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QTL analysis in Aromatic Rice of Assam, India

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Abstract

The study was carried out to identify quantitative trait loci (QTLs) controlling 12 morphological traits in rice using a F_2 derived from *Ranjit* and *Kola Joha* cross. A framework linkage map of 1387.9cM was developed using 102 SSR markers and other few markers linked to aroma. QTL analysis based on composite interval mapping identified 24 QTLs was for 12 traits. Among them two QTLs were identified for grain aroma each on chromosome 5 and chromosome 8, out of which the QTLs between Aro1-BAD2 is in similar position with aroma gene of *Basmati* rice. Most of the QTLs identified in the current study, showed a range of partial to over-dominance effects, indicating complexity of the traits under consideration. Some genomic regions were associated with more than one trait, indicating linkage and/or pleiotropic effects. Marker linked to the QTLs can be considered for use in marker assisted breeding as being confirmatory to other reports.

Introduction

Northeast India (NE) particularly Assam is a rich source of genetic diversity of rice [1]. The farmers of this region still use their traditional cultivars which not only suit to their taste but also provide crop security. The NE, India is also the home to many locally adapted aromatic and quality rice land races. Among the various classes of cultivated rice varieties, Assam has a unique class of scented rice, locally called as '*Joha*', which is very popular among the farmers of this region. *Joha* rice is primarily used in the social and religious festivals. The cultivation of few *Joha* rice land races in Assam in spite of the onslaught from new high yielding varieties, demonstrate its popularity and utility among the masses. *Joha* rice occupies a premium position in the local markets than other classes of rice and there is immense possibility for export of this class of rice. Except cooked grain elongation ratio, *Joha* cultivars of Assam have compatible aroma and quality as that of other scented rice of India. However, the class of aromatic rice has not been studied by researchers [2]. As a result of which basic genetic insights in the genetics of aroma and yield attributes are becoming a limiting factor for genetic improvement of *Joha* rice.

Lorieux et al. [3] reviewed the genetics of aroma and concluded that a single recessive gene was responsible for the production of aromatic rice plants. This single recessive fragrance gene (*fgr*) was earlier identified to be linked to the RFLP clone RG28 on chromosome 8, at genetic distance of 4.5 cM [4]. Fine mapping and sequence analysis identified a betaine aldehyde dehydrogenase gene (BADH2) associated with the fragrant phenotype [5]. Though Talukdar et al. [6] reported the presence of similar gene for aroma in *Joha* rice based on association study using SSR markers, this results need confirmation to facilitate the breeders to deploy markers linked to aroma in a *Joha* rice improvement programme. There is complicacy in formulating the breeding programme for genetic manipulation of aroma in *Joha* rice due to limited knowledge in genetics of aroma and difficulty in objective assessment of aroma during selection programme. In such circumstances, QTL analysis is one of the best options to elucidate the underlying genetics of aroma and other traits in *Joha* rice and this will also facilitate marker aided selection of useful genes for aroma in the variety development programme for development of high yielding *Joha* rice.

Materials and Methods

The rice mapping population used in this study was a set of 96 F_2 plants derived from a class between *Ranjit*, a high yielding variety of Eastern India developed by AAU, Jorhat, and *Kola Joha*, a popular aromatic rice landrace of Assam. F_2 plants were grown in two numbers of blocks in Augmented RBD design along with parents *Ranjit* and *Kola Joha*. Data on individual plant basis were recorded for plant height (cm) , tiller number, time of heading (days), panicle length (cm), number of grains per plant, grain length (mm), grain width (mm), grain length/grain width ratio, decorticated grain length (mm), decorticated grain width (mm), decorticated grain length/grain width ratio, and yield per plant (g). Aroma in leaves of the mapping population was determined according to the method described by Sood and Siddiq [7]. The data were subjected to analysis of variance following Augmented design II [8]. Skewness (K_3), the third degree statistics and Kurtosis (K_4), the fourth degree statistics were estimated according to Snedecor and Cochran [9] to understand the nature of distribution of different traits as described by Fisher et al. [10] and number of genes controlling the traits as by Robson respectively. [11]

Molecular marker analysis

DNA from each F_2 plant was extracted from fresh leaves following the protocol of Plasckhe et al. [12] with slight modification. A total of 137 primer pairs were selected and primer sequences were obtained

from Gramene (http://www.gramene.org). From these 102 SSR polymorphic markers were used for linkage map construction. Seven aromatic primers were selected for analyzing the genetic variability to aroma in F_2 plants (Table 1). The amplification conditions were based on the procedure of Rathi and Sarma [13].

S No.	Primer name	Chromosome No.	Forward sequence (5`-3`/)	Reverse sequence (5`-3`)	Reference
1	BADEX7-5	8	TGTTTTCTGTTAGGTTGCATT	ATCCACAGAAATTTGGAAAC	[14]
2	Aro1	8	CATCTATCCTCCTCGGGCAACA	GGCGGCGTCATATCCAACA	[15]
3	Aro7	8	ATTTGCCTCCTGAGTCTG	GAGGATGGGGAAGATAAA	[15]
4	BAD2	8	TTGTTTGGAGCTTGCTGATG	AGTGCTTTACAAAGTCCCGC	[16]
5	RM5474	3	AAGTGTTGGTGAGCATAGC	TTTGTGTTTGGAGAGACGAG	[17]
6	RM282	3	CTGTGTCGAAAGGCTGCAC	CAGTCCTGTGTTGCAGCAAG	[17]
7	RM223	8	GAGTGAGCTTGGGCTGAAAC	GAAGGCAAGTCTTGGCACTG	[18]

Table 1: List of primers linked to aroma used in association analysis and linkage mapping.

Linkage map construction and QTL analysis

Based on the marker segregation data of polymorphic SSR loci, linkage map was constructed using software Mapmaker v 3.0 [19] with a threshold of 49 cM for mapping distance and 2.5 LOD. The recombination frequencies were converted into genetic distances using Kosambi mapping function [20].

QTL mapping was done using Composite interval mapping (CIM) using the Windows QTL Cartographer 2.5 [21]. A LOD score of 3.0 was taken as criteria to define a putative QTL. The relative contribution of a genetic component (R_2) was calculated as the proportion of the phenotypic variation explained (PVE). The QTLs explaining more than 20 per cent phenotypic variation were considered as major QTLs. The additive effects and R_2 of the detected QTL were estimated by the *Zmapqtl* procedure inbuilt in the QTL Cartographer. The linkage map diagram showing the QTLs positions was generated using MapChart [22]. Average levels of dominance (h) were estimated using the ratio dominance (d)/additive effects (a) [23]. Gene action was determined on the basis of the average level of dominance by using the criteria of Stuber et al. [23]: additive (A)=0 to 0.20; partial dominance (PD)=0.21 to 0.80; dominance (D)=0.81 to 1.20; and over dominance (OD)>1.20.The naming for loci with significant additive effect followed the rules of nomenclature [24], while for the loci with non-significant additive effect and significant epistatic effect, the first letter 'q' was omitted contrasting with those foregoing loci.

Results and Discussion

Genetic variability among F_2 population

The analysis of variance for F_2 population (Table 2) of the *Ranjit* X *Kola Joha* cross revealed the existence of significant variation among F_2 lines for all the characters except for plant height, grain width and yield/plant. Parents differed significantly from segregating lines which might be due to recombination of genes from both parents.

Trait distribution pattern

In this present investigation all the traits under study showed transgressive segregation. Most of the characters showed asymmetrical distribution rather than normal distribution compared to parents in Table 2. They are positively or negatively skewed. According to Rieseberg et al. [25], transgressive segregation resulted from recombination between parental lines that possess quantitative trait loci (QTLs) with antagonistic effects (*i.e.* QTLs with effects that are in the opposite direction to parental differences for those traits). Transgressive segregation provides an opportunity for the production of extreme phenotypes at both above and below the species level and helps in adaptive evolution and speciation. Transgressive segregation observed in the F_2 population offers scope of identifying desirable segregants to develop improved breeding lines as varieties.

SSR Markers	Linkage group												
Chromosome no	1	2	3	4	5	6	7	8	9	10	11	12	Total
Total marker surveyed	15	9	10	9	14	12	10	19	10	8	12	8	136
Monomorphic makers	3	1	2	2	4	1	2	2	1	0	1	2	21
Polymorphic markers	12	8	8	7	10	10	8	17	9	8	11	6	114
Percent polymorphism	80	88.9	80	77.8	71.4	83.3	80	89.5	90	100	91.7	75	83.8
Marker used for map construction	9	8	7	6	9	9	7	14	9	8	10	6	102

Table 2: SSR markers used for map construction in the F2 lines of the cross Ranjit x Kola Joha.

The gene action for the quantitative traits in the segregating generations was found out based on the frequency distribution of traits through third and fourth order statistics viz., skewness and kurtosis. Kurtosis which is always negative or near to zero in the absence of gene interaction and positive only in the presence of gene interaction [26-28]. For a normal distribution, skewness is equal to zero in the absence of gene interaction, while it is greater and smaller than zero in the presence of complementary and duplicate gene interactions, respectively. In a frequency distribution of a segregating generation, Skewness could result when certain combinations of genes are lethal, presence of incomplete linkage of certain genes, presence of epistasis and one gene has a much larger effect than others [29]. Accordingly, complementary gene interaction might be attributed for traits plant height, no of grains/panicle, grain length/grain width, decorticated grain length/decorticated grain width and grain yield/plant in the F_2 population in this study (Table 2). Similar findings were also reported by Ashwini et al. [30] in rice, warranting intense selection is needed for those traits with complementary gene action [31]. Duplicate gene interaction with equal frequencies of positive and negative alleles was observed for traits tiller number/plant, grain length, and time of heading. The positive values of kurtosis indicates leptokurtic curve and negative kurtosis indicates platykurtic curve [32]. In this study, except grain length, remaining all the significant characters showed leptokurtic distribution. Traits showing leptokurtic distribution are usually under the control of few segregating genes and traits showing a platykurtic distribution usually represent characters that are controlled by many genes [29]. This indicated that the genetic control of grain length in the F_2 mapping population might be under the control of many genes and those remaining traits showing leptokurtic distribution might be considered under the control of few segregating genes.

Negatively skewed and leptokurtic distribution are considered as an evidence for involvement of fewer number of dominant genes [31] with increasing effects, and also coefficient of skewness significantly deviates from zero indicating presence of duplicate gene interaction for inheritance of traits [33]. Maximizing the genetic gain in respect of these traits with negatively skewed distribution requires mild selection from the existing variability [31].

The results on gene interaction in this study needs to be further confirmed with more detailed genetic analyses like, diallel analysis, generation mean analysis etc. due to the exploratory nature of third degree and fourth degree statistics.

QTL mapping

The linkage map was constructed using software Mapmaker v 3.0 [19]. The molecular linkage map was consisted of 102 SSR markers and seven markers linked to aroma covering total genetic distance 1387.9 cM with an average distance of 13.6 cM between adjacent markers (Figure 1). The details of the number of polymorphic markers given in Table 3 showed that the chromosome-wise total number of polymorphic SSR marker per loci ranged from 6 to 12. Comparison of the resulting linkage map and the maps of the Chen et al. [34], Temnykh et al. [18] and McCouch et al. [35] showed that all markers were located in the expected order on the chromosomes.

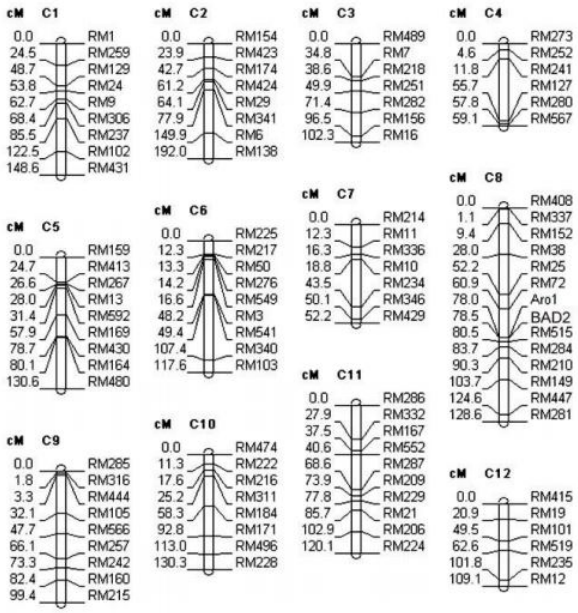

Figure 1: Framework linkage map of f2 mapping population from ranjit x kola joha cross.

	Block (ignoring Treatments)	Treatment(eliminating Blocks)	Parents	Entries (ignoring Blocks)	Plants	Parents vs. plants	Error	Range	Skewness (K3)	Kurtosis (K4)	Mean ± std.error
df	2	95	1	95	93	1	2				
Plant height	41.23	190.26	1362.94*	189.49	120.01	5476.94**	23.51	91.542 - 157.217	0.593*	1.476*	122.003 ± 1.302
Tiller no.	16.03*	26.88**	4.17 *	27.19**	27.64**	8.64 *	0.17	3.167 - 32.667	-0.16	0.462	16.385 ± 0.531
Panicle length/ plant	6.11*	8.87*	75.40**	8.94*	7.56*	70.86**	0.11	17.552 - 31.537	0.304	0.176	25.493 ± 0.306
No. of grains	140.74	423.96	28.17	425.84	244.51	17687.04**	26.17	94.000 - 161.500	0.646*	1.075*	131.724 ± 1.832

Grain Length (GL)	0.24	0.60*	0.95*	0.60*	0.60*	0.68*	0.02	6.412 - 9.777	-0.178*	-0.823	8.155 ± 0.084
Grain width (GW)	0.02	0.04	0.05	0.05	0.05	0.03	0.01	1.977 - 3.037	-0.457	2.227*	2.466 ± 0.022
GL/GW Decorticated Grain Length(LDG	0.18	0.2	0.02	0.2	0.2	0.38	0.03	2.780 - 4.580	1.178*	1.886*	3.333 ± 0.046
Decorticated Grain Length (LDG)	0.04	0.47	0.17	0.47	0.46	1.65*	0.05	5.000 - 8.000	0.166	-0.306	6.030 ± .069
Decorticated Grain Width (WDG)	0.06*	0.04*	0	0.04*	0.04*	0.14**	0	1.467 - 2.142	0.347	1.654*	1.991 ± 0.021
LDG/ WDG	0.24*	0.26*	0.01	0.26*	0.25*	1.35**	0	1.881 - 4.494	1.066*	1.548*	3.050 ± 0.051
Time of heading	278.30*	44.71	4.17	50.46	48.69	259.88	4.67	110.000 - 133.000	-6.873*	58.492*	122.583 ± 1.454
Yield/plant (g)	0.04	0.19	0.15	0.19	0.11	7.88**	0.02	20.74 - 38.95	0.633*	1.104*	2.847 ± 0.039

Table 3: Analysis of variance for yield and yield attributing characters for F2 population derived from Ranjit x Kola Joha cross along with third degree and forth degree statistics.

Among the traits studied, tiller number/plant, panicle length, grain width, decorticated grain length, and decorticated grain width were normally distributed while remaining traits including aroma showed skewed distribution. Thus before QTL analysis log transformation was used to normalize the data. A total of 25 QTLs affecting 12 morphological as well as grain quality traits were identified by QTL cartographer software using its composite interval mapping (CIM) function at 3.0 cut off LOD score (Table 4). The two QTLs for plant height identified each on chromosomes 1 and 10, showed a positive additive effect contributed by parent *Ranjit*. The QTL on chromosome 10 exhibited dominance for plant height and the QTL on chromosome 1 for the same trait showed overdominance gene action towards increased or decreased plant height. Rice chromosome 1 harbour the semi-dwarf gene *sd-1* for plant height [36]. The QTL detected in this study on chromosome 1 explained largest amount of variation amongst the QTLs for plant height detected and its allelic contribution was from semi-dwarf variety *Ranjit*. The QTLs detected on chromosomes 1 in the present study might be considered as confirmation to the QTL detected by earlier reports [37, 38]. So this QTL may be regarded as the same with *Sd-1*. However, the allelic relationship with *Sd-1* could not be explained from this study. The QTLs detected on chromosomes 1 in the present study might be considered as confirmation to the QTL detected by earlier reports [37, 38]. Since, no information of QTL for plant height on chromosome 10 was reported earlier, so the QTL on chromosome 10 in this study may be considered as novel located in *Joha* rice warranting further investigation.

Characters	Chromosome	Marker Interval	QTL name	QTL Position	LOD Score	Additive effect(a)	Dominant effect(d)	Gene action (d/a)	% of variation
Plant Height	1	RM9-RM306	plh_cim1-1	68.41	3.172	2.572	6.695	OD	17.3
	10	RM184-RM171	plh_cim10-1	67.31	4.034	6.708	-6.352	D	11.986
Tiller No.	12	RM101-RM519	tn_cim12-1	49.51	3.284	-1.318	-3.302	OD	5.3
Panicle Length	10	RM184-RM171	pl_cim10-1	59.31	4.353	0.944	-1.862	OD	9.667
	12	RM415-RM19	pl_cim12-1	12.01	3.435	1.873	0.837	PD	11.43
Grain No. / panicle	5	RM267-RM13	gn_cim5-1	26.61	4.33	5.22	10.81	OD	3.6
	10	RM184-RM171	gn_cim10-2	69.31	3.639	6.39	-16.73	OD	9.341
Grain Length(GL)	9	RM444-RM105	gl_cim9-1	19.31	3.493	-0.095	1.24	OD	14.501
Grain Width (GW)	1	RM237-RM102	gw_cim1-1	105.51	14.597	-0.494	-0.008	A	17.671
	2	RM341-RM6	gw_cim2-1	121.91	5.327	0.234	0.266	D	3.02
	5	RM159-RM413	gw_cim5-1	24.71	3.388	-0.016	0.149	OD	9.162

Decorticated Grain Length(LDG)	9	RM444-RM105	dgl_cim9-1	25.31	3.579	0.13	0.761	OD	2.3
Decorticated Grain Width(WDG)	10	RM171-RM496	dgw_cim10-2	99.81	3.332	0.096	0.137	OD	1.109
LDG/WDG	8	RM447-RM281	dglwr_cim8-1	125.61	3.902	-0.293	-0.251	D	5.534
Time of Heading	2	RM341-RM6	fl_cim2-1	102.91	10.155	7.152	6.565	D	11.653
	3	RM156-RM16	fl_cim3-1	98.51	4.602	-3.083	6.105	OD	4.179
	5	RM169-RM430	fl_cim5-3	68.91	5.513	-0.31	10.807	OD	9.537
	6	RM541-RM340	fl_cim6-2	77.41	7.475	6.343	8.006	OD	9.723
	7	RM10-RM234	fl_cim7-1	32.81	6.527	6.566	7.68	D	4.797
	10	RM184-RM171	fl_cim10-1	76.31	4.093	5.538	8.738	OD	4.566
	11	RM552-RM287	fl_cim11-1	53.61	4.242	-1.231	13.457	OD	3.242
Yield/Plant	5	RM267-RM13	yld_cim5-1	26.61	4.33	0.113	0.234	OD	5.932
Aroma	5	RM169-RM430	aro_cim5-2	57.91	3.296	0.035	0.572	OD	3.084
	8	Aro1-BAD2	aro_cim8-2	78.51	16.312	-1.108	-0.567	PD	17.687

Table 4: QTLs for different characters through Composite Interval Mapping (CIM) in F2 mapping population of Ranjit x Kola Joha and their genetic effects.

For tiller number one QTL was identified on chromosome 12. A total of 14 QTLs that significantly influenced tiller number were reported on rice chromosomes 1, 2, 4, 5, 6, 7, 8 and 10 by Bian et al. [39](2013) in *Japonica* rice. The QTLs for tiller number on chromosome 12 identified in this study needs further investigation, since available reports do not indicate existence of such QTL for tiller number on chromosome 12.

Two QTLs detected for panicle length on chromosomes 10 and 12 showed positive additive effect contributed by *Ranjit*. The QTL on chromosome 10 exhibited partial dominance gene action while QTLs on chromosome 12 exhibited overdominace. In previous research, QTLs for panicle length were reported on chromosome 8 [40, 41], chromosome 9 [40-42], chromosomes 2, 4, 11, and 12 [43] chromosomes 3,6,10 [44], chromosomes 2, 8, 9, 10, 11 and 12 [38]. Thus the *tqo* QTLs detected in this study confirmed the presence of QTLs for tiller number on chromosomes 10 and 12 as reported by others.

Grain number per panicle is an important quantitative trait directly contributing towards yield. In this study two QTLs for grain number per panicle were identified in chromosome 5 and chromosome 10. Both the QTLs for gains per panicle showed positive additive effect which indicated the contribution of parent *Ranjit* to this trait and showed overdominance gene action. For grains per panicle earlier reported QTLs on chromosomes 1, 2, 3, 4, 5, 6, 9, 11, and 12 [38,40-48] in rice. The presence of QTL for grains per panicle on chromosomes 5 might be similar to that reported in available literature. Since, no information of QTL for grains per panicle on chromosome 10 was reported earlier, so the QTL on this chromosome in this study may be considered as novel located in *Joha* rice which needs further investigation.

The lone QTL for grain length detected on chromosome 9 in the marker interval RM444-RM105 was responsible for 14.50 per cent variation with an additive effect. Earlier, Tsunematsu et al. [49] mapped two QTLs for grain length on chromosomes 3 and 7. The presence of a QTL for grain length on chromosome 7 was detected by several workers [50-52]. However, Redona and Mackill [51] detected additional QTLs for grain length on chromosome 3. Five QTLs were identified for grain length on chromosomes 2, 3, 5, 7 and 8 by Rabiei et al. [53](2004) in *Iranian* rice. However, the presence of QTL for grain length on chromosome 9 is not confirmed by available literature. Since, no information of QTL on chromosome 9 was reported, the present QTL may be considered as novel located in *Assam* rice.

For grain width three QTLs were detected each on chromosomes 1, 2 and 5 by composite interval mapping. The QTL on chromosome 1 had the highest the highest LOD score contributing 17 per cent to the trait variation, with a negative additive effect contributed by parent *Kola Joha*. Two QTLs for grain width on chromosomes 5 and 9 were detected by Tsunematsu et al. [49](1996). Rabiei et al. [53](2004) detected Seven QTLs were mapped for grain breadth on chromosome 2, 3, 5, 6, 7, 8 and 9. Ya-dong et al. [54](2013) detected six grain width QTLs of which, three were on chromosome 2, two on chromosome 5 and one on chromosome 9. Wan et al [55](2008) also reported the presence of QTLs for this trait on chromosomes 1, 5 and 9. Our results were confirmatory to those reported by other workers.

Single QTL was identified for decorticated grain length by composite interval mapping on chromosome 9 in the marker interval RM444-RM105 was responsible for 2.30% variation. Similarly, single QTL for decorticated grain width on chromosome 10 in the marker interval RM171-RM496 respectively. Only one QTL was detected for decorticated grain length /decorticated grain width by composite interval mapping on chromosome 8 in the marker interval RM447-RM281 was responsible for 5.534% of variation. Rabiei et al. [53] have identified two major QTLs for grain shape on chromosomes 3 and 8,

which coincided with the major QTLs for grain length and grain breadth.

Seven significant QTLs for flowering time, which altogether explained for 50 per cent of variation in flowering time in the mapping population. Despite showing no difference in flowering time between parents, detection of many QTLs suggested the existence positive and negative alleles in both parents. The QTL for flowering time on chromosome 2 was a major QTL with LOD score of 10.15 for 11.65% of variation with a positive additive effect of 7 days towards reduced flowering days. The QTL on chromosome 6 has been identified between at 77.4 cM explains minor variation of 0.7%, since there is a major gap in between the RM541 and RM340. Through Association mapping in *Joha* rice of Assam, Talukdar et al. [6] identified eight QTLs to be associated with the time of heading on chromosomes 3, 5, 7, 8, 10 and 12, and among which the QTL linked to chromosome 3 explained the highest variation. Using F_2 and BIL populations of cross *Nipponbare*/*Kasalath* (NK), eight QTLs for heading date, Hd1–Hd5, Hd7, Hd8 and Hd11, were detected [56]. The same group later detected six more QTLs including Hd6 [57], Hd9 [58], Hd10 and Hd12– Hd14 [59]. Bian et al. [39] identified QTLs for heading time on chromosome 1, 4, 5, 6, 10 and 12. Therefore the QTLs detected for flowering time in this present study might be considered as confirmation to the QTL detected by Yano et al. [56] and Bian et al. [39].

For grain yield, single QTL identified on chromosome 5 exhibited overdominance gene action towards increased grain yield. For this trait positive additive effect was contributed by parent *Ranjit*. From earlier findings, QTLs for grain yield were detected on chromosome 1, 2, 3, 4, 7, 8 and 12 [60], three QTLs on chromosomes 2 and 8 [38].

In this present investigation three QTLs were identified for aroma by QTL cartographer through composite interval mapping, one on chromosome 5 and two on chromosome 8, out of which the QTLs aro_cim8-1 and aro_cim8-2 were major QTLs in the marker intervals RM38-RM25 and Aro1-BAD2 respectively. A major QTL for aroma was detected in *Joha* rice on chromosome 8 by Talukdar et. al. [6], which has been validated by the present investigation. In this study the additive effect for the major QTL showed that the aroma was contributed from the parent *Kola Joha*. Amarawathi et al. [52] found single QTL for aroma in each chromosome 3, 4 and two QTLs in chromosome 8 in a set of *Basmati* rice cross population. These indicated the potentiality of Aro1 and BAD2 marker in MAS of *Joha* rice.

According to MCcouch and Doerge [60], it is necessary to sacrifice population size in favor of data quality, and this trade-off meant that only QTLs with a relatively large effect could be detected. Considering these, a population size of 94 F_2 individual was considered as a prelimanry study to identify QTLs. Most of the QTLs identified in the current study, showed a range of partial to overdominance effects, indicating complexity of the traits under consideration (Table 4). In most of the cases, degree of dominance was high, suggesting the importance of dominance or over dominance effects for the respective QTLs. These high levels of dominance can be related to heterosis. Therefore, these results will provide important information for further functional analysis of genes for yield and its attributing traits and aroma in rice. Again the major QTLs identified in this study can be considered in the breeding programmes for *Joha* rice improvement. Some genomic regions were associated with more than one trait, indicating linkage and/or pleiotropic effects. For example on chromosome 10 there are QTLs for plant height, panicle length, grain no/panicle, time of heading or there are QTLs on chromosome 5 grain no/panicle and yield/plant. The significant correlations between these traits can be explained by these genomic regions containing pleiotropic or tight linkage QTLs [61]. Few QTLs detected in this study were identified to be previously known QTL position on different chromosomes. But, it is hard to precisely compare the chromosomal location of these QTLs because of different genetic materials and lack of common markers used for mapping, and therefore additional studies are needed to clarify the allelic relationship of these QTLs.

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