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Generation mean analysis for bacterial blight resistance and yield traits in rice

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Abstract
Profiling genetic architecture of quantitative traits like yield and contributing traits is essential for success of any breeding Programme. Genetic components of variation are key factors determines fate of any crop improvement program. Assessment of genetic component of variation is imperative in maximizing genetic gain with precision. This study revealed the existence of highest number of genes for increasing breeding value, additive (d) effect and dominant × dominant (l) gene interaction were the only significant portion of gene controlling grain yield per plant of the rice and spikelet fertility of plants. The additive and dominance gene effects were found important in controlling bacterial leaf blight disease reaction. The plus sign in the additive gene effect implies that HUR 917 contributes positively to the trait as compared to IRBB66 and *vice versa*.

Keywords: Generation mean analysis, scaling test, epistatic, gene action

Introduction
Rice (*Oryza sativa* L.) is major food crop in the world grown under various regions and ecosystems. It covers around half of the area and approximately 90.4% of the world's rice production for over 2.7 billion populations (Salim *et al.*, 2003; Cantrell and Hettel, 2004) [27, 3]. Besides, it generates employment for over one billion people directly/indirectly involved in the venture (Dat, 2004) [6]. In India, rice has played substantial role in realization of 'Green Revolution', covers largest area among cereals (44.6 mha; 23.3% of gross cropped area of the country) and ranks second in production next to China (Verma *et al*, 2016). However, under dynamic demographic (8.5 billion till 2030) and climatic scenario meeting world food demand (about 40% more rice) is challenging, needs further exhaustive breeding attention in rice (Gurdev, 2006) [10]. Nonetheless, the water scarcity, decrease in arable land, the constant battle against the new emerging pathogens and pest and possible adverse effects from climate change going to be great challenges for rice breeder and agriculture scientists.
Genetic improvement depends primarily on the parental selection and effectiveness of selection among progenies that differ in genetic value. The additive and dominant effects and their interactions are reported to be associated with breeding value. Genetic analysis using generation mean analysis (GMA) has been used to estimate the gene actions controlling the quantitative traits, and knowledge of additive, dominance and epistatic effects which are prerequisite in designing the most appropriate breeding strategies for substantial genetic gain enhancement in rice. It is a simple and very effective technique for estimating gene effects for polygenic traits, able to partitioned/estimate total epistatic/interaction gene effects into additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) effects.

Materials and Methods
This study was conducted at research Farm of Institute of Agricultural Sciences, BHU, Varanasi, Uttar Pradesh and research Fram of ICAR-NRRI, Cuttack during Kharif 2016 to Rabi 2017-18. The experimental site was fertile alluvial loam supplemented with fertilizer dose of 120 kg N, 60 kg P_2O_5 and 40 kg K_2O per hectare at both season and locations.
The *indica* rice cultivars HUR-917 and IRBB66 were sown with 7 days intervals under raised nursery bed and transplanted with 25 days old healthy seedling with same time staggering. The F1 crosses were generated between BB susceptible rice variety HUR-917 and BB donor parent IRBB66 (*Xa21, xa13, Xa7, xa5* and *Xa4*) where HUR-917 used as female and IRBB 66 as

male. During Rabi-2017-18, total 150 F1 seeds were sown along with parents, F2, BC1 and BC2 generation with three replications in RBD design with normal plant spacing (20cm x15 cm) and recommended agro-practices. Observations were recorded for 15 quantitative traits, days to panicle initiation, days to 50% flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grains per panicle, spikelet fertility, test or 1000-seed weight, grain yield per plant, head rice recovery, kernel length, kernel breadth, kernel length/ breadth ratio and disease severity from 5 randomly selected plants from each replication. The pathogenicity test in parents, F_1, F_2 and BC generations was done through leaf-clipping method (Kauffman *et al*., 1973) with 8 different virulent strain of *Xanthomonas oryzae* pv. *Oryzae* maintained at NRRI, Cuttack. Data on pathogenity test were recorded every 24 hours time interval to note the appearance of disease symptoms, and lesion length were measured at 14, 21and 28days after inoculation (DAI) on randomly selected ten plants and five leaves per plant in each generation.

Statistical Analysis

Genic action was analyzed by following scaling test (Mather, 1949 [21] and Hayman and Mather, 1955) [14]. Hayman (1958) [12] and Jinks and Jones (1958) [15] devised the six parameter model for the estimation of various genetic components. Cavalli (1952) [4] gave the method 'Joint scaling test' which includes any combination of families at a time. The 'weighted least square method' developed by Nelder (1960) [24] and Hayman (1960) [13] was used to estimate the parameters m, d and h. Here, the weights are defined as the reciprocal of standard error. From these estimates, the expected generation means were calculated and compared with the observed generation mean values using a χ^2 test. A significant χ^2 value indicates that the model is not adequate and the non-allelic interactions are added in the model.

Result and Discussion

Estimates from scaling tests

The gene action of the traits undertaken in the study were analyzed based on simple additive × dominance model to understand the pattern of the gene action of the target (*Xa21, xa13, xa5*) as well as product profile traits (basic trait of recurrent parent like duration, height, grain dimension and cooking quality and productivity) undertaken in this study (Table-1). The scaling test analysis showed all scale, A, B, C and D were significant for the traits like days to panicle initiation, days to 50% flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grain per panicle, spikelet fertility, grain yield per plant indicates presence of epistasis/non-alleliec interaction in expression of these traits. Whereas, A scale was not-significant for disease severity, kernel breadth, and kernel L/B ratio; scale B was also non-significant for disease severity, kernel length and kernel L/B ratio; scale C was non-significant for test weight, disease severity; and scale D was also non-significant for head rice recovery. All the basic (yield and related) and value added traits (bacterial leaf blight resistance) in the present study were reported significant in either one of the scales or in combination representing the existence of epistatic interactions between the genes involved.

Further, goodness of fit of this model was tested by following chi-square test analysis. The adequacy of simple additive-dominance model suggests the absent of non-allelic interaction effect (epistasis) and means value of different generations depends only on additive × dominance gene interaction or effect of the gene. The chi-squire test analysis revealed that all the 15 traits studied in the cross of HUR-917/IRBB-66 were found significant value which indicates presence of epistatic effect between these traits. The results showed the data does not fit into simple additive × dominance model; role of epistatic is prevalent which is not fit into three parameter model hence data were further subjected to be analyzed under six-parameter model.

Estimation of gene effects based on six generation means

Digenic non-allelic/intergenic/epistatic interaction model with six parameters namely m, d, h, i, j and l revealed that the epistatic interaction model was found adequate to explain the gene action in the traits days to panicle initiation, days to panicle emergence, days to fifty percent flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grain per panicle, spikelets fertility, test weight, grain yield per plant, disease severity, head rice recovery, kernel length, kernel breadth, and kernel L/B ratio. The estimates of gene effect clearly illustrate high variation in the observed traits (Table-1). Mean and additive components for days to panicle initiation, days to panicle emergence, days to fifty percent flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grain per panicle, spikelets fertility, test weight, grain yield per plant, disease severity, head rice recovery, kernel length, kernel breadth, and kernel L/B ratio were highly significant.

The six parameter analysis of cross HUR-917/IRBB-66, revealed the dominance (h) and dominance × dominance (l) gene interaction or effects opposite signs (opposite direction) for the traits *viz*., panicle length, grain yield per plant, disease severity and kernel length indicates duplicate epistasis. The values of most of the traits except panicle length, grain yield per plant, head rice recovery and kernel length shows same sign for dominance (h) and dominance × dominance (l) interaction were fit into complementary epistasis model.

The classification of gene interactions depends on the magnitudes and signs of the estimates of dominance (h) and dominance × dominance (l) gene interaction or effects, when there are many pairs of interacting genes. The sign associated with the estimates of (d) and (h) indicates the parent that concentrates the highest number of genes for increasing the trait. Additive (d) effect and dominant × dominant (l) gene interaction were the only significant portion of gene controlling grain yield per plant of the rice and spikelet fertility of plants. Finally, additive and dominance gene effects were found important in controlling bacterial leaf blight disease reaction. The plus sign in the additive gene effect implies that HUR 917 contributes positively to the trait as compared to IRBB 66 and vice versa. The positive sign for the additive (d) effects was observed in the all studied traits except number of grains per panicle and spikelet fertility (%), while the negative sign for (h) was observed in the traits panicle length, grain yield per plant, disease severity and kernel length (Table-1).

Profiling genetic architecture of quantitative traits like yield and contributing traits is essential for success of any breeding programme. Genetic components of variation are key factors determines fate of any crop improvement program. Assessment of genetic component of variation is imperative in maximizing genetic gain with precision. The basic biometrical concept for estimation of genetic component of variation

'generation mean analysis' was developed by Hayman (1958) [12] and Jinks and Jones (1958) [15]. The generation mean analysis is a powerful statistical tool for detection of epistasis/non-alleliec interaction among genes using several basic generations' *viz*. parents, their F1, F2 and backcross B1 and B2 of biparental crosses. In addition to additive and dominance gene effects, epistatic effects have great impact towards genotypic mean of any population (Viana, 2000) [31]. These effects define specific additive × additive and additive × dominant epistatic components. As such components are not estimable their relative importance cannot be assessed. These epistatic effects can cause bias in the estimates of the additive and dominance components of the bias depends on the relative values of the epistatic effects, comparatively to deviations d and h, type of prevailing epistatic and direction of dominance.

The mean values of different generations over replications are used for estimation of gene effects. The biometrical analysis consists of two main steps *viz*. testing the model for epistasis and estimation of gene effects. The testing of epistasis (non-alleliec) is very crucial for estimating the different components of genetic variation, hence analyses priortingly before advance estimation for gene effect. The test which determines the presence or absence of non-allelic interactions is known as scaling test.

The information about nature of gene action for complex traits like yield and resistance/tolerant mechanisms are prerequisite in making trait development strategies to achieve maximum genetic gain/ improvement for yield and tolerant/resistant to biotic/abiotic stresses. It provides information on the relative importance of the average effects of the genes (additive effects), dominance effects and effects due to non-allelic genic interactions in determining genotypic values of the individuals and consequently genotypic mean values of families and generations. It is a simple but useful technique for estimating gene effects for polygenic traits; its greatest merit lying in the ability to estimate epistatic gene effects such as additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) effects.

Scaling tests were performed to understand the adequacy of simple additive-dominance model. In the present study, scaling test showed that all A, B, C and D scales were significant for days to panicle initiation, days to 50% flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grain per panicle, spikelet fertility, grain yield per plant indicates presence of epistasis/non-alleliec interaction in expression of these traits. Whereas, A scale was not-significant for disease severity, kernel breadth, and kernel L/B ratio; scale B was also non-significant for disease severity, kernel length and kernel L/B ratio; scale C was non-significant for test weight, disease severity; and scale D was also non-significant for head rice recovery. Results indicated that the basic traits (yield and related) and value added traits (bacterial leaf blight resistance) in the present study were reported significant in either one of the scales or in combination representing the existence of epistatic interactions between the genes involved.

All the traits related to yield as well as bacterial leaf blight resistance in the present study were significant in either one of the scales or in combination representing the existence of epistatic interactions between the genes involved. Further, goodness of fit of this model was tested by following chi-square test analysis. The adequacy of simple additive-dominance model suggests the absent of non-allelic interaction effect (epistasis) and means value of different generations depends only on additive × dominance gene interaction or effect of the gene. The chi-squire test analysis revealed that all the 15 traits studied in the cross of HUR-917/IRBB-66 were found significant value which indicates presence of epistatic effect between these traits. The generation means involves substantial non-alleliec interaction in the expression of target traits which is also clear that only selective R gene combination reported to be responding R reaction in NILs. This result has full agreement with the findings of Mahalingam and Nadarajan, 2010 [20]; Gnanamalar and Vivekanandan, 2013 [9]; and Kiani, 2013 [17], reported the presence of epitasis for all the characters studied in the combination of TS29 / Basmati-370. The results showed the data does not fit into simple additive × dominance model; role of epistatic is prevalent which is not fit into three parameter model hence data were further subjected to be analyzed under six-parameter model (Hayman, 1958) [12].

Digenic non-allelic/intergenic/epistatic interaction model with six parameters namely m, d, h, i, j and l revealed that the epistatic interaction model was found adequate to explain the gene action in the traits days to panicle initiation, days to panicle emergence, days to fifty percent flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grain per panicle, spikelets fertility, test weight, grain yield per plant, disease severity, head rice recovery, kernel length, kernel breadth, and kernel L/B ratio. The estimates of gene effect clearly illustrate high variation in the observed traits. Mean and additive components for days to panicle initiation, days to panicle emergence, days to fifty percent flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grain per panicle, spikelets fertility, test weight, grain yield per plant, disease severity, head rice recovery, kernel length, kernel breadth, and kernel L/B ratio were highly significant (Murugan and Ganesan 2006) [23].

The six parameter analysis of cross HUR-917/IRBB-66 revealed the dominance (h) and dominance × dominance (l) gene interaction or effects with opposite signs (opposite direction) for the traits *viz*., panicle length, grain yield per plant, disease severity and kernel length indicates duplicate epistasis. These results are in conformity with the earlier reports of Hasib *et al*. (2002) [11], Kiani *et al*. (2013) [17], Magda (2013) [19] and Divya *et al*. (2014) [7] for plant height, number of productive tillers, panicle length, days to first flowering, filled spikelet per panicle, total spikelet per panicle, spikelet fertility, spikelet sterility, test weight, single plant yield and disease incidence. The values of most of the traits except panicle length, grain yield per plant, head rice recovery and kernel length shows same sign for dominance (h) and dominance × dominance (l) interaction were fit into complementary epistasis model. It was reported that gene effects are known to be cross specific and fits into complementary recessive epistasis for grain yield (Azizi *et al*. 2006 [8], Thirugnana Kumar *et al*., 2007 [29], Divya *et al*. 2014) [7].

The classification of gene interactions depends on the magnitudes and signs of the estimates of dominance (h) and dominance × dominance (l) gene interaction or effects, when there are many pairs of interacting genes (Mather and Jinks, 1982) [22]. The sign associated with the estimates of (d) and (h) indicates the parent that concentrates the highest number of genes for increasing the trait. Additive (d) effect and dominant × dominant (l) gene interaction were the only

significant portion of gene controlling grain yield per plant of the rice and spikelet fertility of plants (Asm *et al*. 2012, Gnanamalar *et al*, 2013) [1, 9]. Finally, additive and dominance gene effects were found important in controlling bacterial leaf blight disease reaction. This result has complete agreement with the finding of Divya *et al*. (2014) [7] reported complementary epistatic for number of productive tillers, economic yield, lesion number, infected leaf area and potential disease incidence. The plus sign in the additive gene effect implies that HUR 917 contributes positively to the trait as compared to IRBB66 and vice versa. The positive sign for the additive (d) effects was observed in the all studied traits except the number of grains per panicle and Spikelet fertility (%), while the negative sign for (h) was observed in the traits Panicle length, grain yield per plant, disease severity and kernel length as observed earlier (Paul *et al*., 2003; Cruz *et al*., 2006; Thirugnanakumar *et al*., 2007 [25, 5, 29]; Li *et al*., 2010) [18] which explained dominance genetic effect in yield and disease related traits in rice. On the contrary, Ray and Islam (2008) [26] and Sharifi *et al*. (2011) [28] have reported the importance of additive effects.

Table 1: Scaling test and generation mean analysis for yield and quality traits with disease severity in the parents P_1, P_2 and combinations F_1, F_2, B_1 and B2 of HUR-917 x IRBB66

Traits/ Parameters	Scaling test				Generation mean analysis						$\Sigma\chi^2$	Gene action/ Epistasis
	A	B	C	D	m (Hayman)	d (Hayman)	h (Hayman)	I (Add × Add)	J (Add × Dom)	L (Dom × Dom)		
Days to panicle initiation (days)	10.25 **	-23.45 **	-2.34 **	33.68 **	49.93 **	3.90 **	3.75 **	7.60 **	-7.39	17.71 **	1955.85 **	C
Days to 50% flowering (days)	22.54 **	32.14 **	12.00 **	8.66 **	52.61 **	4.13 **	3.79 **	-1.72 **	2.50 **	85.33 **	1120.45 **	C
Days to maturity (days)	6.47 **	12.80 **	-4.34 **	22.36 **	52.78 **	2.92 **	2.95 **	3.18 **	4.91 **	23.42 **	872.33 **	C
Plant height (cm)	48.00 **	19.65 **	24.32 **	10.60 **	31.07 **	52.59 **	1.78 **	2.81 **	-5.03	1.69 **	1034.27 **	C
Number of ear bearing tillers (No.)	-9.89 **	-24.28 **	15.08 **	8.12 **	1.44 **	54.72 **	37.89 **	24.65 **	13.88 **	24.01 **	1436.02 **	C
Panicle length (cm)	14.00 **	-5.48 **	7.29 **	-22.54 **	11.44 **	27.67 **	-0.42	0.16	-11.64 **	4.88 **	659.25 **	_
Number of grains per panicle	37.26 **	-17.73 **	-25.50 **	-22.52 **	49.21 **	-16.01 **	12.34 **	57.74 **	-2.90	2.17 **	1604.87 **	C
Spikelet fertility (%)	12.41 **	5.91 **	-2.80 **	7.55 **	61.25 **	-4.87 **	3.21 **	-1.62	2.038 **	35.43 **	953.57 **	C
Test or 1000-seed weight (g)	0.83 **	2.44 **	-0.95	3.42 **	14.99 **	1.74 **	3.27 **	1.87 **	11.74 **	22.51 **	715.04 **	C
Grain yield per plant (g)	4.6 **	-8.40 **	3.71 **	2.32 **	5.45 **	22.65 **	-15.55 **	-1.82	18.65 **	17.25 **	142.13 **	D
Head rice recovery (%)	1.32 **	4.21 **	6.08 **	-0.77	12.08 **	1.57 **	10.84 **	3.47 **	-4.87	-1.62	236.85 **	_
Kernel length (mm)	-0.24 **	-0.28	1.25 **	1.57 **	1.22 **	2.85 **	-3.65 **	-1.65 **	-0.31 **	1.86 **	120.82 **	D
Kernel breadth (mm)	0.42	0.08 *	0.10 **	0.09 **	0.25 **	1.62 **	0.68 **	-0.28 **	-0.14	0.87 **	634.21 **	C
Kernel length/ breadth ratio	0.05	-0.11	0.42 **	0.17 **	2.58 **	1.47 **	2.35 **	1.98 **	0.87	1.68 **	56.47 **	C
Disease severity (%)	-1.36	0.59	-0.48	-0.85 **	-14.87 **	18.28 **	-25.10 **	23.42 *	-1.98	-2.44	642.14 **	_

Note: *, ** is significant at 5% and 1% probability level

Conclusion

This study revealed the existence of highest number of genes for increasing breeding value, additive (d) effect and dominant × dominant (l) gene interaction were the only significant portion of gene controlling grain yield per plant of the rice and spikelet fertility of plants. The additive and dominance gene effects were found important in controlling bacterial leaf blight disease reaction. The plus sign in the additive gene effect implies that HUR 917 contributes positively to the trait as compared to IRBB66 and *vice versa*.

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