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Research Article

Study of association between morphological traits and QTLs governing sheath blight resistance in rice (*Oryza sativa L.*)

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Abstract
Rice sheath blight is one of the most serious diseases of rice. In the current study, the relationship between morphological traits and sheath blight resistance was investigated by using 1545 recombinant inbred lines. Correlation analysis showed that culm angle, flag leaf angle, flag leaf length and plant height were significantly correlated with sheath blight resistance. Genome-wide association studies revealed that a gene controlling culm angle (*TAC1*), three quantitative trait loci (QTL) governing plant height (q*PHT1-1*), penultimate leaf angle (q*PLA-1*) and days to 50% flowering (q*DFF-7*) were found to be adjacent to the regions of q*SB9*, q*SBR1-1* and q*SB7*, the QTLs conferring sheath blight resistance. Except for these cases, no QTL underlying other traits was detected near the chromosomal region associated with sheath blight resistance. The results concluded that the morphological traits were not the main factors responsible for the sheath blight resistance but had some indirect influence to evade infection of the pathogen. An efficient approach in resistance breeding for sheath blight would be to pyramid major QTLs for sheath blight resistance and select those morphological traits that favour resistant reaction.

Keywords: QTL, morphological characters, correlation, GWAS, sheath blight resistance

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most vital and staple food crops in the world for more than 50% of the global population. Rice provides 35–75% of the total calories to more than three billion Asians (Rudresh *et al*., 2021). Considering the increase in human population and decline in natural resources, the development of new high yielding rice varieties has become essential (Christina *et al*., 2021). Rice sheath blight is considered one of the devastating diseases of rice worldwide leading to significant yield losses in many rice

growing counties, it is caused by a necrotrophic pathogen *Rhizoctonia solani* (Rao *et al.*, 2020). Because of the unique symptoms exhibited by this disease, it is referred as "rotten foot stalk", "mosaic foot stalk" and "snake skin disease" (Molla *et al*., 2020; Zhang *et al.,* 2019). This disease has become widespread recently because of the intensification of rice-cropping systems with the development of new short stature, high tillering, high yielding cultivars, high plant densities and an increase in nitrogen fertilization. These factors promote disease spread by providing a favourable microclimate for the disease agent due to a dense leaf canopy with an increased leaf-to-sheath and leaf-to-leaf contact (Banniza *et al*., 2007).

The necrotrophic sheath blight pathogen possesses a broad range of hosts, there are few germplasm lines in rice that are known to show resistant reactions against this pathogen, and most of the breeders are focused on harnessing these resistant sources to breed cultivars. Upon intensive study, it is believed to be controlled by many genomic regions dispersed across the genome (Pinson *et al*., 2005; Zuo *et al*., 2013). It is widely believed that the quantitative nature of resistance could be advantageous for evolving varieties with durable/ horizontal resistance (Poland *et al*., 2009). More than 60 quantitative trait loci (QTLs) have been identified to govern sheath blight resistance (Zeng *et al*., 2011).

Several studies have indicated that ecological and morphological traits have a great influence on sheath blight resistance, such as tiller angle, plant compactness, width and length of flag leaf, plant height, days to heading and leaf morphology (Pinson *et al.,* 2005; Zou *et al.,* 2000; Zuo *et al*., 2014). The rate of infection and development of the disease is controlled not only by genes but also by the microclimate prevailing in the paddy field. Certain morphological traits do influence the speed with which infection spreads, hence it is of utmost importance to understand the association between morphological traits and sheath blight resistance. The objective of this study was to understand the correlation between morphological characters and sheath blight resistance and to locate the chromosomal regions responsible for morphological traits to examine the association between these regions and QTLs responsible for sheath blight resistance.

MATERIALS AND METHODS

The material used for the present study consisted of 1545 RILs created by crossing resistant lines with agronomically superior susceptible lines involving Jasmine 85, Tetep & MTU 9992 as resistant parents and TN1, Swarna-Sub1, II32B, IR54 & IRBB4 as susceptible parents. A total of eleven crosses were used for the study (Jasmine 85 × TN1, Jasmine 85 × Swarna-Sub1, Jasmine 85 × II32, Jasmine 85 × IR54, Tetep × TN1, Tetep × Swarna-Sub1, Tetep × II32B, Tetep × IR54, MTU 9992 × TN1, MTU 9992 × II32B and MTU 9992 × IRBB4). The RILs were generated by following the single seed descent method (SSD) at Rapid Generation Advancement/ Speed breeding facility of Pioneer Hi-Bred Pvt. Ltd. Research Centre at Tunkikalsa village, Medak district, Telangana. All the 1545 RILs derived from eleven crosses were phenotyped for sheath bight reaction and morphological characters in two hot spot locations (Seethanagaram and Draksharam) of East Godavari District of Andhra Pradesh state, India (Latitude $16^0$08' N and Longitude $81^0$08' E, Latitude $17^0$10'N and Longitude $81^0$41' E).

The experiment comprising of RILs along with parental lines was planted in a randomized complete design with two replications. Row length of 1.2 m with a row-to-row distance of 15 cm and plant to plant distance of 10 cm was considered to ensure a dense population which was congenial for the development of disease. TN1 was used as a susceptible check and was sown after every two rows as well as all along the border to increase the disease pressure so as to serve as spreader rows. In the present study, the virulent local East Godavari isolate of rice sheath blight pathogen was utilized for disease screening. Before the inoculation, the fungus was cultivated in potato dextrose agar medium at optimal temperature for 3–4 days, followed by transferring of the disc of medium with mycelia for multiplication. To ensure stringent screening for better disease development, artificial inoculation was done by spraying the mycelia uniformly at the base of the plant at the maximum tillering stage. The data of sheath blight score (SHBSC) was recorded at peak milking stage to dough stage by visualizing the relative lesion length to height (%) using a 1-9 scale based on the development of lesion from the lower to the upper part of the plant on a scale from 1 (Resistant) to 9 (Susceptible) thereby getting total of six phenotypic classes, where score 1: no infection, score 2: 1-20%, score 3: 21-30%, score 5: 31-45%, score 7: 46-65%, score 9: 66-100%.

Data on six characters were collected from four individual plants in each replication, the average value was used for analysis. The characters used for the study were, days to 50% flowering (DFF), plant height (PHT), flag leaf length (FLL), flag leaf width (FLW), penultimate leaf angle (PLA) and culm angle (CLA). All the RILs used for the study were genotyped using the Infinium marker platform which is a fixed plex comprising 6564 markers. The SNP genotyping was done at the marker technology lab of Pioneer Hi-Bred International Limited at Johnston, Iowa State, United States of America. Simple Pearson's correlation coefficients were estimated among morphological traits and sheath blight disease scores (SHBSC). The analysis was done with "**TASSEL**" application. TASSEL known as **T**rait **A**nalysis by a**SS**ociation**, E**volution and **L**inkage. In the current study, the analysis was done with the MLM model as it is the most robust in terms of correcting population structure.

MLM model equation: $y = S_{i+} Q/PCA/PCoA + K + e$

[phenotype (y) and markers (Si) one at a time, where i=1 to m, and m is the number of markers, Q/PCA/PCoA is population structure term, kinship(K) and residuals (e)]

Analysis was done separately for populations involving resistant parents Jasmine 85, Tetep and MTU 9992 to systematically trace the genomic regions governing sheath blight resistance. For the identification of QTLs controlling morphological traits, the association analysis was done by combining all 1545 RILs from eleven populations.

RESULTS AND DISCUSSION

The frequency distribution of 1545 RILs evaluated showed continuous variation across all populations studied for sheath blight (**Fig. 1, 2 and 3**). The genotypic analysis was done with the large number of markers which were uniformly distributed throughout the genome (**Table 1**), polymorphic markers between parents across populations studied ranged from 1407 to 2849, MTU 9992XTN1 and MTU 9992XIRBB4 possessed the lowest and the highest number of informative markers (**Table 1**).

Pearson's correlation coefficients were estimated among all the 6 morphological traits and SHBSC (**Table 2**). Significant negative correlations were detected between

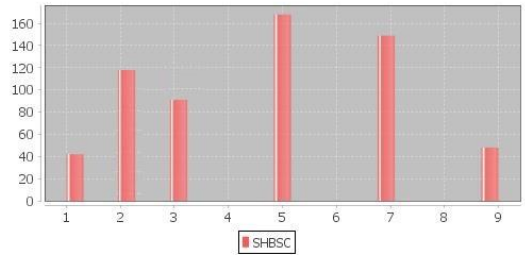

Fig. 1. Frequency distribution of SHB scores of RILs involving populations of Jasmine 85

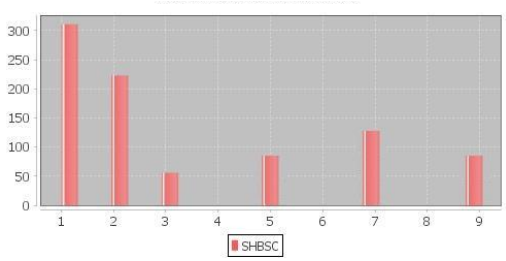

Fig. 2. Frequency distribution of ShB scores of RILs involving populations of Tetep

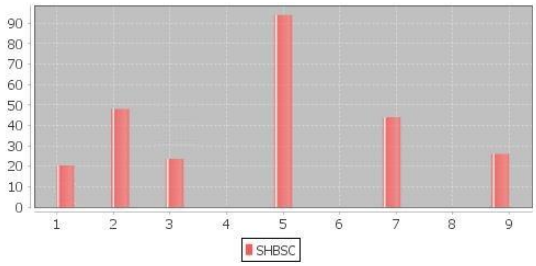

Fig. 3. Frequency distribution of ShB scores of RILs involving populations of MTU 9992

Table 1. List of informative markers available across the genome for each population used for analysis

Populations	Number of RILs	Total Markers	Polymorphic Markers
Jasmine 85/TN1	121	6564	2522
Jasmine 85/Swarna-Sub1	139	6564	2627
Jasmine 85/II32B	144	6564	2586
Jasmine 85/IR54	161	6564	2663
Tetep/TN1	221	6564	2806
Tetep/Swarna-Sub1	158	6564	2278
Tetep/II32B	241	6564	2702
Tetep/IR54	94	6564	2796
MTU 9992/TN1	50	6564	1407
MTU 9992/II32B	122	6564	2314
MTU 9992/IRBB4	94	6564	2849
Total	**1545**		

Table 2. Pearson's correlation coefficient (r) among morphological traits and sheath blight score

Character	SHBSC[a]	CLA[b]	PLA[c]	FLW[d]	FLL[e]	PHT[f]	DFF[g]
SHBSC	1	-0.487*	-0.47*	0.041	-0.356*	-0.485*	-0.139
CLA		1	0.888**	-0.134	0.52*	0.682*	0.001
PLA			1	-0.112	0.498*	0.669*	0.014
FLW				1	-0.156	-0.181	0.013
FLL					1	0.563*	-0.005
PHT						1	0.01
DFF							1

* and** indicate a significant difference at $p < 0.1$ and $p < 0.05$ level of probability, respectively. [a]Sheath blight scores, [b]Culm angle, [c]Penultimate leaf angle, [d]Flag leaf width, [e]Flag leaf length, [f]Plant height, [g]Days to 50% flowering

SHBSC and CLA (-0.487*), SHBSC and PLA (-0.47*), SHBSC and FLL (-0.356*) and SHBSC and PHT (-0.485*), similar results were observed in earlier researches also (Han *et al*., 2003 and Hossain *et al*., 2016). However, from our observations, we found that culm angle (tiller angle), penultimate leaf angle, flag leaf length and plant height were significantly correlated with sheath blight resistance. The flag leaf and penultimate leaf in rice plants contribute significantly to grain yield in rice. The angle between the stem and leaf (leaf angle) controls the influence of the flag and penultimate leaves. For example, a genotype with semi erect leaf attitude produces less shade in the plant canopy and captures more light in comparison with the droopy phenotype, particularly at the lower part of the plant. Sheath blight pathogenicity is fundamentally favored by the shady, hot and humid microenvironment in the paddy field. This is the reason why sheath blight is commonly less predominant in the upper part of the plant than the lower part. Since, semi erect leaf morphology reduces the shading effect at the lower part of the plant, a genotype with semi erect leaves escapes an attack by sheath blight pathogen and shows low ShB invasion. Similar results were also observed by Loan *et al.* (2004) and Channamallikarjuna *et al*. (2010).

The association mapping with a mixed linear model (MLM) discovered sixteen QTLs from mapping populations (RILs) of three sources of resistance on different chromosomes. In Jasmine 85, five QTLs were found on Chr1 (Q*Rh1*), Chr3 (q*SB-3* l), Chr9 (q*SB-9*), Chr10 (q*SBR10-1*) and Chr11 (q*SB-11-1*) with $-\text{Log}_{10}$ (*P*-Value) more than 3 and R^2 value ranged from 5.0 to 5.5% (R^2 value depicts the amount of phenotypic variance explained by the marker linked to QTL). The signals detected were near the proximity where some of the QTLs were already discovered earlier, but the one detected on Chr 10 (q*SBR10-1*) was a novel QTL (**Fig. 4 and Table 3**).

In Tetep, eight QTLs were observed on Chr1 (q*SBR1-1*), Chr2 (q*SBR2-1*), Chr5 (q*SBR5-1* and q*SBR5-2*), Chr6 (q*SBR6-1*), Chr7 (q*SBR7-1*), Chr8 (q*SBR8-1*) and Chr11 (q*SBR11-1*) with $-\text{Log}_{10}$ (*P*-Value) more than 4 and R^2 values ranged from 7.7% to 19.1%. Apart from QTLs reported earlier, four new QTLs were detected on Chr2 (q*SBR2-1*), Chr5 (q*SBR5-1* and *qSBR5-2*) and Chr6 (q*SBR6-2*) (**Fig. 5 and Table 3**).

However, in MTU 9992, all the three QTLs discovered were novel, Chr2 (q*SBR2-2*), Chr6 (q*SBR6-2*) and

Chr11 (q*SBR11-2*) with $-Log_{10}$ (*P*-Value) more than 3 and R^2 values ranged from 5.2% to 6.4% (**Fig.6 and Table 3**). ShB QTLs were reported in many studies on multiple chromosomes in Jasmine 85 (Zou *et al*., 2000; Liu *et al*., 2009) and Tetep (Sha and Zhu, 1989; Channamallikarjuna *et al.,* 2010).

Table 3. Detailed information on ShB QTLs detected on different chromosomes

Trait	Marker	Chr	Source	Reported QTL	New QTL	-Log_{10}(*P*-value)	R^2 (%)
SHBSC	SNP101TP5-001	1	Jasmine 85	Q*Rh1*		3.345	5.4
SHBSC	SNP101WMR-001	3	Jasmine 85	q*SB-3*		3.407	5.5
SHBSC	SNP102151-001	9	Jasmine 85	q*SB-9*		3.283	5.3
SHBSC	SNP101U6D-001	10	Jasmine 85		q*SBR10**	3.383	5.5
SHBSC	SNP101UHW-001	11	Jasmine 85	q*SB-11-1*		3.377	5.5
SHBSC	SNP03790-1	1	Tetep	q*SBR1-1*		16.1	19.1
SHBSC	SNP101VHF-001	2	Tetep		q*SBR2-1**	7.154	11.6
SHBSC	SNP101XV7-001	5	Tetep		q*SBR5-1**	4.757	7.7
SHBSC	SNP01177-1	5	Tetep		q*SBR5-2**	4.757	7.7
SHBSC	SNP05385-1	6	Tetep		q*SBR6-1**	6.159	10
SHBSC	SNP13515-001	7	Tetep	q*SBR7-1*		10.842	15.6
SHBSC	SNP10208P-001	8	Tetep	q*SBR8-1*		9.568	13.5
SHBSC	SNP101UWB-001	11	Tetep	q*SBR11-1*		5.224	8.5
SHBSC	SNP101W2M-001	2	MTU 9992		q*SBR2-2**	3.231	5.2
SHBSC	SNP101YH1-001	6	MTU 9992		q*SBR6-2**	3.412	5.5
SHBSC	SNP07570-1	11	MTU 9992		q*SBR11-2**	3.923	6.4

*, new QTL was named with trait abbreviation plus chromosome number. If more than one QTL affecting a trait was identified along the same chromosome, they were distinguished by number.

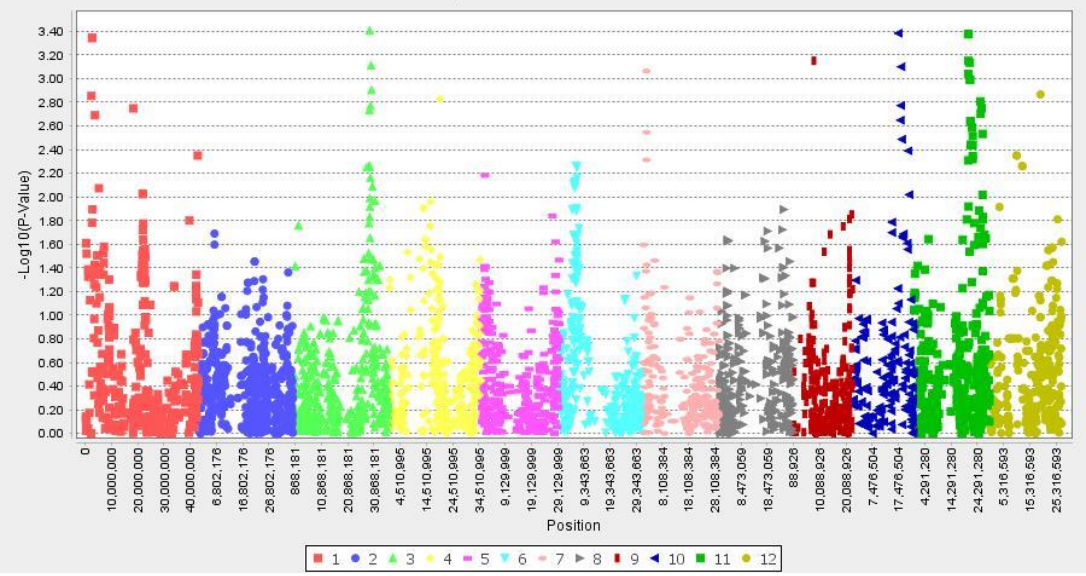

Fig. 4. Manhattan plot depicting genome-wide association results for sheath blight in Jasmine 85 populations using mixed linear model (MLM) for analysis

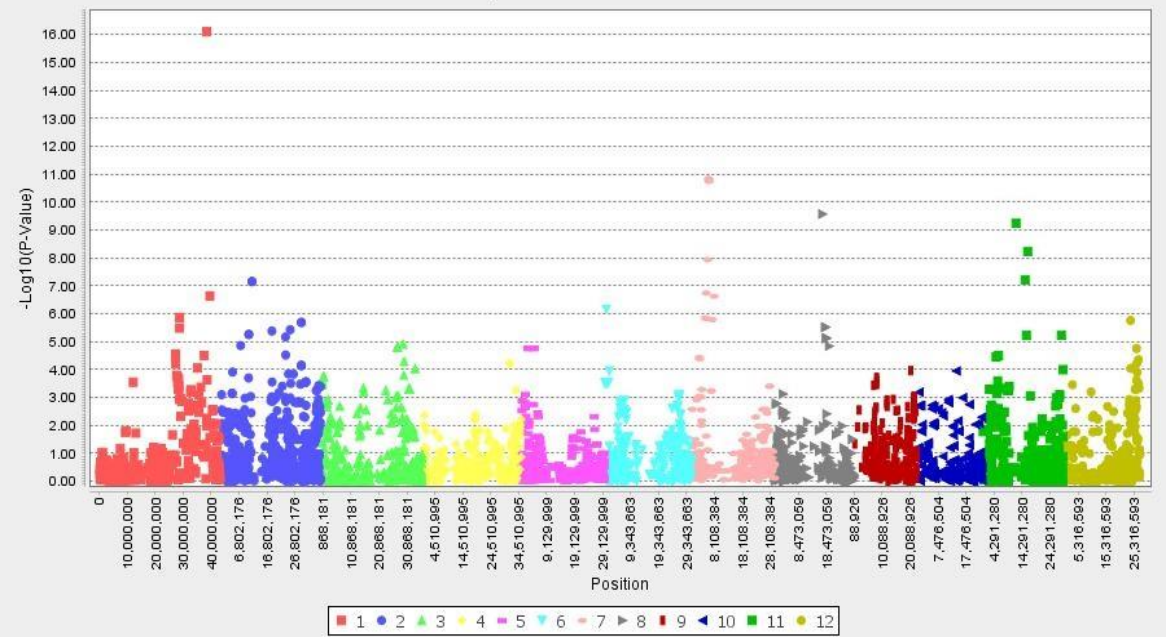

Fig. 5. Manhattan plot depicting genome-wide association results for sheath blight trait of Tetep populations using mixed linear model (MLM) for analysis

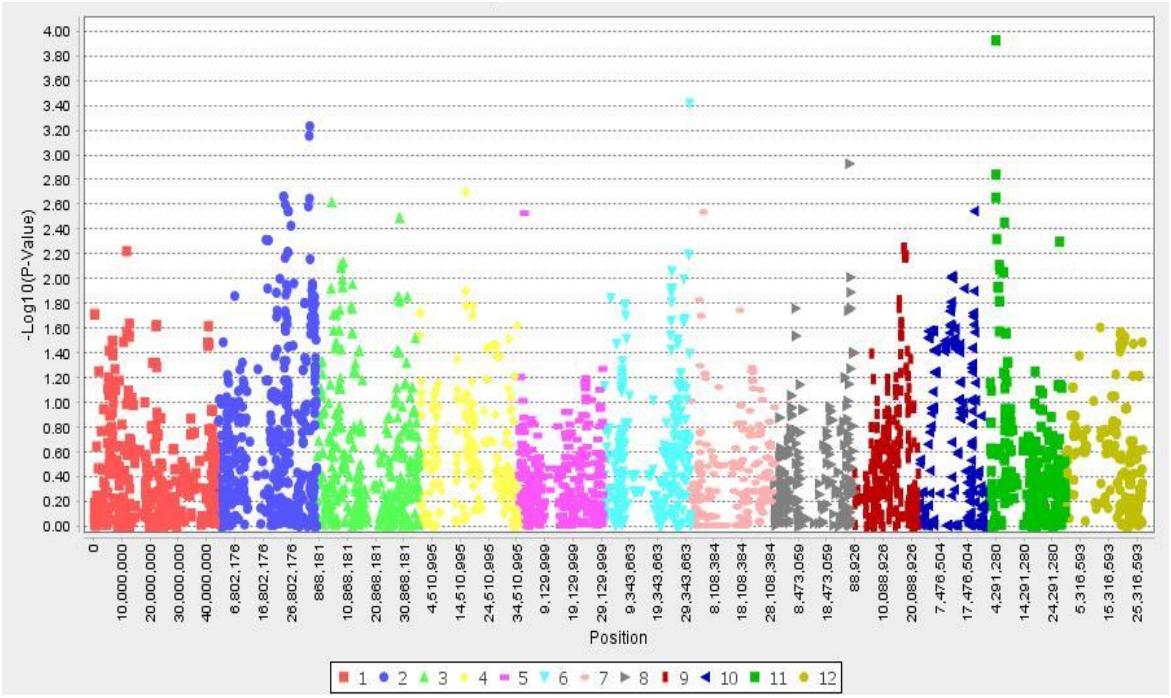

Fig. 6. Manhattan plot depicting genome wide association results for sheath blight trait of MTU 9992 populations using mixed linear model (MLM) for analysis

Table 4. Information on QTLs of morphological characters detected on different chromosomes

Trait	Marker Name	Chromosome	QTL Detected	-Log10(P-Value)	R^2 (%)
CLA[a]	SNP102151-001	9	*TAC1*	11.505	10.105
PLA[b]	SNP03790-1	1	q*PLA-1*	12.972	11.572
	SNP06850-1	8	q*PLA-8*	14.375	12.975
FLW[c]	SNP101U5F-001	10	q*FLW-10-1*	6.55	5.15
	SNP101U5B-001	10	q*FLW-10-2*	6.078	4.678
FLL[d]	R17859-001	1	q*FLL-1*	11.646	10.246
	SNP05073-1	4	q*FLL-4*	12.693	11.293
DFF[e]	SNP13515-001	7	q*DFF-7*	14.225	12.825
	SNP01781-1	6	q*DFF-6*	12.307	10.907
PHT[f]	SNP03790-1	1	q*PHT-1*	17.066	15.666
	SNP06850-1	8	q*PHT-8*	11.858	10.458

[a]Culm angle, [b]Penultimate leaf angle, [c]Flag leaf width, [d]Flag leaf length, [e]Days to 50% flowering and [f]Plant height

From the mapping populations (1545 RILs) studied eleven QTLs were detected controlling six morphological traits on different chromosomes (**Table 4**). One QTL was detected on Chr9 (q*CLA-9*) controlling culm angle with $-Log_{10}$ (*P*-Value) 11.505 and R^2 values of 10.1 per cent. Two QTLs were discovered on Chr2 and Chr8 (q*PLA-1* and q*PLA-8*) controlling penultimate leaf angle with $-Log_{10}$ (*P*-Value) 12.972 and 14.375 and R^2 values of 11.5% and 12.9 per cent, respectively. Two QTLs were identified on Chr10 (q*FLW-10-1* and q*FLW-10-2*) controlling flag leaf width with $-Log_{10}$ (*P*-Value) 6.55 and 6.07 and R^2 values of 5.1% & 4.6% respectively. Two QTLs were detected on Chr1 and Chr4 (q*FLL-1* and q*FLL-4*) controlling flag leaf length with $-Log_{10}$ (*P*-Value) 11.64 & 12.69 and R^2 values of 10.2 and 11.2 per cent, respectively. Two QTLs were discovered on Chr6 and Chr7 (q*DFF-6* and q*DFF-7*) controlling days to 50% flowering with $-Log_{10}$ (*P*-Value) 12.3 and 14.22 and R^2 values of 10.9 and 12.8 per cent, respectively. Two QTLs were detected on Chr1 and Chr8 (q*PHT-1* and q*PHT-8*) controlling plant height with $-Log_{10}$ (*P*-Value) 17 and 11.85 and R^2 values of 15.6 and10.4 per cent, respectively.

The information about the markers linked to QTLs of morphological traits helped to detect was there any QTL governing sheath blight was linked to the same marker indicating co-segregation and the possibility of enhanced resistance reaction by such QTL in the genotype possessing favorable allele .

In the current study, a marker SNP03790-1 (Chr1) was linked to QTLs (q*PLA-1* and q*PHT-1*) controlling penultimate leaf angle and plant height, respectively and was also linked to q*SBR1-1*, one of the large effects QTL controlling sheath blight resistance. The linkage between plant height QTL (q*PHT-1*) and sheath blight QTL (q*SBR1-1*) was reported by Srinivasachary *et al*. (2011). Also, a marker SNP102151-001 linked to gene *TAC1* governing culm angle (tiller angle) was found to be linked to a large effect QTL q*SB-9* which governs sheath blight resistance, such observation was made by Zuo *et al*. (2014). Similarly, one more QTL q*DFF-7* controlling days to 50% flowering was linked to SNP13515-001 marker which was close to q*SB7* QTL of sheath light resistance, the results conformed to results of Li *et al*. (1995).

In the present study, findings from the analysis of molecular data and morphological data supported each other strongly for a few traits only, only three ShB QTLs were observed to be linked to regions controlling a few morphological traits. For most morphological traits, their inheritance was independent of sheath blight resistance, and the associations between them and sheath blight resistance were not significant.

Pyramiding all the QTLs identified so far into a susceptible variety is a challenging task as resistance is governed not only by several large effect QTLs but also by medium to small effect QTLs as well. The inheritance of disease resistance is complex, hence genomic selection approach could be rewarding to breeding for sheath blight resistance. Genomic selection considers marker effects of all loci dispersed across the genome to provide genomic estimated breeding values which can be used for the selection of breeding lines with resistance to sheath blight.

The results of the current investigation facilitated to discover a new regions controlling sheath blight resistance and helped to have a better understanding of the genetic basis for sheath blight resistance in rice. The study showed that rice sheath blight resistance is genetically controlled but also influenced by certain morphological characters such as plant height, leaf and culm angle. To conclude

the strategy to breed a sheath blight resistant rice cultivar should be through genomic selection to identify a line with a congregation of many QTLs for sheath blight resistance and selection of morphological traits which favor resistant reaction.

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