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# GENE INTERACTIONS AND ASSOCIATION ANALYSIS FOR SHEATH BLIGHT RESISTANCE IN RICE (*Oryza sativa* L.)

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## SUMMARY

Rice sheath blight is one of the most destructive diseases worldwide, resulting in heavy yield loss every year. It is prevalent in almost all rice growing areas of the world as well as India, and has become a major constraint to rice production during the last 2 decades. An experiment was conducted to determine the nature and magnitude of gene action governing the resistance to sheath blight and association between yield related traits with area under disease progress curve. Six generations *viz*., $P_1$, $P_2$, $F_1$, $F_2$, $B_1$ and $B_2$ were developed from the cross involving high yielding susceptible rice variety HUR 105 and resistant Tetep. The interaction was duplicate for days to 50% flowering, plant height, number of effective tillers per plant, fertile spikelet per panicle, total number of spikelet panicle, spikelet fertility percentage, test weight, grain yield per plant and area under disease progress curve, while complementary for days to maturity, panicle length and flag leaf length. The number of effective factors for sheath blight ranged from 1.31 to 4.14 indicated that 1 to 4 genes were involved in the inheritance of resistance. The area under disease progress curve showed significant positive association with days to 50% flowering, days to maturity, number of effective tillers per plant, flag leaf length, fertile spikelet per panicle, spikelet fertility percentage, test weight and grain yield per plant while significant negative with plant height. The trait days to 50% flowering contributed highest positive direct effect on area under disease progress curve followed by spikelet fertility percentage, grain yield per plant, plant height, test weight, fertile spikelet per panicle and number of effective tillers per plant. Thus, the information on genetics of various contributing traits of resistance will further aid plant breeders in choosing appropriate breeding strategy for sheath blight resistance and yield enhancement in rice.

**Key words:** Correlation, grain yield, gene action, resistance, sheath blight

**Key findings:** The gene action for sheath blight and yield attributing traits indicated that additive, dominance and epistatic genetic components are important for the expression of traits, and gives useful information for plant breeders to develop new rice varieties resistant to sheath blight with desirable yield component traits.

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## INTRODUCTION

Rice (*Oryza sativa* L.) is one of the oldest domesticated crops, which provides food for more than half of the world's population and constitutes a major source of calories for urban and rural inhabitants (Khush, 2005). Rice sheath blight (ShB) caused by the soil borne fungal pathogen *Rhizoctonia solani Kuhn*, is one of the most destructive diseases worldwide (Savary *et al*., 2006). It has been reported to cause 20-30% yield loss depending on the severity of infection and approximately 50% yield reduction in test plots of susceptible rice cultivars (Savary and Mew, 1996). Growing resistant cultivars is the most economical and environmentally sound strategy in managing ShB. The accurate measurement of ShB resistance under field conditions depends on a range of environmental factors (Eizenga *et al*., 2002) and plant morphological traits, such as plant height (Zou *et al*., 2000; Pinson *et al*., 2005), which interact, resulting in the observed variation in resistant/susceptible phenotypes. Resistance to rice sheath blight is a complex, quantitative trait controlled by polygenes (Pinson *et al*., 2005). Presently, about 50 sheath blight resistance quantitative trait loci have been detected on all the 12 rice chromosomes (Jia et al., 2009; Zuo *et al*., 2010; Xu *et al*., 2011; Fu *et al*., 2011; Wang *et al*., 2012). Breeding for ShB resistance has been difficult, mainly because of the lack of identified resistant donors in cultivated varieties (Bonmann *et al*., 1992), but an *indica* rice line, Tetep is a well-documented source of durable and broad spectrum resistance to sheath blight (Channamallikarjuna *et al*., 2010).

The expression of trait is affected not only by large number of genes governing them but also by environmental effect. Frequently, these genes interact with each other causing distortions in Mendelian ratios and leading to novel phenotypes (Phillips, 1998). The estimation of epistasis assumes more significance in view of these fact that in its presence, variance component estimates are likely to be biased hence inferences drawn from such estimates are more likely to be misleading. Generation mean analysis is a powerful statistical tool for detection of epistasis using several basic generations from a cross between two parents. To achieve the desired genetic improvement towards the development of better cultivars, it is essential to gather information about genetic architecture of quantitative traits including grain yield. Before placing strong emphasis on breeding for yield improvement trait, knowledge on the association between disease severity and yield attributes will immense help the breeder in the improvement of yield. The existence of correlation may be attributed to the presence of linkage or pleiotropic effect of genes or physiological and development relationship or environmental effect or in combination of all (Oad *et al*., 2002). Path coefficient is being widely used by plant breeders to understand the nature of complex interrelationships among traits and to identify the sources of variation in yield. To accumulate yield contributing traits together with sheath blight resistance, it is essential to know the association among various traits along with path coefficients between the major contributors and the target trait. Therefore, the present investigation was undertaken to estimate the types of gene action of sheath blight resistance in rice, yield and yield contributing traits through generation mean analysis, and association between yield related traits with area under disease progress curve in rice.

## MATERIALS AND METHODS

### Plant material and experimental design

The two *indica* rice varieties HUR 105 and Tetep were staggered planted at Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India during *Kharif* 2012. The variety HUR 105 is most widely grown in North East India owing to its high yielding, semi dwarf, medium duration, long slender grain with acceptable grain quality but susceptible to sheath blight, while Tetep showed resistance. The HUR 105 used as recurrent parent and crossed with Tetep which is used as donor parent to produce $F_{1s}$. Five hundred seeds of $F_1$ were produced, and only two hundred seeds were planted in *Rabi season* 2012 at Central Rice Research Institute, Cuttack, Odissa, India. At flowering stage, the

two backcrosses namely $B_1$ ($F_1 \times P_1$) and $B_2$ ($F_1 \times P_2$) were made and their three hundred seeds of each cross combination were produced. Fifty $F_1$ plants were also selfed to produce about 500 g of $F_2$ seeds. Six generations, namely, $P_1$, $P_2$, $F_1$, $F_2$, $B_1$ and $B_2$ were raised in a complete randomized block design with three replications at Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India during *Kharif* 2013. Twenty days old single seedlings were transplanted in separate plot size 3 × 1 m with spacing 20 × 15 cm apart. The recommended packages of practices were followed to raise healthy crops.

**Strain revival and pathogenicity test**

The most aggressive isolate A-1 of *Rhizoctonia solani* was used for resistance screening. The fungus was maintained on oat meal agar medium (OMA-Himedia Laboratories Pvt. Ltd.) for the production of sclerotia. The pure culture of *R. solani* was maintained in petri dishes on potato dextrose agar medium. After 20 days the sclerotia were formed on the medium. All the uniform sized sclerotia were selected for the preparation of inoculums. The sclerotia of same age obtained from *R. solani* culture were cut into uniform size (2 mm), using sterilized blade and carefully inserted behind the sheath of the third leaf (from the top) with forceps at the first stem elongation stage of growth (~60 days after sowing) during August and September.

**Observation recorded**

The phenotypic traits were assessed on each individual entry in the segregating generations and observations were recorded for twelve quantitative traits; days to 50% flowering (DF), days to maturity (DM), plant height (PH), number of effective tillers per plant (ET), panicle length (PL), flag leaf length (FLL), fertile spikelet per panicle (FSP), total number of spikelet per panicle (TSP), spikelet fertility percentage (SF%), test weight (TW), grain yield per plant (GYP) and percent disease severity. Ten plants from both parents, 25 plants from $F_1$, $B_1$ & $B_2$ and 35 plants from $F_2$ generation per replication were randomly selected and tagged for recording data on twelve quantitative traits, and mean values were used for statistical analysis.

**Statistical 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. 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 calculated. The standard errors of A, B, C and D were obtained as square root of the variances VA, VB, VC and VD, respectively and 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. The significance of the scales was evaluated using calculated *P* values for respective calculated't' values. Joint scaling test (Cavalli, 1952) was conducted which combines several scaling test into one and tests the adequacy of additive-dominance model using a $\chi 2$ test.

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 six genetic parameters were calculated. The least squares computation method was used for arriving at different gene effects.

The number of effective factors controlling resistance was estimated by five methods:

Method 1 was proposed by Wright (1968); $EF_1 = (P_2 - P_1)^2 [1.5 - 2h (1 - h)] / 8 [\sigma^2_{F2} - 0.25 (\sigma^2_{P1} + \sigma^2_{P2} + 2\sigma^2_{F1})]$. Where $F_1$, $P_1$ and $P_2$ are average, $\sigma^2_{P1}$, $\sigma^2_{P2}$, $\sigma^2_{F1}$ and $\sigma^2_{F2}$ are variance of the respective generations and $h = F_1 - P_1 / P_2 - P_1$.

Method 2 was proposed by Mather and Jinks (1982); $EF_2 = [0.5 (P_2 - P_1)]^2 / [2\sigma^2_{F2} - (\sigma^2_{B1} + \sigma^2_{B2})]$. Where $P_1$ and $P_2$ are average and $\sigma^2_{F2}$, $\sigma^2_{B1}$ and $\sigma^2_{B2}$ are variances of the respective generations.

Methods 3 to 5 were proposed by Lande (1981); $EF_3 = (P_2 - P_1)^2 / 8 [\sigma^2_{F2} - 0.25 (\sigma^2_{P1} + \sigma^2_{P2} + 2\sigma^2_{F1})]$; $EF_4 = (P_2 - P_1)^2 / 8 [2\sigma^2_{F2} - (\sigma^2_{B1} + \sigma^2_{B2})]$ and $EF_5 = (P_2 - P_1)^2 / 8 [\sigma^2_{B1} + \sigma^2_{B2} - (\sigma^2_{F1} + 0.5\sigma^2_{P1} + 0.5\sigma^2_{P2})]$. Where $P_1$ and $P_2$ are average, $\sigma^2_{P1}$, $\sigma^2_{P2}$, $\sigma^2_{F1}$, $\sigma^2_{F2}$, $\sigma^2_{B1}$ and $\sigma^2_{B2}$ are variances of the respective generations.

All formulas are based on the assumption that genes segregating for sheath blight resistance, located in the resistant parent, are linked, having equal effects on the resistance, and absence of epistatic effect, dominance effect and genotype × environment effects (Wright, 1968).

The pathological data were observed after every 24 hours time interval to note the appearance of disease symptoms, and percent disease severity was recorded at $7^{th}$, $14^{th}$ and $21^{st}$ days after inoculation (DAI). The area under disease progress curve (AUDPC) was calculated according to the formula given by Madden *et al*. (2007). Correlation and path coefficient analyses were estimated adopting the procedure suggested by Dewey and Lu (1959). OPSTATE (developed by CCS-HAU, Hisar, Haryana, India) statistical software was used for generation mean, correlation and path coefficient analyses**.**

## RESULTS AND DISCUSSIONS

### Generation mean analysis

Progenies of the cross between HUR 105 × Tetep were advanced to $F_2$, $B_1$ (HUR 105 × $F_1$) and $B_2$ (IRBB 55 × $F_1$) to isolate high yielding segregants with introgressed sheath blight resistance genes. To elucidate the nature of gene action for yield traits and sheath blight 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 12 quantitative traits are presented in Table 1. $F_1$ (83.93 and 113.73 days) along with $B_2$ (84.38 and 115.20 days) segregating population flowered and matured earlier than parent HUR 105 (98.37 and 129.77 days) and Tetep (88.73 and 119.10 days), which was statistically significant and desirable in further selections. The segregating population $F_2$ (90.16 and 120.90 days) and $B_1$ (93.62 and 125.35 days) flowered and matured intermediate compared with parents. Plant height in $F_1$ (110.02 cm) and $F_2$ (109.69 cm) were slightly shorter than non-recurrent parent Tetep (112.25 cm), $B_1$ population (97.31 cm) had comparable plant height to recurrent parent HUR 105 (97.11 cm), and $B_2$ population (116.91 cm) was taller than both parents. The $F_1$ (13.38), $F_2$ (11.80) and $B_1$ (13.41) population recorded intermediate number of tillers per plant while $B_2$ population (9.13) had lesser number of tillers per plant than both parent HUR 105 (14.67) and Tetep (10.62). The very less difference (0.63 cm) for panicle length was observed between parents which was statistically non-significant. Among all generation materials panicle length was comparable to both parents. The flag leaf length in $F_1$ (24.65 cm) and $F_2$ (23.15 cm) populations were comparable to recurrent parent HUR 105 (24.02 cm). $B_1$ (26.44 cm) and $B_2$ (18.57 cm) segregants showed taller and smaller flag leaf length than both parents (HUR 105: 24.02 cm and Tetep: 19.20 cm), respectively. $F_1$ (176.18 and 197.68) along with three segregating populations $F_2$ (184.06 and 207.16), $B_1$ (182.02 and 209.35) and $B_2$ (181.10 and 210.58) had comparable number of fertile and total spikelet per panicle to recurrent parent HUR 105 (186.07 and 205.63), which was higher than non-recurrent parent Tetep (128.40 and 148.20). $F_1$ (88.88%) along with three segregating populations $F_2$ (88.86%), $B_1$ (87.02%) and $B_2$ (85.80%) had intermediate spikelet fertility percentage compared with both parent HUR 105 (90.38%) and Tetep (86.49%). The $F_1$ (22.79 g),

Table 1. Mean performance of 6 generation materials of the cross HUR 105 × Tetep for 12 quantitative traits.

| Traits | $P_1$±SEm | $P_2$±SEm | $F_1$±SEm | $F_2$±SEm | $B_1$±SEm | $B_2$±SEm |
|---|---|---|---|---|---|---|
| DF | 98.37±0.70 | 88.73±0.78 | 83.93±1.13 | 90.16±1.05 | 93.62±0.86 | 84.38±0.77 |
| DM | 129.77±1.27 | 119.10±0.85 | 113.73±1.04 | 120.90±1.03 | 125.35±0.94 | 115.20±0.84 |
| PH (cm) | 97.11±1.69 | 112.25±1.14 | 110.02±0.68 | 109.69±1.19 | 97.31±0.69 | 116.91±0.71 |
| ET | 14.67±1.18 | 10.62±0.58 | 13.38±0.69 | 11.80±0.72 | 13.41±1.06 | 9.13±0.55 |
| PL (cm) | 23.52±0.34 | 24.15±0.59 | 22.86±0.63 | 22.16±0.64 | 23.51±0.54 | 21.76±0.64 |
| FLL (cm) | 24.02±0.70 | 19.20±0.52 | 24.65±0.81 | 23.15±0.77 | 26.44±0.62 | 18.57±0.76 |
| FSP | 186.07±5.89 | 128.40±3.98 | 176.18±6.86 | 184.06±4.04 | 182.02±4.88 | 181.10±6.00 |
| TSP | 205.63±5.75 | 148.20±3.89 | 197.68±6.71 | 207.16±4.21 | 209.35±4.73 | 210.58±5.96 |
| SF% | 90.38±0.63 | 86.49±0.70 | 88.88±0.98 | 88.86±0.70 | 87.02±1.36 | 85.80±0.61 |
| TW (g) | 23.59±0.46 | 20.07±0.40 | 22.79±0.63 | 23.15±0.46 | 24.13±0.53 | 20.80±0.43 |
| GYP (g) | 42.94±1.16 | 23.96±0.50 | 36.41±0.91 | 31.63±0.96 | 44.25±0.66 | 25.57±0.82 |
| AUDPC | 546.81±11.71 | 95.22±4.09 | 356.64±21.51 | 311.99±16.77 | 138.89±9.40 | 120.70±8.09 |

$F_2$ (23.15 g) and $B_2$ (20.80 g) populations had intermediate test weight compared with both parent HUR 105 (23.59 g) and Tetep (20.07 g), while $B_1$ population (24.13 g) showed slightly higher test weight than recurrent parent HUR 105 (23.59 g), which is desirable for selecting transgressive segregants. HUR 105 (42.94 g) recorded higher grain yield per plant compared with Tetep (23.96 g) while the $B_1$ (44.25 g) yielded more compared with both the parents, but in the $F_1$ (36.41 g) and $F_2$ (31.63 g) populations grain yield was intermediate and $B_2$ (25.57 g) segregating generation give slightly higher grain yield per plant than non-recurrent parent Tetep (23.96 g). The disease progress curve in different generations of cross HUR 105 × Tetep are presented in Figure 1. The sheath blight susceptible parent HUR 105 showed continuous increase in disease severity at an increasing rate from 28.12% at 7$^{th}$ DAI to 49.43% at 21$^{st}$ DAI, while resistant parent Tetep showed lower level of disease severity ranged from 4.83% at 7$^{th}$ DAI to 8.44% at 21$^{st}$ DAI. The $F_1$ (16.88% to 33.04%) and $F_2$ (15.96% to 28.10%) population showed intermediate disease severity compared with both parents, but $F_2$ population showed slightly lower disease severity than $F_1$ population. The backcross generation $B_1$ (7.36% to 12.54%) and $B_2$ (6.17% to 10.98%) showed slightly higher but comparable disease severity than resistant parent Tetep (4.83% to 8.44%). The sheath blight susceptible parent HUR 105 showed high area under disease progress curve (546.81) compared

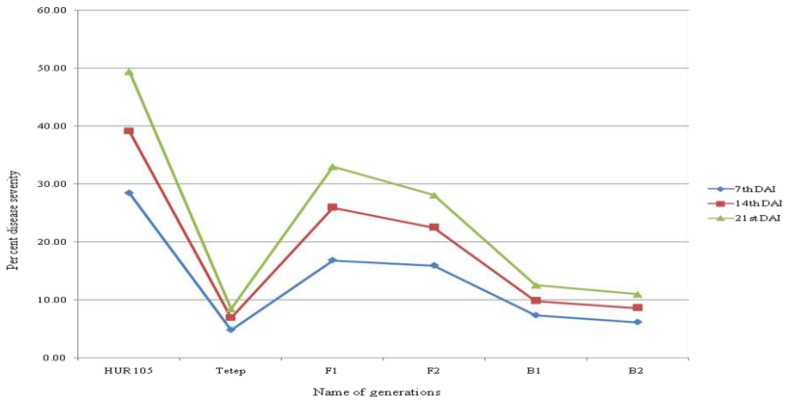


Figure 1. Disease progress curve in different generations of cross HUR 105 × Tetep.

with resistant parent Tetep (95.22) while intermediate in $F_1$ (356.64) and $F_2$ (311.99) populations but both backcross generation $B_1$ (138.89) and $B_2$ (120.70) showed slightly higher area under disease progress curve than resistant parent. Most of the above results of present investigation are in conformity with the findings of Reddy *et al.* (2012).

**Scaling and joint scaling tests**

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 plant height and grain yield per plant indicating presence of epistasis. All the traits related to yield as well as sheath 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, joint scaling test was adopted 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. The adequacy of simple additive-dominance model suggests non-allelic interaction effect (epistasis) is absent and generation means depends only on additive-dominance effect of the gene. Chi square values were significant for all 12 traits in the present 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).

**Gene action**

Digenic non-allelic 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. The estimates of gene effect clearly illustrate high variation in the observed traits (Table 3). Mean and additive components for days to 50% flowering, days to maturity, plant height, number of effective tillers per plant, panicle length, flag leaf length, test weight and grain yield per plant were highly significant. The dominance (*h*) and dominance × dominance (*l*) gene effects displayed opposite signs for the traits *viz*., days to 50% flowering, plant height, number of effective tillers per plant, fertile spikelet per panicle, total number of spikelet panicle, spikelet fertility percentage, test weight, grain yield per plant and area under disease progress curve indicating presence of duplicate epistasis. These results are in conformity with the earlier report of Divya *et al.* (2014) for plant height, number of productive tillers, leaf length, leaf width, panicle length, days to first flowering, filled grains per panicle, total grains per panicle, spikelet fertility, spikelet sterility, test weight, single plant yield and disease incidence. The values of dominance (*h*) and dominance × dominance (*l*) interaction were in the same direction for days to maturity, panicle length and flag leaf length, and the interaction 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 (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). Additive and dominance gene effects were found important in controlling sheath blight disease reaction. The plus sign in the additive gene effect implies that HUR 105 contributes positively to the trait as compared to Tetep, and vice versa. Therefore, the positive sign for (*d*) in the traits like days to 50% flowering, days to maturity, number of effective tillers per plant, panicle length, flag leaf length, fertile spikelet per panicle, spikelet fertility percentage, test weight, grain yield per plant and area under disease progress curve indicates that the high yielding susceptible parent HUR 105 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 Tetep as observed earlier (Paul *et al*., 2003; Cruz *et al*., 2006; Thirugnanakumar et al., 2007; Li *et al*., 2010; Alam *et al*., 2014) which explained dominance genetic effect in yield and disease related traits in rice. On the contrary, Ray and Islam (2008) and Sharifi *et al*. (2011) have reported the importance of additive effects.

**Table 2.** Estimates from scaling and joint scaling tests for twelve quantitative traits.

| Traits | Scaling test | | | | Joint Scaling test | | | |
|---|---|---|---|---|---|---|---|---|
| | Scale A±SE | Scale B±SE | Scale C±SE | Scale D±SE | m±SE | d±SE | h±SE | χ2 |
| DF | -4.93**±1.26 | 3.90**±1.19 | -5.67*±2.83 | 2.32±1.39 | 93.56**±0.29 | -5.57**±0.28 | -9.22**±0.62 | 40.93** |
| DM | -7.20**±1.44 | 2.43±1.25 | -7.27*±2.80 | 1.25±1.39 | 125.31**±0.39 | -6.73**±0.37 | -10.82**±0.72 | 37.51** |
| PH | 12.52**±1.32 | -11.55**±1.12 | -9.36**±3.09 | 5.16**±1.49 | 103.41**±0.43 | 13.52**±0.40 | 7.12**±0.66 | 235.88** |
| ET | 1.24±1.46 | 5.73**±0.82 | 4.87*±1.99 | 1.05±1.08 | 12.11**±0.33 | -2.47±0.33 | -0.14±0.53 | 49.82** |
| PL | -0.65±0.75 | 3.50**±0.89 | 4.75**±1.70 | -0.95±0.89 | 23.54**±0.18 | -0.04±0.18 | -1.23**±0.38 | 23.34** |
| FLL | -4.21**±0.94 | 6.71**±1.04 | -0.06±2.08 | 1.28±1.06 | 21.81**±0.23 | -3.28**±0.23 | 2.64±0**.48 | 78.23** |
| FSP | -1.78±7.68 | -57.62**±8.30 | -69.40**±12.91 | 5.00±6.46 | 159.76**±1.87 | -25.54**±1.84 | 32.70**±3.93 | 67.19** |
| TSP | -15.38±7.48 | -75.28**±8.21 | -79.43**±13.06 | -5.62±6.55 | 180.73**±1.83 | -25.88**±1.80 | 38.06**±3.86 | 96.98** |
| SF% | 5.22*±1.71 | 3.77**±0.99 | -0.83±2.04 | 4.91**±1.18 | 88.16**±0.25 | -2.17**±0.25 | -0.35±0.55 | 26.52** |
| TW | -1.89±0.76 | 1.26±0.66 | -3.37*±1.34 | 1.37*±0.66 | 21.93**±0.17 | -2.04**±0.16 | 1.15**±0.35 | 20.94** |
| GYP | -9.15**±1.14 | 9.23**±1.12 | 13.18**±2.56 | -6.55**±1.26 | 34.79**±0.31 | -11.77**±0.30 | 0.75±0.60 | 215.46** |
| AUDPC | 625.67**±30.88 | 210.46**±27.22 | 107.37±80.65 | 364.38**±35.76 | 273.70**±5.68 | -175.16**±5.49 | -155.75**±14.03 | 480.41** |

** and *: Significant at 1 and 5% level, respectively.

**Table 3.** Estimation of gene effects based on six generation means.

| Traits | m±SE | d±SE | h±SE | i±SE | j±SE | l±SE |
|---|---|---|---|---|---|---|
| DF | 90.16**±0.61 | 9.23**±0.67 | -14.25**±2.87 | -4.63±2.78 | 8.83**±1.47 | 3.60±3.89 |
| DM | 120.90**±0.59 | 10.15**±0.73 | -13.20**±2.88 | -2.50±2.78 | 9.63**±1.70 | -2.27±4.04 |
| PH | 109.69**±0.69 | -19.61**±0.57 | -4.99±3.06 | -10.33**±2.98 | -24.07**±1.64 | 11.29**±3.85 |
| ET | 11.80**±0.41 | 4.28**±0.69 | -1.36±2.22 | -2.10±2.15 | 4.49**±1.57 | 9.07**±3.39 |
| PL | 22.16**±0.37 | 1.76**±0.48 | 0.92±1.82 | 1.90±1.77 | 4.14**±1.04 | 0.95±2.57 |
| FLL | 23.15**±0.45 | 7.87**±0.57 | 0.48±2.18 | -2.56±2.11 | 10.92**±1.24 | 5.05±3.07 |
| FSP | 184.06**±2.33 | 0.92±4.47 | 8.95±13.67 | -10.00±12.92 | -55.83**±9.83 | -49.40*±22.04 |
| TSP | 207.16**±2.43 | -1.23±4.39 | 32.00*±13.81 | 11.23±13.10 | -59.90**±9.66 | -101.90**±21.90 |
| SF% | 88.86**±0.40 | 1.22±0.86 | -9.37**±2.44 | -9.82**±2.36 | -1.45±1.81 | 18.81**±4.00 |
| TW | 23.15**±0.27 | 3.34**±0.39 | -1.78±1.38 | -2.75*±1.32 | 3.15**±0.86 | 2.12±2.06 |
| GYP | 31.63**±0.55 | 18.68**±0.61 | 16.06**±2.60 | 13.09**±2.52 | 18.38**±1.42 | -13.01**±3.53 |
| AUDPC | 311.99**±16.77 | 18.19±12.40 | -693**.14±74.94 | -728.76**±71.52 | -415.20**±27.73 | 1564.89**±94.68 |

** and *: Significant at 1 and 5% level, respectively.

**Number of effective factors**

The estimates of effective factors controlling sheath resistance and yield related traits are presented in Table 4. Estimation of number of effective factors becomes essential to carry out efficient selection in the segregating population. It is important to note that the estimation of number of effective factors is based on independent segregation; if loci are linked a large number will be involved (Parlevliet and Kupier, 1985). The number of effective factors ranged from 1.31 to 4.14 indicated that 1 to 4 genes were involved in the inheritance of resistance to sheath blight. The number of effective factors for grain yield per plant ranged from 0.88 to 1.94, days to 50% flowering from 0.19 to 2.76, days to maturity from 0.27 to 1.67,

plant height from 0.31 to 2.80, fertile spikelet per panicle from 3.77 to 10.32, total number of spikelet per panicle from 1.60 to 5.81 and test weight from 0.20 to 3.25. These results are conformity with the earlier report of Alam *et al.* (2014).

**Character association and path analysis**

The estimates of correlation coefficient (phenotypic) are presented in Table 5. The area under disease progress curve and yield attributing traits was investigated for their relationship with yield as well as themselves. The area under disease progress curve showed significant positive association with days to 50% flowering (0.232*), days to maturity (0.128*), number of effective tillers per plant (0.297**), flag leaf length (0.251**), fertile spikelet per panicle (0.247**), spikelet fertility percentage (0.418**), test weight (0.297**) and grain yield per plant (0.309**), while negative significant with plant height (-0.220*). Grain yield per plant showed positive significant association with days to 50% flowering (0.497**), days to maturity (0.461**), number of effective tillers per plant (0.565**), panicle length (0.232*), flag leaf length (0.692**), fertile spikelet per panicle (0.246**), total number of spikelet per panicle (0.238**), spikelet fertility percentage (0.224*) and test weight (0.539**) indicated that high yielding rice genotypes derived from these materials can be obtained by selecting high number of effective tillers per plant, panicle length, spikelet fertility percentage and test weight which will increase grain yield per plant. Similar trend was observed in the earlier findings (Singh *et al*., 2014 a and b) for plant height, panicle length, fertile spikelet per panicle, total grains per panicle, spikelet fertility and test weight, although their studies were based on pure lines.

**Table 4.** Estimation of minimum number of effective factors (EF) controlling sheath blight resistance and yield related traits.

| Effective factors | Traits | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | DF | DM | PH | FSP | TSP | TW | GYP | AUDPC |
| $EF_1$ | 1.20 | 1.67 | 0.86 | 8.83 | 3.81 | 0.49 | 1.94 | 4.14 |
| $EF_2$ | 0.37 | 0.54 | 0.61 | 7.53 | 3.20 | 0.40 | 1.75 | 2.62 |
| $EF_3$ | 0.40 | 0.56 | 0.69 | 7.26 | 3.02 | 0.43 | 1.85 | 4.09 |
| $EF_4$ | 0.19 | 0.27 | 0.31 | 3.77 | 1.60 | 0.20 | 0.88 | 1.31 |
| $EF_5$ | 2.76 | 1.31 | 2.80 | 10.32 | 5.81 | 3.25 | 1.05 | 3.67 |
| Mean | 0.98 | 0.87 | 1.05 | 7.54 | 3.49 | 0.95 | 1.49 | 3.17 |

**Table 5.** Correlation coefficient (Phenotypic) between area under disease progress curve and yield related traits.

| Traits | DF | DM | PH | ET | PL | FLL | FSP | TSP | SF% | TW | GYP |
|---|---|---|---|---|---|---|---|---|---|---|---|
| DM | 0.956** | | | | | | | | | | |
| PH | -0.608** | -0.602** | | | | | | | | | |
| ET | 0.297** | 0.266** | -0.492** | | | | | | | | |
| PL | 0.201* | 0.158 | -0.250** | 0.168 | | | | | | | |
| FLL | 0.317** | 0.318** | -0.556** | 0.489** | 0.174 | | | | | | |
| FSP | 0.103 | 0.115 | -0.141 | 0.106 | -0.124 | 0.263** | | | | | |
| TSP | 0.094 | 0.101 | -0.121 | 0.030 | -0.139 | 0.248** | 0.941** | | | | |
| SF% | 0.126 | 0.122 | -0.160 | 0.318** | 0.028 | 0.284** | 0.386** | 0.115 | | | |
| TW | 0.454** | 0.421** | -0.504** | 0.341** | -0.002 | 0.437** | 0.292** | 0.275** | 0.186* | | |
| GYP | 0.479** | 0.461** | -0.771** | 0.565** | 0.232* | 0.692** | 0.246** | 0.238** | 0.224* | 0.539** | |
| AUDPC | 0.232* | 0.188* | -0.220* | 0.297** | -0.042 | 0.251** | 0.247** | 0.150 | 0.418** | 0.297** | 0.309** |

** and *: Significant at 1 and 5% level, respectively.

The association between area under disease progress curve and yield related traits were partitioned into direct and indirect effects through path coefficient analysis (Table 6). The partitioning of correlation into direct and indirect effects revealed that the days to 50% flowering (0.523) contributed highest positive direct effect on area under disease progress curve followed by spikelet fertility percentage (0.316), grain yield per plant (0.206), plant height (0.108), test weight (0.105), fertile spikelet per panicle (0.088) and number of effective tillers per plant (0.084). Kumar and Saravanan (2012); Singh *et al*. (2013) reported similar results for days to maturity, number of productive tillers per plant, panicle length, filled grains per panicle and spikelet fertility percentage, although their studies were based on pure lines. Days to maturity (-0.429) showed high negative direct effect on area under disease progress curve followed by panicle length (-0.107), total number of spikelet per panicle (-0.047) and flag leaf length (-0.037). Plant height (0.108) showed direct positive effect on area under disease progress but it showed negative significant association (-0.216*) with area under disease progress, which was only due to high negative indirect effect of days to 50% flowering (-0.318) and grain yield per plant (-0.159). Similar observation was also made by Minnie *et al.* (2013) for plant height, days to 50% flowering and test weight**.** The residual effect observed was 0.70 indicating that other important disease resistance contributing traits need to be included.

**Table 6.** Path coefficient (phenotypic) between area under disease progress curve and yield related traits.

| Traits | DF | DM | PH | ET | PL | FLL | FSP | TSP | SF% | TW | GYP | Correlation with AUDPC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DF | 0.523 | -0.411 | -0.066 | 0.025 | -0.022 | -0.011 | 0.009 | -0.004 | 0.038 | 0.048 | 0.099 | 0.228* |
| DM | 0.500 | -0.429 | -0.065 | 0.022 | -0.017 | -0.011 | 0.010 | -0.005 | 0.037 | 0.044 | 0.095 | 0.182* |
| PH | -0.318 | 0.258 | 0.108 | -0.041 | 0.027 | 0.020 | -0.012 | 0.006 | -0.050 | -0.054 | -0.159 | -0.216* |
| ET | 0.156 | -0.115 | -0.053 | 0.084 | -0.018 | -0.018 | 0.009 | -0.001 | 0.101 | 0.037 | 0.117 | 0.298** |
| PL | 0.106 | -0.069 | -0.028 | 0.014 | -0.107 | -0.007 | -0.011 | 0.007 | 0.008 | -0.001 | 0.048 | -0.040 |
| FLL | 0.162 | -0.132 | -0.060 | 0.042 | -0.019 | -0.037 | 0.023 | -0.012 | 0.088 | 0.046 | 0.144 | 0.245** |
| FSP | 0.054 | -0.050 | -0.015 | 0.009 | 0.013 | -0.010 | 0.088 | -0.044 | 0.122 | 0.031 | 0.051 | 0.248** |
| TSP | 0.049 | -0.043 | -0.013 | 0.003 | 0.015 | -0.009 | 0.082 | -0.047 | 0.036 | 0.029 | 0.049 | 0.150 |
| SF% | 0.063 | -0.051 | -0.017 | 0.027 | -0.003 | -0.010 | 0.034 | -0.005 | 0.316 | 0.018 | 0.046 | 0.418** |
| TW | 0.237 | -0.181 | -0.055 | 0.029 | 0.001 | -0.016 | 0.026 | -0.013 | 0.056 | 0.105 | 0.112 | 0.300** |
| GYP | 0.250 | -0.198 | -0.084 | 0.048 | -0.025 | -0.026 | 0.022 | -0.011 | 0.070 | 0.057 | 0.206 | 0.309** |

Residual effect = 0.70; Value in diagonal indicate direct effect.

## CONCLUSION

The gene action for sheath blight and yield attributing traits indicated that additive, dominance and epistatic genetic components are important for the expression of traits studied. Since considerable amount of dominance effect was also present for most of the traits, selection of superior segregants has to be postponed to later generations until homozygosity is achieved. The traits days to 50% flowering, spikelet fertility percentage, grain yield per plant, test weight, fertile spikelet per panicle and number of effective tillers per plant exhibited positive and significant association, as well as had positive direct effect on area under disease progress curve. Thus, the information on nature and magnitude of gene action for sheath blight resistance gives useful information for plant breeders to develop new rice varieties resistant to sheath blight with desirable yield component traits having high positive direct effect and positive significant association with area under disease progress curve.

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