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Research Article

Study on gene action of yield and its attributes in rice (*Oryza sativa* L.) under phosphorus-deficient conditions using Griffing's approach

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Abstract
Phosphorus (P) deficiency drastically limits rice production in tropical soils, necessitating the development of P-efficient varieties. The present study evaluated the combining ability of eight rice parents and their 28 F_1 hybrids, which were produced from a half-diallel cross, at the UBKV Research Farm in West Bengal during *Kharif* 2021–2023 under deficient P soil condition. The experiment was laid out in a randomized block design with three replications and genotypes evaluated for 14 yield related traits. Combining ability was analyzed using Griffing's Method II, Model I, to estimate general (GCA) and specific (SCA) combining ability effects. Significant genetic variation was observed, with GCA exceeding SCA for traits like plant height and grains per panicle, indicating strong additive effects, while SCA dominated for P uptake and yield, suggesting non-additive contributions. Parents like MTU 7029 and Ranjit appeared as superior combiners, while crosses such as CR Sugandh Dhan 909 × BBII and Paolum Sali × Ranjit exhibited high hybrid vigor. Dominance variance surpassed additive variance across traits, favoring hybrid breeding strategies. These findings indicate prospective parents and crosses that can improve rice production and P-use efficiency in low-P soils, especially in the *Terai* Zone of West Bengal.

Keywords: Rice, combining ability, diallel, phosphorus, GCA, SCA

INTRODUCTION

Rice (*Oryza sativa* L.) is a staple food for more than half of the global population (Fairhurst and Dobermann, 2002, Susmi *et al.*, 2025) and its production has significant challenges due to phosphorus (P) deficiency, which is a common issue in tropical and subtropical soils (Birla *et al.*, 2017)). Rice yields are limited by the poor availability of phosphorus in weathered soils (Nishigaki *et al.*, 2019), especially in rainfed and upland systems (Kato *et al.*, 2016). Phosphorus is an essential mineral for plant growth and supports metabolic processes including photosynthesis and energy transfer (Malhotra *et al.*, 2018). The P shortage in about 50% of rice-growing regions is further exacerbated by soil fixation and limited fertilizer supplies for smallholder farmers (Liu *et al*., 2024)). In order to solve this limitation in a sustainable manner, recent developments in breeding have placed a strong focus on developing rice cultivars with increased P-use efficiency (PUE) (Vandamme *et al*., 2016; Rose and Wissuwa, 2012). A promising approach to improving rice resilience is provided by genetic diversity for P-deficiency tolerance combined with present phenotyping and genomic technologies (Heuer *et al*., 2017).

Understanding the combining ability of parents and their hybrids, along with the type of gene action governing trait inheritance, is highly valuable for plant breeders in selecting suitable parents and identifying promising crosses for breeding programs (Sudharani *et al*., 2013). Combining ability analysis provides a solid basis for separating additive and non-additive gene effects in rice breeding (Devi *et al*., 2015), which is essential to understanding the genetic basis of P-deficiency tolerance (Chaubey *et al*., 1994). Specific combining ability (SCA) captures non-additive effects, which is essential for hybrid development, whereas general combining ability (GCA) represents additive genetic contributions, making it perfect for pure-line selection (Shamuyarira *et al*., 2023).

According to studies, important characteristics including root architecture, P uptake and yield components can be improved to perform better in low-P environments (Niu *et al*., 2013; Lynch, and Brown, 2001). Improved P acquisition has been associated with genes such as *PSTOL1*, which promotes marker-assisted breeding (Azevedo *et al*., 2015; Neelam *et al*., 2017). Diallel crosses have the ability to find superior parents and hybrids, as indicated by recent field experiments in P-deficient soils that showed significant GCA and SCA impacts for yield and P uptake (Mutale, 2020; Santos *et al*., 2022). The present study evaluates the ability of rice to grow under phosphorus-deficient soil conditions in *Tera*i Zone of West Bengal, India. The soil conditions in the Terai Zone of West Bengal, India, are characterized by low phosphorus availability and acidic pH, as reported by Chand and Mandal (2000), Ghosh *et al*. (2005), Maji *et al*. (2012), and Vishnupriya *et al*. (2024) The recent researches shows that use of half-diallel mating design to study hybrid vigor and additive genetic effects under phosphorus-deficient soil conditions, aiming to identify parent lines and crosses with strong general and specific combining ability (GCA and SCA) for traits important in phosphorus stress tolerance. Therefore, it is essential to develop P-efficient rice cultivars due to nutrient scarcity and climate variability endanger global food security (Navea *et al*., 2024).

MATERIALS AND METHODS

The field experiments were conducted at the Research Farm of Uttar Banga Krishi Viswavidyalaya (UBKV), Pundibari, Cooch Behar, West Bengal, India, across the *Kharif* seasons of 2021 to 2023. The Terai agroecological zone is located at 26°23’59” N latitude, 89°23’22” E longitude, and 72 meters above sea level, the site features phosphorus-deficient soils typical of the region. During *Kharif,* 2021, a preliminary evaluation of rice genotypes was performed under low-P conditions (available P - 11.08 kg/ha) by Vishnupriya *et al*. (2024) to select eight diverse parents: CR Sugandh Dhan 909, Paolum Sali, Ranjit, Banga Bandhu (white), Uttar Lakshmi, BBII, MTU 7029, and Uttar Sona. Selection criteria included agronomic performance and P-acquisition potential. In *Kharif* 2022, these parents were crossed in a half-diallel design without reciprocals (Griffing, 1956), producing 28 F_1 hybrids. The 28 hybrids and along with their eight parents were evaluated in P-deficient soil, in a randomized block design with three replications, during *Kharif* 2023. Fourteen traits, namely, days to 50% flowering, days to 100% flowering, plant height (cm), number of productive tillers, flag leaf length (cm), flag leaf width (cm), number of panicles per plant, panicle length, number of grains per panicle, number of spikelets per panicle, test weight (g), dry shoot weight (g/plant), phosphorus uptake (mg/plant) and grain yield (g/plant) were observed. Phosphorus uptake was quantified using the Ammonium metavanadate method after tissue triple acid digestion (Jackson and Patterson, 1973).

Assessment of GCA and SCA was done by Griffing’s Method II, Model I (fixed effects) for a half-diallel cross (Griffing, 1956). Variance components (σ^2GCA and σ^2SCA) were derived to evaluate additive and dominance effects, with ANOVA partitioning the total variance into GCA, SCA and error components (Hayman, 1954). Data were analyzed using SPAR DOS-Box software with significance levels set at $P < 0.05$ and $P < 0.01$.

RESULTS AND DISCUSSION

The combining ability analysis of eight rice parents and their 28 F1 crosses under phosphorus-deficient conditions revealed assessment of genetic variation and breeding potential for developing phosphorus-deficiency-tolerant rice varieties under low phosphorus soil condition. Mean performances of the parents and crosses (**Table 1**) showed significant trait diversity among parents and hybrids. The cross CR Sugandh Dhan 909 × BBII exhibited the earliest flowering, a trait associated with efficient resource allocation under P stress (Feng *et al*., 2021). Early flowering may allow plants to complete their reproductive phase before severe P depletion occurs, reducing yield losses (Malhotra., 2018). The cross, **Uttar** Lakshmi × BBII showed delayed flowering, possibly due to prolonged P acquisition efforts, as observed in P-stressed genotypes with enhanced root foraging (Nadeem et al., 2022). However, delayed maturity under P deficiency can be detrimental if P availability remains critically low during grain filling stage (Rose et al., 2013; Rose et al., 2016). Among the crosses, Banga Bandhu (white) × Uttar Sona and Paolum Sali × Ranjit represented tall and shortest plant respectively. Shorter genotypes, such as Uttar Sona, may exhibit better P-use efficiency (PUE) by reducing vegetative biomass and allocating more P

Table 1. Mean performance of parents and crosses under phosphorus-deficient field condition

S.No	Parents	DFF	DHF	PH	NPT	FLL	FLW	NPP	PL	NGP	NSP	TW	DSW	PU	GY
1	CR sugandh dhan 909	127.33	134.33	155.40	32.67	23.70	1.77	8.33	25.77	120.33	134.33	14.73	24.57	7.13	35.60
2	Paolum Sali	104.67	111.33	170.30	21.33	26.03	1.13	14.67	18.47	144.67	173.33	22.70	37.97	0.73	46.03
3	Ranjit	126.33	131.67	148.80	17.33	21.30	1.43	15.67	28.57	111.33	136.33	16.63	32.83	2.43	62.87
4	Banga Bandhu (White)	110.00	117.67	112.47	13.33	18.10	1.53	10.33	23.57	134.33	151.00	20.40	32.17	0.97	57.50
5	Uttar Lakshmi	95.00	97.67	136.40	27.33	29.47	1.27	9.33	19.93	127.33	170.67	23.77	34.27	3.43	31.23
6	BBII	109.33	117.33	107.37	12.33	22.70	1.67	11.33	15.93	91.33	105.67	17.73	30.13	0.13	42.80
7	MTU 7029	114.33	121.00	124.27	19.33	35.20	1.03	13.67	22.60	117.33	171.67	25.27	39.47	4.73	22.83
8	Uttar Sona	94.67	97.33	90.60	9.33	25.10	1.83	12.33	17.77	142.33	171.33	19.20	32.90	1.87	24.20
Crosses															
9	CR Sugandh Dhan 909 x Paolum Sali	129.33	134.33	163.37	24.67	23.47	1.77	13.33	22.53	150.67	156.33	15.43	34.67	6.73	52.73
10	CR Sugandh Dhan 909 x Ranjit	109.33	114.33	142.53	22.67	25.43	1.17	16.33	18.67	169.67	180.33	16.17	22.97	7.13	48.60
11	CR Sugandh Dhan 909 x Banga Bandhu (White)	124.67	129.33	120.70	19.67	24.47	1.67	12.33	23.13	159.67	188.67	14.73	12.70	5.47	45.60
12	CR Sugandh Dhan 909 x Uttar Lakshmi	113.33	115.33	134.03	17.33	22.43	1.23	14.33	20.27	144.67	167.67	15.83	30.30	8.27	53.93
13	CR Sugandh Dhan 909 x BBII	88.33	91.33	118.53	15.67	23.93	1.83	15.67	25.37	134.33	173.33	17.27	18.33	6.07	30.73
14	CR Sugandh Dhan 909 x MTU 7029	109.67	112.33	128.37	21.33	25.93	1.33	13.33	19.90	154.67	183.33	14.43	28.53	8.93	50.00
15	CR Sugandh Dhan 909 x Uttar Sona	115.33	118.33	116.23	18.67	22.93	1.53	14.67	24.77	147.67	168.67	16.67	25.67	7.43	46.10
16	Paolum Sali x Ranjit	94.67	99.33	159.67	16.67	26.47	1.07	17.33	26.97	137.33	146.67	19.77	15.67	1.97	60.13
17	Paolum Sali x Banga Bandhu (White)	119.67	122.67	138.53	13.67	23.97	1.53	13.67	21.57	162.33	210.67	20.57	9.20	1.77	58.03
18	Paolum Sali x Uttar Lakshmi	104.33	106.67	121.83	11.33	23.47	1.17	15.67	26.17	141.33	158.67	19.13	20.47	1.47	62.37
19	Paolum Sali x BBII	111.33	116.67	132.13	9.33	24.43	1.77	16.33	20.37	129.33	179.33	20.27	8.27	2.13	49.93
20	Paolum Sali x MTU 7029	99.33	101.33	125.83	14.67	24.97	1.63	12.67	25.83	139.67	158.33	21.63	17.93	2.77	57.87
21	Paolum Sali x Uttar Sona	114.67	119.33	114.90	12.67	26.47	1.43	13.67	19.30	132.67	187.33	18.97	14.03	1.67	55.90
22	Ranjit x Banga Bandhu (White)	129.67	131.67	142.73	14.67	22.93	1.23	19.67	22.00	174.67	220.33	17.57	11.40	1.23	55.40
23	Ranjit x Uttar Lakshmi	107.67	109.33	130.37	12.33	24.97	1.43	16.67	18.30	179.67	227.33	18.37	25.50	1.03	61.80
24	Ranjit x BBII	123.67	127.33	124.67	10.67	23.47	1.37	18.67	23.17	164.67	192.33	16.93	15.43	0.83	43.77
25	Ranjit x MTU 7029	118.33	122.33	136.90	13.33	23.93	1.57	17.67	19.97	172.33	212.67	18.07	24.63	1.67	59.70
26	Ranjit x Uttar Sona	121.33	126.33	126.27	11.33	25.93	1.17	15.67	25.03	167.33	195.67	16.63	20.63	1.17	52.57
27	Banga Bandhu (White) x Uttar Lakshmi	94.67	97.67	115.93	10.33	25.93	1.77	11.67	27.07	154.33	199.67	21.13	7.43	0.77	65.67
28	Banga Bandhu (White) x BBII	117.67	121.33	105.63	8.67	22.97	1.83	12.33	21.07	144.33	200.33	20.47	5.73	0.93	37.57
29	Banga Bandhu (White) x MTU 7029	99.33	104.67	110.13	9.33	24.97	1.63	10.33	26.30	149.67	178.67	22.07	10.63	1.23	63.03
30	Banga Bandhu (White) x Uttar Sona	97.33	100.67	98.30	7.33	24.47	1.77	11.33	20.13	157.67	167.33	20.87	8.13	0.57	54.13
31	Uttar Lakshmi x BBII	134.33	139.33	128.47	7.67	23.97	1.23	10.33	22.00	79.67	119.33	19.37	13.37	0.33	32.67
32	Uttar Lakshmi x MTU 7029	124.67	127.67	118.43	8.33	26.43	1.43	11.67	18.50	89.67	107.33	20.53	28.33	0.63	58.00
33	Uttar Lakshmi x Uttar Sona	129.67	134.33	106.30	6.67	23.43	1.37	9.33	23.87	99.67	127.33	18.77	24.40	0.43	49.50
34	BBII x MTU 7029	104.67	109.67	120.00	10.67	24.43	1.53	12.33	27.33	119.67	155.67	22.93	19.47	3.23	41.70
35	BBII x Uttar Sona	112.00	115.67	112.17	9.67	24.97	1.67	11.33	21.07	109.33	124.67	21.13	15.53	2.63	38.87
36	MTU 7029 x Uttar Sona	94.67	98.67	105.00	11.67	25.93	1.33	10.33	26.73	124.33	156.67	22.47	30.77	4.07	56.23

DFF – Days to 50% of flowering; DHF - Days to 100% of flowering; PH-Plant height (cm); NPT-No. of tillers per plant; FLL – Flag leaf length (cm); FLW – Flag leaf width (cm); NPP- No. of panicle per plant; PL-Panicle length (cm); NGP – No. of grains per panicle; NSP- No. of spikelet per panicle; TW- Test weight (g); DSW – Dry shoot weight (g); PU-Phosphorus uptake (mg/plant); GY- grain yield (g/plant) to grain development (Heuer *et al*., 2017). Also, taller genotypes like Paolum Sali may require higher P uptake to sustain growth, making them more susceptible to P deficiency (Chin et al., 2011). Ranjit × Uttar Lakshmi produced the highest number of grains and spikelets per panicle, indicating strong combining ability for yield under P stress. This could be attributed to improved P remobilization from vegetative tissues to grains (Khan et al., 2023). On the other hand, Uttar Lakshmi × BBII had the lowest grain count, possibly due to poor P assimilation or sink strength under stress (Xu et al., 2022). Banga Bandhu (white) × Uttar Lakshmi achieved the highest grain yield, while MTU 7029 had the lowest, strengthening the importance of parental selection for P-stress tolerance. High-yielding crosses may possess superior P-partitioning mechanisms, ensuring sufficient P allocation to developing grains (Rao et al., 1999). CR Sugandh Dhan 909 × MTU 7029 showed the highest P uptake, likely due to enhanced root exudation of organic acids or phosphatase enzymes that solubilize soil P (Hocking, 2001; Israr *et al*., 2016). **BBII** had the lowest P uptake, possibly due to inefficient P transporters or restricted root proliferation (Hasan *et al*., 2016).

Analysis of variance (**Table 2**) revealed highly significant genetic variability among parents and crosses for all traits except days to 100% flowering, exhibiting significant diversity exploitable for breeding phosphorus-efficient rice varieties. The stability of flowering time across generations suggests strong physiological regulation under P stress, while the significant general (GCA) and specific (SCA) combining ability effects revealed complementary genetic architectures with additive effects dominating morphological and yield-related traits (plant height, panicle characteristics, test weight) and non-additive effects contributing substantially to all traits. This genetic architecture suggests dual breeding strategies such as leveraging high-GCA parents like those with superior panicle traits or shoot biomass for pure-line improvement through recurrent selection (Gunasekaran *et al*., 2023), while simultaneously exploiting heterosis in high-SCA crosses for yield and P uptake (Singh *et al*., 2025). The results emphasis the potential of hybrid breeding for overcoming P limitation, as evidenced by significant SCA effects, while maintaining the ability to make predictable gains in important agronomic traits through additive genetic effects.

Table 2. Analysis of variance of morphological characters for parents and crosses by Griffing's approach

Source of variation	df	Mean sum of squares						
		Days to 50% flowering	Days to 100% flowering	Plant height (cm)	No. of productive tillers	Flag leaf length (cm)	Flag leaf width (cm)	No. of panicles per plant
Replication	2	11.731	3.009	17.612	1.083	3.480	73.542	6.481
Treatments	35	459.380**	492.733**	1003.023**	109.162**	20.077**	0.175**	23.451**
Parents	7	460.567**	564.615*	2170.570**	186.185*	82.727*	0.261*	20.232**
Crosses	27	473.137*	492.346**	714.467**	69.373**	4.276**	0.159**	22.598**
Parents Vs Crosses	1	796.252**	2.199	621.944*	644.292**	8.143*	0.010**	69.001**
Error	70	8.179	7.762	14.886	0.369	0.381	0.003	0.341
Total	107	16674.296	17794.991	36182.656	3848.667	729.489	6.3777	844.769

*, ** Significant at 5% and 1% levels of probability, respectively

Table 2 (Continued)

Source of variation	df	Mean sum of squares						
		Panicle length (cm)	No. of grains per panicle	No. of spikelet per panicle	Test weight (g)	Dry shoot weight (g/plant)	Phosphorus uptake (mg/plant)	Grain yield (g/plant)
Replication	2	0.430	3.028	20.083	0.371	0.355	0.013	0.363
Treatments	35	31.967**	1868.571**	2737.760**	22.264**	274.520**	19.826*	390.732**
Parents	7	55.783**	92.804**	1829.610**	40.372*	63.493**	16.521**	648.321**
Crosses	27	26.001*	1934.379**	2762.937*	17.414**	194.813*	21.368**	252.692**
Parents Vs Crosses	1	26.353**	6675.482**	8415.027**	26.479**	3903.749**	1.357**	2314.759**
Error	70	0.390	9.856	21.245	0.161	0.389	1.120	0.602
Total	107	1147.003	66096.000	97348.917	791.276	9636.169	66062.106	62575.290

*, ** Significant at 5% and 1% levels of probability, respectively

The observed variability in general combining ability (GCA) and specific combining ability (SCA) (**Table 3**) suggests that both additive and non-additive gene effects influence P-deficiency tolerance. Parents with high GCA such as CR Sugandh Dhan 909 likely possess dominant alleles for PUE traits, such as root architecture or P transporters (Van et al., 2016). Superior crosses such as Ranjit × Uttar Lakshmi may benefit from complementary gene interactions, enhancing P acquisition and utilization (Wang et al, 2010). The identification of high-performing crosses such as CR Sugandh Dhan 909 × BBII for earliness, Ranjit × Uttar Lakshmi for grain yield, provides a foundation for breeding programs targeting P-deficient soils.

The general combining ability (GCA) analysis (**Table 4**) identified several parental lines with significant genetic contributions to key traits under phosphorus-deficient conditions, providing valuable resources for breeding programs targeting improved P-use efficiency. Five parents such as Uttar Sona, MTU 7029, Paolum Sali, Uttar Lakshmi, and Banga Bandhu (white) showed significant negative GCA effects for days to flowering, revealing their high capacity to pass on earliness alleles to offspring, an essential adaption mechanism that permits the reproductive cycle to be completed before significant P depletion takes place (Balemi and Negisho, 2012). For plant height, Uttar Sona exhibited the most dramatic negative GCA effect, followed by BBII**,** Banga Bandhu (white), MTU 7029 and Uttar Lakshmi, suggesting these parents carry valuable alleles for developing compact varieties with reduced lodging risk and improved resource allocation under phosphorus limited conditions (Lynch, 2017). The analysis revealed distinct parental strengths for yield components, with Ranjit showing high positive GCA for panicles per plant, panicle length, and grains per panicl**e,** Banga Bandhu (white) excelling in spikelets per panicle and grain yield and MTU 7029 indicating superior GCA for flag leaf length**,** test weight, dry shoot weight and P uptake, confirming its known PUE potential through enhanced photosynthetic capacity and nutrient acquisition efficiency. The consistent GCA patterns across multiple traits indicate predominantly additive genetic control, supporting their use in pure-line breeding through conventional pedigree (Yan *et al*., 2017) or recurrent selection methods (Ayiecho and Nyabundi., 2025), while also offering opportunities for strategic trait pyramiding by combining complementary parents (Peng *et al*., 2014) like Uttar Sona (early maturity), Banga Bandhu (high yield), and MTU 7029 (PUE) in single varieties.

The analysis of specific combining ability (SCA) analysis (**Table 5**) revealed significant non-additive genetic interactions revealing the potential for exploiting heterosis in rice breeding programs. The crosses such as CR Sugandh Dhan 909 × BBII and Banga Bandhu (white) × Uttar Lakshmi exhibits strong negative SCA for days to 50% flowering, indicating hybrid vigor for earliness as a potential P-stress adaptation mechanism (Rao, 2021), while other combinations like Ranjit × Banga Bandhu (white) showed delayed flowering, suggesting alternative strategies for P acquisition (Zemunik *et al*., 2015). For grain yield, superior crosses including Paolum Sali × Ranjit, CR Sugandh Dhan 909 × BBII and Banga Bandhu (white) × Uttar Sona exhibited significant positive SCA effects, reflecting robust heterosis for productivity under P limitation. Phosphorus uptake was particularly enhanced in CR Sugandh Dhan 909 × BBII (24.517) and Paolum Sali × Ranjit, indicating specific hybrid advantages in P acquisition efficiency through complementary root architectures (Lambers *et al*., 2006) or P transporter systems (Gu *et al*., 2016). The negative SCA effects were observed for vegetative traits such as plant height (Paolum Sali × MTU 7029) and tiller number (Uttar Lakshmi × MTU 7029) revealed adaptive reductions in vegetative growth under P stress which helps in the hybrid combinations can overcome P stress through various mechanisms, including altered phenology, improved resource partitioning, enhanced nutrient acquisition, and modified growth patterns (Nord *et al*., 2011), providing useful knowledge for developing high-performing rice varieties for low-P environments through targeted exploitation of non-additive genetic effects.

The genetic variance estimates (**Table 6**) revealed a complex interaction between additive and non-additive genetic effects, with dominance variance (σ^2SCA) exceeding additive variance (σ^2GCA) for all traits, indicating the predominant role of non-additive gene action in phenotypic variation under low-phosphorus soil conditions (Bispo, 2024). However, the σ^2GCA/σ^2SCA ratio exceeded unity for key developmental and yield-related traits including days to 50% flowering, days to 100% flowering, plant height, grains per panicle, and spikelets per panicle, indincating that additive effects remain substantial for these traits, particularly in controlling flowering time and panicle architecture. The exceptionally high dominance variance observed for number of spikelets per panicle suggests strong potential for exploiting heterosis through hybrid breeding (Meena *et al*., 2017), especially for complex yield components and phosphorus uptake efficiency, as shown by superior performance of specific crosses including CR Sugandh Dhan 909 × MTU 7029 and Banga Bandhu (white) × Uttar Lakshmi in mean performance. These indicates that the non-additive effects dominate overall genetic architecture and therefore, breeding approaches that focus on both additive variance through recurrent selection of superior parents like Ranjit and MTU 7029 is used for pure-line improvement, and dominance variance through targeted hybridization to maximize heterotic effects is used for yield and nutrient efficiency traits in low-phosphorus environments.

The present study on combining ability analysis of eight rice parents and their 28 F_1 hybrids under phosphorus-

Table 3. Analysis of variance for combining ability for morphological characters under phosphorus-deficient condition

Sources of variation	Df	DFF	DHF	PH	NPT	FLL	FLW	NPP	PL	NGP	NSP	TW	DSW	PU	GY
GCA	7	277.381**	298.255**	4135.360**	366.229**	47.302*	0.360*	66.721**	15.831**	3784.771**	3195.083**	80.893**	392.411**	422.863**	394.797**
SCA	28	504.880**	541.353**	219.948**	44.895**	13.269**	0.129*	12.633**	36.001*	389.521**	2623.429**	7.608**	245.046*	2250.813**	2134.581**
Error	70	8.179	7.762	14.886	0.369	0.381	0.003	0.341	0.390	9.856	21.245	0.161	0.389	1.120	0.602

*, ** Significant at 5% and 1% levels of probability, respectively, DFF – Days to 50% of flowering; DHF - Days to 50% of flowering; PH-Plant height (cm); NPT-No. of tillers per plant; FLL – Flag leaf length (cm); FLW – Flag leaf width (cm); NPP- No. of panicle per plant; PL-Panicle length (cm); NGP – No. of grains per panicle; NSP- No. of spikelet per panicle; TW- Test weight (g); DSW – Dry shoot weight (g); PU-Phosphorus uptake (mg/plant); GY- grain yield (g/plant).

Table 4. General combining ability (gca) effects for parents for morphological characters under phosphorus-deficient condition

S. No	Parents	DFF	DHF	PH	NPT	FLL	FLW	NPP	PL	NGP	NSP	TW	DSW	PU	GY
1	CR Sugandh Dhan 909	3.830**	3.992**	9.867**	7.433**	-0.617*	0.078*	-0.442	0.367**	5.700	-2.775**	-3.215*	2.619**	-3.587**	0.360**
2	Paolum Sali	-2.370**	-2.108**	16.097**	1.467**	0.313**	-0.065	1.092**	-0.283	3.767	2.925**	0.902**	0.006**	-4.277**	-0.110**
3	Ranjit	5.100**	4.992**	12.484**	0.533	-0.644	-0.142	3.225**	0.874**	14.333	13.325**	-1.538	0.579**	1.150**	2.850**
4	Banga Bandhu (White)	-0.330**	-0.075**	-7.899	-2.067	-1.627	0.122**	-0.908*	0.591	12.633	15.292**	0.605**	-6.654**	3.950**	5.753**
5	Uttar Lakshmi	-0.770**	-1.842**	-0.773	-0.233	0.739	-0.112**	-1.275**	-0.646*	-10.133**	-6.608**	0.852**	2.223**	-4.567**	-5.533**
6	BBII	0.430**	1.192**	-7.956	-3.400*	-0.861	0.128**	-0.142*	-1.026	-18.100	-15.842**	0.168**	-3.971**	-0.330	-3.370**
7	MTU 7029	-2.700**	-2.542**	-4.269**	-0.300	2.483	-0.075	-0.542*	0.727*	-6.033	-1.875**	2.052*	4.313**	4.210**	2.120**
8	Uttar Sona	-3.200**	-3.608**	-17.553*	-3.433	0.216	0.065	-1.008	-0.606**	-2.167	-4.442	0.175	0.886**	3.450**	-2.070**

DFF – Days to 50% of flowering; DHF - Days to 50% of flowering; PH-Plant height (cm); NPT-No. of tillers per plant; FLL – Flag leaf length (cm); FLW – Flag leaf width (cm); NPP- No. of panicle per plant; PL-Panicle length (cm); NGP – No. of grains per panicle; NSP- No. of spikelet per panicle; TW- Test weight (g); DSW – Dry shoot weight (g); PU-Phosphorus uptake (mg/plant); GY- grain yield (g/plant).

Table 5. Specific combining ability (sca) effects for morphological characters under phosphorus-deficient condition

S.No	Parents	DFF	DHF	PH	NPT	FLL	FLW	NPP	PL	NGP	NSP	TW	DSW	PU	GY
1.	CR Sugandh Dhan 909 x Paolum Sali	16.052**	16.441**	11.192*	1.211**	-0.914	0.277*	-0.770	-0.051	2.867	-12.122	-1.381*	10.252	15.463**	19.583*
2.	CR Sugandh Dhan 909 x Ranjit	-11.415	-10.659**	-6.028	0.144**	2.009**	-0.246	0.096**	-5.074	11.300**	1.478	1.792	-2.021	-18.830	-25.477
3.	CR Sugandh Dhan 909 x Banga Bandhu (White)	9.352**	9.407*	-7.478	-0.256	2.026*	-0.009**	0.230*	-0.324	3.000**	7.844**	-1.784	-5.055	24.370**	29.653**
4.	CR Sugandh Dhan 909 x Uttar Lakshmi	-1.548	-2.826	-1.272	-4.422*	-2.374**	-0.209	2.596**	-1.954**	10.767	8.744	-0.931	3.669**	-12.713	-17.593
5.	CR Sugandh Dhan 909 x BBII	-27.748**	-29.859*	-9.588*	-2.922	0.726**	0.151	2.796**	3.526	8.400	23.644**	1.186**	-2.105	24.517**	31.643**
6.	CR Sugandh Dhan 909 x MTU 7029	-3.281	-5.126	-3.442	-0.356	-0.618	-0.146	0.863	-3.694**	16.667	19.678	-3.531	-0.188	-23.157	-25.447
7.	CR Sugandh Dhan 909 x Uttar Sona	2.885**	1.941	-2.292	0.111	-1.351	-0.086	2.663	2.506	5.800**	7.578	0.579	0.372	17.737	35.277**
8.	Paolum Sali x Ranjit	-19.881	-19.559	4.875*	0.111**	2.112**	-0.203	-0.437**	3.876	-19.100	-37.889	1.276	-6.708	29.060**	38.993**
9.	Paolum Sali x Banga Bandhu (White)	10.552	8.841	4.125*	-0.289	0.596**	0.001	0.030	-1.241	7.600**	24.144**	-0.068**	-5.941*	-21.607	-28.643
10.	Paolum Sali x Uttar Lakshmi	-4.348	-5.393	-19.702	-4.456	-2.271	-0.133	2.396	4.596	9.367	-5.956**	-1.748	-3.551	11.577	19.277
11.	Paolum Sali x BBII	1.452**	1.574*	-2.219	-3.289	0.296*	0.227*	1.930	-0.824	5.333**	23.944	0.069	-9.558	-14.460	-19.220
12.	Paolum Sali x MTU 7029	-7.415	-10.026	-12.205**	-1.056	-2.514	0.297	-1.337	2.889	3.600	-11.022	-0.448	-8.175	22.067	37.090**
13.	Paolum Sali x Uttar Sona	8.419	9.041	-9.855	0.078**	1.252	-0.043	0.130	-2.311	-7.267	20.544*	-1.238	-8.648**	-19.740	-21.187
14.	Ranjit x Banga Bandhu (White)	13.085**	10.741**	11.938	1.644**	0.519	-0.223**	3.896**	-1.964	9.367	23.411*	-0.628	-4.315	-32.367	-29.103
15.	Ranjit x Uttar Lakshmi	-8.481	-9.826**	-7.555	-2.522	0.186	0.211	1.263*	-4.427	37.133**	52.311**	-0.074	0.909	21.450	9.983**
16.	Ranjit x BBII	6.319**	5.141	-6.072	-1.022	0.286	-0.096	2.130*	0.819**	30.100	26.544**	-0.824*	-2.965	-26.853	-23.080
17.	Ranjit x MTU 7029	4.119	3.874	2.475	-1.456**	-2.591*	0.307	1.530*	-4.134	25.700**	32.911**	-1.574	-2.048	26.773	3.763**
18.	Ranjit x Uttar Sona	7.619	8.941**	5.125	-0.322	1.676	-0.233*	-0.004	2.266*	16.833	18.478	-1.131	-2.621	-30.833*	-24.080
19.	Banga Bandhu (White) x Uttar Lakshmi	-16.048**	-16.426**	-1.605*	-1.922	2.136	0.281	0.396	4.623	13.500**	22.678	0.549	-9.925	-25.917	-23.720**
20.	Banga Bandhu (White) x BBII	5.752	4.207	-4.722	-0.422	0.769	0.107**	-0.070	-0.997	11.467	32.578**	0.566	-5.431	30.747	23.183
21.	Banga Bandhu (White) x MTU 7029	-9.448	-8.726**	-3.908	-2.856	-0.574	0.111*	-1.670	2.483**	4.733	-3.056	0.282**	-8.815	-34.027	-31.673
22.	Banga Bandhu (White) x Uttar Sona	-10.948	-11.659	-2.458**	-1.722**	1.192	0.104*	-0.204	-2.351	8.867**	-11.822*	0.959	-7.888	14.533	15.183**
23.	Uttar Lakshmi x BBII	22.852**	23.974	10.985*	-3.256	-0.598	-0.259	-1.704*	1.173	-30.433	-26.522	-0.781	-6.675	34.763**	26.670
24.	Uttar Lakshmi x MTU 7029	16.319**	16.041*	-2.735	-5.689	-1.474	0.144*	0.030	-4.081	-32.500	-52.489**	-1.498*	0.009	-25.977**	-17.887**
25.	Uttar Lakshmi x Uttar Sona	21.819**	23.774*	-1.585**	-4.222*	-2.208	-0.063	-1.837	2.619	-26.367**	-29.922**	-1.388	-0.498	29.017	22.537**
26.	BBII x MTU 7029	-4.881	-4.993	6.015*	-0.189	-1.874	0.004*	-0.437	5.133*	5.467	5.078	1.586	-2.665	30.987**	0.150
27.	BBII x Uttar Sona	2.952	2.074	11.465*	1.944**	0.926**	-0.003*	-0.970*	0.199	-8.733**	-23.356**	1.662	-3.171	-29.887	-14.427
28.	MTU 7029 x Uttar Sona	-11.248**	-11.193	0.611	0.844**	-1.451*	0.065	-1.570**	4.113	-5.800	-5.322**	1.112*	3.779	-34.627	-22.117**

DFF – Days to 50% of flowering; DHF - Days to 50% of flowering; PH-Plant height (cm); NPT-No. of tillers per plant; FLL – Flag leaf length (cm); FLW – Flag leaf width (cm); NPP- No. of panicle per plant; PL-Panicle length (cm); NGP – No. of grains per panicle; NSP- No. of spikelet per panicle; TW- Test weight (g); DSW – Dry shoot weight (g); PU-Phosphorus uptake (mg/plant); GY- grain yield (g/plant.

Table 6. Estimates of genetic components of variance and degree of dominance for morphological characters under phosphorus-deficient condition

Sources of variation	DFF	DHF	PH	NPT	FLL	FLW	NPP	PL	NGP	NSP	TW	DSW	PU	GY
σ^2_{gca}	0.076	0.072	0.138	0.003	0.004	0.00003	0.0003	0.003	0.091	0.197	0.001	0.004	0.0001	0.016
σ^2_{sca}	0.239	0.226	0.434	0.011	0.111	0.00009	0.0100	0.011	0.287	0.620	0.005	0.011	0.0330	0.018
$\sigma^2_{gca}/\sigma^2_{sca}$	1.696	1.610	3.086	0.077	0.079	0.00067	0.0710	0.081	2.044	4.406	0.033	0.081	0.2320	0.125
$(\sigma^2_{gca}/\sigma^2_{sca})^{0.5}$	2.242	2.273	4.078	0.101	0.105	0.00088	0.0930	0.107	2.701	5.823	0.044	0.107	0.3070	0.165
σ^2_A	0.545	0.517	0.992	0.025	0.025	0.00021	0.0230	0.026	0.657	1.416	0.011	0.026	0.0750	0.040
σ^2_D	3.272	3.105	5.952	0.148	0.153	0.00129	0.1360	0.156	3.943	8.498	0.064	0.016	0.4480	0.241
σ^2_A/σ^2_D	4.907	4.657	8.928	0.221	0.229	0.00193	0.0019	0.205	5.914	12.747	0.097	0.234	0.0070	1.038
$\sigma^2_A/\sigma^2_A+\sigma^2_D$	0.436	4.140	7.936	0.197	0.203	0.00172	0.1820	0.208	5.257	11.331	0.086	0.208	0.0062	0.567

gca = general combining ability, sca = specific combining ability, σ^2_{gca} = gca variance, σ^2_{sca} = sca variance, $(\sigma^2_{gca}/\sigma^2_{sca})^{0.5}$ = degree of dominance, σ^2_A = additive variance, σ^2_D = dominance variance, $\sigma^2_A/(\sigma^2_A+\sigma^2_D)$ = predictability ratio, DFF – Days to 50% of flowering; DHF - Days to 50% of flowering; PH-Plant height (cm); NPT-No. of tillers per plant; FLL – Flag leaf length (cm); FLW – Flag leaf width (cm); NPP- No. of panicle per plant; PL-Panicle length (cm); NGP – No. of grains per panicle; NSP- No. of spikelet per panicle; TW-Test weight (g); DSW – Dry shoot weight (g); PU-Phosphorus uptake (mg/plant); GY- grain yield (g/plant).

deficient conditions reveals substantial genetic potential for developing low-P-tolerant varieties. Significant GCA effects in parents like MTU 7029, Ranjit, and Banga Bandhu (white) for traits such as phosphorus uptake, grain yield, and yield components showed their value as donors of additive genetic effects, suitable for pure-line breeding. High SCA effects in crosses like CR Sugandh Dhan 909 × BBII and Paolum Sali × Ranjit for P uptake and grain yield exhibits non-additive gene action, favoring hybrid development. The predominance of dominance variance over additive variance across traits suggests that exploiting heterosis could maximize gains in P-stressed environments, while the additive effects for flowering and height traits support selection-based breeding program in the Terai Zone's P-deficient soils. Crosses combining early maturity, efficient P uptake and high yield potential are particularly promising for sustainable agriculture amid nutrient constraints.

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