RESEARCH ARTICLE

Gene interactions and genetics of blast resistance and yield attributes in rice (*Oryza sativa* L.)

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Abstract

Blast disease caused by the pathogen *Pyricularia oryzae* is a serious threat to rice production. Six generations *viz*., P_1, P_2, F_1, F_2, B_1 and B_2 of a cross between blast susceptible high-yielding rice cultivar ADT 43 and resistant near isogenic line (NIL) CT13432-3R, carrying four blast resistance genes *Pi1*, *Pi2*, *Pi33* and *Pi54* in combination were used to study the nature and magnitude of gene action for disease resistance and yield attributes. The epistatic interaction model was found adequate to explain the gene action in most of the traits. The interaction was complementary for number of productive tillers, economic yield, lesion number, infected leaf area and potential disease incidence but duplicate epistasis was observed for the remaining traits. Among the genotypes tested under epiphytotic conditions, gene pyramided lines were highly resistant to blast compared to individuals with single genes indicating that the nonallelic genes have a complementary effect when present together. The information on genetics of various contributing traits of resistance will further aid plant breeders in choosing appropriate breeding strategy for blast resistance and yield enhancement in rice.

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Introduction

Rice (*Oryza sativa* L.) has close relationship with humans for ages and it is the most important staple food worldwide (Khush 2005). Blast disease caused by the fungus *Pyricularia oryzae* is one of the most serious constraints for rice production at the global level. The disease has been reported to destroy rice enough to feed an estimated 60 million people each year (Barman and Chattoo 2005). To avoid the use of chemical measures for the control and management of blast, which are not only harmful to ecology but also uneconomical, plant breeders have achieved significant progress towards the enhancement of host plant resistance albeit with limited success in the development of cultivars with durable resistance which is complicated by the extreme level of variation in the pathogen (Jia 2003). More than 96 blast R genes (Sharma *et al.* 2012) have been described and mapped by previous workers but a limited number of reports are available on the genetics of blast resistance in rice. Resistance of rice varieties to blast is governed mostly by dominant genes, but in few cases recessive genes are also responsible (Padmanabhan *et al.* 1973; Marchetti *et al.* 1987). Both major and minor genes can contribute to durable resistance (Wang *et al.* 1994) against rice blast. This study is focussed on the deployment of blast resistance genes to develop resistant high-yielding varieties and to elucidate the gene action associated with various yield and resistance attributes through generation mean analysis. Information concerning the nature of gene action on complex traits such as yield and resistance mechanisms would be a valuable tool for breeding high-yielding cultivars with disease resistance. In addition, an attempt has been made to estimate various kinds of gene effects through standard biometrical and statistical procedures. Quantitative traits of economic importance are governed by complex interaction mechanisms. Genetics of such traits and knowledge on interactions would help to develop a suitable breeding strategy.

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Keywords. blast; gene action; generation mean analysis; resistance; yield.

Materials and methods

The present research work was conducted at the Centre for Plant Breeding and Genetics (CPBG), Tamil Nadu Agricultural University, Coimbatore during 2009–2012. Field trials and crossing blocks were laid out at the experimental plots of the Paddy Breeding Station (PBS), Centre for Plant Breeding and Genetics (CPBG), Tamil Nadu Agricultural University, Coimbatore (11° 00′ N, 77° 00′ E; 426.72 m above mean sea level (MSL)). The disease reaction was evaluated in Uniform Blast Nursery in two hotspots, one at PBS, Coimbatore and the other at Hybrid Rice Evaluation Centre, Gudalur (11°30′ N, 76°30′ E; 1117.00 MSL). Parents for this study include a popular rice variety ADT 43 as recurrent parent for the improvement and a blast resistant NIL, CT13432-3R carrying four blast resistance genes *Pi1*, *Pi2*, *Pi33* and *Pi54* in combination as donor parent. ADT 43 is one of the most widely grown cultivars in South India owing to its high yield, short duration and acceptable grain quality. It also showed tolerance to various biotic stresses *viz*., green leaf hopper, brown plant hopper, shoot borer (SB) and gall midge. Near isogenic line (NIL) CT13432-3R pyramided with four blast resistance genes (*Pi1*, *Pi2*, *Pi33* and *Pi54*) in the background of a susceptible *indica* variety CO 39 was used as the donor parent and has resistance against nine lineages of blast pathogen (Mackill and Bonman 1992; Correa Victoria *et al.* 2002; Yanoria *et al.* 2011).

Crossing programme

The crossing programme included (i) effecting crosses between susceptible and resistant parents, to generate F_1s and (ii) raising F_1s to develop F_2 and backcross progenies (B_1 and B_2) and (iii) evaluation of six generation materials (parents, F_1, F_2, B_1 and B_2) for blast resistance and yield attributes. The breeding strategy is illustrated in figure 1.

During Rabi 2011, six generations of the promising cross ADT 43 × CT13432-3R (P_1, P_2, F_1, F_2, B_1 and B_2) was raised in the open field conditions as well as epiphytotic conditions in the Uniform Blast Nursery. Phenotypic traits were assessed on each individual entry in the segregating generations and observations were recorded for yield and morphological traits like plant height (PH), number of tillers (NOT), number of productive tillers (PRT), leaf length (LL), leaf width (LW), panicle length (PL), days to first flowering (FF), total grains per panicle (TGP), filled grains per panicle (FGP), spikelet fertility (SPF), spikelet sterility (SPS), 100 grain weight (GWT100), single plant yield (SPY), biological yield (BY), dry weight (DWT), economic yield (EY) and harvest index (HI). These lines were also screened for blast resistance contributing traits like leaf blast (LB), lesion number (LN), lesion type (LT), infected leaf area (ILA), potential disease incidence per cent (PDI), seedling vigour (VIG) and blast resistance (RES) adopting standard evaluation system (SES) for rice (IRRI 2002). Study of these component traits to yield and disease resistance, and their phenotypic analysis will aid in understanding the contribution of the introgressed genes in improving these traits in desirable direction. The performance of genotypes was assessed and behaviour of the introgressed blast resistance genes were quantified and analysed through generation mean analysis.

Generation mean analysis

The generation mean analysis was performed according to Hayman (1958) and Jinks and Jones (1958) for the estimation of genetic components of variation, epistasis model and gene effects in two steps (i) testing for epistasis to determine the presence or absence of interallelic interaction and (ii) estimation of gene effects, variances and the type of epistasis involved.

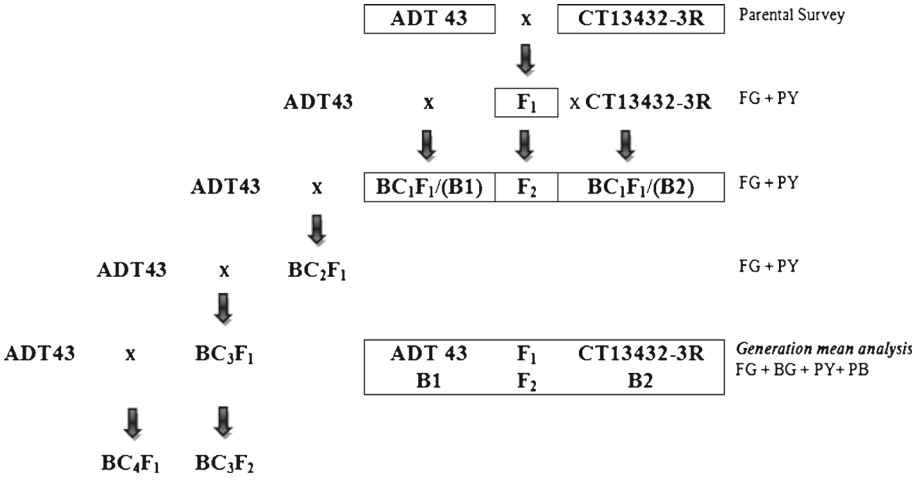

Figure 1. Breeding scheme for generation mean analysis and marker assisted backcross breeding. FG, foreground screening of Pi genes; BG, background screening of recurrent parent genome; PB, phenotyping for blast resistance traits; PY, phenotyping for yield and morphology related traits.

Scaling test

Scaling test for A, B, C and D scales as suggested by Hayman and Mather (1955) and Mather and Jinks (1971) was applied to test the adequacy of simple additive–dominance model. Utilizing the means of different generations, the values of A, B, C and D scales were constructed using the following formulae. $A = 2B_1 - P_1 - F_1$; $B = 2B_2 - P_2 - F_1$; $C = 4F_2 - 2F_1 - P_1 - P_2$; $D = 2F_2 - B_1 - B_2$; where, P_1, P_2, F_1, F_2, B_1 and B_2 are the means of parent 1, parent 2, F_1, F_2 and backcross generations B_1 and B_2, respectively. Utilizing the variance of different generations, the variances of A, B, C and D scales were computed as follows: $V_A = 4VB_1 + VP_1 + VF_1$; $V_B = 4VB_2 + VP_2 + VF_1$; $V_C = 16VF_2 + 4VF_1 + VP_1 + VP_2$; $V_D = 4VF_2 + VB_1 + VB_2$; where, VP_1, VP_2, VF_1, VF_2, VB_1 and VB_2 are the variances of means of the P_1, P_2, F_1, F_2, B_1 and B_2 generations, respectively e.g.,$VP_1 = V(P_1)/n_{P1}$, where $V(P_1)$ and n_{P1} are variances and number of observation of the P_1 generation. The standard errors of A, B, C and D were obtained as square root of the variances VA, VB, VC and VD, respectively and were utilized for testing the significance of the deviations of the respective scales from zero. To test the significance of the scales, the 'Student's *t*' values for each of these quantities were calculated as follows: $t(A) = A/SE(A)$; $t(B) = B/SE(B)$; $t(C) = C/SE(C)$; $t(D) = D/SE(D)$; where standard error (SE) is the square root of respective variance e.g., $SE(A) = (VA)^{1/2}$. The significance of the scales was evaluated using calculated *P* values for respective calculated '*t*' values.

Joint scaling test

Joint scaling test (Cavalli 1952) was conducted which combines several scaling test into one and tests the adequacy of additive–dominance model using a χ^2 test. The following relationship between respective generation mean and genetic effects was calculated by a weighted least square analysis using reciprocal of the respective variance of the generation means as given; $P_1 = m + (d)$; $P_2 = m - (d)$; $F_1 = m + (h)$; $F_2 = m + 1/2\,(h)$; $B_1 = m + 1/2\,(d) + 1/2\,(h)$; $B_2 = m - 1/2\,(d) + 1/2\,(h)$.

Estimation of gene effects using six generation means

The generation means were analysed by the method suggested by Hayman (1958) to provide information on the inheritance of various traits. The generation means were used to estimate the six genetic parameters *viz*., *m*, (*d*), (*h*), (*i*), (*j*) and (*l*) of digenic interaction model representing mean, additive genetic effect, dominance genetic effect, additive × additive gene interaction effect, additive × dominance interaction effect and dominance × dominance gene effects, respectively assuming that no linkage and no higher order gene interaction exists. Considering the generation means as reference values, the above six genetic parameters were calculated following relationship between respective generation mean and genetic effects. $P_1 = m + (d) + (i)$; $P_2 = m - (d) + (i)$; $F_1 = m + (h) + (1)$; $F_2 = m + 1/2\,(h) + 1/4\,(1)$; $B_1 = m + 1/2\,(d) + 1/2\,(h) + 1/4\,(i) + 1/4\,(j) + 1/4\,(1)$; $B_2 = m - 1/2\,(d) + 1/2\,(h) + 1/4\,(i) - 1/4\,(j) + 1/4\,(1)$.

Accordingly, by least squares computation method, the following formulae were used for arriving at different gene effects. Mean $= m = F_2$; additive effect $= (d) = B_1 - B_2$; dominance effect $= (h) = 2B_1 + 2B_2 + F_1 - 4F_2 - 1/2P_1 - 1/2P_2$; additive × additive epistatic effect $= (i) = 2B_1 + 2B_2 - 4F_2$; additive × dominance epistatic effect $= (j) = B_1 - 1/2P_1 - B_2 + 1/2P_2$; dominance × dominance interaction effect $= (l) = P_1 + P_2 + 2F_1 + 4F_2 - 4B_1 - 4B_2$.

The variance of these gene effects involving the variance of means of the generations were calculated as follows: $V_m = VF_2$; $V_d = VB_1 + VB_2$; $V_h = VF_1 + 16VF_2 + 1/4VP_1 + 1/4VP_2 + 4VB_1 + 4VB_2$; $V_i = 4VB_1 + 4VB_2 + 16VF_2$; $V_j = VB_1 + VB_2 + 1/4VP_1 + 1/4VP_2$; $V_l = VP_1 + VP_2 + 4VF_1 + 16VF_2 + 16VB_1 + 16VB_1$.

Square roots of the variance provided respective standard errors. The standard errors were used to calculate the '*t*' values for testing significance of the corresponding gene effects, $t(d) = d/SE(d)$, where $SE(d) = [V_d]^{1/2}$.

Estimation of variance components for different characters

Phenotypic variance is calculated by the variance of the F_2 and environmental variance is estimated from mean variance of the nonsegregating generations (P_1, P_2, and F_1) (Wright 1968). A difference in the variances of the backcrosses (B_1, B_2) from twice the phenotypic (F_2) variance gives additive variance, assuming absence of linkage and environment interaction (Warner 1952). The information is used to estimate the broad and narrow sense heritability. Estimates of phenotypic (V_P), environmental (V_E), genotypic (V_G), additive (V_A) and dominance (V_D) variances from generation variances are obtained using the following formulae (Warner 1952; Wright 1968).

$$V_P = V(F_2);$$

$$V_E = \left\{V(P_1) + V(P_2) + 2^*V(F_1)\right\}/4;$$

$$V_G = V_P - V_E;$$

$$V_A = 2 \times V(F_2) - \{V(B_1) + V(B_2)\};$$

$$V_D = V_G - V_A;$$

where $V(P_1)$, $V(P_2)$, $V(F_1)$, $V(F_2)$, $V(B_1)$ and $V(B_2)$ are different generation variances.

Results and discussion

Progenies of the cross between ADT 43 × CT13432-3R were advanced to F_2, B_1(ADT 43 × F_1) and B_2 (CT13432-3R × F_1) to isolate high yielding segregants with introgressed blast resistance genes. To elucidate the nature of gene

action for yield traits and blast resistance, generation mean analysis was carried out using the data recorded from six generations of the above cross combination. The mean performances of the six generation materials P_1, P_2, F_1, F_2, B_1 and B_2 for 20 quantitative traits are presented in table 1. The values of individual scaling tests and estimates of gene effects *viz*., *m, d, h, i, j* and *l* for different characters in this cross were estimated (tables 2 and 3). Information on these aspects in genetic architecture of the various traits is essential for proper selection of parents and breeding methodology. Epistatic gene effects were not detected for biological yield (BY), dry weight (DWT) and harvest index (HI) and hence, these values are not included in table 3 as there is no epistasis identified from scaling test.

Plant height in F_1 was higher than both the parents, ADT 43 and CT 13432-3R, but in the three segregating populations (F_2, B_1 and B_2), plants were slightly taller than non-segregating generations. F_1 hybrid recorded maximum number of tillers per plant. However, leaf length was intermediate when compared with both parents. Panicle length among all generation materials varied from 20.86 to 24.76 cm with F_1 manifesting the highest value. F_1 flowered earlier compared with the high-yielding parent ADT 43 which was desirable in further selections. Filled grains per panicle showed a range of values across the generations studied. However, F_2 segregants possessed less filled grains per panicle than F_1s while further improvement in filled grains per panicles was noticed in the backcross progenies. The F_1 showed narrow improvement in spikelet fertility reflecting positively in spikelet sterility when compared with the parent ADT 43 correlating well to the means and scaling tests as it is a derived trait. Because of bold grains, CT13432-3R recorded higher grain weight than medium slender ADT 43 and their progenies. However, the 100-grain weight of F_1 was intermediate to the parents, which is desirable considering consumer preference. ADT 43 recorded higher single plant yield compared with CT13432-3R and the F_1 yielded more compared with both the parents. Harvest index was high in F_1 hybrid as compared with the parents and backcross generations.

Blast infection measured in terms of lesion number in resistant parent (CT13432-3R) at Coimbatore and Gudalur, was 5.4 (table 1), whereas it was 31.0 in the susceptible parent ADT 43. The same was the lowest in F_1 while in the segregating generations i.e. F_2, B_1 and B_2 it was in the intermediate range between those of the two parents. In terms of infected leaf area, F_1 recorded desirable value while in F_2 and backcross progenies (B_1 and B_2) it was within their parental values and closer to the resistant parent. Potential disease incidence (PDI) was low in F_1 hybrid compared to all other generations.

Scaling and joint scaling tests were performed to understand the adequacy of simple additive–dominance model (table 2). The scaling test (Hayman and Mather 1955) showed all A, B, C and D scales were significant for panicle length indicating presence of epistasis. All the traits related to yield as well as blast resistance in this study were significant in either one of the scales or in combination representing the existence of epistatical interactions between

Table 1. Mean performance of six generation materials of the cross ADT 43 × CT13432-34 for various quantitative traits.

Introduce	Trait[#]	P_1	P_2	F_1	F_2	B_1	B_2
1	PH	64.80 ± 0.80	73.00 ± 0.89	76.40 ± 1.47	78.97 ± 0.77	78.23 ± 0.83	78.29 ± 0.80
2	NOT	26.80 ± 0.97	22.00 ± 0.71	33.40 ± 1.36	26.76 ± 0.66	26.32 ± 0.65	25.59 ± 0.63
3	PRT	26.60 ± 0.93	21.60 ± 0.51	33.40 ± 1.36	23.84 ± 0.65	23.74 ± 0.64	22.90 ± 0.61
4	LL	38.10 ± 1.35	27.66 ± 1.33	34.36 ± 1.82	26.46 ± 0.38	26.48 ± 0.41	26.70 ± 0.40
5	LW	1.18 ± 0.04	1.36 ± 0.02	1.48 ± 0.06	1.33 ± 0.01	1.33 ± 0.02	1.33 ± 0.01
6	PL	23.60 ± 1.11	21.44 ± 0.29	24.76 ± 0.28	23.21 ± 0.17	20.92 ± 0.27	20.86 ± 0.28
7	FF	93.20 ± 0.80	82.80 ± 0.37	88.80 ± 0.37	88.46 ± 0.46	88.90 ± 0.46	88.50 ± 0.45
8	TGP	138.00 ± 19.91	118.80 ± 1.99	131.20 ± 17.30	121.68 ± 2.69	170.94 ± 5.31	170.65 ± 5.44
9	FGP	157.60 ± 21.00	132.60 ± 4.71	152.00 ± 24.62	142.50 ± 2.94	186.69 ± 5.57	185.74 ± 5.77
10	SPF	87.09 ± 2.05	89.87 ± 2.01	87.76 ± 3.70	85.40 ± 0.79	91.48 ± 0.63	91.77 ± 0.56
11	SPS	12.91 ± 2.05	10.13 ± 2.01	12.24 ± 3.70	14.60 ± 0.79	9.47 ± 0.76	9.20 ± 0.71
12	GWT100	1.50 ± 0.01	2.15 ± 0.16	1.96 ± 0.06	1.88 ± 0.03	1.80 ± 0.03	1.83 ± 0.03
13	SPY	51.89 ± 9.42	42.24 ± 5.62	53.84 ± 10.11	49.30 ± 1.69	24.51 ± 1.25	37.15 ± 2.02
14	BY	128.40 ± 1.36	155.60 ± 1.44	212.40 ± 3.59	167.18 ± 3.32	169.05 ± 3.87	177.56 ± 4.64
15	DWT	110.80 ± 4.53	120.20 ± 2.85	147.20 ± 5.24	126.87 ± 1.66	128.07 ± 1.98	133.27 ± 2.59
16	EY	60.24 ± 4.74	44.36 ± 8.72	82.99 ± 2.23	62.56 ± 1.89	63.59 ± 1.91	66.16 ± 2.15
17	HI	54.34 ± 3.49	37.26 ± 7.88	56.76 ± 2.95	49.12 ± 1.3	49.60 ± 1.30	49.49 ± 1.30
18	LN	31.00 ± 2.92	5.40 ± 0.68	3.60 ± 0.68	12.63 ± 1.2	14.57 ± 1.30	13.60 ± 0.94
19	ILA	74.00 ± 1.87	3.40 ± 0.68	4.60 ± 0.51	25.52 ± 3.04	28.44 ± 3.24	24.72 ± 2.18
20	PDI	84.44 ± 4.44	15.56 ± 2.72	11.11 ± 0.00	35.19 ± 3.14	39.34 ± 3.32	31.28 ± 2.39

[#] PH, plant height; NOT, number of tillers; PRT, productive tillers; LL, leaf length; LW, leaf width; PL, panicle length; FF, days to first flowering; TGP, total grains per panicle; FGP, filled grains per panicle; SPF, spikelet fertility; SPS, spikelet sterility; GWT100, 100 grain weight; SPY, single plant yield; BY, biological yield; DWT, dry weight); EY, economic yield and HI, harvest index ; LB, leaf blast; LN, lesion number, LT, lesion type, ILA, infected leaf area and PDI, potential disease incidence per cent VIG, seedling vigour and RES, blast resistance.

Table 2. Estimates from scaling and joint scaling tests.

Trait	Scaling test				Joint scaling test			
	Scale A	Scale B	Scale C	Scale D	*m*	*d*	*h*	χ^2
PH	15.25** ± 2.36	7.19** ± 2.35	25.26 ± 4.43	1.41** ± 1.93	70.06** ± 0.57	−3.37** ± 0.53	13.86** ± 1.25	51.09**
NOT	−7.56** ± 2.12	−4.22** ± 1.99	−8.55 ± 3.98	1.61** ± 1.60	23.59** ± 0.55	1.76** ± 0.50	6.31** ± 1.18	13.10**
PRT	−12.52** ± 2.09	−9.20** ± 1.90	−19.63 ± 3.92	1.04** ± 1.58	22.88** ± 0.48	1.67** ± 0.45	3.31** ± 1.07	42.73**
LL	−19.49** ± 2.40	−8.62** ± 2.39	−28.66 ± 4.37	−0.27** ± 0.95	29.97** ± 0.85	1.23* ± 0.49	−6.18** ± 1.70	69.43**
LW	−0.00 ± 0.08	−0.17* ± 0.07	−0.16 ± 0.14	0.01** ± 0.04	1.28** ± 0.02	−0.05** ± 0.02	0.12** ± 0.04	10.08*
PL	−6.52** ± 1.27	−4.47* ± 0.69	−1.73** ± 1.45	4.63** ± 0.52	20.71** ± 0.27	−0.33 ± 0.28	3.47** ± 0.46	98.60**
FF	−4.20** ± 1.28	5.39 ± 1.05	0.25 ± 2.16	−0.47 ± 1.12	87.44** ± 0.35	3.88** ± 0.35	1.71** ± 0.56	41.45**
TGP	72.68* ± 28.44	91.30 ± 20.54	−32.50* ± 41.40	−98.24** ± 9.31	125.96** ± 5.90	6.88 ± 5.74	22.98 ± 12.24	113.03**
FGP	63.78 ± 34.22	86.88 ± 27.59	−24.20 ± 55.01	−87.43* ± 9.94	141.46** ± 7.10	7.66 ± 6.26	31.79* ± 14.76	78.65**
SPF	8.11 ± 4.41	5.92* ± 4.35	−10.87 ± 8.53	−12.45** ± 1.79	89.02** ± 1.34	−0.83 ± 0.73	2.27 ± 2.73	49.94**
SPS	−6.20 ± 4.49	−3.97* ± 4.44	10.87 ± 8.53	10.52** ± 1.88	11.27** ± 1.34	0.80 ± 0.84	−0.60 ± 2.75	31.68**
GWT100	0.15 ± 0.08	−0.45 ± 0.18	−0.05 ± 0.23	0.13 ± 0.07	1.60** ± 0.03	−0.10** ± 0.03	0.43** ± 0.06	17.68**
SPY	−56.70** ± 14.04	−21.79 ± 12.25	−4.61 ± 23.98	36.94 ± 4.13	34.24** ± 4.42	−15.16** ± 2.09	4.93 ± 9.01	97.56**
BY	−2.71 ± 8.65	−12.89** ± 10.05	−40.10 ± 15.24	−12.25** ± 8.99	141.62** ± 0.98	−13.46** ± 0.98	65.88** ± 3.10	7.71
DWT	−1.87 ± 7.98	−0.86* ± 7.90	−17.93 ± 13.52	−7.60** ± 4.66	114.70** ± 2.33	−4.82* ± 2.02	28.97** ± 4.84	3.34
EY	−16.05* ± 6.49	4.97* ± 9.98	−20.32 ± 13.26	−4.62** ± 4.76	48.88** ± 2.60	1.38 ± 2.43	32.10** ± 4.18	8.86*
HI	−11.89* ± 5.25	4.95 ± 8.81	−8.65 ± 11.67	−0.85** ± 3.18	46.22** ± 2.37	2.15 ± 1.64	7.22 ± 4.45	6.57
LN	−5.46 ± 3.96	18.20** ± 2.11	6.93 ± 5.81	−2.91* ± 2.88	17.54** ± 0.95	10.16** ± 0.99	−12.14** ± 1.30	79.27**
ILA	−21.72** ± 6.75	41.44** ± 4.45	15.47 ± 12.38	−2.12* ± 7.23	38.51** ± 0.95	34.10** ± 0.95	−33.44** ± 1.09	99.14**
PDI	−16.87* ± 7.98	35.90** ± 5.50	18.52 ± 13.59	−0.26* ± 7.49	52.60** ± 2.07	27.77** ± 2.17	−41.49** ± 2.07	48.37**

*$P<0.05$ and ** $P<0.01$

Non significant traits in chi-square test are underlined.

Table 3. Estimation of gene effects based on six generation means (Hayman 1958).

Trait	*m*	*d*	*h*	*i*	*j*	*l*
PH	78.97**± 0.77	−0.08 ± 1.15	4.68 ± 5.10	−2.82 ± 3.85	4.03**± 1.30	−19.62**± 6.39
NOT	26.76**± 0.66	0.73 ± 0.91	5.77 ± 4.46	−3.23 ± 3.20	−1.67 ± 1.09	15.00**± 5.38
PRT	23.84**± 0.65	0.84 ± 0.88	7.22 ± 4.42	−2.09 ± 3.16	−1.66 ± 1.03	23.80**± 5.28
LL	26.47**± 0.38	−0.22 ± 0.57	2.02 ± 4.58	0.54 ± 1.90	−5.44**± 1.11	27.57**± 4.93
LW	1.33**± 0.01	−0.01 ± 0.02	0.19 ± 0.15	−0.02 ± 0.07	0.08**± 0.03	0.20 ± 0.16
PL	23.21**± 0.17	0.06 ± 0.39	−7.03**± 1.34	−9.27**± 1.04	−1.02 ± 0.69	20.26**± 2.13
FF	88.46**± 0.46	0.40 ± 0.65	1.74 ± 2.42	0.94 ± 2.23	−4.80**± 0.78	−2.12 ± 3.37
TGP	121.68**± 2.69	0.29 ± 7.60	199.27**± 44.09	196.47**± 18.62	−9.31 ± 12.57	−360.40**± 51.36
FGP	142.50**± 2.94	0.95 ± 8.02	181.76**± 59.51	174.86**± 19.89	−11.55 ± 13.42	−325.50**± 63.68
SPF	85.40**± 0.79	−0.29 ± 0.84	24.18**± 9.12	24.90**± 3.57	1.10 ± 1.67	−38.92**± 9.18
SPS	14.60**± 0.79	0.27 ± 1.03	−20.32*± 9.20	−21.03**± 3.77	−1.12 ± 1.77	31.20**± 9.48
GWT100	1.88**± 0.03	−0.03 ± 0.04	−0.11 ± 0.21	−0.25 ± 0.14	0.30**± 0.09	0.55*± 0.28
SPY	49.30**± 1.69	−12.63**± 2.37	−67.11**± 24.69	−73.88**± 8.26	−17.46**± 5.98	152.37**± 25.79
EY	62.56**± 1.89	−2.58 ± 2.88	39.93**± 11.84	9.24 ± 9.52	−10.51 ± 5.74	1.84 ± 17.56
LN	12.63**± 1.20	0.97 ± 1.60	−8.78**± 6.14	5.82 ± 5.76	−11.83**± 2.19	−18.57*± 8.64
ILA	25.52**± 3.04	3.72 ± 3.90	−29.86*± 14.54	4.24 ± 14.46	−31.58**± 4.03	−23.96 ± 19.92
PDI	35.19**± 3.14	8.06*± 4.09	−38.37*± 15.20	0.52 ± 14.98	−26.38**± 4.85	−19.55 ± 21.26

* $P<0.05$ and ** $P<0.01$.

the genes involved except in case of 100-grain weight with none of the scales showing significance. Further, joint scaling test was adapted to fit the data to three parameter model to estimate mean (*m*), additive gene effects (*d*) and dominant gene effects (*h*) and to evaluate adequacy of simple additive–dominance model (Cavalli 1952). Chi square test was conducted to evaluate the goodness of fit of this model. For three traits *viz*., biological yield, dry weight and harvest index, chi square values were not significant indicating the absence of digenic nonallelic interaction in these cases. The adequacy of simple additive–dominance model suggests nonallelic interaction effect (epistasis) is absent and generation means depends only on additive–dominance effect of the gene. Chi square values were significant for remaining 17 traits in this study indicating the data does not fit into simple additive–dominance model. The role of epistatic interactions was identified by lack of goodness of fit into three parameter model and the data was further subjected to six parameter model (Hayman 1958).

Digenic nonallelic interaction model with six parameters namely *m, d, h, i, j* and *l* (Hayman 1958) revealed that the epistatic interaction model was found adequate to explain the gene action in the traits like plant height, number of tillers, productive tillers, leaf length, panicle length, days to first flowering, filled grains per panicle, 100-grain weight, lesion number, infested leaf area and potential disease incidence per cent (table 3). In ADT 43 × CT13432-3R cross, dominance (*h*) and dominance × dominance (*l*) gene effects displayed opposite signs for the traits *viz*., plant height, panicle length, days to first flowering, days to maturity, filled grains per panicle, total grains per panicle, spikelet fertility, spikelet sterility, 100-grain weight and single plant yield indicating duplicate epistasis. The values of dominance (*h*) and dominance × dominance (*l*) interaction were in the same direction for traits like number of tillers, productive tillers, leaf length, leaf width, economic yield, lesion number, infested leaf area and potential disease incidence per cent and the interaction fit into complementary epistasis model. It was reported that gene effects are known to be crossspecific and fits into complementary recessive epistasis for grain yield (Thirugnanakumar *et al.* 2007).

The classification of gene interactions depends on the magnitudes and signs of the estimates of dominance and dominance × dominance effects, when there are many pairs of interacting genes (Mather and Jinks 1982). The sign associated with the estimates of (*d*) and (*h*) indicates the parent that concentrates the highest number of genes for increasing the trait (Falconer 1989). Therefore, the positive sign for (*d*) in the traits like number of tillers, productive tillers, panicle length, days to first flowering and filled grains per panicle indicates that the high yielding susceptible parent, ADT 43 (P_1) showed the highest number of genes for increasing the yield and the negative sign for (*h*) demonstrated that the dominance was towards the resistant parent (P_2) CT13432-3R as observed earlier (Paul *et al.* 2003; Cruz *et al.* 2006; Thirugnanakumar *et al.* 2007; Li *et al.* 2010) which explained dominance genetic effect in yield and stress-related traits in rice. On the contrary, Ray and Islam (2008) and Sharifi *et al.* (2011) have reported the importance of additive effects.

Variance estimation using the six generation values revealed that variation due to dominant genetic effect was predominant for the traits under study (table 4). Estimation of variance components in these six generation materials indicates that dominance genetic variance was higher than additive variance for the traits under study. Additive genetic variance was more pronounced for traits like spikelet fertility and 100-grain weight. Variance estimates also revealed that degree of dominance (H/D) was more than one for traits like spikelet fertility and 100-grain weight. Yield parameters *viz*.,

Table 4. Estimation of variance component (Warner 1952; Wright 1968).

Traits	V_P	V_E	V_G	V_A	V_D	HerN	HerB
PH	67.70	7.20	60.50	−3.03	63.53	−0.05	0.89
NOT	49.60	6.45	43.15	13.97	29.18	0.28	0.87
PRT	48.63	6.05	42.58	15.94	26.64	0.33	0.88
LL	16.52	12.74	3.78	−0.71	4.49	−0.04	0.23
LW	0.02	0.01	0.01	0.00	0.01	0.03	0.51
PL	3.39	1.84	1.55	−9.00	10.55	−2.66	0.46
FF	23.61	1.33	22.29	3.84	18.45	0.16	0.94
TGP	822.56	1249.20	−426.60	−4361.00	3934.50	−5.30	−0.52
FGP	984.82	2094.00	−1109.00	−4719.00	3610.10	−4.79	−1.13
SPF	70.54	44.48	26.06	67.07	−41.01	0.95	0.37
SPS	70.54	44.48	26.06	29.85	−3.79	0.42	0.37
GWT100	0.11	0.04	0.07	0.08	−0.01	0.76	0.64
SPY	325.47	406.01	−80.53	67.35	−147.90	0.21	−0.25
BY	1259.40	37.05	1222.40	−1274.00	2496.30	−1.01	0.97
DWT	315.64	104.45	211.19	−469.20	680.36	−1.49	0.67
EY	408.69	135.55	273.14	−44.05	317.19	−0.11	0.67
HI	192.52	114.59	77.93	33.04	44.89	0.17	0.41
LN	163.21	12.35	150.86	59.36	91.50	0.36	0.92
ILA	1056.10	5.60	1050.50	522.21	528.32	0.49	1.00
PDI	1122.90	33.95	1089.00	504.53	584.47	0.45	0.97

panicle length, filled grains per panicle, 100-grain weight, spikelet fertility, harvest index and single plant yield in this cross expressed higher degree of dominance variance than additive variance. Hence, it is concluded that these characters are governed by non additive gene action; it is also evident from the superior performance of F_1s than advanced lines (Manickavelu *et al.* 2006; Saleem *et al.* 2010). The predominance of non additive gene action for these characters under study indicated that improvement of these characters could be possible through heterosis breeding. To obtain better genotypes through recombination breeding, hybridization followed by selection at later generations is suggested for exploiting dominance gene action and this method was followed in the present study.

Sobita Devi *et al.* (2006) and Verma *et al.* (2006) reported the predominance of additive gene action for plant height, number of productive tillers and days to 50% flowering in rice. Additive genetic variance was predominant in case of 100-grain weight and spikelet fertility and it is associated with homozygosity and hence it is fixable in nature and selection for these characters will be very effective. Selection is the reliable breeding method for improving varieties for the characters with predominant additive variance. If the dominance is high, the selection has to be postponed to later generation. Heterosis breeding is not desirable in case of epistasis but it would be possible to isolate segregants as good as that of F_1 in the subsequent filial generations. More reliance should be placed on selection between families and lines for the traits with relatively high epistatic variance.

Introgression of blast resistance genes in the segregating population was analysed using reported linked molecular markers (results not presented) simultaneously with this study. Based on both phenotypical as well as molecular screening of introgressed lines, it was observed that there was a difference in response of the single gene when it acts alone or in combination (table 5). Expression of other resistance genes or QTLs in the population which are not examined in this study may be responsible for the differential disease reaction of the same genotypes. Epistatic interactions for blast resistance traits were also identified through generation mean analysis and it may be another reason behind differential response of these genes individually and in combination. The epistatic effects among resistance genes have been reported earlier in several gene combinations during pyramiding process (Yoshimura *et al.* 1995; Fukuta *et al.* 1998; Fujita *et al.* 2010). QTLs/genes with different levels of dominant, overdominant and epistatic effects have been mapped in rice (Mei *et al.* 2003, 2005; Luo *et al.* 2011). In case of stress-related QTLs, the results of the marker-assisted selection are limited (Tuberosa *et al.* 2002; Steele *et al.* 2006) owing to difficulties such as QTL that have epistatic interactions and do not contribute uniformly in different genetic backgrounds. Thus, knowledge of the resistance spectrum of genes and gene action should be taken into consideration for the successful conduct of resistance breeding programme.

The epistatic nonallelic interaction model was found adequate to explain the gene action in most of the traits under study through generation mean analysis using six generations of the cross ADT43 × CT13432-3R. The presence of duplicate nonallelic interactions was identified for most of the traits examined. Complementary epistasis was observed in the inheritance of blast resistance and the contributing traits like lesion number, potential disease incidence and infected leaf area. Among the genotypes tested under epiphytotic

Table 5. Resistance response of BC_2F_1 lines at two hot-spot locations of blast disease.

Genotypes	Gene combinations	Coimbatore								Gudalur							
		LB	LN	LT	ILA	PDI%	VIG	RES	RES	LB	LN	LT	ILA	PDI%	VIG	RES	RES
ADT 43	NIL	9.00	33.00	9.00	73.00	81.00	6.00	7.00	S	8.00	32.94	7.88	77.19	88.89	6.19	7.00	S
CT13432-3R	*Pi1+Pi2+Pi33+Pi54*	0.00	2.00	0.00	1.00	0.00	1.00	1.00	R	1.00	5.00	1.00	1.00	11.11	1.00	1.00	R
Gene combinations	*Pi1+Pi2+Pi33+Pi54*	1.00	5.00	1.00	5.00	9.00	1.00	0.00	HR	2.00	9.57	1.57	15.00	22.22	1.00	1.00	R
in BC_2F_1 lines	*Pi1+Pi2+Pi33*	2.00	7.00	3.00	10.00	18.00	1.00	1.00	R	2.33	13.00	3.00	25.00	25.89	3.67	1.67	R
	Pi1+Pi2+Pi54	5.00	22.00	7.00	25.00	45.00	6.00	7.00	MR	2.67	21.67	6.33	36.67	29.67	5.00	3.00	MR
	Pi1+Pi33+Pi54	3.00	28.00	5.00	30.00	27.00	3.00	3.00	MR	2.50	14.25	3.50	29.50	27.78	1.50	2.00	R
	Pi2+Pi33+Pi54	3.00	15.00	3.00	25.00	27.00	1.00	3.00	MR	2.25	12.25	3.00	16.25	25.00	1.50	1.50	R
	Pi1+Pi2	5.00	28.00	5.00	30.00	45.00	3.00	3.00	MR	3.00	16.33	3.67	30.00	33.33	1.00	3.00	MR
	Pi1+Pi33	1.00	9.00	3.00	20.00	9.00	1.00	1.00	R	1.80	13.00	2.40	16.90	20.00	2.00	1.50	MR
	Pi1+Pi54	3.00	22.00	3.00	30.00	27.00	3.00	3.00	MR	1.46	7.15	2.38	12.77	16.22	1.00	0.54	R
	Pi2+Pi33	1.50	15.00	3.00	20.00	13.50	5.00	3.00	MR	2.25	11.75	3.00	16.25	25.00	1.50	1.50	MR
	Pi2+Pi54	3.00	20.00	3.00	25.00	27.00	3.00	3.00	MR	1.33	10.00	1.67	15.00	14.78	1.00	1.00	R
	Pi33+Pi54	3.00	20.00	3.00	30.00	27.00	3.00	3.00	MR	4.00	27.00	5.00	41.67	44.44	4.33	3.67	MR
	Pi1	3.00	20.00	3.00	20.00	27.00	5.00	3.00	MR	2.56	15.33	3.31	22.22	28.44	3.14	2.32	MR
	Pi2	5.00	10.00	1.00	14.00	45.00	3.00	1.00	MR	3.89	8.67	2.33	13.00	43.22	2.33	1.00	MR
	Pi33	1.00	8.00	1.00	10.00	9.00	1.00	1.00	R	2.00	7.27	2.27	13.64	22.22	1.00	1.00	R
	Pi54	4.65	9.00	1.00	10.00	41.85	3.00	1.00	MR	3.00	7.14	2.14	12.71	33.33	3.00	1.00	MR

LB, leaf blast; LN, lesion number; LT, lesion type; ILA, infected leaf area; PDI, potential disease incidence; VIG, vigour; RES, leaf blast resistance (IRRI 2002).

condition at two different environments, the gene pyramided lines were highly resistant to blast disease than individuals with single genes indicating that the nonallelic genes have a complementary effect when present together (table 5). The information on genetics of various contributing traits will further aid plant breeders in the selection of breeding programmes for simultaneous improvement of blast resistance and yield related traits in rice.

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