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Study on Gene Action of Yield and its Attributes in Rice (*Oryza sativa* L.) under Phosphorus-deficient Conditions using Haymans Approach

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ABSTRACT

The study was conducted during *kharif* (July, 2022–January, 2023) at the Instructional Agricultural Farm, Uttar Banga Krishi Vishwavidhyalaya, Cooch Behar, West Bengal, India to measure gene action and inheritance of yield and its attributing characteristics of rice under phosphorus-deficient soil conditions. The experimental material comprised eight diverse rice genotypes and their 28 direct crosses grown under phosphorus-deficient soil conditions in a randomized block design with three replications. Data on 14 quantitative characters were recorded and tested using the t^2 test. Regression of Wr on Vr and genetic components of variance were estimated, and graphical analysis was performed using Hayman's methodology. Non-significance of the t^2 test for all characters implied that there was no epistatic gene interaction. Estimation of genetic components revealed the presence of both additive and non-additive genes. The graphical approach indicated over-dominance gene action for the characters, flag leaf length, flag leaf width, no. of panicles plant^{-1}, and grain yield, whereas the remaining ten characters exhibited partial dominance. The rice genotype, CR Sugandh Dhan 909, exhibited dominance for phosphorus uptake and Paolum Sali for grain yield. Under phosphorus-deficient conditions, dominant alleles and significant additive gene effects facilitated early-generation fixability of traits. Overdominance played a significant role in certain traits like flag leaf dimensions and grain yield, indicating efficient selection possibilities in later generations.

KEYWORDS: Gene action, haymans approach, variability, Wr-Vr graph

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1. INTRODUCTION

Over 90% of the world's population is fed by Asian cultivated rice (*Oryza sativa* L.), making it one of the most significant crops in the world (Hour et al., 2020). Rice fields are heavily fertilized to maintain rice production which accounts for 50% of global fertilizer usage, respectively (Anonymous., 2017). Among the fertilizers, phosphorus is very important for boosting rice growth because it ensures maximum grain production and strong root development, which both improve global food security and agricultural sustainability. A lack of soil phosphorus causes stunting of rice plants in their early growth, bronzing of older leaves, reduced tillering, delayed flowering, and reduced grain yields (Dobermann, 2000). Phosphorus deficiency is particularly acute in tropical and subtropical regions, where weathered soils, such as Oxisols and Ultisols, dominate and exhibit low phosphorus availability due to high iron and aluminum oxide content (Fageria et al., 2011). This exacerbates the challenge of maintaining rice productivity in regions heavily reliant on rice as a staple crop. P availability is frequently low despite the long-term application of phosphate fertilizers to boost crop yields because of phosphate's strong affinity for the solid phase of soil (Zhu et al., 2018). Soil P frequently needs to be replaced repeatedly to meet plant demand, even when other constraints may also limit production. This is partly because soil P is rapidly taken from the dissolved (plant-available) form by sorption, precipitation and microbial immobilization (Roberts and Johnston, 2015). The issue has been resolved to some extent by phosphate fertilization, but not sustainably because the phosphate rock needed to produce fertilizer is a limited resource (Baker et al.., 2015). Therefore, one of the main goals of plant breeders is to lessen dependence on high phosphate intake, especially in rice crops. To achieve this, knowledge of gene action is needed to develop a low phosphorus tolerance rice variety. To comprehend the nature of gene action involved in the quantitative characters, diallel mating design has been widely applied in both self- and cross-pollinated species (Sabouri et al., 2013). The genetic information controlling the inheritance of the studied characteristics determines an efficient and successful breeding program (Riyanto et al., 2023). Therefore, understanding additive and non-additive genetic effects is essential for developing successful breeding methods. While non-additive gene effects influence features such as heterosis and direct particular breeding approaches, additive effects help achieve long-term genetic progress through predictable selection. Diallel design mating system gives a variety of information through two approaches such as Griffings approach to find the combining ability between the selected parents for the crossing program and Hayman's approach to know about the type of gene action that controls the inheritance of the character. The Hayman (1954) variance analysis approach was utilized for the genetics analysis in this study since it was determined to be more comprehensive than the Griffing (1956) variance analysis method (Sabouri et al., 2013). Hayman's numerical and graphical approach was used to estimate gene action and its inheritance for yield and its attributing characters in various crops like rice (Bano and Singh,2019; Riyanto et al., 2023; Gunasekaran et al., 2020), wheat (Chaudhari et al., 2023; Abdi and Fotokian, 2018), corn (Erfani Moghadam, 2023), *Ocimum* spp (Singh, 2020). Hence, the present study was initiated to estimate the genetic components and type of gene action its inheritance pattern of yield, and its attributing characters in rice under phosphorus-deficient soil conditions using a numerical and graphical approach.

2. MATERIALS AND METHODS

The study was conducted during *kharif* (July, 2022-January, 2023) at the Instructional Agricultural Farm, Uttar Banga Krishi Vishwavidhyalaya, Cooch Behar, West Bengal, India. The experimental material consisted of eight morphologically diverse rice genotypes such as CR Sugandh Dhan 909, Paolum Sali, Ranjit, Banga Bandhu (White), Uttar Lakshmi, BBII, MTU 7029, and Uttar Sona and their 28 direct crosses, i.e., the F1 populations obtained through half diallel mating design. All 36 treatments (8 parents and 28 crosses) were grown under phosphorus-deficient soil conditions (>8 kg ha^{-1}) in a randomized block design with three replications at the Instructional Agricultural Farm, Uttar Banga Krishi Vishwavidhyalaya, Cooch Behar, West Bengal, India, during the Kharif season of 2023. The observations were recorded on five randomly selected plants for each treatment, and the mean data was calculated for further analysis. The data were recorded for 14 characters such as 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 plant^{-1}, panicle length (cm), no. of grains panicle^{-1}, no. of spikelets panicle^{-1}, test weight (g), dry shoot weight (g plant^{-1}), phosphorus uptake (mg plant^{-1}), and grain yield (g plant^{-1}). The ammonium vanadate molybdate method (Ma et al., 2022) was used to detect Pi concentration and then multiplied with dry weight to obtain phosphorus uptake (mg plant^{-1}). Further analysis was done using AGD-R software version 3.0 (CIMMYT software based on R script).

The material under the study was tested for agreement with assumptions such as (i) diploid segregation, (ii) no differences between reciprocal crosses, (iii) absence of epistasis, i.e., independent action of non-allelic genes in the diallel cross, (iv) homozygous parent, (v) no linkages, i.e., genes independently distributed between the parents, and (vi) no multiple allele effect (Hayman, 1954a). Tests like the t^2 test and regression of Wr on Vr were used to test the assumptions. The presence of significance in the t^2 test implied that the assumptions were true.

Genetic components of variance were estimated using Hayman's (1954a) methodology. These included genetic variance due to additive effects of genes (D), genetic variance due to dominant gene effects of the genes (H1), genetic variance due to dominance effects corrected for the distribution of the genes (H2), the mean of F over the arrays, where F was the dominance effects in a single array (F), and overall dominance effects of heterozygous loci (h^2).

The graphical analysis was computed according to Hayman (1954b). The V_r (Variance of the r^{th} array) and W_r (covariance of the r^{th} array) points for the parents were depicted along the V_r and W_r axes. V_{ri} values were used to draw parabola and calculated using the formula

$W_{ri}=(V_{ri}\times V_0L_0)^{0.5}$

Expected W_{rei} values were calculated to draw a regression line as per the formula

$W_{rei}=Wr-bV_r+bV_r$

The point of interception (a) on W_r ordinate by the regression line is formulated by the formula

$a=W_r-bV_r$

3. RESULTS AND DISCUSSION

In Table 1, the matrix means of the 14 characters examined for parents and F_1 were provided. According to Jana (1975), the ANOVA was to detect the differences between Wr-Vr arrays. For all the characters under investigation, there were significant differences between the genotypes according to Hayman's (1954a) analysis of variance for half-diallel (Table 2). For every character under investigation, significant additive and non-additive effects were noted. All the characters had high levels of additive effects (a) except flag leaf length and width. The F_1's mean deviation from the mid-parental value (b_1) suggested that there was no ambi-directional dominance and that F_1 resembled either parent which resulted in heterosis for all the characters.

An asymmetric gene distribution was shown by significant values of (b_2) for each of the 14 characters, indicating that each parent had a sufficient number of dominant genes in comparison to the other parents. For the characters under investigation, each F_1 (b_3) had a unique residual dominance, which was significant and implied that each character had a dominant influence that was not fully understood. The block effect was not significant, showing homogeneity, concerning the number of panicles panicle^{-1}, test grain weight (g), flag leaf length, flag leaf breadth, no. of grains panicle^{-1}, no. of spikelets panicle^{-1} and phosphorus uptake. Therefore, none of the other variables interacting with the blocks had any significance. On account of the dominance effects importance, a further study was conducted to ascertain the variance and covariance components.

3.1. Testing validity of the hypothesis

The 't^2' test was employed to assess if the additive-dominance model was appropriate or not. (Table 3). The non-significant findings for all characters suggested Vr-Wr were consistent across arrays, indicating a strong fit for the additive-dominance hypothesis. The non-significant t^2 value shows that the assumptions have been fulfilled and there was no epistasis. It was expected that the Wr-Vr graph's regression slope (b) would differ significantly from zero but not significantly from unity (Hayman, 1954). Also, it was crucial to observe how the regression line deviated from one (b=0), as this served to verify the additive-dominant model's underlying assumptions. (Satheeshkumar et al., 2021). All the characters under study were significant for (b=0) indicating that all assumptions were true. For every character, the regression coefficient ($H=b_1$) with a unit slope was found in the absence of non-allelic interaction. After the additive dominance model was found to be adequate, the components of genetic diversity-D, H_1, H_2, E, F, and h^2 were determined.

3.2. Estimation of components of variation: (Numerical approach)

For all the characters under study, estimates of the genetic components were calculated (Table 4). For every trait, the F component values were significant and positive, suggesting that there was a higher proportion of dominant alleles than recessive alleles. It was further supported by the KD/KR value which was more than unity for all the characters indicating the existence of more dominant genes. According to the dominant hypothesis (Davenport, 1910), the favorable genes that control growth and development were dominant. Also, both dominant and overdominance theory suggested that heterosis was due to the effect caused by a single allele locus. So, the presence of more dominant alleles than recessive ones helped in the improvement of the rice genotypes with desired characteristics under phosphorus-deficient condition. The additive effect of genes (D), was significant for all characteristics except days to 100% flowering. This implied that except for days to 100% flowering, all the characters were easily fixable in the early generation. Non-significance of additive effects of genes for flowering parameters was observed by Hassan et al., 2016.

The estimations of H_1 and H_2 showed non-additive (dominance or epistatic) genetic influences, and they were a substantial factor in the inheritance of these characters (Ali et al., 2018). It was evident from the significant values of the non-additive (H_1 and H_2) and additive (D) components that both fixable and non-fixable components played a dominant role. Similar findings were also reported by Sharma and Jaiswal (2021). Furthermore, the magnitude of the non-additive (H_1) component was greater than the additive (D) component, for plant height, no. of productive tillers, flag leaf length, and test weight indicating the significance of overdominance for these characters. A similar interpretation

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

Sl. No.	Parents	DFF	DHF	PH	NPT	FLL	FLW	NPP
1.	CR sugandh dhan 909	127.33	134.33	155.40	32.67	23.70	1.77	8.33
2.	Paolum Sali	104.67	111.33	170.30	21.33	26.03	1.13	14.67
3.	Ranjit	126.33	131.67	148.80	17.33	21.30	1.43	15.67
4.	Banga Bandhu (White)	110.00	117.67	112.47	13.33	18.10	1.53	10.33
5.	Uttar Lakshmi	95.00	97.67	136.40	27.33	29.47	1.27	9.33
6.	BBII	109.33	117.33	107.37	12.33	22.70	1.67	11.33
7.	MTU 7029	114.33	121.00	124.27	19.33	35.20	1.03	13.67
8.	Uttar Sona	94.67	97.33	90.60	9.33	25.10	1.83	12.33
Crosses								
9.	CR Sugandh Dhan 909×Paolum Sali	129.33	134.33	163.37	24.67	23.47	1.77	13.33
10.	CR Sugandh Dhan 909×Ranjit	109.33	114.33	142.53	22.67	25.43	1.17	16.33
11.	CR Sugandh Dhan 909×Banga Bandhu (White)	124.67	129.33	120.70	19.67	24.47	1.67	12.33
12.	CR Sugandh Dhan 909×Uttar Lakshmi	113.33	115.33	134.03	17.33	22.43	1.23	14.33
13.	CR Sugandh Dhan 909×BBII	88.33	91.33	118.53	15.67	23.93	1.83	15.67
14.	CR Sugandh Dhan 909×MTU 7029	109.67	112.33	128.37	21.33	25.93	1.33	13.33
15.	CR Sugandh Dhan 909×Uttar Sona	115.33	118.33	116.23	18.67	22.93	1.53	14.67
16.	Paolum Sali×Ranjit	94.67	99.33	159.67	16.67	26.47	1.07	17.33
17.	Paolum Sali×Banga Bandhu (White)	119.67	122.67	138.53	13.67	23.97	1.53	13.67
18.	Paolum Sali×Uttar Lakshmi	104.33	106.67	121.83	11.33	23.47	1.17	15.67
19.	Paolum Sali×BBII	111.33	116.67	132.13	9.33	24.43	1.77	16.33
20.	Paolum Sali×MTU 7029	99.33	101.33	125.83	14.67	24.97	1.63	12.67
21.	Paolum Sali×Uttar Sona	114.67	119.33	114.90	12.67	26.47	1.43	13.67
22.	Ranjit×Banga Bandhu (White)	129.67	131.67	142.73	14.67	22.93	1.23	19.67
23.	Ranjit×Uttar Lakshmi	107.67	109.33	130.37	12.33	24.97	1.43	16.67
24.	Ranjit×BBII	123.67	127.33	124.67	10.67	23.47	1.37	18.67
25.	Ranjit×MTU 7029	118.33	122.33	136.90	13.33	23.93	1.57	17.67
26.	Ranjit×Uttar Sona	121.33	126.33	126.27	11.33	25.93	1.17	15.67
27.	Banga Bandhu (White)×Uttar Lakshmi	94.67	97.67	115.93	10.33	25.93	1.77	11.67
28.	Banga Bandhu (White)×BBII	117.67	121.33	105.63	8.67	22.97	1.83	12.33
29.	Banga Bandhu (White)×MTU 7029	99.33	104.67	110.13	9.33	24.97	1.63	10.33
30.	Banga Bandhu (White)×Uttar Sona	97.33	100.67	98.30	7.33	24.47	1.77	11.33
31.	Uttar Lakshmi×BBII	134.33	139.33	128.47	7.67	23.97	1.23	10.33
32.	Uttar Lakshmi×MTU 7029	124.67	127.67	118.43	8.33	26.43	1.43	11.67
33.	Uttar Lakshmi×Uttar Sona	129.67	134.33	106.30	6.67	23.43	1.37	9.33
34.	BBII×MTU 7029	104.67	109.67	120.00	10.67	24.43	1.53	12.33
35.	BBII×Uttar Sona	112.00	115.67	112.17	9.67	24.97	1.67	11.33
36.	MTU 7029×Uttar Sona	94.67	98.67	105.00	11.67	25.93	1.33	10.33

Table 1: Continue...

Sl. No.	Parents	PL	NGP	NSP	TW	DSW	PU	GY
1.	CR sugandh dhan 909	25.77	120.33	134.33	14.73	24.57	7.13	35.60
2.	Paolum Sali	18.47	144.67	173.33	22.70	37.97	0.73	46.03
3.	Ranjit	28.57	111.33	136.33	16.63	32.83	2.43	62.87
4.	Banga Bandhu (White)	23.57	134.33	151.00	20.40	32.17	0.97	57.50
5.	Uttar Lakshmi	19.93	127.33	170.67	23.77	34.27	3.43	31.23
6.	BBII	15.93	91.33	105.67	17.73	30.13	0.13	42.80
7.	MTU 7029	22.60	117.33	171.67	25.27	39.47	4.73	22.83
8.	Uttar Sona	17.77	142.33	171.33	19.20	32.90	1.87	24.20
Crosses								
9.	CR Sugandh Dhan 909×Paolum Sali	22.53	150.67	156.33	15.43	34.67	6.73	52.73
10.	CR Sugandh Dhan 909×Ranjit	18.67	169.67	180.33	16.17	22.97	7.13	48.60
11.	CR Sugandh Dhan 909×Banga Bandhu (White)	23.13	159.67	188.67	14.73	12.70	5.47	45.60
12.	CR Sugandh Dhan 909×Uttar Lakshmi	20.27	144.67	167.67	15.83	30.30	8.27	53.93
13.	CR Sugandh Dhan 909×BBII	25.37	134.33	173.33	17.27	18.33	6.07	30.73
14.	CR Sugandh Dhan 909×MTU 7029	19.90	154.67	183.33	14.43	28.53	8.93	50.00
15.	CR Sugandh Dhan 909×Uttar Sona	24.77	147.67	168.67	16.67	25.67	7.43	46.10
16.	Paolum Sali×Ranjit	26.97	137.33	146.67	19.77	15.67	1.97	60.13
17.	Paolum Sali×Banga Bandhu (White)	21.57	162.33	210.67	20.57	9.20	1.77	58.03
18.	Paolum Sali×Uttar Lakshmi	26.17	141.33	158.67	19.13	20.47	1.47	62.37
19.	Paolum Sali×BBII	20.37	129.33	179.33	20.27	8.27	2.13	49.93
20.	Paolum Sali×MTU 7029	25.83	139.67	158.33	21.63	17.93	2.77	57.87
21.	Paolum Sali×Uttar Sona	19.30	132.67	187.33	18.97	14.03	1.67	55.90
22.	Ranjit×Banga Bandhu (White)	22.00	174.67	220.33	17.57	11.40	1.23	55.40
23.	Ranjit×Uttar Lakshmi	18.30	179.67	227.33	18.37	25.50	1.03	61.80
24.	Ranjit×BBII	23.17	164.67	192.33	16.93	15.43	0.83	43.77
25.	Ranjit×MTU 7029	19.97	172.33	212.67	18.07	24.63	1.67	59.70
26.	Ranjit×Uttar Sona	25.03	167.33	195.67	16.63	20.63	1.17	52.57
27.	Banga Bandhu (White)×Uttar Lakshmi	27.07	154.33	199.67	21.13	7.43	0.77	65.67
28.	Banga Bandhu (White)×BBII	21.07	144.33	200.33	20.47	5.73	0.93	37.57
29.	Banga Bandhu (White)×MTU 7029	26.30	149.67	178.67	22.07	10.63	1.23	63.03
30.	Banga Bandhu (White)×Uttar Sona	20.13	157.67	167.33	20.87	8.13	0.57	54.13
31.	Uttar Lakshmi×BBII	22.00	79.67	119.33	19.37	13.37	0.33	32.67
32.	Uttar Lakshmi×MTU 7029	18.50	89.67	107.33	20.53	28.33	0.63	58.00
33.	Uttar Lakshmi×Uttar Sona	23.87	99.67	127.33	18.77	24.40	0.43	49.50
34.	BBII×MTU 7029	27.33	119.67	155.67	22.93	19.47	3.23	41.70
35.	BBII×Uttar Sona	21.07	109.33	124.67	21.13	15.53	2.63	38.87
36.	MTU 7029×Uttar Sona	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 productive tillers panicle^{-1}; FLL: Flag leaf length (cm); FLW: Flag leaf width (cm); NPP: No. of panicle panicle^{-1}; PL: Panicle length (cm); NGP: No. of grains panicle^{-1}; NSP: No. of spikelet panicle^{-1}; TW: Test weight (g); DSW: Dry shoot weight (g); PU: Phosphorus uptake (mg plant^{-1}); GY: grain yield (g plant^{-1})

could also be determined based on the mean degree of dominance (>1). According to Kreiger et al. (2010), the overdominance effect could be used for artificial breeding.

The breeder could select certain desirable characteristics without compromising any other desirable characters since both positive and negative alleles are distributed equally (Wricke and Weber, 2010). For every trait, H_1 was greater than H_2, suggesting that the frequency of gene distribution in the parental lines was unequal. This was further supported by the ratio of $H_2/4H_1$ (<0.25), which suggested that the parents' asymmetrical (unbalanced) distribution of genes at the loci implied dominance for every trait. Mather and Jinks (1971) proposed that $(H_1/D)0.5$ at each locus was true only for a major degree of dominance and that the distribution of genes might have an impact on the estimate of the mean degree of dominance.

The h^2/H_2 value was 2.854 for no. of productive tillers, 3.082 for dry shoot weight, and 4.582 for grain yield. The number of genes or gene groups responsible for a given trait was essential for the genetic advancement achieved by selection Gene distribution correlation occurs when complementary gene interactions take place (Liang et al. 1968) or when the ratio of all the genes involved was not equal in terms of quantity and distribution (Jinks and Jones, 1958). All characters except flag leaf length and flag leaf breadth had estimated narrow sense heritability that was high. High heritability suggested that additive genes regulated most of the yield attributes under phosphorus-deficient condition. Flag leaf length and width were influenced by both additive and non-additive genes, with non-additive genes predominating, which aided in selection in the later generations. The majority of the characters showed a negative correlation between the parental mean (Yi) and order of dominance (Vr+Wr), except plant height, the number of productive tillers, flag leaf length, flag leaf width, test grain weight, and dry shoot weight. These results suggested that recessive alleles have a role in increasing the mean values of many characters.

3.3. Graphical approach

The Wr-Vr graph for all the 14 characters were depicted from Figure 1 to Figure 14. The number represented the genotypes as follows 1-CR Sugandh Dhan 909, 2–Paolum Sali, 3–Ranjit, 4–Banga Bandhu (white), 5–Uttar Lakshmi, 6–BBII, 7-MTU 7029 and 8–Uttar Sona for all the graphs.

3.4. Days to 50% flowering

For days up to 50% flowering, the regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crossing the Wr axis was above the origin (intercept=59.16), suggesting that partial dominance was influencing this trait (Figure 1). Similar findings were also observed by Ganapati et al. (2020). The regression coefficient (-0.247) was low and negative. MTU 7029 had a higher dominant gene, followed by Paolum Sali and Ranjit, whereas Uttar Lakshmi had a higher number of recessive alleles. The intermediate allele belongs to CR Sugandh Dhan 909 and Uttar Sona. Given that the gene was positioned away from the regression line, the genotypes Banga Bandhu (White) and BBII might have an inter-allelic interaction gene.

Table 2: Analysis of variance of morphological characters for parents and crosses under phosphorus-deficient condition by Hayman's approach

Sources of variation	df	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 plant^{-1}
Replication	2	11.731	3.009	17.859	1.083	0.030	0.007	0.065
Treatment	35	459.380**	492.733**	1003.046**	109.162**	20.077**	0.175**	23.451**
a	7	277.381**	298.255**	4135.527**	366.229**	47.312**	0.360**	66.721**
b	28	504.880**	541.353**	219.926**	44.895*	13.268**	0.129*	12.633**
b_1	1	79.636*	0.032*	622.032**	644.292**	8149**	0.010*	69.001**
b_2	7	349.831**	422.438**	192.529**	69.762**	39.809**	0.211*	20.701**
b_3	20	580.409**	610.039**	209.410**	6.222*	4.235*	0.107**	6.990**
a×Block	14	7.288**	11.912**	19.408**	0.321*	0.296**	0.003*	0.150
b×Block	56	8.402**	6.724**	13.739*	0.381*	0.403*	0.003*	0.389**
b_1×Block	2	3.501*	5.479**	13.148*	1.542*	0.107	0.003**	0.703*
b_2×Block	14	8.388**	11.084**	15.211*	0.383*	0.421*	0.002	0.356**
b_3×Block	40	8.652*	5.260*	13.254*	0.322*	0.412*	0.004**	0.385*
Residuals	70	8.179	7.762	14.873	0.369	0.382	0.003	0.341

Table 2: Continue...

Sources of variation	df	Panicle length (cm)	No. of grains panicle^{-1}	No. of spikelets panicle^{-1}	Test weight (g)	Dry shoot weight (g plant^{-1})	Phosphorus uptake (mg plant^{-1})	Grain yield (g plant^{-1})
Replication	2	0.426	3.028	20.083	0.381	0.350	0.014	0.387
Treatment	35	31.967**	1868.571**	2737.760**	22.265**	274.519**	19.826**	390.733**
a	7	15.831**	3784.771**	3195.083**	80.894**	392.412**	80.201**	834.005**
b	28	36.001**	1389.521**	2623.429**	7.608**	245.046**	4.733**	279.915**
b_1	1	26.349**	6675.482**	8415.006**	26.481**	3903.750**	1.357**	2314.744**
b_2	7	47.503**	2458.711**	4107.212**	11.846**	294.897**	12.416**	655.309**
b_3	20	32.458**	751.007**	1814.525**	5.181*	44.663**	2.213*	46.786**
a×Block	14	0.580*	12.993**	12.140**	0.056	0.342*	0.014*	1.306**
b×Block	56	0.343**	9.072*	23.521**	0.187*	0.402**	0.011**	1.836**
b_1×Block	2	0.962**	5.669**	7.685	0.254*	0.594*	0.000	1.168**
b_2×Block	14	0.298*	6.989	26.310**	0.144*	0.612*	0.013**	1.978*
b_3×Block	40	0.327**	9.971*	23.337**	0.199**	0.318**	0.011**	1.819**
Residuals	70	0.390	9.856	21.245	0.161	0.390	0.012	1.730

*, ** Significant at p=0.05 and p=0.01 levels of probability, respectively

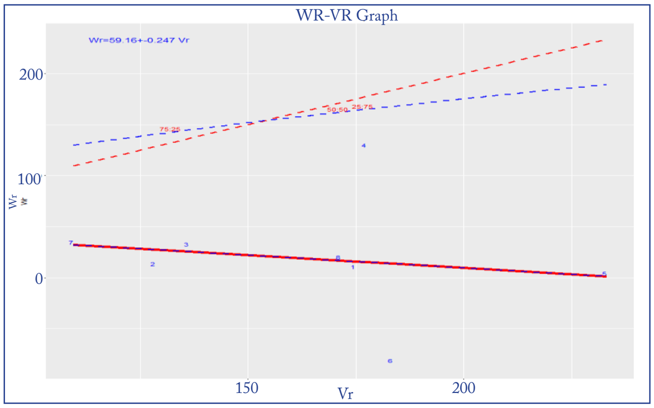

Figure 1: Vr-Wr graph of days to 50% flowering (Wr=59.16+ -0.247 Vr)

3.5. *Days to 100% flowering*

For days to 100% flowering, the regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crossing the Wr axis was above the origin (intercept=88.419), suggesting that this trait was under the influence of partial dominance (Figure 2). The regression coefficient (-0.385) was a low and negative value. MTU 7029 was the genotype with the most dominant gene, followed by Paolum Sali and Ranjit, while Uttar Lakshmi had the most recessive alleles. The intermediate allele belonged to CR Sugandh Dhan 909 and Uttar Sona. Given that the gene was positioned away from the regression line, the genotypes Banga Bandhu (White) and BBII might have an inter-allelic interaction gene.

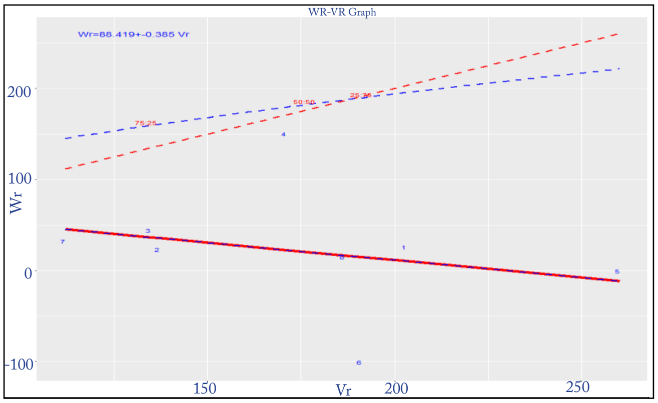

Figure 2: Vr-Wr graph of days to 100% flowering (Wr= 88.419+-0.365 Vr)

3.6. *Plant height (cm)*

For plant height, the array variance (Vr) with the unit slope across the Wr axis and the regression line for the parent-offspring covariance (Wr) array was above the origin (intercept=116.111), suggesting partial dominance was influencing this trait (Figure 3). The regression coefficient (0.926) was a very high value. The genotypes Uttar Lakshmi, BBII, MTU 7029 Uttar sona, and Ranjit had more dominant genes, while Paolum Sali had more recessive alleles. An intermediate allele was present in the parents Banga Bandhu (White) and CR Sugandh Dhan 909.

3.7. *No. of productive tillers plant^{-1}*

The number of productive tillers plant^{-1}, the regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crossing the Wr

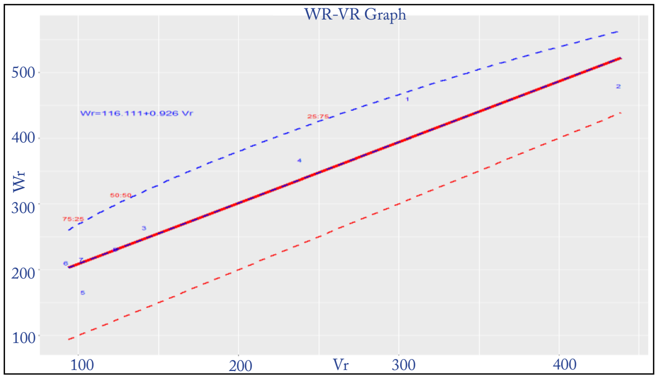

Figure 3: Vr-Wr graph of plant height (cm) (Wr=116.111+0.926 Vr)

axis was above the origin (intercept=5.576), suggesting that partial dominance was marginally influencing this feature (Figure 4). Similar results for obtaining partial dominance of panicle length in rice were also obtained by Akram et al. (2007). The regression coefficient (0.774) was almost at a high value. The BBII genotype had a higher dominant gene, followed by Uttar Sona, whereas the recessive alleles were more prevalent in CR Sugandh Dhan 9090 and Uttar Lakshmi. An intermediate allele was present in the parents MTU 7029, Banga Bandhu (White), and Ranjit.

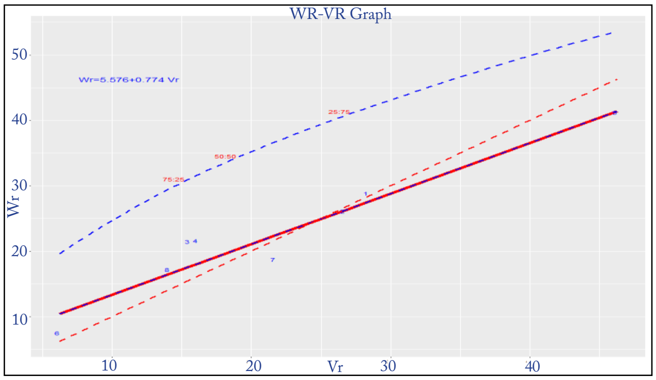

Figure 4: Vr-Wr graph of no. productive tillers plant^{-1} (Wr=5.575+0.774 Vr)

3.8. *Flag leaf length (cm)*

The regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crossing the Wr axis was below the origin (intercept=-0.49) for flag leaf length, indicating that overdominance was only slightly impacting this feature (Figure 5). The regression coefficient was nearly at a high value of 1.284. CR Sugandh Dhan 909, Uttar Sona, BBII, and Paolum Sali possessed more dominant gene whereas MTU 7029 had more recessive genes. Ranit, Banga Bandhu (white) and Uttar Lakshmi exhibited intermediate alleles.

3.9. *Flag leaf width (cm)*

Flag leaf length was shown to be influenced by overdominance, as indicated by the regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crossing the Wr axis being above the origin (intercept=-0.027) (Figure 6). The regression coefficient is remarkably high at 0.913. Banga Bandhu (White) had more dominant genes, Uttar Lakshmi had more recessive alleles, and Paolum Sali had more recessive alleles. The parents of the intermediate allele were BBII and CR Sugandh Dhan 909. The genotypes Uttar Sona and Ranjit might include genes with inter-allelic interactions.

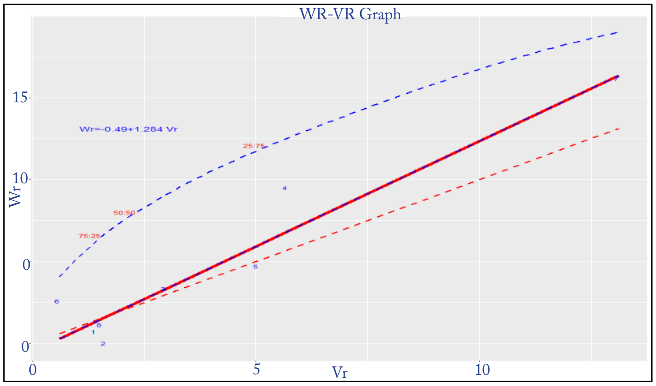

Figure 5: Vr-Wr graph of flag leaf length (cm) (Wr=0.49+1.284 Vr)

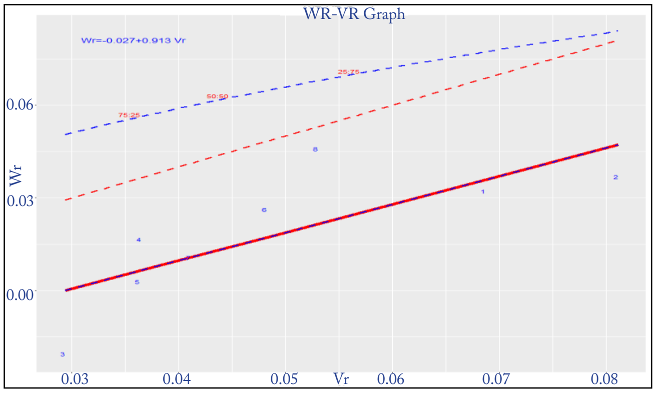

Figure 6: Vr-Wr graph of fFlag leaf width (cm) (Wr=-0.027+0.913 Vr)

3.10. *No. of panicles plant^{-1}*

The regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crosses the Wr axis was above the origin (intercept=-0.825) for panicles plant^{-1} indicating that this trait was slightly under the influence of over dominance (Figure 7). Similar results of over-dominance by no. of panicle^{-1} were also reported by Luo et al. (2001). The regression coefficient (0.913) was exceptionally high. Paolum Sali had more recessive alleles, while Uttar Lakshmi had more dominant genes, followed by Banga Bandhu (White). The intermediate allele belongs to CR Sugandh Dhan 909 and BBII, the parents. Genes with inter-allelic

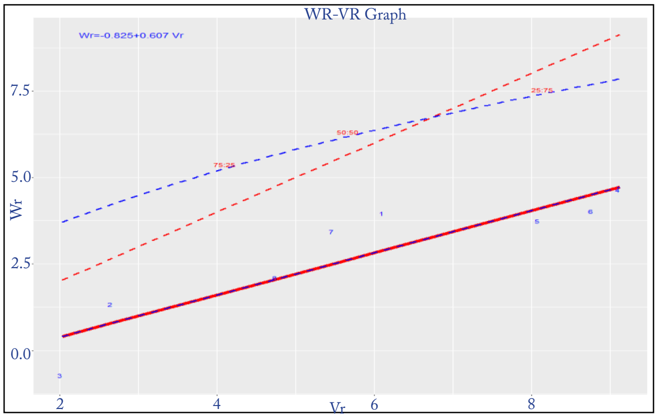

Figure 7: Vr-Wr graph of no. of panicles plant^{-1} (Wr=-0.825+0.607 Vr)

interactions might be present in the genotypes Uttar Sona and Ranjit.

3.11. Panicle length (cm)

The regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crosses the Wr axis was above the origin (intercept=2.915) for panicle length indicating partial dominance of this character (Figure 8). Similar results

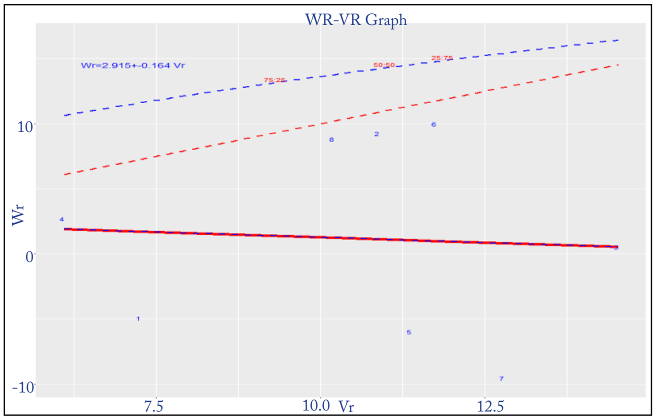

Figure 8: Vr-Wr graph of panicle length (cm) (Wr=2.915+-0.164 Vr)

Table 3: Estimation of genetic components under phosphorus-deficient condition

Components	DFF	DHF	PH	NPT
E (Estimate±SE)	8.179±18.60*	7.762±23.13*	14.873±9.06*	0.369±0.96*
Additive gene effects (D)	145.343±55.81*	180.443±69.40	708.648±27.18*	61.692±2.88*
F_r mean (F)	220.861±131.88*	279.513±164.00*	240.970±64.24*	33.426±6.81*
Non-additive gene effect (H_1)	714.615±128.31*	779.665±159.55*	275.474±62.50*	58.503±6.62*
Dominat or epistatic gene effect (H_2)	611.427±111.63*	653.475±138.81*	226.464±54.37*	36.979±5.76*
h^2	9.487±74.86*	0.000±93.09*	95.545±36.46*	105.543±3.86*
Mean degree of dominance $(H_1/D)^{0.5}$	2.217	2.079	0.623	0.974
Prop. of genes w/+ or -effects in par. (H_2/4H)	0.214	0.210	0.206	0.158
Prop. of dominant & reces. genes in par. (KD/KR)	2.043	2.188	1.750	1.771
r between Wr+Vr and Yr	-0.187	-0.139	0.652	0.778
Pred. for meas. of comp. dom. and res. Parent	0.035	0.019	0.425	0.605
No. of grps. w c-1 control char and exh. dom.	0.016	0.000	0.422	2.854
Additive variance	13.835	13.560	258.345	24.895
Phenotypic variance	174.870	184.690	329.833	34.509
Genotypic variance	166.691	176.929	314.961	34.140
Heritability in narrow sense	0.079	0.073	0.783	0.721
Broad-sense heritability	0.953	0.958	0.955	0.989
Mean covariance of additive and dominance effects	220.861	279.513	240.970	33.426
Intercept of regression line	59.160	88.419	116.111	5.576
Variance for components of variation	269.253	281.961	657.023	7.385
t_2	2.217	2.079	0.623	0.974
B	0.214	0.210	0.206	0.158
SE(b)	2.043	2.188	1.750	1.771
H_0:b=0	-0.187*	-0.139*	0.652*	0.778*
H_0:b=1	0.035	0.019	0.425	0.605

Table 3: Continue...

Components	FLL	FLW	PPP
E (Estimate±SE)	0.382±0.48*	0.003±0.00*	0.341±0.32*
Additive gene effects (D)	27.194±1.46*	0.084±0.01*	6.403±0.96*
F$_r$ mean (F)	35.964±3.45*	0.096±0.02*	1.974±2.29*
Non-additive gene effect (H$_1$)	23.936±3.36*	0.203±0.02*	18.350±2.22*
Dominat or epistatic gene effect (H$_2$)	11.781±2.92*	0.139±0.02*	12.137±1.93**
h^2	1.170±1.96*	0.000±0.01*	11.171±1.30*
Mean degree of dominance (H$_1$/D)$^{0.5}$	0.938	1.556	1.693
Prop. of genes w/+ or -effects in par. (H$_2$/4H)	0.123	0.172	0.165
Prop. of dominant & reces. genes in par. (KD/KR)	5.776	2.177	1.200
r between Wr+Vr and Yr	0.549	0.260	-0.810
Pred. for meas. of comp. dom. and res. Parent	0.301	0.068	0.656
No. of grps. w c-1 control char and exh. dom.	0.099	0.001	0.920
Additive variance	1.692	0.025	5.321
Phenotypic variance	5.019	0.063	8.697
Genotypic variance	4.637	0.060	8.356
Heritability in narrow sense	0.337	0.400	0.612
Broad-sense heritability	0.924	0.949	0.961
Mean covariance of additive and dominance effects	35.964	0.096	1.974
Intercept of regression line	-0.490	-0.027	-0.825
Variance for components of variation	1.903	2.100	0.835
t$_2$	0.938	1.556	1.693
B	0.123	0.172	0.165
SE(b)	5.776	2.177	1.200
H$_0$:b=0	0.549*	0.260*	-0.810*
H$_0$:b=1	0.301	0.068	0.656

Components	PL	GPP	SPP	TGW
E (Estimate±SE)	0.390±2.07*	9.856±85.54*	21.245±127.31*	0.161±0.42*
Additive gene effects (D)	18.204±6.21*	299.491±56.64*	588.626±381.93*	13.297±1.25*
F$_r$ mean (F)	31.895±14.67*	355.782±06.34*	1224.76 0±902.47*	6.060±3.02*
Non-additive gene effect (H$_1$)	55.286±14.28*	2147.526±34.27*	4034.270±878.00*	11.371±2.94*
Dominat or epistatic gene effect (H$_2$)	40.734±12.42*	1386.571±13.29*	2766.700±763.86*	7.790±2.55*
h^2	4.152±8.33*	1090.884±11.29*	1371.292±512.28*	4.274±1.71*
Mean degree of dominance (H$_1$/D)0.5	1.743	2.678	2.618	0.925
Prop. of genes w/+ or -effects in par. (H$_2$/4H)	0.184	0.161	0.171	0.171
Prop. of dominant & reces. genes in par. (KD/KR)	3.022	1.570	2.319	1.654
E (Estimate±SE)	-0.544	-0.339	-0.257	0.867
Additive gene effects (D)	0.296	0.115	0.066	0.752
No. of grps. w c-1 control char & exh. dom.	0.102	0.787	0.496	0.549
Additive variance	0.431	352.332	315.718	5.409
Phenotypic variance	11.004	708.831	1028.638	7.517
Genotypic variance	10.614	698.975	1007.393	7.356
Heritability in narrow sense	0.039	0.497	0.307	0.720

Table 3: Continue...

Components	PL	GPP	SPP	TGW
Broad-sense heritability	0.965	0.986	0.979	0.979
Mean covariance of additive and dominance effects	31.895	355.782	1224.760	6.060
Intercept of regression line	2.915	21.757	14.375	1.244
Variance for components of variation	34.304	548.387	164.907	1.455
t_2	1.743	2.678	2.618	0.925
B	0.184	0.161	0.171	0.171
SE(b)	3.022	1.570	2.319	1.654
H_0:b=0	-0.544*	-0.339*	-0.257*	0.867*
H_0:b=1	0.296	0.115	0.066	0.752

Components	DSW	PU	GY
E (Estimate±SE)	0.390±6.57*	0.012±0.28*	1.730±8.26*
Additive gene effects (D)	20.775±19.73*	5.495±0.85*	214.377±24.79*
F_r mean (F)	34.193±46.62*	0.000±2.02*	292.365±58.59*
Non-additive gene effect (H_1)	299.621±45.35*	8.578±1.96*	443.110±57.00*
Dominat or epistatic gene effect (H_2)	207.758±39.75*	4.707±1.71*	239.623±49.59*
h^2	640.289±26.46*	0.218±1.14*	379.006±33.25*
Mean degree of dominance (H_1/D)0.5	3.798	1.249	1.438
Prop. of genes w/+ or -effects in par. (H_2/4H)	0.173	0.137	0.135
Prop. of dominant & reces. genes in par. (KD/KR)	1.553	1.000	2.804
E (Estimate±SE)	0.656	-0.131	-0.756
Additive gene effects (D)	0.431	0.017	0.571
No. of grps. w c-1 control char & exh. dom.	3.082	0.046	1.582
Additive variance	39.222	4.683	62.749
Phenotypic variance	91.551	5.872	124.385
Genotypic variance	91.162	5.860	122.655
Heritability in narrow sense	0.428	0.798	0.504
Broad-sense heritability	0.996	0.998	0.986
Mean covariance of additive and dominance effects	34.193	-3.397	292.365
Intercept of regression line	5.080	1.493	-26.862
Variance for components of variation	346.028	0.651	546.507
t_2	3.798	1.249	1.438
B	0.173	0.137	0.135
SE(b)	1.553	1.000	2.804
H_0:b=0	0.656*	-0.131*	-0.756*
H_0:b=1	0.431	0.017	0.571

Wr: Covariance between families within the ith array; Vr: The variance among family (F_1) means within an array; Yr: Mean parental value; *significant at $p<0.05$, DFF: Days to 50% of flowering; DHF: Days to 100% of flowering; PH: Plant height (cm); NPT: No. of productive tillers plant^{-1}; FLL: Flag leaf length (cm); FLW: Flag leaf width (cm); NPP: No. of panicle plant^{-1}; PL: Panicle length (cm); NGP: No. of grains panicle^{-1}; NSP: No. of spikelet panicle^{-1}; TW: Test weight (g); DSW: Dry shoot weight (g); PU: Phosphorus uptake (mg plant^{-1}); GY: Grain yield (g plant^{-1})

for obtaining partial dominance of panicle length in rice were also obtained by Akram et al. (2007). The regression coefficient (-0.164) was small and negative. The genotype Banga Bandhu (White) possessed a more dominant gene and Ranjit possessed more recessive alleles. The fact that other genotypes were positioned outside of the shortened region suggested that these genotypes might contain genes that interacted between alleles.

3.12. *No. of grains plant^{-1}*

For grains panicle^{-1} was under the impact of partial dominance, as indicated by the regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope across the Wr axis being above the origin (intercept=21.757) (Figure 9). The regression coefficient is nearly at a high value of 0.774. The predominant gene for the BBII genotype was higher in Uttar Sona and CR Sugandh Dhan 9090, while the recessive alleles were more prevalent in Uttar Lakshmi and Uttar Sugandh Dhan 9090. The parents of MTU 7029, Banga Bandhu (White), and Ranjit have an intermediate allele.

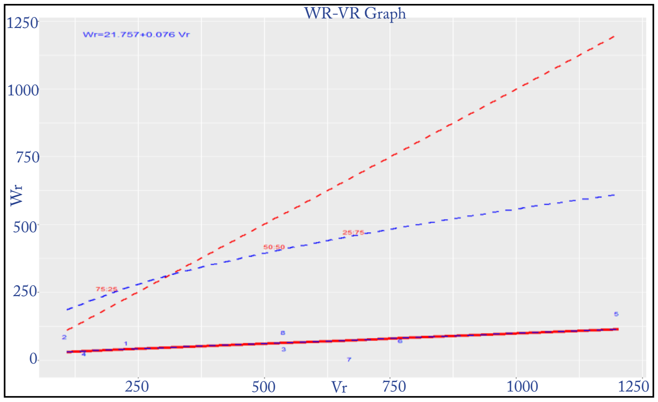

Figure 9: Vr-Wr graph of no. of grains panicle^{-1} (Wr=21.757+0.076 Vr)

3.13. *No. of spikelets plant^{-1}*

The array variance (Vr) with the unit slope crossing the Wr axis and the regression line for the array of parent-offspring covariance (Wr) were above the origin (intercept=14.375) for the number of spikelets panicle^{-1}, showing partial dominance of this trait (Figure 10). The regression coefficient was negative and modest (-0.027). In the genotype CR Sugandh Dhan 909, Uttar Lakshmi had more recessive alleles, while Paolum Sali, Banga Bandhu (White), and Uttar Sona had more dominant genes. The intermediate allele was associated with BBII, Ranjit, and MTU 7029.

3.14. *Test weight (g)*

The regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crosses the Wr axis was above the origin (intercept=1.244) for test weight indicating that this trait was under the influence of partial dominance (Figure 11). The regression coefficient of 0.824 was high. Whereas MTU 7029 had more recessive alleles, the Ranjit genotype had more dominant genes. An intermediate allele was present in the parents Paolum Sali, BBII, Uttar Lakshmi, and Banga Bandhu (White). There might be a gene with inter-allelic interaction in CR Sugandh Dhan 909.

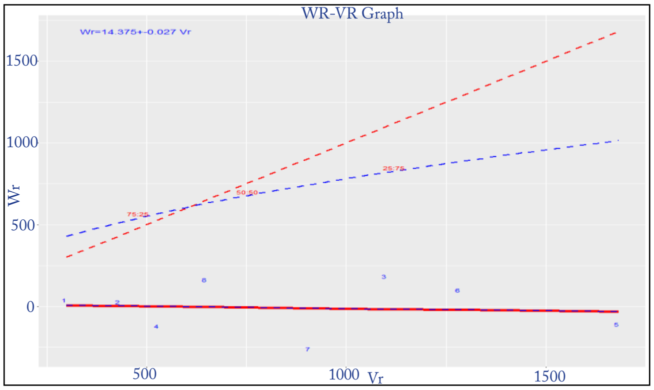

Figure 10: Vr-Wr graph of no. of spikelets panicle^{-1} (Wr=14.375+0.027 Vr)

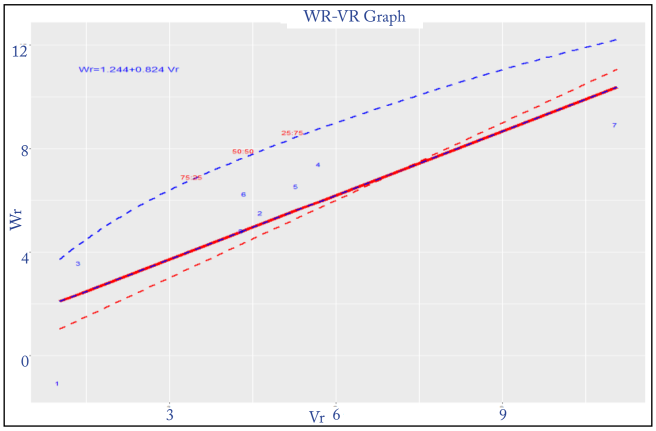

Figure 11: Vr-Wr graph of test weight (g) (Wr=1.244+0.824 Vr)

3.15. *Dry shoot weight (mg plant^{-1})*

The dry shoot weight array's regression line (intercept=5.08) for the parent-offspring covariance (Wr) array on the array variance (Vr) with the unit slope crossing the Wr axis was above the origin, suggesting partial dominance of this feature (Figure 12). The regression coefficient is negative and modest, at -0.044. After BBII, the genotypes Paolum Sali and Ranjit had more recessive alleles and the genotype CR Sugandh Dhan 909 had more dominant genes. The parents of MTU 7029, Uttar Sona, Banga Bandhu (White), and Uttar Lakshmi carry an intermediate allele.

3.16. *Phosphorus uptake (mg plant^{-1})*

The regression line for the array of parent-offspring

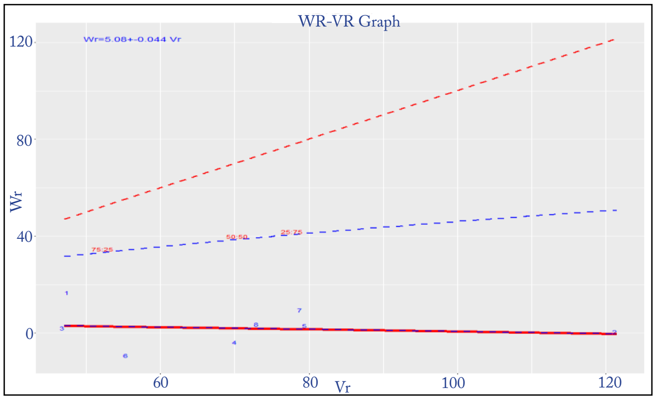

Figure 12: Vr-Wr graph of dry shoot weight (g) (Wr=5.08+-0.044 Vr)

covariance (Wr) on the array variance (Vr) with the unit slope crosses the Wr axis was above the origin (intercept=1.493), which was on par with unity for phosphorus uptake indicating that this trait was slightly under the influence of partial dominance (Figure 13). The regression coefficient was low (0.481). The genotype CR Sugandh Dhan 909 possessed a more dominant gene followed by Banga Bandhu (White) whereas Uttar Lakshmi and MTU 7029 possessed more recessive alleles. The parents Paolum Sali, BBII, Ranjit, and Uttar Sona have an intermediate allele.

3.17. Grain yield (g plant^{-1})

Grain yield was shown to be under the impact of overdominance when the regression line for the array of parent-offspring covariance (Wr) on the array variance (Vr) with the unit slope crosses the Wr axis was below the origin (intercept=-26.862) indicating over-dominance of this character (Figure 14). Zhou et al. (2012) quoted that the over-dominance of grain yield might be due to pseudo-overdominance but according to Luo et al. (2001), there was no proof that the over-dominant QTL for grain yield originated from pseudo-overdominance resulting from the repulsive linkage of totally or partially dominant QTL for yield components. The regression coefficient (0.663) was almost excessively high. Paolum Sali genotype had a more dominant gene than Ranjit, BBII, and CR Sugandh Dhan 9090, while MTU 7029 and Uttar Lakshmi genotypes had more recessive alleles. While Banga Bandhu (White) was positioned distant from the regression line, suggesting that this genotype might contain a gene with inter-allelic interaction, the parent Uttar Sona possesses an intermediate allele.

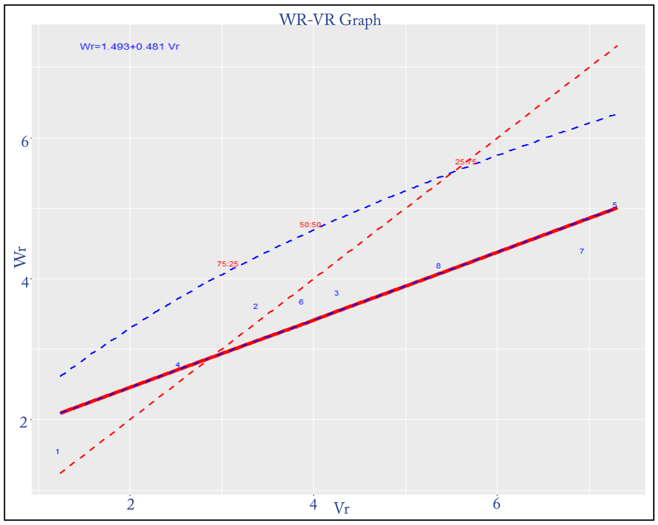

Figure 13: Vr-Wr graph of phosphorus uptake (mg plant^{-1}) (Wr=1.493+0.491 Vr)

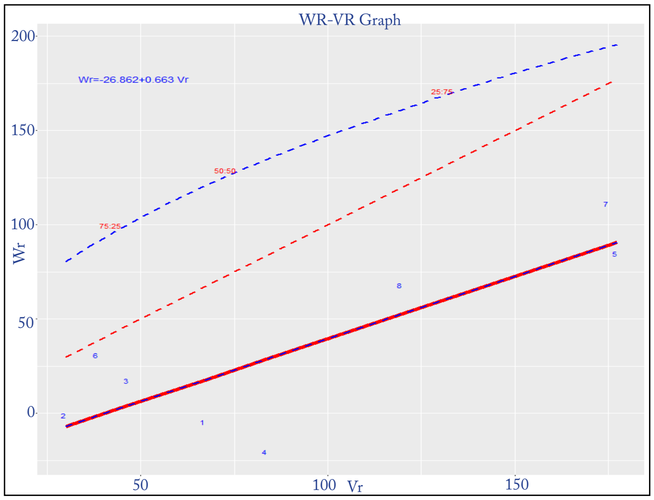

Figure 14: Vr-Wr graph of grain yield (g plant^{-1}) (Wr=-26.862+0.663 Vr)

The main genetic foundation of heterosis in rice appeared to be overdominance and epistasis rather than dominance, according to observations made by Li et al. (2001). According to Zhuang et al. (2001), over-dominance was crucial for the genetic regulation of heterosis in rice. Therefore, exploiting the characters such as flag leaf length, flag leaf width, no. of panicle plant^{-1} and grain yield could result in more positive heterosis in rice improvement programs under phosphorus-deficient condition.

The numerical approach showed overdominance for plant height, no. of productive tillers, flag leaf length, and test weight whereas in the graphical approach flag leaf length, flag leaf width, no. of panicles plant^{-1}, and grain yield exhibited over dominance. Remaining all other characters displayed partial dominance. Such contradictory results were also obtained by Sharma and Jaiswal (2021). According to Comstock and Robinson (1952), the appearance of over-dominance might not be regarded as an indicator of real over-dominance since the degree of dominance might be skewed by linkage, epistasis, or both.

Most of the characters exhibited a predominance of incomplete dominance except for flag leaf length, flag leaf width, no. of panicles^{-1}, and grain yield. The prevalence of additive gene action for these characters indicated that selection for improving rice production through yield components under phosphorus-deficient condition might be postponed segregating populations.

4. CONCLUSION

The eight parents and their 28 crosses under phosphorus-deficient conditions exhibited more dominant alleles than recessive alleles. Additive gene effects (D) were significant, suggesting early-generation fixability. However, higher non-additive effects (H1>D) for traits like flag leaf length, width, panicles per plant, and grain yield indicated overdominance. CR Sugandh Dhan 909 exhibited dominance for phosphorus uptake, while Paolum Sali for grain yield. Genotypes like MTU 7029 and Banga Bandhu (White) exhibited balanced allele combinations.

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