



Research Article

Genetic inheritance studies in rice (*Oryza sativa* L.) for grain protein, quality and yield

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Abstract

The present study was undertaken to investigate the genetic parameters of yield component and quality traits of the F₃ population from BPT 5204 and JAK-686 cross in rice. High heritability and high genetic advance as a percentage of the mean were recorded for productive tillers per plant, grains per panicle, panicle length and grain yield per plant indicating the effectiveness of direct phenotypic selection for improvement of these traits. For traits such as grains per panicle, 1000 grain weight, amylose content and grain protein content, the magnitude of additive (d) effects surpassed dominance (h) gene effects. This implies that phenotypic selection using methods like pureline selection, mass selection would be beneficial. Gel consistency exhibited complimentary gene interaction. Furthermore, duplicate gene interaction was prevalent in traits like days to 50% flowering, productive tillers per plant, plant height, panicle length, grain yield per plant, kernel length, kernel breadth, and kernel L/B ratio, making selection in later generations more effective. The inheritance studies highlighted the importance of selecting desired recombinants from the segregating population to enhance rice quality as well as grain yield.

Keywords: Rice, Grain protein content, Quality, Variability, Heritability, Gene action

INTRODUCTION

Rice (*Oryza sativa* L.) stands as the most widely consumed cereal, contributing to 21% of human caloric needs and up to 76% of calorie intake in Southeast Asia. It is a dietary staple for over half of the global population, particularly in Asia, Africa, and Latin America. India leads in acreage under rice (43.9 million hectares) and is second in production (114.45 million tonnes of milled rice), following China (Agricultural statistics at a glance, 2022). As a crucial component of the human diet, understanding and enhancing the nutritional aspects of rice are vital to address energy malnutrition.

In recent times, there is an increasing demand for rice varieties with higher yields while maintaining favourable agronomic traits. Consequently, current rice breeding programs focus on developing varieties with high yields

and desirable grain quality. The evaluation of rice grain quality involves assessment of characters such as grain size, shape, amylose content, protein content, colour *etc.* (Gong *et al.*, 2023). The digestibility of the rice depends on the properties of starch, including its crystallinity and amylose to amylopectin ratio (Amirtham and Radha, 2023). The foundation of crop improvement programs relies on genetic variability and appropriate selection techniques (Allard, 1960). Hybridization is acknowledged as a valuable tool in rice breeding to combine desired traits and introduce genetic variability. The selection process predominantly relies on evaluating the performance of lines from F₂ or F₃ generations, assuming that early-generation performance (is indicative of its performance at homozygosity), particularly in self-pollinating crops like rice (Mallimar *et al.*, 2015).

While the coefficient of variation quantifies trait variability, it does not offer insights into the hereditary component. To gain a more comprehensive understanding, heritability, along with genetic advance and genetic advance as a percentage of the mean, is also calculated. Furthermore, understanding gene interactions is essential for genetic improvement of polygenic traits like yield and quality. Generation mean analysis is a valuable method for estimating gene actions. Studying the genetics of yield and quality attributes is crucial for developing a breeding strategy to improve production while maintaining rice quality (Bano *et al.*, 2017; Solanke *et al.*, 2019).

In this context, the present study focuses on identifying various genetic factors and gene actions within the segregating population derived from the cross between Samba Mahsuri (BPT 5204) and JAK-686 (an improved breeding line) for traits attributing grain yield and quality.

MATERIALS AND METHODS

The current study was conducted at ICAR-Indian Institute of Rice Research, Hyderabad. Genetically pure seeds of Samba Mahsuri (BPT 5204) and JAK-686 (an improved breeding line), were acquired from ICAR-IIRR, Rajendranagar, Hyderabad. The planting material comprised of five generations (P_1 , P_2 , F_1 , F_2 and F_3) of BPT 5204 x JAK-686. All the material was planted in a randomized block design with three replications having 15 plants in each of P_1 and P_2 ; 15 plants of F_1 , 60 plants of F_2 and 40 plants of F_3 population per replication during *rabi*, 2022-23. Throughout the crop's growth cycle, recommended agronomic practices and pest control measures were employed to ensure the cultivation of a healthy crop. Thirteen characteristics, *viz.*, plant height (cm), productive tillers per plant, panicle length (cm), grains per panicle, days to 50 % flowering, 1000-grain weight (g), grain yield per plant (g), kernel length (mm), kernel breadth (mm), length-to-breadth ratio (L/B), gel consistency (mm), amylose content (%) and grain protein content (%), were recorded for each P_1 , P_2 , F_1 , F_2 and F_3 plant in all the three replications. The collected data was subjected to statistical analyses. Genetic variability parameters, which includes Genotypic Coefficient of Variation (GCV) and Phenotypic Coefficient of Variation (PCV), were calculated using the formula proposed by Burton and Dewane (1953). Heritability was determined using the formula provided by Allard (1960), and genetic advance as a percentage of the mean was calculated using the formula from Johnson *et al.* (1955). Johnson *et al.* (1955) classified heritability as low: 30%, moderate: 30-60% and high: > 60%. GAM *i.e.*, genetic advance as per cent of mean was categorized (Johnson *et al.*, 1955) into low: 0-10%, moderate: 10-20% and high: >20%. All the above statistical analyses were performed using R software version 1.4.1717.

To validate the additive-dominance model proposed by Singh and Chaudhary (1985), the scaling test (A, B, C, and D) as outlined by Mather (1949) was conducted.

In five-parameter model, only scales C and D were employed to detect the existence of epistasis.

$$\text{Scale C} = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2 = 0$$

$$\text{Scale D} = 4\bar{F}_3 - 2\bar{F}_2 - \bar{P}_1 - \bar{P}_2 = 0$$

Estimates of various gene effects were computed by a five parameter model of Hayman (1958) and Jinks and Jones (1958) by the following equations:

$$\text{Mean} = (m) = \bar{F}_2$$

$$\text{Additive effect} = (d) = (\bar{P}_1 - \bar{P}_2)/2$$

$$\text{Dominance effect} = (h) =$$

$$1/6(4\bar{F}_1 + 12\bar{F}_2 - 16\bar{F}_3)$$

$$\text{Additive} \times \text{Additive epistatic effect} = (i) =$$

$$\bar{P}_1 - \bar{F}_2 - 1/2(\bar{P}_1 - \bar{P}_2)$$

$$\text{Dominance} \times \text{Dominance interaction effect} = (l) =$$

$$1/3(16\bar{F}_3 - 24\bar{F}_2 + 8\bar{F}_1)$$

where,

\bar{P}_1 , \bar{P}_2 , \bar{F}_1 , \bar{F}_2 and \bar{F}_3 are mean values of P_1 , P_2 , F_1 , F_2 , and F_3 generations, respectively.

RESULTS AND DISCUSSIONS

The study of variation is crucial to understand the extent of diversity present in the genetic material. Utilizing the broader range of variability within a population has the potential to enhance a character through the process of selection. Hence, variability in thirteen traits was assessed by calculating mean, phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), heritability (broad sense), and genetic advance as a percentage of the mean (GAM) in F_3 population, as detailed in **Table 1**. Analysis of genetic variability indicated that the PCV values only slightly exceeded the corresponding GCV estimates for all the traits under study, thus indicating the significant role of genotype in determining phenotyping variation. Selection based on phenotype could be effective for the traits under study. Similar results were reported by Adjah *et al.* (2020), Babu *et al.* (2012) and Karuppaiyan *et al.* (2013). Furthermore, gel consistency (GC) exhibited highest PCV and GCV, while plant height (PH), panicle length (PL), grains per panicle (GPP), grain yield per plant (GYPP) and productive tillers per plant (PTPP) demonstrated moderate PCV and GCV, ranging from 10% to 20%. In contrast, traits such as days to 50% flowering (DFF), 1000 grain weight (TGW), kernel length

Table 1. Estimation of Variability in F₃ population of BPT 5204 x JAK-686

Traits	Mean±SE	Range	GV	PV	GCV	PCV	Hbs	GA	GAM
DFF	115.4±2.2	96-145	42.98	57.96	5.68	6.59	74.16	11.63	10.07
PH	112.9±3.3	84.8-147.5	211.1	244.01	12.86	13.83	86.51	27.84	24.64
PL	19.9±0.41	14.7-26.2	10.48	11	16.2	16.6	95.3	6.51	32.59
PTPP	18.04±0.38	12.7-25.7	8.05	8.5	15.72	16.16	94.65	5.68	31.51
GPP	120.1±2.5	86.4-164.9	530	548.86	19.16	19.5	96.56	46.6	38.78
TGW	21.4±0.58	17.3-28.3	4.04	5.06	9.37	10.49	79.85	3.7	17.25
GYPP	18.4±0.52	10.1-28.1	7.64	8.45	15	15.78	90.35	5.41	29.37
KL	5.24±0.10	4.72-5.98	0.03	0.06	3.21	4.84	43.94	0.23	4.38
KB	2.23±0.02	1.86-2.38	0.01	0.01	4.25	4.59	85.71	0.18	8.11
LB	2.35±0.05	2.09-2.82	0.01	0.02	5.1	6.33	64.86	0.2	8.46
AC	24.46±0.24	21.5-27.8	1.87	2.05	5.58	5.85	91.25	2.69	10.99
PC	11.26±0.11	9.9-12.9	0.54	0.57	6.51	6.73	93.51	1.46	12.97
GC	35.15±0.81	22-59.1	88.21	90.2	26.71	27.01	97.79	19.13	54.42

PV: Phenotypic variance; GV: Genotypic variance; PCV: Phenotypic coefficient of variation; GCV: Genotypic coefficient of variation
Hbs: Broad sense heritability; GA: Genetic advance; GAM: Genetic Advance as percent of mean

DFF- Days to 50% flowering, **PH**-Plant height, **PL**- Panicle length, **PTPP**-Productive tillers per plant, **GPP**- Grains per panicle, **TGW**-1000 – grain weight, **GYPP**- Grain yield per plant, **KL**- Kernel length, **KB**- Kernel breadth, **LB** – Length-to-breadth ratio, **AC**-Amylose content, **PC**- Grain protein content, **GC**- Gel consistency.

(KL), kernel breadth (KB), kernel L/B ratio (LB), amylose content (AC) and grain protein content (PC) displayed low PCV and GCV. Similar results were also recorded by Devi *et al.* (2022), Aditya and Bhartiya (2013), Uma Devi *et al.* (2010), Kole *et al.* (2008) and Akanda *et al.* (1997).

Heritability denotes the proportion of variability in observable traits attributable to genetic factors. The heritability values varied from 43.94% to 97.79%, with KL and GC having the lowest and highest values, respectively. High heritability was observed for GC (97.79 %), followed by GPP (96.54 %), PL (95.30%), PTPP (94.65 %), PC (93.51 %), AC (91.25 %), GYPP (90.35 %), PH (86.51 %), KB (85.71 %), TGW (79.85 %) and DFF (74.16 %). On the contrary, LB and KL demonstrated moderate heritability. These findings were in agreement with Devi *et al.* (2022), Manjunatha *et al.* (2017) and Gupta *et al.* (2020). The GAM for the thirteen traits ranged from 4.38% to 54.42%, with KL and GC displaying the lowest and highest values, respectively. High GAM was observed for GC (54.42 %), GPP (38.78 %), PL (32.59 %), PTPP (31.51 %), GYPP (29.37 %) and PH (24.64 %). Whereas, TGW, PC, AC, and DFF demonstrated moderate GAM, indicating the influence of both additive and non-additive gene effects on the expression of these traits. On the other hand, KL, KB and LB exhibited low GAM.

The characters PH, PTPP, PL, GPP, GYPP and GC exhibited both high heritability and high GAM. Similar findings were also reported by Chaudhari *et al.* (2007). These characteristics, primarily influenced by additive gene action, show potential for enhancement through direct selection (Panse, 1957). Choosing these traits

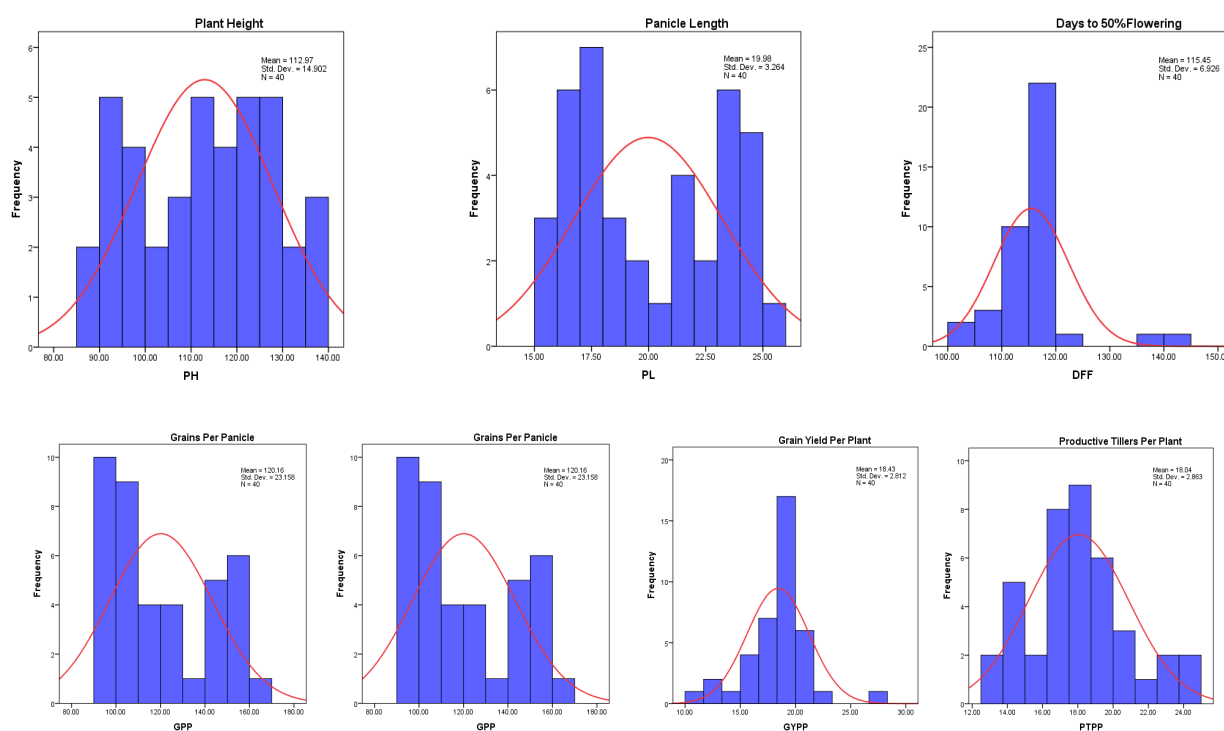
for selection in the early generations could enhance the genotypic value of the individuals beyond their parents, as indicated by Bruno *et al.* (2017) and Roychowdhury and Tah (2011). Selection can be accomplished by using simple crop improvement techniques such as pure line selection, mass selection, and pedigree. While PC and AC exhibited high heritability, the GAM was low to moderate due to low GCV. This suggests the impact of environmental factors and presence of non-additive gene action, indicating that simple phenotypic selection may not effectively contribute to their genetic enhancement (Panse, 1957). To improve these traits, a selection process followed by progeny testing is recommended (Thongbam *et al.*, 2012).

The mean values of BPT 5204, JAK-686 and the F₃ population resulting from BPT 5204 x JAK-686 is furnished in **Table 2**. The presence of transgressive segregants were evident in the range of trait values illustrated in **Fig 1** and **Fig 2**. Transgressive segregation, occurring in one or both directions, was observed in all traits except for KB. This phenomenon is likely attributed to the combination of favourable and unfavourable alleles inherited from the parental lines 'BPT 5204' and 'JAK-686'. Lou *et al.* (2009) reported similar findings, noting transgressive segregation in one or both directions for all traits except grain length. Indurkar *et al.* (2015) observed a continuous distribution for all traits, while Chattopadhyay *et al.* (2019) reported a normal distribution for all traits except for plant yield and 100-grain weight. They also observed transgressive segregation for all traits, indicating the presence of multiple alleles and epistatic interactions between quantitative trait loci (QTLs).

Table 2. Mean performance of F₃ population for grain yield, yield attributing and quality traits

Trait Name	BPT5204	JAK-686	F ₃ Mean	F ₃ Range
DFF	103	67.8	115.4±2.2	96-145
PH	74.5	99.2	112.9±3.3	84.8-147.5
PL	20.9	21.5	19.9±0.41	14.7-26.2
PTPP	12	11.8	18.04±0.38	12.7-25.7
GPP	172.5	84.3	120.1±2.5	86.4-164.9
TGW	14.7	23.8	21.4±0.58	17.3-28.3
GYPP	20.3	18.7	18.4±0.52	10.1-28.1
KL	5.11	5.39	5.24±0.10	4.72-5.98
KB	1.88	2.38	2.23±0.02	1.86-2.38
LB	2.71	2.26	2.35±0.05	2.09-2.82
AC	23.93	25.69	24.46±0.24	21.5-27.8
PC	7.4	11.6	11.26±0.11	9.9-12.9
GC	23.5	40.5	35.15±0.81	22-59.1

DFF- Days to 50% flowering, **PH**-Plant height, **PL**- Panicle length, **PTPP**-Productive tillers per plant, **GPP**- Grains per panicle, **TGW**- 1000 – grain weight, **GYPP**- Grain yield per plant, **KL**- Kernel length, **KB**- Kernel breadth, **LB** – Length-to-breadth ratio, **AC**-Amylose content, **PC**- Grain protein content, **GC**- Gel consistency.

Fig 1. Frequency distribution for grain yield and yield component traits in F₃ population of BPT 5204 x JAK-686

With a view to study the nature and mode of gene action for yield, yield attributes and quality traits, generation mean analysis was carried out utilizing mean data of five basic generations viz., P₁, P₂, F₁, F₂ and F₃ of BPT 5204 X JAK-686. The F₁ hybrids outperformed both parents in the traits viz., DFF, PTPP and GYPP, indicating

overdominance of F₁ hybrids. Intermediate performance of F₁s, were observed in traits such as TGW, KL, KB, PH, PL, GPP, LB, AC, PC and GC (Table 3). The scaling test, which determines the presence or absence of non-allelic interactions (epistasis), was conducted for BPT 5204 X JAK-686 across five basic generations for 13 traits

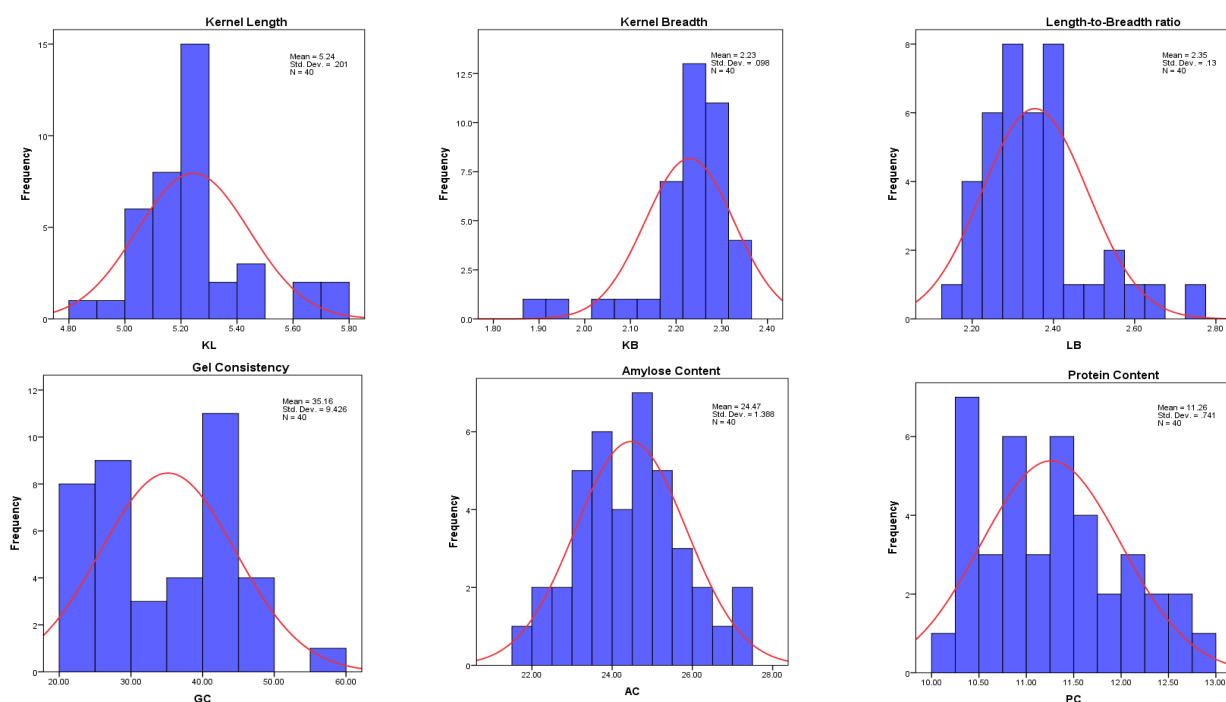


Fig. 2. Frequency distribution for quality traits in F₃ population of BPT 5204 x JAK-686

Table 3. Mean performance of different generations in the cross BPT 5204 x JAK-686

Characters	P ₁	P ₂	F ₁	F ₂	F ₃	Mean
Days to 50% flowering	101	67	108	112	115	101
	±0.95	±0.74	±2.62	±6.33	±2.51	±1.02
Plant height (cm)	74.1	100.3	83	90.6	112.9	92.2
	±0.50	±1.25	±2.41	±4.02	±5.14	±2.44
Panicle length (cm)	21.1	21.6	21.3	17.7	19.9	20.3
	±0.32	±0.25	±0.48	±0.98	±1.09	±0.08
Productive panicles per plant	12.2	12	14.1	11.2	18	13.5
	±0.26	±0.56	±0.41	±1.25	±0.95	±0.14
Grains per panicle	172	86	124	106	120	121.6
	±4.66	±3.19	±8.012	±10.26	±7.7	±1.68
1000 grain weight (g)	14.4	23.92	21.6	20.5	21.4	21.6
	±0.18	±0.42	±0.61	±0.70	±0.74	±0.07
Grain yield per plant (g)	20.5	18.6	22.1	14.8	18.4	18.9
	±0.48	±0.36	±0.49	±1.78	±0.95	±0.14
Kernel length (mm)	5.1	5.4	5.1	5.6	5.2	5.3
	±0.068	±0.083	±0.119	±0.075	±0.083	±0.012
Kernel breadth (mm)	1.8	2.4	2	2	2.2	2.1
	±0.0132	±0.026	±0.055	±0.036	±0.033	±0.011
Kernel L/B ratio	2.7	2.2	2.4	2.7	2.3	2.5
	±0.032	±0.039	±0.0723	±0.059	±0.049	±0.0114
Amylose content (%)	23.9	26.3	24.7	23.7	24.4	24.6
	±0.25	±0.31	±0.54	±0.61	±0.47	±0.054
Protein Content (%)	7.5	11.7	10.4	10.3	11.2	10.2
	±0.058	±0.066	±0.806	±0.57	±0.249	±0.085
Gel consistency (mm)	23.9	40.6	27.2	35	35.1	32.4
	±0.49	±1.187	±2.822	±2.717	±3.125	±0.353

(Table 4). The results of the scaling test, indicated the inadequacy of the additive-dominance model for all the traits. Among the 13 traits, nine (including PH, PTPP, GPP, KL, KB, LB, AC and GC) showed significance for both scale C and D. Scale C was significant for PL and GYPP, while scale D was significant for DFF, TGW and GPC.

The study of gene actions indicated the preponderance of dominance (h) gene effects along with dominance x dominance (l) type of non-allelic interactions for DFF, PH, PTPP, GYPP, KL, KB and LB (Table 5). It suggests that heterosis breeding could be beneficial for improving these traits. Duplicate gene interaction, prevalent for these

traits, tends to diminish or nullify heterotic effects, making selection in later generations more effective. At the same time, population improvement method like recurrent selection, which can maintain considerable variability and heterozygosity could be effective for improving the traits exhibiting non additive gene action. Recurrent selection is very beneficial for grain yield and yield related traits along with other traits that show polygenic inheritance. It helps in increasing the frequency of the alleles if favourable and decreasing if undesirable. These findings align with studies of Bano *et al.* (2017) and Sreelakshmi and Babu (2022). For gel consistency, complimentary gene interaction was predominant, suggesting that heterosis breeding is advantageous for improving this trait, and

Table 4. Scaling tests for yield, yield attributing and grain quality traits in BPT 5204 x JAK-686

Characters	Scaling tests	
	C	D
Days to 50% flowering	3.39 ^{NS}	46.50*
Plant height (cm)	21.87*	96.18**
Panicle length (cm)	-14.70**	1.66 ^{NS}
Productive tillers per plant	-7.41*	25.43**
Grains per panicle	-81.70**	10.50*
1000 grain weight (g)	0.27 ^{NS}	6.45**
Grain yield per plant (g)	-24.03**	4.68 ^{NS}
Kernel length (mm)	1.81**	-0.94**
Kernel breadth (mm)	-0.16*	0.39*
Kernel L/B ratio	1.01**	-0.95**
Amylose content (%)	-4.94**	0.14*
Protein Content (%)	1.21 ^{NS}	5.12*
Gel consistency (mm)	21.09**	5.80*

*Significant at 5 % level, ** Significant at 1 % level

Table 5. Estimation of gene effects for yield, yield attributing and quality traits in BPT 5204 x JAK-686

Characters	m	d	h	i	l	Epistasis
Days to 50% flowering	112.17**	16.92**	-10.88*	-1.66	8.93*	Duplicate
Plant height (cm)	90.62**	-13.10**	-64.64**	-86.68**	99.09**	Duplicate
Panicle length (cm)	17.72**	-0.25	-3.57	-4.05	21.83*	-
Productive tillers per plant	11.27**	0.10	-16.15**	-17.99**	43.80**	Duplicate
Grains per panicle	106.16**	43.07**	-25.25	65.51**	123.03**	-
1000 grain weight (g)	20.50**	-4.75**	-1.73	-13.75*	8.24**	-
Grain yield per plant (g)	14.88**	0.96*	-4.62**	-5.22	38.30**	Duplicate
Kernel length (mm)	5.68**	-0.17**	0.81**	0.60*	-3.69**	Duplicate
Kernel breadth (mm)	2.09**	-0.28**	-0.38**	-0.86**	0.75*	Duplicate
Kernel L/B ratio	2.73**	0.24**	0.83**	1.29**	-2.62**	Duplicate
Amylose content (%)	23.71**	-1.18**	-1.34	-3.28*	6.80*	-
Protein Content (%)	10.34**	-2.09**	-2.37	-7.40**	5.21	-
Gel consistency (mm)	35.08**	-8.35**	-5.43**	-17.05*	-20.39**	Complementary

*Significant at 5 % level, ** Significant at 1 % level

selection could be conducted in the early generations, as proposed by Krishna *et al.* (2013).

The study of gene effects further revealed the presence of additive (d) gene action, along with additive x additive (i) and dominance x dominance (l) non-allelic interactions for traits such as GPP, TGW, AC and PC. The magnitude of additive (d) effects exceeded that of dominance (h) gene effects. The significance of additive (d) gene effects indicates that simple selection techniques and hybridization followed by pedigree method would be effective. This aligns with the findings of Thongbam *et al.* (2012), suggesting that phenotypic selection using methods like pureline selection and mass selection could be employed for traits governed by additive gene action.

In conclusion, traits such as PH, PTPP, PL, GPP, GYPP and GC exhibited both high heritability and high GAM, indicating the predominance of additive gene action. Therefore, these traits are crucial for enhancing both yield and grain quality. Improvement of these traits can be carried out by employing methods like pure line selection and mass selection. Hence, prioritizing these characters during the selection process is essential to identify superior lines with high yield and desirable quality. KL exhibited low heritability; SSD is recommended for improvement of this trait. On the contrary, the remaining traits, characterized by low to moderate estimates of genetic advance, are likely more influenced by non-additive gene effects. Duplicate gene interaction, prevalent for DFF, PH, PTPP, GYPP, KL, KB and LB suggests that selection in later generations could be more effective. For gel consistency, complimentary gene interaction was predominant. Hence, selection could be conducted in the early generations for this trait. The significance of additive (d) gene effects for GPP, TGW, AC and PC indicates that simple selection techniques and hybridization followed by pedigree method would be effective. The nature and inheritance studies suggested that the selection of desired recombinants from segregating population is essential for enhancing rice quality, in addition to achieving high grain yield per plant. This is because both additive and non-additive gene actions played a critical role in the expression of nearly all the studied traits.

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