness and kurtosis, offer valuable insights into the type of gene action and the number of genes influencing traits within segregating generations (Fisher et al. 1932; Robson 1956). Therefore, understanding the extent of genetic variability and the distribution pattern of the F_2 segregates would be effective tools to identify superior segregates with high yield and better market acceptability (Bassuony et al. 2022). Grain yield is a complex trait governed by polygenic loci, which in turn depends upon many independent contributing characteristics such as the number of productive tillers (Kalaivani et al. 2023), panicle length (Muthuvijayaragavan and Jebaraj, 2022), panicle weight (Nofal et al. 2024), thousand seed weight (Kalaivani et al. 2023), and filled grains per panicle (Bassuony et al. 2022). Therefore, direct selection for yield is often not effective. A better understanding of their association with single plant yield would be essential for formulating an effective breeding strategy, attributing traits as effective indicators in selection. In this context, the present study was designed to analyze the statistics and quantify the level of genetic variation present within the F_2 (segregating) generation for yield, yield-attributing, and grain quality traits.

2 Materials and Methods

The study was conducted at the Department of Rice, TNAU, Coimbatore, Tamil Nadu, India (11° N latitude and 77° E longitude). Hybridization was carried out between a popular high-yielding fine grain rice variety, CO 55, with three drought-tolerant landraces *viz.*, IC 457996, IC 464685, and IC 115439 during *Rabi* 2022, and the resulting F_1s were evaluated during Summer 2023. True hybrids were distinguished based on their distinct morphological characteristics, such as the pigmentation of basal leaf sheath in CO 55 (green) × IC 115439 (purple) (Figure 1), as well as grain colour in CO 55 (white) × IC 464685 (red) and CO 55 (white) × IC 115439 (red). Subsequently, all identified hybrids were further subjected to molecular confirmation using polymorphic marker RM1 between CO 55 and IC 464685 and RM3412 between CO 55 and IC 115439. Due to the lack of a visual morphological marker in CO 55 × IC 457996, polymorphic marker RM208 was used for identifying the true F_1s between CO 55 and IC 457996 (Figure 1). The heterozygous plants obtained from each cross CO 55 × IC 457996 (cross I), CO 55 × IC 464685 (cross II), and CO 55 × IC 115439 (cross III) were advanced to F_2 generation during *Kharif* 2023. Seedlings were transplanted on twenty-one days, with a single seedling per hill, while maintaining a spacing of 30 cm between the rows and 20 cm between the plants. The crop was grown adopting recommended agronomic practices. Qualitative characteristics like basal leaf sheath colour were individually assessed in the F_2 segregants of cross III. Likewise, grain colour was observed in crosses II and III using a single panicle from each plant. Six yield attributing traits *viz.*, days to first flowering (DFF in days), plant height (PH in cm), productive tillers per plant (NPT), panicle length (PL in cm), hundred seed weight (HSW in g) and single plant yield (GYPP in g) along with two physical grain quality traits, grain length (KL in mm) and grain width (KB in mm) were recorded from 380, 391 and 217 F_2 plants in crosses I, II and III, respectively.

The inheritance pattern for qualitative traits was assessed through the χ^2 (Chi-square) test (Fisher 1936). Shapiro-Wilks' W test was carried out to test the normality of the F_2 populations using R software (Shapiro et al. 1968). Skewness and kurtosis were computed to understand the extent of the distribution pattern for yield and quality attributes in the segregating population by using SPSS Statistics version 29.0.2.0 (Snedecor and Cochran 1989). The Genotypic and Phenotypic Coefficient of Variation (GCV and PCV) were calculated as per the formula given by Burton, 1952. The broad sense heritability (h^2) and genetic advance as a percentage of the mean (GAM) were calculated as per Lush (1940) and Johonson et al. (1955). Pearson's pairwise correlation among variables was computed to analyze their mutual linear relationship using the '*corrplot'* statistical package in R software.



Note: L - Ladder (100bp); P1 - CO 55; P2 - IC 457996;

True F1s - 3,4,5,6,7,8,10,12,12,14,14,16

Figure 1 Hybrid confirmation using morphological and molecular markers

Table 1 Segregation pattern of the progenies for qualitative traits in F_2 generation

Basal leaf sheath colour							
Name of the cross	P_1/P_2	F_1 Phenotypes	Number of F_2 plants		χ^2 ratio	χ^2 value	p-value
			Purple	Green			
CO 55 × IC 115439	Green/Purple	Purple	119	98	9:7	0.18	0.6752
Grain colour							
Name of the cross	P_1/P_2	F_1 Phenotypes	Number F_2plants		χ^2 ratio	χ^2 value	p-value
			Red	White			
CO 55 × IC 115439	White/Red	Red	175	42	13:3	0.05	0.8194
CO 55 × IC 464685	White/Red	Red	208	183	9:7	1.48	0.2236

3 Results and Discussion

3.1 Inheritance pattern of qualitative traits

True hybrids were identified by their distinct morphological characteristics, such as the pigmentation of basal leaf sheath in CO 55 × IC 115439 and grain colour in CO 55 × IC 464685 and CO 55 × IC 115439. All true F_1s resulting from CO 55 × IC 115439 exhibited red grain colour and purple pigmentation in their leaf sheath (Figure 1). Likewise, in CO 55 × IC 464685 the true F_1s had red grain colour. Besides conferring disease resistance, basal leaf sheath colour is an important morphological marker for distinguishing off types at an early stage. The segregation pattern of the progenies of the cross between green and purple pigmented leaf sheath in the F_2 generation closely fitted to the 9:7 ratio (χ^2 = 0.68) (Table 1). The result herein emphasizes that two genes with complementary gene interaction jointly govern the expression of basal leaf sheath colour in rice (Pandey et al. 2016). Likewise, the proportion of plants exhibiting red and white grain colour in F_2 generation of the cross CO 55 × IC 464685 closely followed a 9:7 ratio (χ^2 = 0.22) (Table 1). Thus, it confirms that the red grain colour in rice is determined by digenic complementary gene interaction. Meanwhile, a segregation ratio of 13:3 (red:white) gave the best fit for grain colour in the cross CO 55 × IC 115439 (χ^2 = 0.82) (Table 1). This indicates that the red grain colour in the cross CO 55 × IC 115439 might be due to dominant suppression epistasis, i.e., two genes with an inhibitory effect jointly govern the expression of the trait (Waghmode et al. 2017).

3.2 *Per se* performance of yield-attributing traits

The *per se* performance of the studied traits in the F_2 segregants indicated a wide range of variation (Table 2, 3, and 4), providing ample opportunities to identify and utilize the most promising segregants in future breeding programs. Days to first flowering in the F_2 segregants of the cross I (CO 55 × IC 457996) ranged from 75.00 to 114.00 days (Table 2), while it was from 76.00 to 105.00 days in cross II (CO 55 × IC 464685) (Table 3) and 79.00 to 117.00 days in cross III (CO 55 × IC 115439) (Table 4). Transgressive segregants with lower values than the early parent are desirable for days to first flowering. Nearly 20% of plants in cross I, 27.59% in cross II, and 5.53% in cross III were identified as early flowering compared to their parent CO 55 (86.4 days). Transgressive segregants with higher values than the high-yielding parent are desirable for yield-attributing traits. The transgressive segregants with higher value of productive tillers per plant were more in the F_2 generation of cross I (93 plants) followed by cross III (55 plants) and cross II (23 plants). Similarly, single plant yield in the F_2 segregants of cross I, varied from 8.97 to 74.52 g, while in cross II, it ranged from 8.11 to 61.96g and in cross III, it ranged from 10.08 to 61.86 g. The wide range of variation for these traits in all three crosses underscores the presence of transgressive segregation. The number of plants in F_2 that outperformed the mean single plant yield of parents was 176 in cross I, 116 in cross II, and 96 in cross III. Koide et al. (2019) indicated

Table 2 Genetic variability estimates of yield and quality attributes in the F_2 population of CO 55 × IC 457996

Traits	W-test	Probability	Mean	Range	Skewness	Kurtosis	PCV	GCV	h^2	GAM
DFF	0.981	0.001	95.26	75.00 - 114.00	-0.08	-0.74	9.68	9.59	97.96	19.54
PH	0.968	0.000	147.11	70.00 - 200.00	-0.51	-0.26	15.23	14.81	94.56	29.66
NPT	0.968	0.000	14.15	5.00 - 28.00	0.55**	-0.12	35.18	30.99	77.61	56.24
PL	0.992	0.039	27.27	20.00 - 35.60	-0.03	-0.02	9.82	8.62	76.94	15.57
HSW	0.996	0.501	2.07	1.43 - 2.84	0.09	-0.05	11.96	11.22	87.97	21.68
KL	0.805	0.000	8.40	7.20 - 9.80	0.17	-0.28	6.61	6.54	97.74	13.31
KB	0.247	0.000	2.44	1.90 - 3.80	0.60**	1.52**	10.45	10.08	92.97	20.02
GYPP	0.963	0.000	34.27	8.97 - 74.52	0.70**	0.12	37.39	34.75	86.35	66.52

**1% level of significance; *5% level of significance; DFF - Days to First Flowering; PH - Plant Height (cm); NPT - Productive Tillers per plant; PL - Panicle Length (cm); HSW - Hundred Seed Weight (g); GYPP - Single Plant Yield (g); KL - Grain Length (mm); KB - Grain Breadth (mm); PCV - Phenotypic Coefficient of Variation; GCV - Genotypic Coefficient of Variation; h2 - Heritability in broad sense; GAM - Genetic Advance as per cent of Mean

Table 3 Genetic variability estimates for yield and quality attributes in the F_2 population of CO 55 × IC 464685

Traits	W-test	Probability	Mean	Range	Skewness	Kurtosis	PCV	GCV	h^2	GAM
DFF	0.965	0.000	91.30	76.00 - 105.00	-0.27	-0.22	6.21	6.01	93.82	11.99
PH	0.936	0.000	122.43	80.00 - 184.00	0.43**	-0.98	19.02	18.39	93.50	36.63
NPT	0.960	0.000	12.53	4.00 - 35.00	0.80**	1.77**	36.77	28.81	61.40	46.51
PL	0.973	0.000	26.08	19.00 - 37.00	0.52**	0.99**	10.17	8.32	67.05	14.04
HSW	0.939	0.000	1.76	1.26 - 2.55	0.99**	0.35	17.64	17.05	93.46	33.96
KL	0.972	0.000	8.41	7.00 - 9.60	-0.58	0.38	5.55	5.44	96.36	11.01
KB	0.984	0.000	2.35	1.40 - 3.50	0.11	-0.54	16.48	16.07	95.07	32.28
GYPP	0.908	0.000	28.78	8.11 - 61.96	0.52**	-0.76	38.53	34.06	78.14	62.03

**Significance at 1% level; *Significance at 5% level

Table 4 Genetic variability estimates for yield and quality attributes in the F_2 population of CO 55 × IC 115439

Traits	W-test	Probability	Mean	Range	Skewness	Kurtosis	PCV	GCV	h^2	GAM
DFF	0.981	0.005	100.65	79.00 - 117.00	-0.34	-0.12	7.32	7.19	96.50	14.56
PH	0.976	0.001	138.82	90.00 - 184.00	-0.39	-0.40	13.99	12.70	82.38	23.75
NPT	0.972	0.000	12.28	4.00 - 28.00	0.58**	0.72*	34.73	30.18	75.52	54.04
PL	0.972	0.000	26.76	18.00 - 32.00	-0.40	0.48	8.42	6.75	64.24	11.14
HSW	0.972	0.000	2.05	1.12 - 2.95	0.18	1.40**	14.18	13.70	93.30	27.26
KL	0.980	0.004	8.29	7.10 - 9.80	0.33	0.37	5.04	4.97	97.37	10.10
KB	0.970	0.000	2.90	2.20 -3.80	0.37*	-0.25	10.77	10.39	93.18	20.67
GYPP	0.980	0.004	31.01	10.08 - 61.86	0.45**	0.47	32.05	26.90	70.43	46.50

**Significance at 1% level; *Significance at 5% level

that transgressive segregation is more common in the F_2 population derived from parents with more proximal phenotypes. Among the obtained high-yielding F_2 segregants, 28 plants in cross I, 16 in cross II, and 4 in cross III were found to be high-yielding and early flowering. Therefore, the promising transgressive segregants thus identified offer significant potential for employing them in breeding programs for evolving short-duration high-yielding rice cultivars.

3.3 Skewness and Kurtosis

Shapiro-Wilks test (W-test) revealed that except for hundred seed weight in Cross I, none of the traits exhibited a normal distribution, suggesting the skewed nature of the segregating population (Table 2, 3, and 4). The nature of gene action governing any trait can be identified based on the sign of skewness and its distribution pattern (Fisher et al. 1932; Robson 1956). Cross I noticed significant positive skewness for productive tillers per plant, grain width, and single plant yield (Table 2). Similarly, in cross II, the traits productive tillers per plant, plant height, panicle length, hundred seed weight, and single plant yield (Table 3) were positively skewed (Figure 2, 3). Likewise, productive tillers per plant, grain width, and single plant yield in cross III were identified to have significant positive skewness (Table 4 and Figure 4). The skewed nature underscores the significance of complementary gene action in determining the expression of these traits. Thus, intensive selection is needed to improve the genetic gain of these traits, as mild selection could lead to slow progress (Riyanto et al. 2021; Bassuony et al. 2022). However, the non-significant values for skewness for the remaining traits in the crosses indicate the existence of additive gene action, implying that early-generation selection will be more effective for these traits. Kurtosis indicates the shape of the distribution curve, and it helps determine the number of genes governing the traits. The significant and positive kurtosis observed for traits such as grain width (in cross I), productive tillers per plant, panicle length (in cross II) as well as productive tillers per plant and hundred seed weight (in cross III) indicate their leptokurtic distribution. This suggests that only a few genes are involved in governing their expression. However, the non-significant kurtosis values for the remaining traits in the crosses suggest a mesokurtic distribution, implying that a larger number of genes will likely determine these traits.

3.4 Estimation of variance component

Understanding the extent of genetic variability within breeding materials is essential for optimizing selection processes in any breeding program. Thus, understanding genetic parameters allows breeders to enhance the effectiveness of selection. For all traits investigated across the three crosses, the Phenotypic Coefficient of Variation (PCV) was consistently higher than the Genotypic Coefficient of Variation (GCV) (Tables 2, 3, and 4). However, a narrow difference between PCV and GCV in the F_2 segregants for all the studied traits signifies a pronounced genetic influence on the phenotypic expression with minimal environmental impact. In cross I, PCV values ranged from 6.61% (grain length) to 37.39% (single plant yield), while in cross II, it varied from 5.55% (grain length) to 38.53% (single plant yield). Likewise, in cross III, PCV values ranged from 5.04% (grain length) to 34.73% (productive tillers per plant). Similarly, GCV values in cross I varied from 6.54% (grain length) to 34.75% (single plant yield), while in cross II, they varied from 5.44% (grain length) to 34.06% (single plant yield). Further, GCV values in cross III varied from 4.97% (grain length) to 30.18% (productive tillers per plant). High GCV estimate (>20%) was observed for productive tillers per plant and single-plant yield in all the crosses. High GCV estimates indicate these traits' inherent high degree of variability, which could augur well for rice improvement programs (Riyanto et al. 2021; Kumar et al. 2023). Plant height, hundred seed weight, and grain width in all crosses displayed moderate GCV estimates (10% to 20%). Conversely, the low estimate of GCV (<10%) was observed for days to first flowering, panicle length, and grain length across all crosses. Low GCV estimates indicate the presence of a limited range of variability for these traits within the population (Thúy et al. 2022; Kalaivani et al. 2023; Kumar et al. 2023). Therefore, selection based on these traits is expected to be less effective.

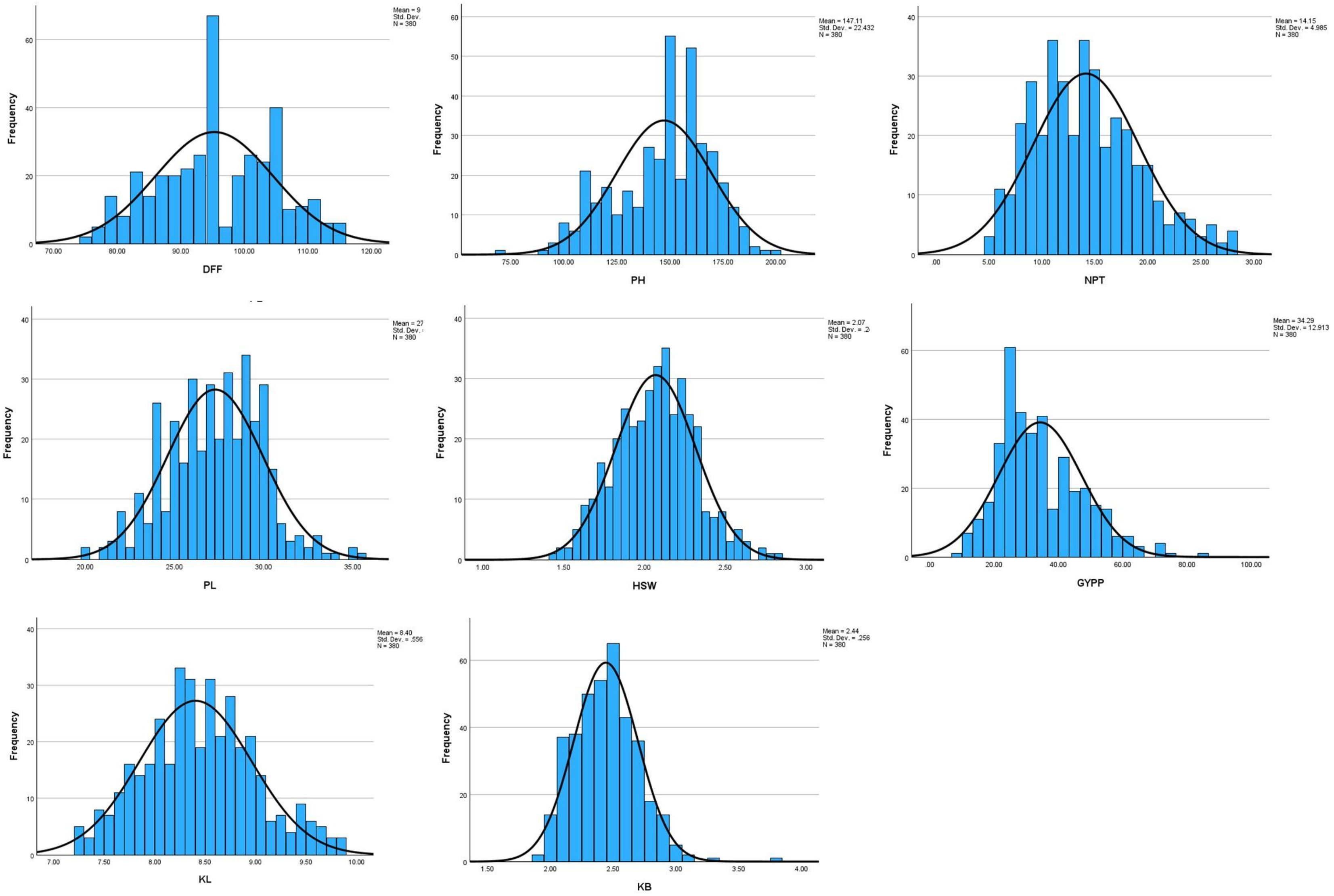


Figure 2 Distribution pattern of yield and quality attributes in the segregating population of CO 55 × IC 457996

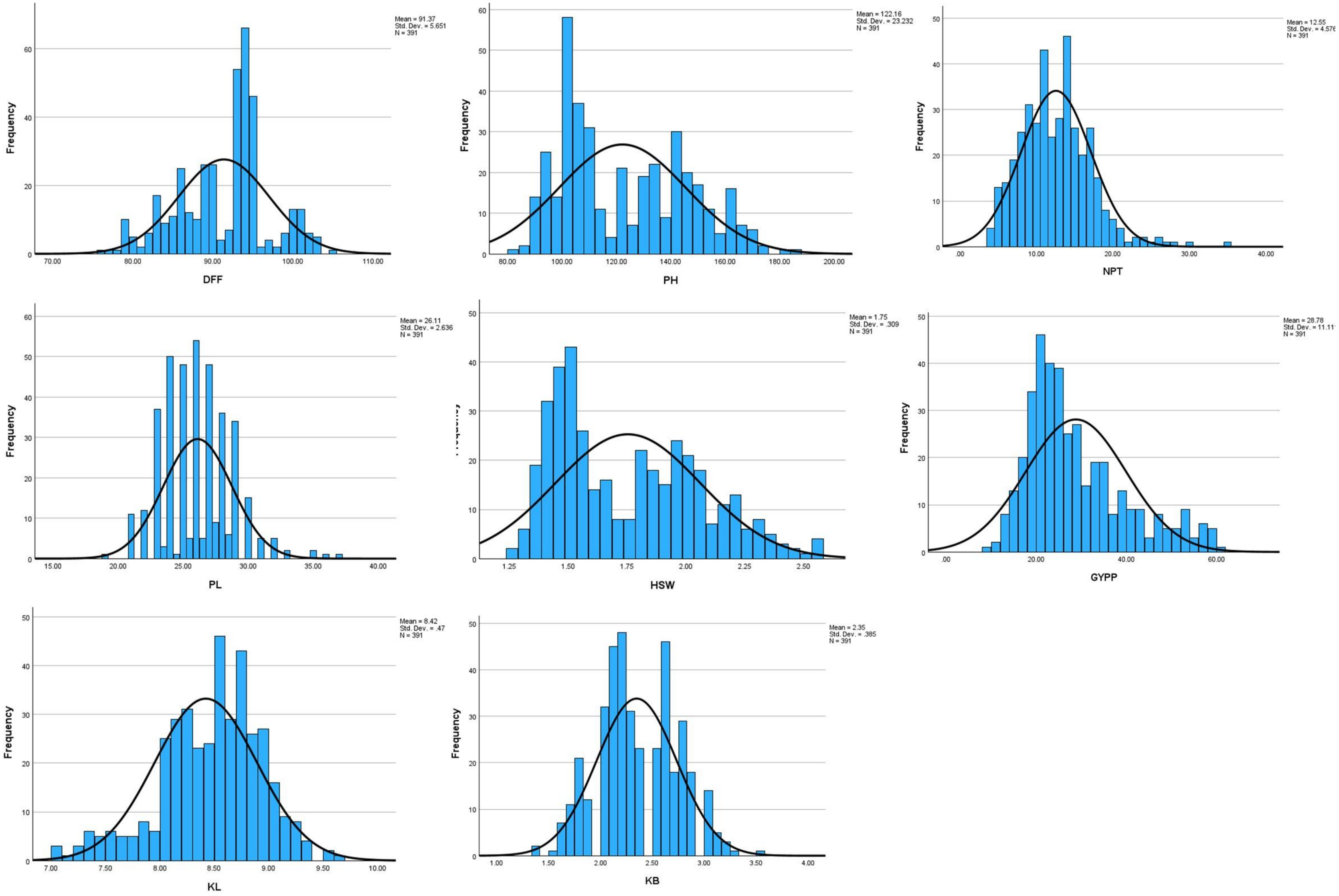


Figure 3 Segregation pattern of yield and quality attributes in the segregating population of CO 55 × IC 464685

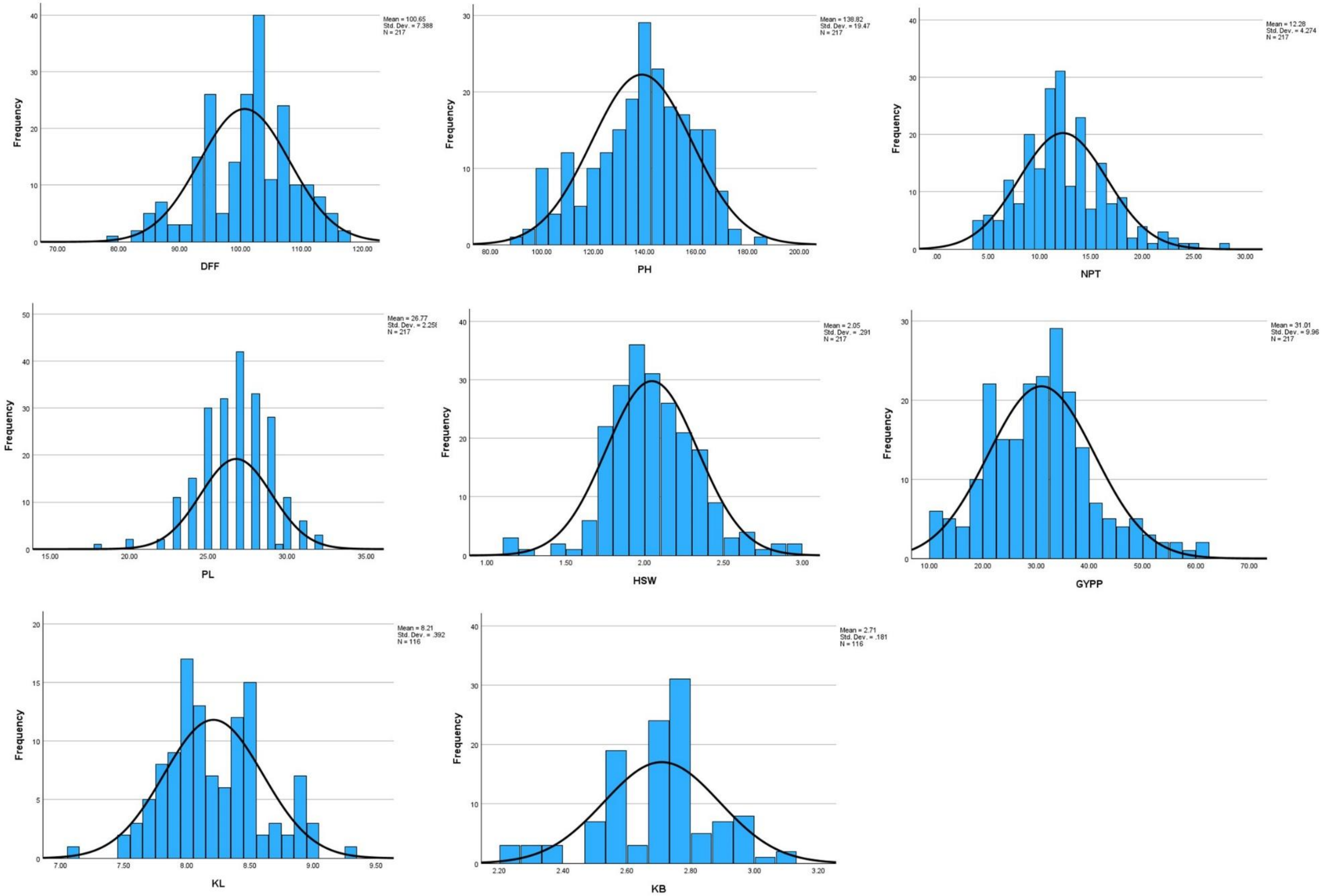


Figure 4 Segregation pattern of yield and quality attributes in the segregating population of CO 55 × IC 115439

3.5 Broad sense heritability and Genetic advance as percent of mean

Although GCV provides insights into the genetic variability present within the population, it alone does not suffice to ascertain the heritable portion of the variation. The efficiency of exploiting the residing genetic variability through selection depends upon the heritability of individual traits. In cross I (Table 2), broad sense heritability ranged from 76.94% (panicle length) to 97.96% (days to first flowering), with genetic advance as a percent of the mean (GAM) varying from 13.31% (grain length) to 66.52% (single plant yield). Similarly, in cross II (Table 3), heritability ranged from 61.40% (productive tillers per plant) to 96.36% (grain length), with GAM ranging from 11.01% (grain length) to 62.03% (single plant yield). In cross III (Table 4), heritability ranged from 64.24% (panicle length) to 97.37% (grain length), with GAM ranging from 11.14% (panicle length) to 54.04% (productive tillers per plant). High broad sense heritability (H^2) observed for all the examined traits across three crosses suggests that environmental factors have minimal influence, with genetic factors predominantly governing these traits. Lestari et al. (2015) suggested that early-generation selection is possible for traits with high heritability as genetic factors predominantly influence the plant phenotype. For effective selection, heritability in consonance with GAM could be useful in predicting the genetic gain under selection (Bassuony et al. 2022). Across all the crosses, high H^2 (>60%) and GAM (>20%) were noticed for single plant yield, productive tillers per plant, plant height, hundred seed weight, and grain width. High broad sense heritability coupled with high GAM emphasis that these traits are predominantly controlled by additive gene action, making them highly amenable to simple phenotypic selection (Prajapati et al. 2022; Kalaivani et al. 2023; Kumar et al. 2023). Furthermore, traits like days to first flowering, panicle length, and grain length exhibited high H^2 (>60%) and moderate GAM (10% to 20%) across all the F_2 segregants. High broad sense heritability coupled with moderate GAM emphasizes that both additive and non-additive gene action play a major role in determining their expression (Yaseen et al. 2020; Prathiksha et al. 2022; Kumar et al. 2023). However, the high heritability in these crosses might be due to environmental factors rather than genotype, rendering selection less rewarding. Consequently, enhancing the genetic gain of these traits can be achieved by intermating superior genotypes within the segregating population.

Table 5 Phenotypic correlation among yield and quality attributes in the segregating population

Traits	Cross	DFF	PH	NPT	PL	HSW	KL	KB
PH	1	0.33**						
	2	0.26**						
	3	0.24**						
NPT	1	0.01	0.24**					
	2	0.11	0.36**					
	3	0.03	0.08					
PL	1	0.37**	0.42**	0.01				
	2	0.23**	0.38**	0.23**				
	3	0.22**	0.38**	0.18**				
HSW	1	0.08	0.11*	-0.01	0.08			
	2	0.15**	0.50**	0.23**	0.11*			
	3	0.00	0.17**	-0.18**	-0.01			
KL	1	0.06	0.03	0.01	0.05	0.29**		
	2	0.06	-0.26**	-0.11*	0.05	-0.27**		
	3	0.13*	-0.08	0.05	-0.02	0.15*		
KB	1	0.04	0.02	-0.07	0.05	0.10	-0.54**	
	2	0.02	0.44**	0.20**	0.03	0.64**	-0.29**	
	3	0.04	0.04	0.04	0.04	0.02	0.13*	
GYPP	1	0.19**	0.42**	0.65**	0.21**	0.12*	0.07	-0.12*
	2	0.15**	0.49**	0.66**	0.20**	0.38**	-0.22**	0.34**
	3	0.43**	0.17**	0.87**	0.27**	0.18**	0.09	0.01

3.6 Correlation analysis

Correlation provides a better insight into the mutual relationship among the traits. Thus, a better understanding of their association with grain yield would make the selection more precise and accurate with the attributing traits as effective indicators in selection. Across all crosses, productive tillers plants (0.65, 0.66, and 0.87) exhibited a strong positive correlation with single plant yield (Table 5). Similarly, the traits *viz*., plant height (0.42, 0.49 and 0.17), panicle length (0.21, 0.20 and 0.27), and hundred seed weight (0.12, 0.38 and 0.18) showed a positive significant association with single plant yield across all the crosses. These results herein show that more tillers might produce more panicles and increased synthesis and translocation of photo-assimilates from the source to sink could significantly improve yield through enhanced grain filling and seed set (Thúy et al. 2022; Kalaivani et al. 2023). In crosses I and II, days to first flowering and single plant yield showed a positive association (0.19 and 0.15). Likewise, within cross II, single plant yield positively correlated with grain width (0.34) while negatively correlated with grain length (-0.22). In general, selecting indicator traits can target high yield through potential traits directly. The results herein show that productive tillers per plant, panicle length, and hundred-seed weight can be indicator traits while selecting high-yielding segregants for grain yield improvement.

Conclusion

The findings of this study emphasize that productive tillers per plant can be used as a reliable trait for direct selection when identifying high-yielding segregants for enhancing grain yield in rice as it exhibits high estimates for PCV and GCV, heritability, and GAM. The positively skewed distribution and leptokurtic nature of the productive tillers per plant suggests the involvement of a limited number of genes governing its expression, and thus, an intense selection from existing genetic variability could significantly enhance the genetic gain of this trait. Moreover, correlation analysis emphasizes that grain yield improvement in rice can be attained by indirectly selecting F_2 segregants with more productive tillers and longer panicles with high hundred seed weights.

Conflict of interest

The authors declare no conflict of interest.

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