



RESEARCH ARTICLE

Identification of genomic regions associated with yield improvement in rice grown under coastal saline soils through correlation and QTL mapping

Vinutna Vinnakota¹, Girija Rani M², Suneetha K^{3*}, Nagendra Rao K⁴ & Ravi Babu M⁵

¹Department of Genetics and Plant Breeding, Agricultural College, Bapatla 522 101, Andhra Pradesh, India

²Regional Agricultural Research Station, Acharya N. G. Ranga Agricultural University, Maruteru, West Godavari 534 122, Andhra Pradesh, India

³ICAR-Indian Institute of Rice Research, Rajendranagar, Hyderabad 500 030, Telangana, India

⁴Agricultural Research Station, Acharya N. G. Ranga Agricultural University, Machilipatnam, Krishna District 521 002, Andhra Pradesh, India

⁵Regional Agricultural Research Station, Acharya N. G. Ranga Agricultural University, Anakapalle, Visakhapatnam District 531 001, Andhra Pradesh, India

*Correspondence email - ponnukota@gmail.com

Received: 13 November 2025; Accepted: 30 March 2026; Available online: Version 1.0: 21 May 2026

Cite this article: Vinutna V, Girija RM, Suneetha K, Nagendra RK, Ravi BM. Identification of genomic regions associated with yield improvement in rice grown under coastal saline soils through correlation and QTL mapping. Plant Science Today (Early Access). <https://doi.org/10.14719/pst.12717>

Abstract

Salt stress is the major limiting factor in rice productivity and is being aggravated in varied climatic conditions. The present study focused on association and identification of genomic regions for yield improvement in coastal saline soils. The association studies indicated that selecting the recombinant inbred lines (RILs) with yield traits like good plant height, more number of tillers, longer panicles, more number of filled grains, higher 100-grain weight and salinity traits like lower Na^+/K^+ ratio and lower salinity scores (< 3) is desirable for breeding salt tolerant varieties. Genetic architecture was studied at $\text{EC } 7.2 \text{ dSm}^{-1}$ by using quantitative trait loci (QTLs). Genotyping using diversity arrays technology (DArT) sequencing platform with 1K-Rice custom amplicon (1K-RICA) panel using 1076 single nucleotide polymorphic markers (SNPs) for 150 RILs accounted 24.72 % of polymorphism. The linkage map spanning the length of 3605.80 cM covering all 12 rice chromosomes was generated using inclusive composite interval mapping (ICIM) software version 4.2. Fourteen QTLs were identified for the yield traits viz., ear bearing tillers hill^{-1} , plant height (cm), panicle length (cm), number of filled grains panicle^{-1} and 100 grain weight (g). However, the major QTLs that are identified for the yield traits-plant height (*qPH5*, *qPH8*) and panicle length (*qPL10*) associated with genes such as *OsGPRP3*, *OsNHX3*, *OsMT2b* and *OsPERK8* might facilitate the genetic improvement of rice through marker-assisted selection for achieving salt tolerance in coastal sector where rice is grown in low-lying lands.

Keywords: inclusive composite interval mapping; 1K-rice custom amplicon; quantitative trait loci; recombinant inbred lines; single nucleotide polymorphic markers

Introduction

Rice (*Oryza sativa* L.) serves as a staple food crop feeding half of the global population. Even though it is one of the main sources to relieve hunger, rice productivity is affected by both biotic and abiotic stresses. Salinity and drought are the two major abiotic stresses that limits rice productivity with increase of salinity caused by adverse conditions (1). Salt stress inhibits photosynthesis and growth, leading to biomass losses and partial sterility, which ultimately results in low rice productivity. According to the global estimates, on an average 683 million ha of land is categorised as saline area. In that, around 6.73 million ha of irrigated land was affected from salt degradation only in India (2). The total saline soils occupy 12.94 lakh ha in coastal India. In terms of their distribution, coastal Gujarat has the highest area (5.28 lakh ha), followed by West Bengal (5.08 lakh ha) and Andhra Pradesh (1.06 lakh ha). In Andhra Pradesh, around 105725 ha of saline soils are distributed within the coastal region, in which 71 % of the area spread within 5 districts, viz., Konaseema (17.9 %), Prakasam (15.8 %), Bapatla (13.4 %), Krishna (12.4 %) and Eluru (11.2 %) (3). About 10 % of yield

loss occurs due to salt stress at 3.5 dSm^{-1} of EC and even up to 50 % of yield losses were reported at $\text{EC } 7.2 \text{ dSm}^{-1}$ (4). To determine trait correlation, associations with yield either positively or negatively were calculated. Correlation can be due to linkage or pleiotropy or both (5). But in certain cases, it also had environmental or genetic bases. In such cases, quantitative trait loci (QTL) mapping can help in resolving this insight by identifying clustered QTLs linked to the correlated traits and comparing their locations and effects (6). As majority of the studies were performed using hydroponics; but farmers rely mostly on natural soils rather than hydroponics to identify genotypes with desirable level of tolerance and to ensure high productivity in real saline conditions (7). Soil plays a major role in plant growth and mineral uptake in salinity stress. Studies on identification of genomic regions for salt tolerance in natural saline soils are limited due to difficulty in achieving perfect phenotypic results at reproductive stage unlike at seedling stage (8). So, breeding salt tolerant rice varieties with stable yield under salinity is necessary to overcome adverse effects of climate variability in such conditions. Currently one of the most significant challenges in rice

breeding for salinity tolerance is to determine the QTLs having the best chance of improving salt tolerance with the least amount of background noise from the tolerant parent (9). The mapping of QTLs requires large segregating bi-parental population such as RILs established by continuous selfing procedures (10). Research is being carried out all over the world for the identification of QTLs for stress conditions (11). *Saltol* a major QTL located on chromosome 1 of rice genome was identified against salinity stress (12, 13). It tolerates only at seedling stage and unable to tolerate salinity stress at reproductive stage. All the salt tolerant lines do not possess *Saltol* region and there are several other genomic regions contributing to salt tolerance which need to be identified for effective breeding of salt tolerant rice varieties (14). Hence, the current study was carried out to identify correlated genomic regions for yield traits and salt tolerance in rice using RILs derived from salt tolerant genetic stock MCM 109 and BRR 0119 under coastal saline soils using 1K-rice custom amplicon (1K-RiCA) panel duly considering character association studies.

Materials and Methods

Phenotypic evaluation

Phenotyping for salinity was carried out to estimate association studies and genetic architecture of F_5 recombinant inbred lines (RILs) population derived from the cross MCM 109 and BRR 0119 along with five checks including susceptible check - BPT 5204 (Samba Mahsuri), resistant checks - MCM 103, MTU 1293, FL 478 and MCM 125 during kharif, 2024 at natural coastal saline soil of Agricultural research station (ARS), Machilipatnam. This centre was located at 81.7° E longitudes and 16.10° N latitudes in Krishna district of Andhra Pradesh. Nursery was raised in normal soil and 35 days old seedlings were transplanted in saline soil with 10 seedlings per genotype. Each genotype was sown in 2 lines (5 seedlings per line) with row length of 3 m with potential of hydrogen (pH) 8.4 and electrical conductivity (EC) 7.2 dSm⁻¹ on 6th September 2024. Alpha-lattice design with 2 replications, 4 blocks was adopted by following spacing of 20 cm for row to row and 15 cm for plant to plant. Phenotypic screening of 150 RILs was conducted in saline soils from September 2024 to December 2024 and then data was recorded on randomly selected 5 plants per RIL for 8 yield and for three salinity traits to compute genotypic correlation. The fertilisers were applied at the rate of 90 kg N, 60 kg P₂O₅ and 60 kg K₂O ha⁻¹ as per recommendations. One third dose of nitrogen and ½ dose of the K₂O ha⁻¹ was applied as first dose. Entire dose of P₂O₅ applied basically in last puddling. The remaining nitrogen was applied in two equal split doses one at 30 days after planting and another at panicle initiation stage along with ½ dose of K₂O ha⁻¹.

Table 1. Heritability of the experiment used for QTL mapping

Traits	Mean	Maximum	Minimum	S. E.	h ² B
PS (%)	94.67	100	54	0.69	0.82
DFF	94.54	118.5	82	0.73	0.96
SS	2.21	7	1	0.08	0.97
PH (cm)	53.9	98.09	42	0.85	0.77
EBT/ hill	3.9	10.25	1	0.16	0.98
PL (cm)	16.08	22.42	6.95	0.17	0.96
FG/ Panicle	59.91	165.3	14	1.67	0.94
RS	2.79	7	1	0.13	0.93
SF (%)	88.31	100	51.87	0.91	0.89
Na ⁺ /K ⁺	0.67	4.25	0.11	0.05	0.95
100 GW (g)	1.57	2.85	1.1	0.02	0.96
GY (g)	4.72	26.74	1.14	0.27	0.92

PS : Plant survival (%); DFF: Days to 50 % flowering; SS: Salinity scoring at seedling stage; PH: Plant height (cm); EBT/hill: Ear bearing tillers hill⁻¹; PL: Panicle length (cm); FG/panicle: Number of filled grains panicle⁻¹; RS: Salinity scoring at reproductive stage; SF: Spikelet fertility (%); Na⁺/K⁺: Shoot sodium to potassium ratio at harvesting stage; 100 GW: Hundred grain weight (g); GY: Grain yield per plant (g).

Salinity scoring and yield traits

Scoring at seedling stage and reproductive stages has 5 different scores ranking from 1 to 9. The score 1 indicates that the line is highly tolerant and score 9 indicates high susceptibility. This scoring discriminated the susceptible from the tolerant and the moderately tolerant genotypes. The scoring was given as per modified standard evaluation system (15). For shoot Na⁺/K⁺ ratio at harvesting stage, RILs were categorised according to scale of (16). Then, data was collected on yield traits like plant survival (%), days to 50 % flowering, plant height (cm), ear bearing tillers hill⁻¹, panicle length (cm), number of filled grains panicle⁻¹, spikelet fertility (%), 100 grain weight (g) and grain yield per plant (g). To remove outliers from the data we used transformation for the traits then mean values for all these traits were used to know phenotypic data quality (Table 1) and to estimate correlation in variability package (gen. var and genotypic correlation) of R software version 4.4.3 (17).

Genotyping and linkage map construction

Genotyping was started by arranging rice grains in 96 well plates at IIRR, Hyderabad (Fig. 1). It was further performed by using diversity arrays technology (DArT) sequencing platform with 1K-RiCA panel by Intertek, Hyderabad, India (18). Genotyping data from 1K-RiCA based single nucleotide polymorphisms (SNPs) (19) was used for mapping the RIL population in the present study. A total of 1076 SNP markers spanning all the 12 rice chromosomes were screened and revealed 266 polymorphic markers accounting 24.72 % of polymorphism. Quantitative trait loci (QTL) analysis using integrated composite inclusive mapping (ICIM) software version 4.2 (20) generated the linkage map spanning the length of 3605.80 cM covering all 12 rice chromosomes. Markers with segregation distortion were deleted and the final genetic linkage map was constructed based on Kosambi mapping function (21) and the number of permutations for the determination of significance levels (at $p = 0.05$) was set to 1000 and the LOD threshold was set to 2.5. At significant LOD peak (≥ 2.5), QTL mapping in terms of QTL effects namely the logarithm of ODDS (LOD), additive effect of the identified loci and phenotypic variation explained (PVE) were estimated. The nomenclature of declared QTLs was followed according to the standard procedure (22) that demonstrated each QTL name should be italicized and start with a lower case letter “q” to indicate that one as a QTL, followed by a 2-5 letter standardised “trait name” (PH for plant height), a number designating the rice chromosome on which it occurs i.e., 1st to 12th chromosome, a period (“.”) and a unique identifier to differentiate individual QTLs (if any) for the same trait that reside on the same chromosome (e.g. *qPH5.1*).

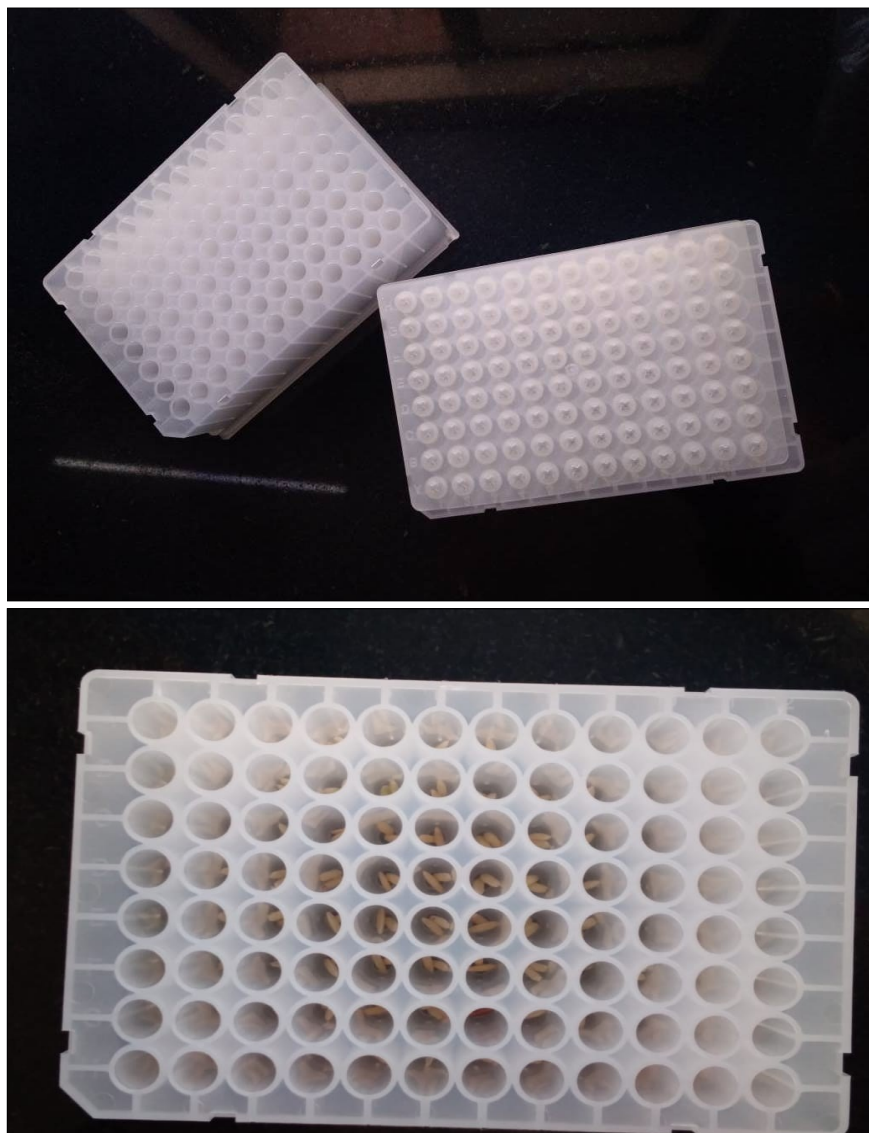


Fig. 1. Rice grain samples prepared and arranged in 96-well plates for genotyping using DArT platform at Intertek, Hyderabad.

Results and Discussion

Heritability and correlation studies

As the heritability estimates for all the traits was high which signifies the good phenotypic data, we proceeded further with the data to estimate correlation analysis and QTL mapping. In the present investigation, correlation was studied between yield and 7 yield attributing characters viz., days to 50 % flowering, plant height (cm), ear bearing tillers hill⁻¹, panicle length (cm), number of filled grains panicle⁻¹, spikelet fertility (%) and 100 grain weight (g). By taking grain yield as dependent variable, correlation studies indicated that grain yield per plant (g) expressed positive association with yield traits like ear bearing tillers hill⁻¹, number of filled grains panicle⁻¹, panicle length (cm), 100 grain weight (g) and plant height (cm) at genotypic level and negative association with salinity traits like plant survival (%), salt tolerance at seedling and reproductive stages and shoot Na⁺/K⁺ ratio at harvesting stage revealing selection of RILs with good plant height, more number of ear bearing tillers, panicle length, filled grains per panicle and 100 grain weight (g) is desirable for salt tolerant genotypes. Ear bearing tillers hill⁻¹ had positive and significant correlation with panicle length (cm), number of filled grains panicle⁻¹ and grain yield per plant (0.510**) signifying selection of RILs with long panicles those possess more filled grains per panicle in saline soil might be useful. These results agree with earlier findings (23) meanwhile number of filled grains panicle⁻¹ had strong

and positively significant association with grain yield per plant (0.51**) exhibiting selection of RILs with more number of filled grains and low Na⁺/K⁺ ratio in evolving salt tolerant high yielding varieties. These findings are partially consistent with the reports (24). The trait panicle length had positive association with 100 grain weight (g) (0.25**) and grain yield per plant (0.51**) demonstrating association of better grain filling and ultimate yield potential for longer panicles. The results were consistent with earlier reports (25). 100 grain weight (g) showed positively significant association with grain yield per plant (0.66*) implicated that grain weight played a crucial role in determining yield performance under saline conditions. These observations are similar to (26). Meanwhile, plant height showed positively significant association with ear bearing tillers hill⁻¹, panicle length (cm) number of filled grains panicle⁻¹ and grain yield per plant (0.47**) declaring that good plant height, ear bearing tillers hill⁻¹, panicle length and number of filled grains panicle⁻¹ are crucial in enhancing of grain yield under salinity. These results agree with earlier findings (27, 28). In conclusion, results of association study revealed selection of RILs with good plant height, more number of ear bearing tillers, panicle length, filled grains per panicle and 100 grain weight (g) duly considering lower values of salt tolerance score (3 or < 3) at seedling and reproductive stage and low Na⁺/K⁺ ratio is desirable in breeding salt tolerant varieties. The results for character association studies are described in Table 2.

Table 2. Genotypic correlation coefficients for salinity and yield related traits of F₅ RILs

Character	SS	DFF	RS	PH (cm)	EBT/ hill	PL (cm)	FG/ Panicle	SF (%)	Na ⁺ /K ⁺	100 GW (g)	GY (g)
PS (%)	0.001	-0.08	0.04	-0.06	-0.05	-0.05	-0.15	-0.02	0.07	-0.08	-0.04
SS	1**	0.26**	0.11	-0.18*	-0.19*	-0.18	0.05	0.004	0.01	-0.14	-0.10
DFF		1**	-0.04	0.01	-0.03	0.05	0.15	0.06	-0.13	0.15*	0.10
RS			1**	0.14	0.15	0.07	-0.02	-0.89**	0.03	-0.12	-0.13
PH (cm)				1**	0.56**	0.53**	0.42**	-0.24**	-0.09	0.19	0.47**
EBT/ hill					1**	0.35**	0.23**	-0.19**	-0.12	0.13	0.51**
PL (cm)						1**	0.59	-0.04	-0.09	0.25**	0.51**
FG/panicle							1**	0.11	-0.14	0.48**	0.51**
SF (%)								1**	0.09	0.10	0.01
Na ⁺ /K ⁺									1**	-0.06	-0.14
100 GW (g)										1**	0.66*
GY (g)											1**

*Significant at 5 % level; **Significant at 1 % level

PS: Plant survival (%); DFF: Days to 50 % flowering; SS: Salinity scoring at seedling stage; PH: Plant height (cm); EBT/hill: Ear bearing tillers hill⁻¹; PL: Panicle length (cm); FG/panicle: Number of filled grains panicle⁻¹; RS: Salinity scoring at reproductive stage; SF: Spikelet fertility (%); Na⁺/K⁺: Shoot sodium to potassium ratio at harvesting stage; 100 GW: Hundred grain weight (g); GY: Grain yield plant⁻¹ (g).

QTL Mapping

The genotypic data from 1K-RiCA custom amplified sequence information was surveyed for polymorphic markers (Table 3) between the two parents MCM 109 and BRR 0119. Out of the 8 yield and 3 salinity traits studied, QTLs for the yield traits plant height (cm), ear bearing tillers hill⁻¹, panicle length (cm), number of filled grains panicle⁻¹ and 100 grain weight (g) under saline soils with logarithm of the ODDS (LOD) and phenotypic variance explained (PVE (%)) ≥ 2.5 % were identified. The identified QTLs were presented in Table 4 and Fig. 2. Three QTLs were observed for plant height viz., *qPH5*, *qPH8* and the remaining one is *qPH12* which is found in consistent with earlier findings (29) who pointed out QTL for plant height that is located at vicinity of 33.7 cM on chromosome 8 for our identified QTL using SSR markers. A total of 5 QTLs were associated with ear bearing tillers hill⁻¹. These are *qEBT2*, *qEBT3*, *qEBT5*, *qEBT6* and *qEBT12*. Some other researchers (30) also identified for the same trait on chromosome 3 (*qTN3-1*, *qTN3-2*, *qTN3-3*) in 250 RILs of F₆ generation at various locations accounting 19–33 % of PVE range with 7K-rice SNP array. For panicle length, we identified only one QTL i.e., *qPL10*. Similarly, with the LOD score of 4.60 (31) identified a major QTL for panicle length in SNPs using RIL population on chromosome 10 flanking between marker 390648-marker 367482 at 37.4 cM. For the trait number of filled grains panicle⁻¹, only one QTL (*qFG5*) was identified. The results were in line with (32) who identified QTL on chromosome 5 (*qPFG5*) explaining PVE of 15.85 % in 96 BC₂F₂ families, with 150 SSR markers using software QGene version 2.30 at 144.3–167.3 cM which is located at distant regions of our identified QTL. *qHGW3*, *qHGW4*, *qHGW8* and *qHGW11* were identified for the trait 100 grain weight (g) contributing moderately to grain weight. Other researchers (33) also identified QTLs for 100 grain weight on

chromosome 8 (*qHGW8*) in F₃ generation of 188 RILs using KASP (Kompetitive allele-specific PCR) mapping with SNP markers at position of 26.44 cM concluding the trait (100 grain weight) noticed superior performance in population than in parents. Among all these 14 QTLs we found potential candidate genes for the major QTLs viz., *qPH5* and *qPL10* through rice annotation project database (RAP-DB|HOME) (34). The potential candidate gene for panicle length *LOC_Os10g0104800* (*OsPERK8*), a proline-rich extensin-like receptor kinase eight acts as regulatory hub which shows response to abscisic acid (ABA) and gibberellin (GA) treatment. As they are important in growth regulating and stress responses, the gene intended its involvement in hormone mediated panicle development by influencing cell elongation in reproductive plant parts to adapt salt stress. Similarly, *LOC_Os10g0544900* (*OSPP2Cs*), a meta-QTL gene was identified on chromosome 10 (35) known for its role in stress tolerance, particularly for the ABA response. For *qPH5*, 2 candidate genes were observed. Firstly, *LOC_Os05g0119200* (*OsGPRP3*) a glycine and proline-rich protein, which help in regulation of, grain size and accumulation of, seed storage protein and lipids to maintain proper seed development and efficient resource allocation under salt stress. The same gene was identified by many of the researchers (36, 37) for salinity in rice. The second gene is *LOC_Os05g0148600* (*OsNHX3*) a salt stress response, Na⁺/H⁺ antiporter gene involved in ion homeostasis by reducing sodium toxicity thereby promoting cellular balance in salinity which has also been reported in previous studies (38) to be located on the same chromosome as identified in the present study and the final one is *LOC_Os05g0111300* (*OsMT2b*) is a metallothionein, reactive oxygen species (ROS) scavenger protein that mainly known for root development and seed embryo germination by supporting plant

Table 3. Chromosome wise number of polymorphic markers used and genome coverage of linkage map

Chromosome number	No. of markers used	No. of polymorphic markers	Polymorphism (%)	Length (cM)
1	122	35	28.92	329.05
2	99	21	21.21	307.81
3	100	29	29.00	317.74
4	86	22	25.58	81.49
5	75	22	29.33	1154.06
6	122	15	12.29	326.79
7	83	9	10.84	165.09
8	91	22	24.44	235.87
9	71	18	25.35	55.15
10	55	22	40.00	192.31
11	101	21	20.79	202.24
12	71	30	40.54	238.14
Total	1076	266	24.72	3605.80

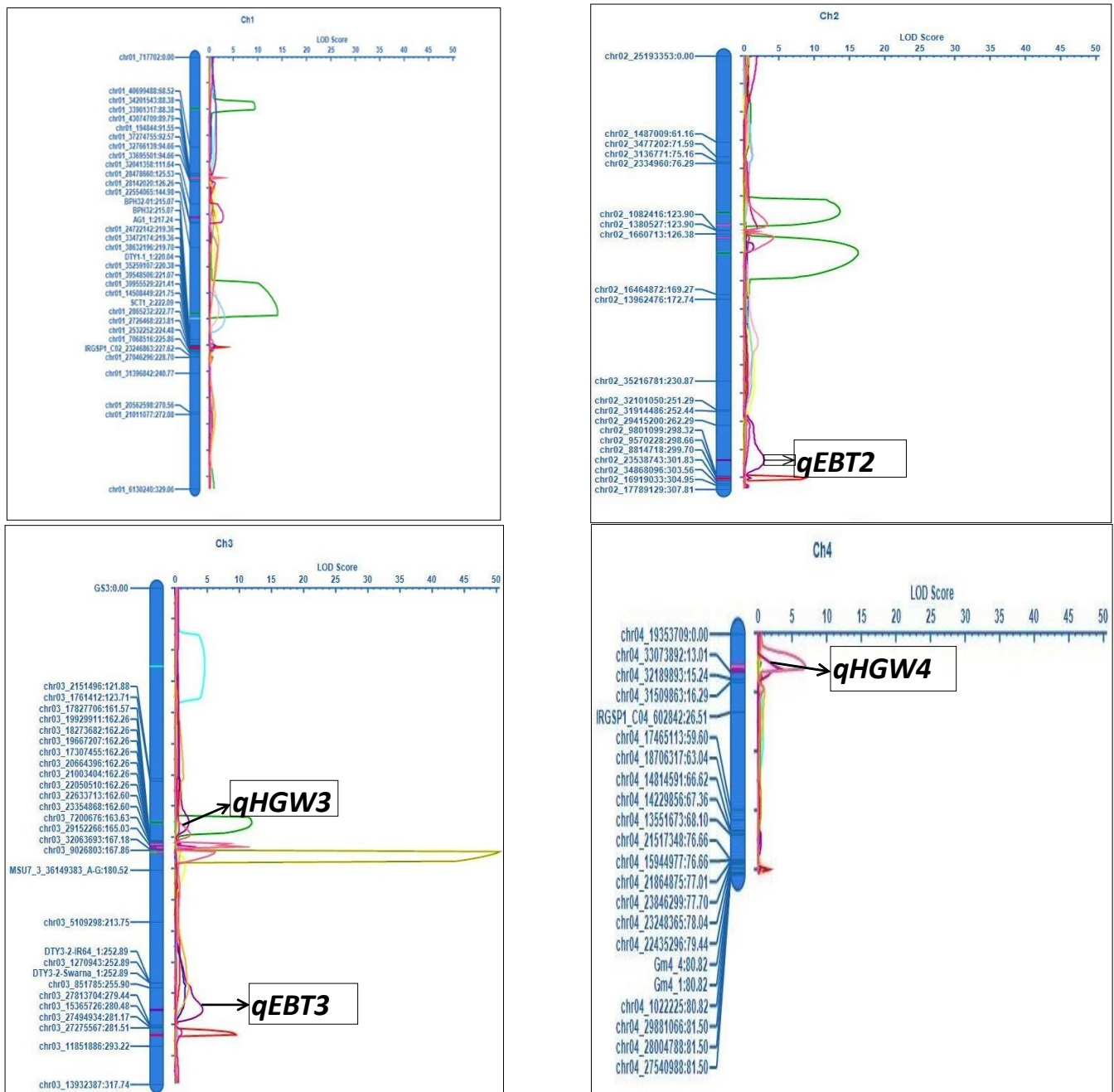
cM: Centimorgan

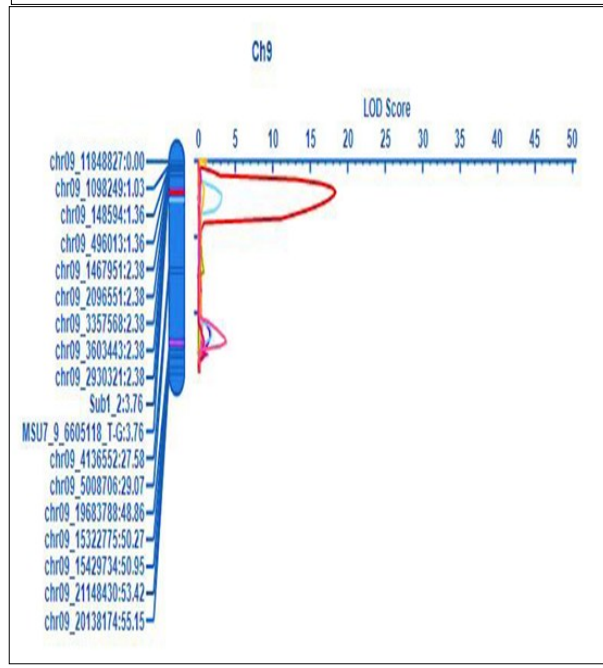
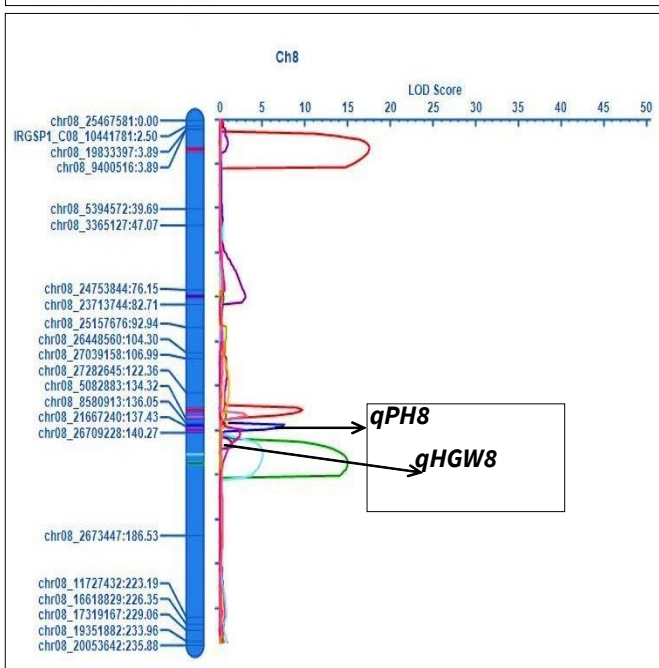
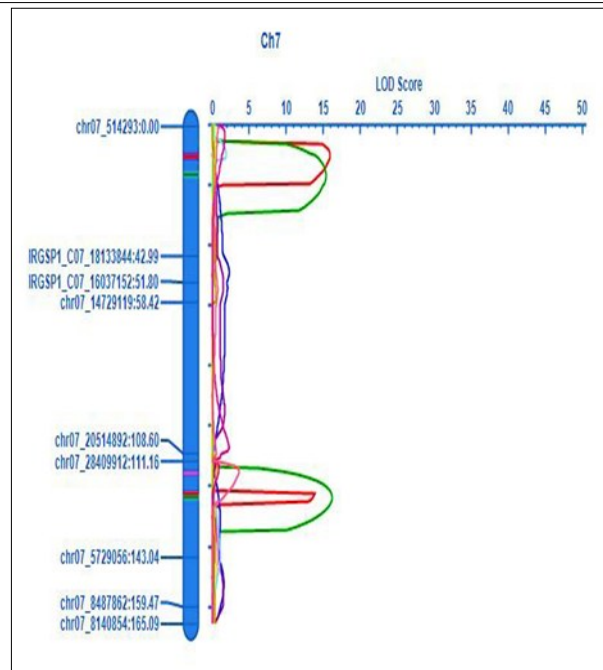
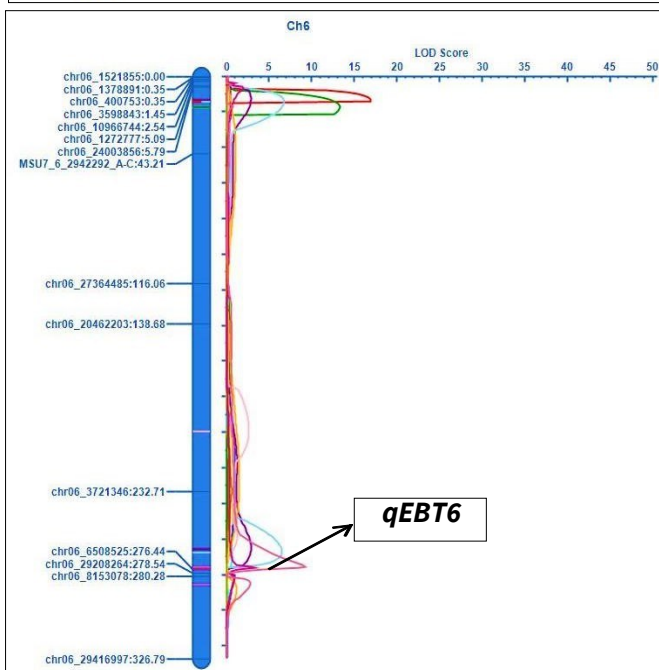
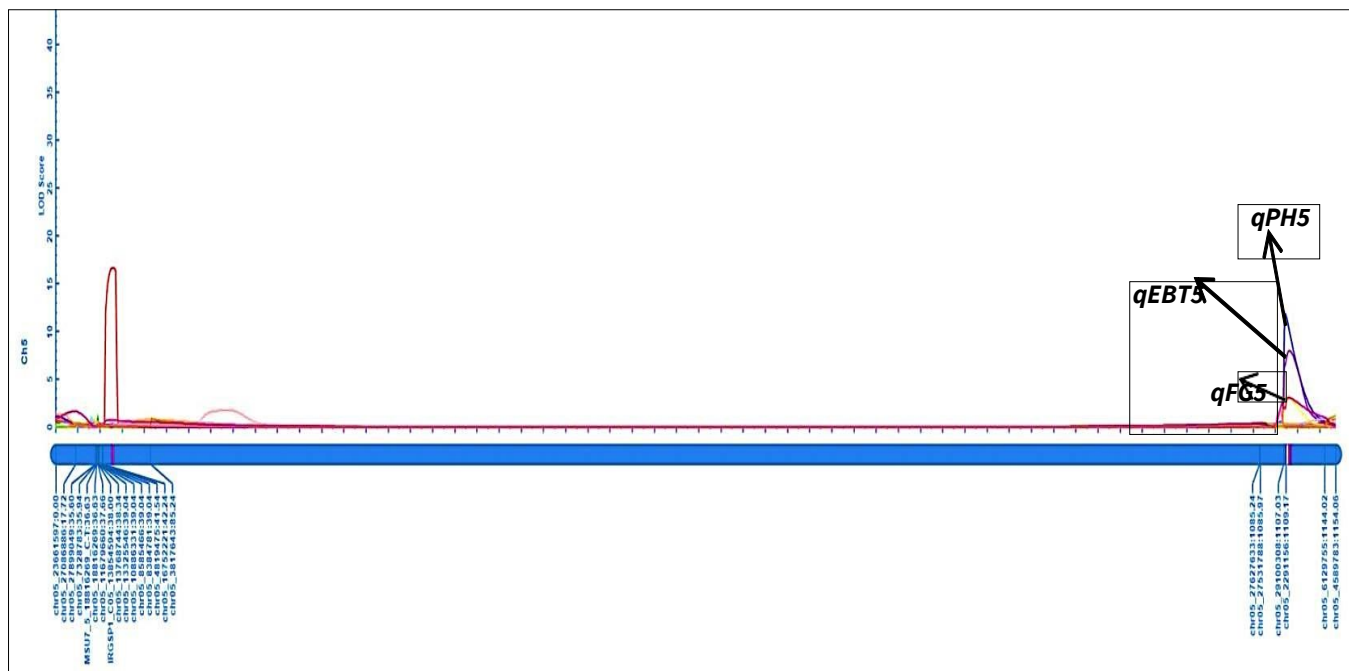
Table 4. Genomic regions associated with 12 traits in 150 F₅ RILs evaluated under salinity stress in rice

Chromosome	Trait name	QTL	Position (cM)	Left marker	Right marker	LOD	PVE (%)	Additive effect	Left CI	Right CI
5	PH	<i>qPH5</i>	1109.00	chr05_29100308	chr05_2291156	11.72	17.26	-10.43	10.50	1111.50
8	PH	<i>qPH8</i>	137.00	chr08_8580913	chr08_21667240	7.45	10.85	11.02	10.50	138.50
12	PH	<i>qPH12</i>	172.00	chr12_26463351	chr12_3285571	4.15	5.34	7.68	10.50	177.50
2	EBT/ hill	<i>qEBT2</i>	287.00	chr02_29415200	chr02_9801099	2.81	5.43	1.45	278.50	293.50
3	EBT/ hill	<i>qEBT3</i>	270.00	chr03_851785	chr03_27813704	7.96	4.93	1.52	263.50	274.50
5	EBT/ hill	<i>qEBT5</i>	1113.00	chr05_2291156	chr05_6129755	2.87	6.14	-1.95	10.50	1117.50
6	EBT/ hill	<i>qEBT6</i>	265.00	chr06_3721346	chr06_6508525	2.98	5.25	-1.52	10.50	274.50
12	EBT/ hill	<i>qEBT12</i>	185.00	chr12_26463351	chr12_3285571	4.00	5.29	1.51	10.50	198.50
10	PL	<i>qPL10</i>	37.00	chr10_19378143	chr10_12145295	3.09	12.63	1.23	10.50	37.50
5	FG/ panicle	<i>qFG5</i>	1110.00	chr05_2291156	chr05_6129755	2.63	9.13	-9.88	10.50	1119.50
3	100 GW	<i>qHGW3</i>	166.00	chr03_29152266	chr03_32063693	3.28	2.88	-0.43	165.50	167.50
4	100 GW	<i>qHGW4</i>	12.00	chr04_19353709	chr04_33073892	3.03	2.89	-0.40	10.50	12.50
8	100 GW	<i>qHGW8</i>	139.00	chr08_21667240	chr08_26709228	3.34	2.68	-0.30	10.50	139.50
11	100 GW	<i>qHGW11</i>	28.00	chr11_21446099	IRGSP1_C11_22303236	2.88	2.87	0.43	10.50	28.50

PH: plant height (cm); EBT/ hill: ear bearing tillers hill⁻¹; PL: panicle length (cm); FG/ panicle: number of filled grains panicle⁻¹; 100 GW: hundred grain weight (g).

QTL: Quantitative trait loci; cM: Centimorgan; LOD: Logarithm of ODDS; PVE: phenotypic variance explained (%); left CI: left confidence interval; right CI: right confidence interval.





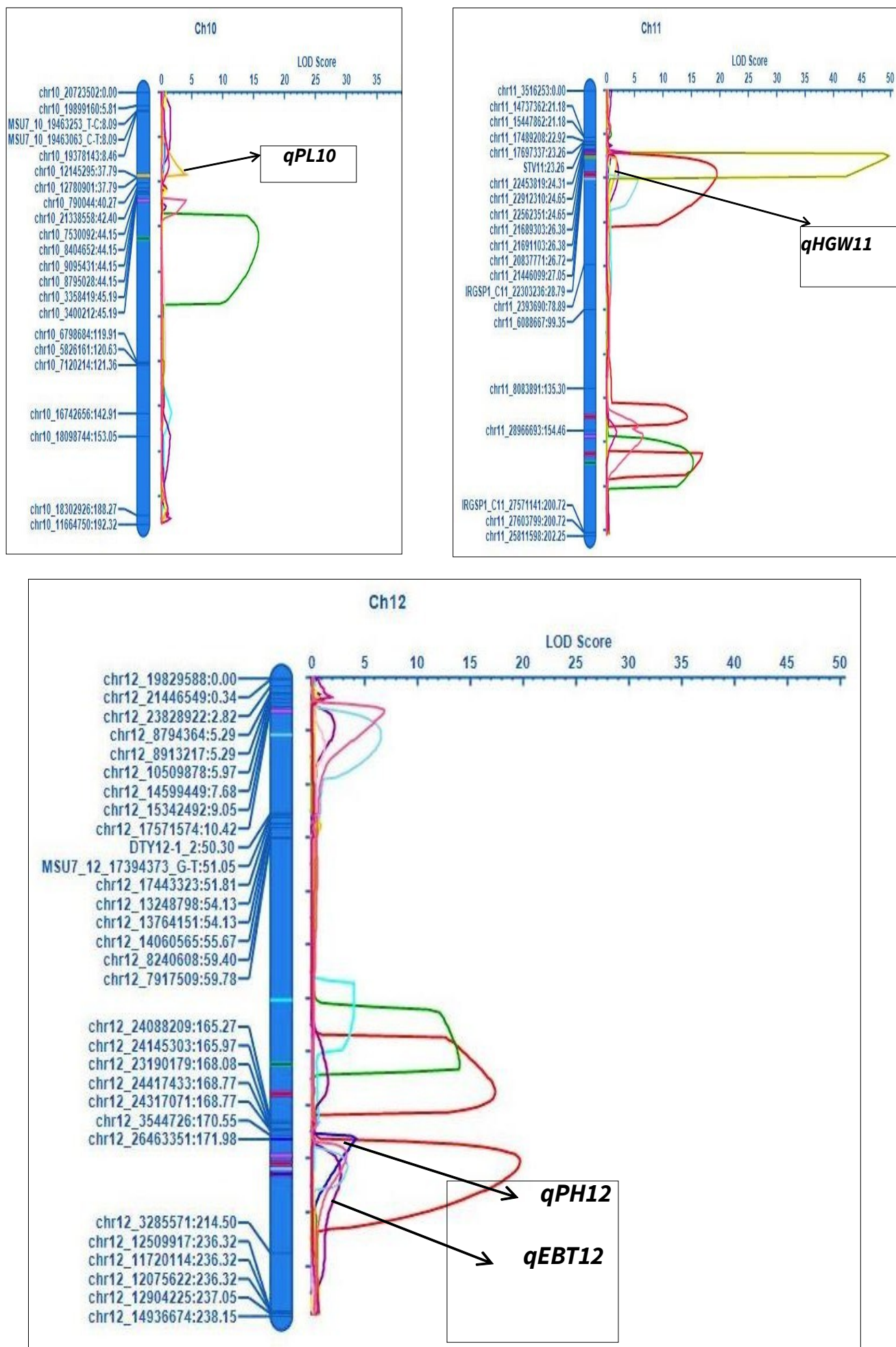


Fig. 2. Chromosome wise linkage map generated using 1076 single nucleotide polymorphic markers with logarithm of ODDS and PVE (%) ≥ 2.5 .

survival in coastal soils. This gene was identified in a manner consistent with previous reports (39) which primarily focused on its functional role in stress tolerance. The positive alleles for the QTLs *qPH8*, *qPH12*, *qEBT2*, *qEBT3*, *qEBT12*, *qPL10* and *qHGW11* were contributed by the tolerant parent MCM 109. Major QTLs for plant height (*qPH5*, *qPH8*) and for panicle length (*qPL10*) identified from RILs of the cross MCM 109/BRR 0119 can be exploited in marker assisted selection with the aid of molecular markers for the development of salt tolerant varieties. Meanwhile, correlation studies indicated that all these traits were positively correlated with grain yield so it might be possible to improve grain yield through genetic improvement of these traits i.e., larger plant height, longer panicles with more number of tillers and finally with good weighted grains.

Conclusion

In conclusion, by unravelling the genetic architecture of salt tolerance in a recombinant inbred lines (RILs) population, the study serves as a foundation for developing rice varieties capable of surviving in saline environments, addressing the challenges posed by coastal soil salinity. Major QTLs identified for the yield traits like plant height (*qPH5* and *qPH8*) and for panicle length (*qPL10*) with the parentage of MCM 109/BRR 0119 can be integrated into breeding programmes such as marker assisted selection to develop high yielding stress resilient varieties in coastal saline soils duly considering other minor QTLs which ultimately result in better yields even in stress conditions, as some of the RILs exhibited extreme levels of salt tolerance in field studies.

Acknowledgements

The authors gratefully acknowledge the support provided by Acharya N. G. Ranga Agricultural University, Guntur, for facilitating this research work. Financial assistance received from the DST-SERB project (CRG/2022/006015) is also duly acknowledged.

Authors' contributions

VV collected and recorded the phenotypic and genotypic data and prepared the initial draft of the manuscript. GRM and NRK supervised and guided the entire experimental work conducted for this study. SK performed the genotypic analyses and contributed to the interpretation of the molecular data, which constituted a major component of the study. RBM assisted in recording the phenotypic data and contributed to manuscript preparation. All authors contributed to the review, revision and finalisation of the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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