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Published in:
Current Research in Biotechnology

DOI:
[10.1016/j.crbiot.2023.100125](https://doi.org/10.1016/j.crbiot.2023.100125)

Published: 01/01/2023

Document Version
Publisher's PDF, also known as Version of record

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Please cite the original version:
Paul, T., Debnath, S., Das, S. P., Natarajan, S., Perveen, K., Alshaikh, N. A., Banik, S., Nath, M., Kumar Kesari, K., & Pramanik, B. (2023). Identification of major and stable QTLs conferring drought tolerance in rice RIL populations. *Current Research in Biotechnology*, 5, 1-10. Article 100125.
<https://doi.org/10.1016/j.crbiot.2023.100125>

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Contents lists available at ScienceDirect

Current Research in Biotechnology

journal homepage: www.elsevier.com/locate/crbiot

Identification of major and stable QTLs conferring drought tolerance in rice RIL populations

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ARTICLE INFO

Keywords:

Drought tolerance (DT)
Microsatellite marker
Moisture stress
QTL
RIL
Rice

ABSTRACT

Rice production in a rain-fed environment during the reproductive period is significantly hindered by drought, which is one of the critical issues limiting yield. Therefore, finding grain yield-related quantitative trait loci (QTL) during the reproductive stage can potentially provide researchers with additional benefits when taken in the context of marker-assisted breeding. CT-9993 and Samba Mashuri were considered to develop recombinant inbred lines (RILs) for tagging QTLs associated with drought tolerance. During the dry and wet experimental conditions, there was a significant difference in the yield and yield-attributing variables. Sixty polymorphic microsatellite markers were utilized to genotype the RILs by employing Inclusive Composite Interval Mapping (ICIM). Especially eight QTLs were identified for four traits viz., plant height, root length, root dry weight and grain yield under stressed and control conditions. QTLs for Root Length (Q_{RL-6-1} and Q_{RL-8-1}) were identified on chromosomes 6 and 8 with PVEs of 20.35% and 10.29%, respectively under stressed situation. A QTL, Q_{PH-4-1} , was also identified on Chromosome 4 with a PVE of 19.73% for plant height under drought stress. Q_{GY-6-1} was identified on Chromosome 6 with a LOD value of 7.95 and a PVE of 22.14% to grain yield under stress. Throughout the growing seasons, two QTLs, Q_{PH-4-1} and Q_{PH-8-1} , were identified for the Plant Height trait, with PVEs of 25.13% and 3.21%, respectively. Three QTLs (Q_{RL-3-1} , Q_{RL-6-1} , and $Q_{RL-11-1}$) were identified as having the highest PVE and LOD score for root length. Two stable quantitative trait loci for grain yield, (Q_{GY-6-1} and Q_{GY-7-1}) were identified. It was flanked by the markers RM19425 and RM19521. These quantitative trait loci might prove to be very beneficial in the marker-assisted breeding of rice that is resilient to climate change, especially drought.

Introduction

Moisture stress has a detrimental impact on rice production and yield stability, posing a problem for agricultural systems as the global climate changes. A minuscule amount of moisture stress, especially during the vegetative growth stage in rice, may have a large influence on grain productivity. As a consequence of this, those who grow rice consider drought to be a critical environmental source of stress. As a straight outcome of this, it is responsible for as much as 15% of the decline in agricultural production in India (Gorantla et al., 2005).

Because of climate change, more than 20 million hectares of land in the southern region of Asia are at risk of suffering from drought (Manrique-Carpintero et al., 2016). A drop in production as a result of drought has emerged as the most important source of climate-related risks. This is because decreased yield is one of the primary limitations of production. (Pandey and Bhandari, 2009). Substantial rain-fed territories in eastern India's drought are evaluated for resilience mostly during the rainy season in selected locales (Verulkar et al., 2010). There are around 17 million hectares of rice fields that are in jeopardy of drought in eastern India and the neighbouring country

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<https://doi.org/10.1016/j.crbiot.2023.100125>

Received 12 November 2022; Revised 25 March 2023; Accepted 27 March 2023

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of Nepal (Huke, 1982). Moisture stress is connected to the length and frequency of water deficits. Insufficient water can be a problem for plants as early as the beginning of the growing season or at any time between blooming and grain filling. It is possible to increase productivity by crossing drought-tolerant cultivars with high-yielding genotypes that are vulnerable to drought.

Breeding for abiotic stresses like drought remains difficult due to the complexity of the genetic system and the occurrence of unanticipated occurrences (Debnath et al., 2023). The advanced molecular technology known as quantitative trait loci analysis is used in the process of identifying genes that are responsible for regulating drought tolerance attributes. Rice genotypes with low water requirements and the ability to produce an economically viable harvest under drought conditions need to be identified as a top priority if additional food scarcities are to be achieved. Several techniques and approaches, such as direct-seeding, aerobic rice, and alternating wetting and drying (AWD) rice-production systems, have been presented as viable ways of saving water in agricultural contexts (Salleh et al., 2020). Grain yield has been utilized as the major criteria for selection in a number of experiments, and the results of these studies have revealed stable, consistent, and major QTLs for grain yield in the face of reproductive-stage drought stress (Ghimire et al., 2012; Mishra et al., 2013; Swamy and Kumar, 2013; Dixit et al., 2014a; Dixit et al., 2014b). A small number of these QTLs have already been put to use in the development of high-yielding, drought-resistant rice varieties (Kumar et al., 2014). Even though the reproductive stage is the growth stage that is least susceptible to drought, it is possible for it to have an effect on the yields of rice in the fields of farmers. Therefore, it is essential to continue searching for QTLs and characteristics that increase rice yields despite varying degrees of drought. To discover QTLs with significant and persistent effects on grain yield, phenotypic screening was performed to directly select for grain yield under reproductive-stage drought stress, non-stress (control), various habitats (upland and lowland), locations, seasons, and years (Kumar et al., 2014; Dixit et al., 2015; Sandhu et al., 2015). Now that co-located genomic regions have been found that are linked to grain yield during drought, root, and seedling establishment traits, there are more ways to improve rice's productivity when it is being affected by drought.

The selection of an extant variety as the drought tolerance donor has been the standard practice in the majority of previous studies that have been published on the topic of identifying major-effect QTLs for rice yield during drought. Even though a lot of traditional upland cultivars were found to be drought-tolerant, this trait often came with others that were less desirable, like low yield potential and/or tall plant height (Vikram et al., 2015). Because of this, it is important to do preliminary tests as soon as possible to prove that the drought-tolerant donor is useful in a breeding program (Kumar et al., 2014). Potential donors include the traditional rice variety CT-9993, which was unearthed during the preliminary screening of rice genotypes with stable grain yield under decreased water abundance and evidence of deep root growth (Bunnag and Pongthai, 2013). The CT-9993 was later acclaimed as one of the best deep-rooted genotypes in a range of upland and lowland drought experiments and as a conventional variety with the ability to maintain significant root elongation throughout the drought (Lanceras et al., 2004; Bunnag and Pongthai, 2013).

A previous study had established CT-9993 as having deeper-rooting capabilities and drought tolerance, it was anticipated that RILs with the best grain production under drought would also be those with the highest yield during water stress. In this study, RILs were generated from a cross between the drought-prone parent, CT-9993, and the low-land-adapted popular rice cultivar Samba Mashuri (Sandhu et al., 2018), and this cross was carried out in order to harness the drought tolerance (yield and other yield attributes) traits of CT-9993 for use in breeding. The goal of this work was to find the genomic regions that are important for grain production and related agronomic

factors in upland and lowland settings, during all stages of reproduction, and when plants are under stress from drought.

Materials and methods

Phenotyping of RILs

The plants used in the study were grown at Visva-Bharati University from December 2018 to April 2021. They were part of a 150 RIL population that came from CT-9993 × Samba Mashuri. CT-9993, a type of upland japonica rice (Lanceras et al., 2004), was used as a female as well as drought-tolerant parent (Bunnag and Pongthai, 2013), and Samba Mashuri, a popular lowland-adapted rice cultivar with a number of economically valuable traits (Sandhu et al., 2018), was used as a drought-sensitive as well as male parent (Rani et al., 2013). Three replications of reproductive-stage drought stress and control experiments were set up in the RCBD in upland sites. With a seeding density of 2.35 g per linear meter of row and a seed rate of around 366 m⁻² and 373 m⁻² during the dry and wet seasons, respectively, seeds were dry-direct-seeded into the soil. Upland trial field management followed the guidelines provided by Bernier et al (2007). During the establishment and the first few weeks of vegetative growth in both years, the Control plots received twice-weekly irrigation, and the RS trials received the same treatment; however, the latter trials' irrigation frequency was reduced 55 and 40 days after sowing, respectively. Plots were regularly re-irrigated when most lines showed signs of wilting and leaf dryness. The stress cycle kept going until the crop was prepared to be harvested. Days to 50% flowering (DFF), Plant height (PH), Number of tillers per plant (NT), Number of panicles per plant (NP), Panicle length (PL), Root Length (RL), Root dry weight (RDW), Flag leaf length (FLL), Single panicle yield (SPY), Plant Biomass (PBM), and Grain yield per plant (GY) were all measured during both crop seasons.

Estimation of genetic parameters of the mapping population

In the process of evaluating mapping populations, each and every component of genetic variability, heritability, and correlation was taken into consideration. ANOVA, phenotypic and genotypic variance, phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), broad sense heritability, and genetic advance as a percentage of mean were calculated as described by Singh and Chaudhary (1977).

Genotyping of RILs

In order to investigate the genetic basis of the many phenotypes important for drought tolerance, genotyping was performed on each of the 150 RIL individuals using sixty unique polymorphic microsatellite markers. Genotyping was carried out with the help of an Agilent BioAnalyzer in accordance with the methodology supplied by the manufacturer (Cheng et al., 2021). This was done so that the genotypic patterns among the markers could be evaluated. Data for genotyping were produced by sixty polymorphic microsatellite markers out of a total of 400 that were originally obtained for this research and were dispersed throughout the twelve chromosomes of rice (McCouch et al., 2002).

Construction of linkage maps and mapping of quantitative trait loci

The QTL analysis, construction of genetic/linkage map, and identification of stable QTLs were carried out using QTL IciMapping software; version 4.2 (Meng et al., 2015), in accordance with the protocol provided by the manufacturer. This was done in order to determine which genomic regions in rice are associated with drought tolerance. A logarithm of odd (LOD) threshold value of 3.0 was used as

a measure of relevance in order to determine the order in which the framework map elements are presented.

Results

Variability, correlation and linkage map

The degree of genetic variability, the heritability for the traits under study, and the genetic advancement of those characteristics are all factors that contribute to the success of breeding programs. It is impossible to improve genetic material without the existence of variation in any population. Measures like genotypic and phenotypic coefficients of variation can be used to figure out how much genetic variation there is between genotypes. During the dry season evaluation, a value of 13.25 g was found to be the mean for Grain yield (g), with a range extending from a minimum of 4.70 to 21.20 g. The values for the standard deviation, kurtosis, and skewness were estimated to be 3.31, -0.57, and -0.26 respectively. It was discovered that the heritability in the broad sense (h^2) was 92.51%, with the GCV coming in at 23.67%, the PCV coming in at 24.61%, and the GA (5%) coming in at 6.22%. It has been observed that the average mean value for grain yield (g) during the wet season was 22.67 g, with a range from 8.90 g to 29.80 g. Based on the information congregated during the study, this number was calculated. The value of the standard deviation has been determined to be 4.28, the kurtosis to be 0.40, and the skewness to be -0.91. The broad sense heritability (h^2) was calculated to have a value of 92.69%, with the genetic advance (GA) accounting for 9.42% and the genetic advance as percentage of mean (at 5% selection intensity) accounting for 55.33%. The percentages that were arrived at for PCV, GCV, and ECV, respectively, were 18.16%, 17.48%, and 4.91%. Similarly, such parameters were recorded for total 11 different yield attributing characters under the study (Table 1, Fig. 1).

The examination of Pearson correlation for the various yield attributing parameters demonstrated how multiple characteristics were connected with one another in our research based on the mean data from two different growing seasons. During the dry season, certain characteristics, such as PH, RL, RDW, NT, NP, PL, SPY were discovered to be positively significant to GY, and these characters positively contributed to the overall grain yield. In the wet season, phenotypic traits such as RDW, NP, SPY, NT were shown to be positive and highly significant to the final Grain yield (GY), which explains the high degree of correlation among the traits. Likewise, correlation was studied for several other traits in both the season to know their magnitude of effect on each other and overall grain yield (Tables 2 and 3). The genetic map was produced using a scaffold linkage map, which covered 1744.33 cM of the rice genome with an average marker density of 29.06 cM.

QTLs identified for different traits for drought tolerance during dry season

In the mapping population, four drought tolerance QTLs in the dry season for traits of plant height (PH), root length (RL), and grain yield (GY) were identified with negative additive effects, implying that majority of introgressed genomic sections came from Samba Mashuri in these regions attributed to trait controlling alleles (Table 4, Fig. 2a). For PH, only one QTL QPH-4-1 was found on Chromosome 1 at the position of 24.00 cM with a LOD score of 7.49 and a PVE of 19.74 %. The QTL was observed in the marker interval of RM 16,251 and RM16341. For the RL, two QTLs, q_{RL-6-1} and q_{RL-8-1} , were found in the dry season. A q_{RL-6-1} was discovered on Chromosome 6 at a position of 1.00 cM with a LOD score of 6.16 and a PVE of 20.36% in the marker interval RM19323 and RM19425. The q_{RL-8-1} was found on Chromosome 8 with a LOD score of 3.34 and a PVE of 10.29 %. QTL q_{RL-8-1} was observed at a position of 23 cM

Table 1 Descriptive Statistics of phenotypic characteristics of RILs derived from mean data for both the season.

Statistics	Traits																					
	PH		DFP		RL		RDW		NT		NP		PL		SPY		FLL		PBM		GY	
	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
Mean	81.36	93.10	99.44	102.81	17.03	15.48	3.10	3.73	4.12	8.59	2.25	4.66	23.35	23.78	3.43	3.86	35.54	38.50	18.09	29.28	13.25	22.67
Standard Deviation	8.81	8.48	8.25	5.75	4.90	2.63	0.96	1.33	1.05	1.94	0.81	1.39	3.25	3.47	0.54	0.18	12.14	11.28	7.85	10.00	3.31	4.28
Kurtosis	3.15	1.68	-0.48	0.64	-1.07	-0.43	-0.77	-0.34	1.36	-0.12	-0.41	-0.22	0.71	1.29	1.98	2.43	-0.82	-0.59	-0.74	-0.29	-0.57	0.40
Skewness	1.39	1.00	0.48	-0.31	-0.32	-0.01	-0.14	0.46	0.69	-0.20	0.11	0.24	0.21	-0.11	-1.58	-0.85	0.33	0.39	0.09	0.57	-0.26	-0.91
Minimum	64.50	75.90	84.00	84.50	2.00	9.50	0.50	1.00	1.71	3.33	0.29	1.50	12.00	10.00	1.30	3.10	11.90	16.50	2.00	9.00	4.70	8.90
Maximum	118.00	126.00	122.00	119.50	25.20	24.40	5.10	7.00	8.57	13.33	4.29	8.50	34.50	36.00	4.00	4.30	64.00	66.00	38.00	54.50	21.20	29.80
PCV	10.83	9.10	8.28	7.48	28.69	15.88	29.81	16.37	23.71	21.19	34.39	27.87	13.67	13.97	15.86	37.82	34.15	29.20	43.36	34.04	24.62	18.16
GCV	10.81	8.98	8.20	4.84	27.76	14.61	28.11	16.19	21.83	19.80	30.86	25.43	13.43	13.04	15.77	20.23	34.11	29.14	43.20	33.95	23.68	17.48
ECV	0.69	1.45	1.16	5.70	7.24	6.23	9.92	2.40	9.27	7.53	15.11	11.40	2.59	5.00	4.55	31.96	1.69	1.95	3.69	2.46	6.73	4.91
(h^2) Broad sense	99.59	97.47	98.03	41.90	93.63	84.59	88.93	97.85	84.76	87.36	80.52	83.27	96.41	87.20	98.87	28.60	99.76	99.56	99.28	99.48	92.53	92.69
GA (5%)	18.08	17.01	16.63	6.62	9.42	4.28	1.69	1.23	1.71	4.91	1.29	4.45	6.34	5.97	1.11	4.14	24.94	23.05	16.04	20.43	6.22	7.86
GAM (5%)	22.22	18.27	16.72	6.46	55.33	27.68	54.61	32.99	41.40	38.13	57.05	47.81	27.16	25.09	32.30	22.28	70.18	59.89	88.66	69.76	46.92	34.67

D = Dry season and W = Wet season

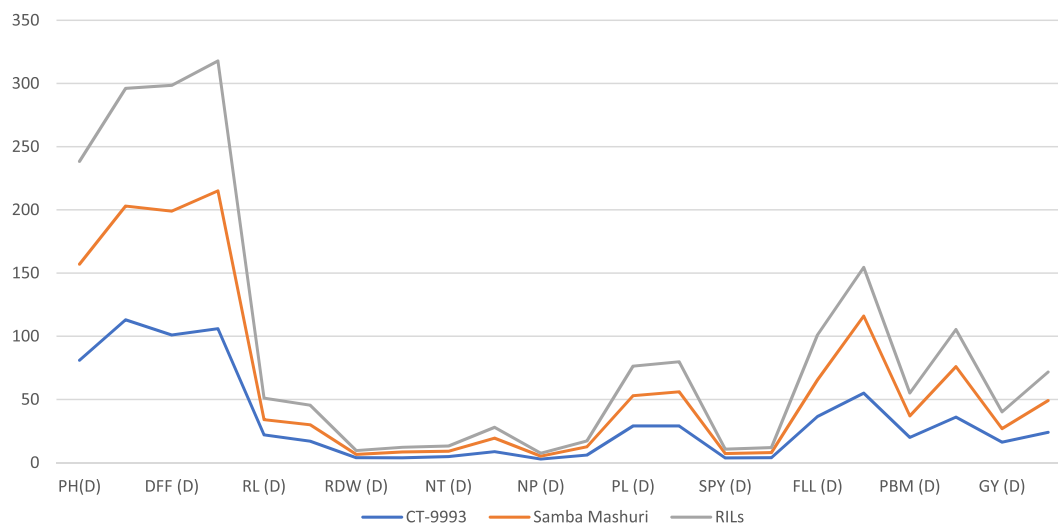


Fig. 1. Distribution of the traits phenotyped and the differences of the parents.

Table 2
Correlation table for different yield attributing traits in Dry season.

Traits	PH	DFF	RL	RDW	NT	NP	PL	SPY	FLL	PBM	GY
PH	1										
DFF	0.044NS	1									
RL	0.058NS	-0.031NS	1								
RDW	0.086NS	0.162**	0.203**	1							
NT	0.027NS	0.088NS	0.197**	0.154**	1						
NP	0.137*	0.019NS	0.033NS	0.202**	0.456**	1					
PL	0.199**	0.052NS	0.045NS	0.093NS	0.197**	0.371**	1				
SPY	0.075NS	-0.049NS	0.064NS	0.102NS	0.037NS	0.149**	0.075NS	1			
FLL	-0.144*	0.038NS	-0.121*	0.130*	0.088NS	-0.007NS	0.005NS	-0.140*	1		
PBM	0.030NS	-0.005NS	-0.026NS	0.264**	0.099NS	0.258**	0.259**	0.139*	0.040NS	1	
GY	0.197**	0.019NS	0.172**	0.150**	0.152**	0.211**	0.121*	0.786**	-0.117*	0.071NS	1

Table 3
Correlation table for different yield attributing traits in Wet season.

Traits	PH	DFF	RL	RDW	NT	NP	PL	SPY	FLL	PBM	GY
PH	1										
DFF	0.029NS	1									
RL	-0.016NS	0.059NS	1								
RDW	-0.037NS	0.160**	0.224**	1							
NT	0.009NS	0.056NS	0.155**	0.204**	1						
NP	0.038NS	0.139*	0.241**	0.253**	0.458**	1					
PL	0.143*	0.151**	0.261**	0.211**	0.206**	0.153**	1				
SPY	-0.111NS	0.089NS	0.047NS	0.177**	0.115*	0.159**	0.189**	1			
FLL	-0.021NS	-0.038NS	-0.011NS	0.074NS	0.040NS	-0.039NS	0.084NS	0.001NS	1		
PBM	0.058NS	0.039NS	0.041NS	0.134*	-0.102NS	0.115*	0.012NS	-0.014NS	0.095NS	1	
GY	-0.126*	0.101NS	0.065NS	0.237**	0.254**	0.233**	0.176**	0.582**	-0.050NS	0.054NS	1

Table 4
Mapping of QTLs conferring drought tolerant traits in Dry and wet season.

Seasons	Trait	Chromosome	QTL	Left marker	Right marker	LOD	PVE (%)	Additive effect
Dry	PH	4	qPH-4-1	RM 16251	RM16341	7.49	19.74	-4.63
	RL	6	qRL-6-1	RM19323	RM19425	6.16	20.36	-2.01
	RL	8	qRL-8-1	RM22300	RM22378	3.34	10.29	-1.43
	GY	6	qGY-6-1	RM19425	RM19521	7.95	22.14	-1.55
Wet	PH	4	qPH-4-1	RM 16251	RM16341	12.76	31.99	-5.17
	RL	10	qRL-10-1	RM24913	RM24969	3.62	7.49	-1.74
	RDW	3	qRDW-3-1	RM14444	RM14653	4.98	14.78	0.22
	GY	7	qGY-7-1	RM20889	RM21002	5.83	17.54	1.75

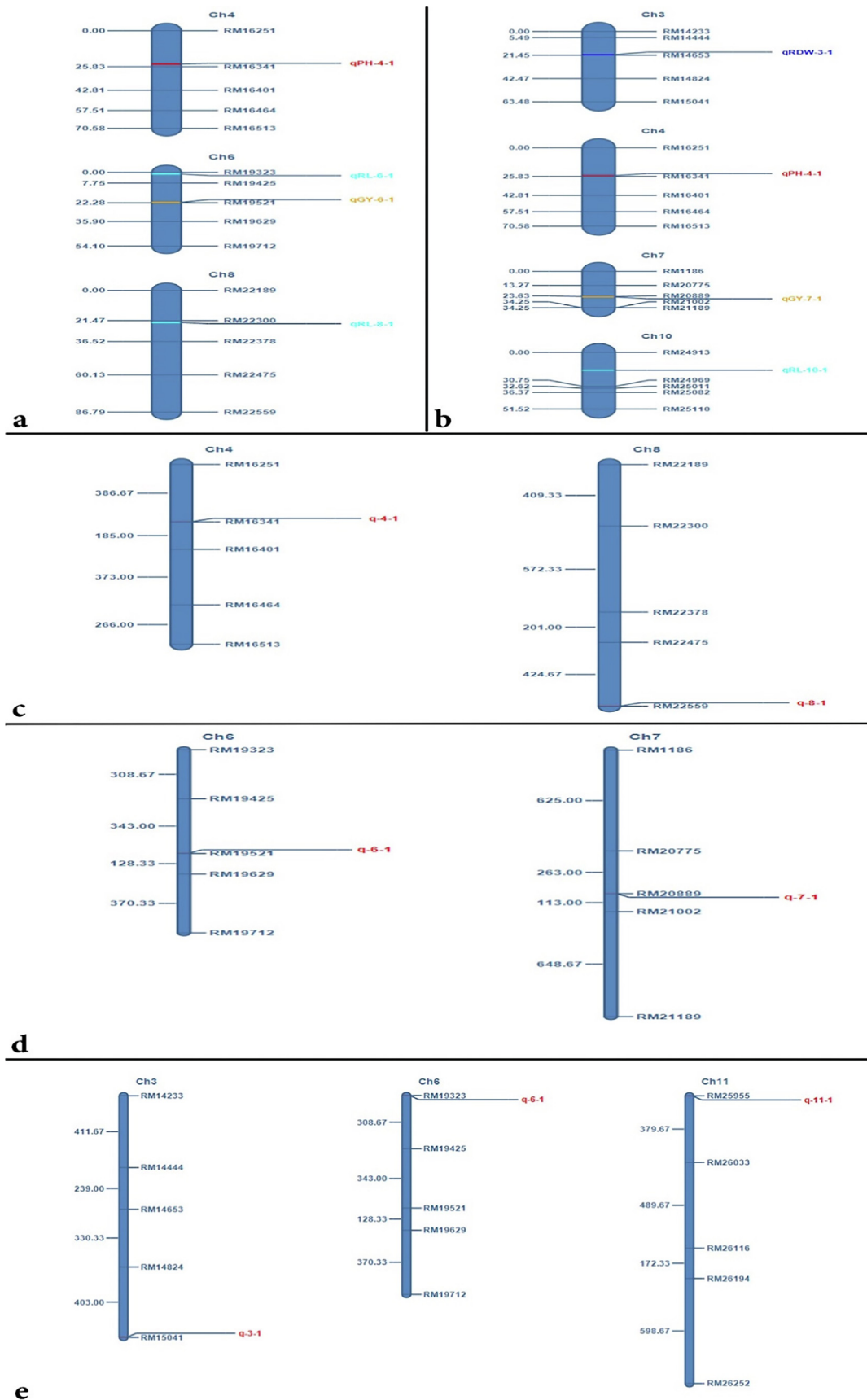


Fig. 2. a. QTLs identified for drought tolerant traits during Dry season over 150 RILs; b. QTLs identified for drought tolerant traits during Wet season over 150 RILs; c. Stable QTLs for Plant Height observed in both the seasons; d. Stable QTLs for Root length observed in both the seasons; e. Stable QTLs for Grain Yield observed in both the seasons.

and also found in the marker intervals RM22300 and RM22378. For GY in the dry season, only one QTL, q_{GY-6-1} , was found on Chromosome 6 with a LOD score of 7.95 and a PVE of 22.14%. QTL $q_{GY-6-1-1}$ was found at position 22 cM and in the marker intervals RM19425 and RM19521.

QTLs identified for different traits for drought tolerance during wet season

Four QTLs for drought resistance were detected during the wet season. These QTLs were revealed for parameters such as plant height (PH), root length (RL), grain yield (GY), and root dry weight (RDW) (Table 4, Fig. 2b). Surprisingly, QTLs for grain yield (GY), and root dry weight (RDW) were identified with positive additive effects, indicating that most of introgressed genomic sections were from CT 9993 whereas QTLs for plant height (PH), root length (RL) were identified with negative additive effects, signifying that most of introgressed genomic sections came from Samba Mashuri. The single QTL that was discovered for the trait PH during the wet period was q_{PH-4-1} , which was located on Chr 4 and had a LOD score of 12.76 and a PVE of 31.99%. The quantitative trait locus q_{PH-4-1} was found to be located at a position of 25 cM, flanking between markers RM 16,251 and RM16341. One QTL, designated $q_{RL-10-1}$, was discovered for the RL during the rainy season. On chromosome 10, the QTL $q_{RL-10-1}$ was discovered, and it had a LOD score of 3.62 and a PVE of 7.49%. It was found at a location of 16 cM, straddling the region between markers RM24913 and RM24969. Only QTL, designated $q_{RDW-3-1}$, was discovered for this RDW trait. On Chr 3, the QTL $q_{RDW-3-1}$ was discovered, and it had a LOD score of 4.98 and a PVE of 14.78%. The quantitative trait locus $q_{RDW-3-1}$ was located on chromosome 3 at a position of 21 cM. In the region between markers RM14444 and RM14653, the QTL designated as $q_{RDW-3-1}$ was detected. There was only one QTL detected for GY during the wet season, and it was located on Chr 7 with a LOD score of 5.83 and a PVE of 17.54%. The quantitative trait locus q_{GY-7-1} was found to be located at a location of 24 cM and was flanked between the markers RM20889 and RM21002.

Validation of identified QTLs for stability over both the seasons

It has been observed that QTLs that are expressed in both seasons are stable QTLs for use throughout the seasons. In this research, certain stable QTLs for characteristics such as PH and GY were discovered. QTLs like q_{GY-7-1} , and q_{GY-6-1} were found in both the seasons. Two QTLs, referred to as q_{PH-4-1} and q_{PH-8-1} , were identified for the Plant Height (PH) trait throughout the course of the growing seasons. On Chr 4, the QTL q_{PH-4-1} was discovered, and it had a LOD score of 18.12 and a PVE of 25.13%. It was discovered that q_{PH-4-1} was located on the chromosome at a location of 438.67 cM and that it was present in the marker interval that stretched between RM 16251 and RM16341. On chromosome 8, the QTL designated as q_{PH-8-1} was found to have a location of 1744.33 cM, a LOD value of 3.05, and a PVE of 3.21%. Between the markers RM22475 and RM22559 is where the QTL q_{PH-8-1} was found to be flanked (Fig. 2c). Three stable QTLs for root length (RL), which are designated as QTL q_{RL-3-1} , q_{RL-6-1} , and $q_{RL-11-1}$ respectively were detected. The quantitative trait locus q_{RL-3-1} was discovered on chromosome 3 at a location of 1524.67 cM with a LOD score of 6 and a PVE of 25.92%. It was flanked by the markers RM14824 and RM15041. On chromosome 6, the quantitative trait locus q_{RL-6-1} was found to be present between the marker intervals of RM19323 and RM19425, with a LOD score of 5.54 and a PVE of 22.14%. This locus was located at a location of 419 cm. On chromosome 11, at a location of 483.67 cM, $q_{RL-11-1}$ was found to be present. It was found that $q_{RL-11-1}$ had a LOD score of 3, and its PVE percentage was 4.35%. It was found inside the marker interval that ranged from RM25955 to RM26033 (Fig. 2d). During the course of the seasons, we found two quantitative trait loci

referred to as q_{GY-6-1} and q_{GY-7-1} . On Chr 6, q_{GY-6-1} was discovered, and it had a LOD score of 13.19 and a PVE of 19.96%. It was discovered that the gene q_{GY-6-1} was located on the chromosome at a location of 1067.00 cM, and it was flanked by the markers RM19425 and RM19521. The quantitative trait locus q_{GY-7-1} was found on chromosome 7 at a location of 1500.00 cM with a LOD value of 4.30 and a PVE of 10.40%. It was present between the marker intervals of RM20889 and RM21002 in the genome (Fig. 2e).

Discussion

According to Zulqarnain et al. (2013), the yield of rainfed lowland rice, which accounts for roughly 25 percent of the world's rice lands, is considerably decreased by drought owing to unexpected, inadequate, and irregular rainfall throughout the growing season. As revealed by Shuxing (2014), rice is very vulnerable to the effects of drought stress. During the reproductive stage, the crop is subjected to drought stress, which has a significant impact on grain output and causes the yield to decline. Zhang et al. (2018) concluded that drought stress imposed on the rice plant during its reproductive stage has a negative impact on the grain filling stage after conducting an experiment to assess the drought response of several agronomic variables in rice.

The analysis of variance carried out in both environments, that is, under stressful and non-stressful settings, showed that there are extremely substantial differences between genotypes for all of the characteristics that were looked into. The findings made it abundantly evident that yield and the components of yield were very variable throughout the RILs that were investigated. Therefore, there is a significant chance for improvement in terms of rice genotypes that may be bred to have greater adaptability to moisture stress in terms of the selection of acceptable genotypes that fulfil the essential needs of the product profile. Researchers like Anis et al. (2016), and Kishore et al. (2018) all found that the variance in features under water stress and non-stress was similar. Most of the traits that were studied during both the wet and dry seasons showed that the phenotypic coefficient of variation had more variation than the genotypic coefficient of variation (Kahani and Hittalmani, 2015; Kumar et al., 2017; Srivastava et al., 2017; Nithya et al., 2020; Nithya et al., 2021).

Based on the correlation analysis done in this study, plant height (0.197**), root length (0.172**), root dry weight (0.150**), number of tillers (0.152**), number of panicles (0.211**), panicle length (0.121**), and single panicle yield (0.786**) were all significantly related to grain yield, while flag leaf length (-0.117**) was significantly related to grain yield under drought stress, but in a negative way. Additional research has shown outcomes that are comparable to these ones (Pantuwan et al., 2002; Yue et al., 2005). As a result of the fact that plant height, root length, root dry weight, number of tillers, number of panicles, panicle length, and single panicle yield all had a significant positive effect on grain yield, these characteristics would be essential selection criteria for the purpose of yield increase under drought stress (Zulqarnain et al., 2013). During the wet season, grain yield had a positive correlation with root dry weight (0.237**), number of panicles (0.223**), single panicle yield (0.582**), and number of tillers (0.254**). Although there was a statistically significant inverse relationship between plant height and grain production (-0.126*), this result explains the considerable correlation that exists between grain yield and yield-attributing characteristics, and prior research has reported findings that are analogous to this one (Bhadru et al., 2011; Bhutta et al., 2019). The estimate of genetic advancement as a percentage of the mean was high for both the plant's biomass and the length of the flag leaf. The grain yield, the yield from a single panicle, the number of panicles, the number of tillers, the root length, and the root dry weight were all moderate. The height of the plant, the number of days before it flowers, 50% of its total buds, and the length of the panicle all showed modest genetic advancement

as a percentage of the mean. It is not always the case that high heritability corresponds to substantial genetic gain; heredity in conjunction with genetic advancement should be utilized when making predictions about the selection of better genotypes (Ali et al., 2012). In this research, high estimates of heritability and high genetic progress were achieved for plant height, days to 50% blooming, flag leaf length, and plant biomass. This finding shows that these qualities may be used for the improvement of upland rice via the process of selection. In addition to this, a high heritability in conjunction with a high genetic advance implies additive gene activity and a strong scope for selection using their phenotypic performance. The findings here are in conformity as reported by Khan et al. (2009) and Kishore et al. (2015) with regard to yield and yield-related components. High heritability with moderate genetic advance observed for grain yield, panicle length, single panicle yield, and root length indicates the role of both additive and non-additive gene action in its inheritance (Lakshmi et al., 2016). Relatively high GCV, heritability, and genetic advance were obtained for plant height, days to 50% flowering, plant biomass, single panicle yield, grain yield, number of tillers, and number of panicles. High heritability with moderate genetic advancement if these traits are passed on to the offspring through hybridization, phenotypic selection could be a good choice.

Environmental factors have a major impact on a considerable number of morpho-physiological traits that are believed to have a role in drought tolerance. Rice breeders have increased their efforts to create new varieties in response to climate change by identifying multiple QTLs that contribute to drought stress. With the advent of new breeding techniques such as marker-assisted breeding (MAB), rice breeders have been able to create new varieties more quickly. Rice has been mapped for QTLs using bi-parental mapping populations, which has led to the discovery of several QTLs. However, because of the crop's diversity, researchers are still looking into the possibility of drought-tolerant QTLs. A quantitative trait locus analysis, also known as a QTL analysis, is a statistical method that combines two different kinds of data—phenotypic data (trait measurements) and genotypic data—in an effort to better understand the relationship between a person's genes and the complex traits they exhibit (typically molecular markers). As a result, QTL analysis has become a significant accomplishment in the field of agricultural science research over the last three decades as a result of advancements in genotyping technology and the advent of quantitative genetic analytical tools. Throughout agricultural history, the vast majority of discovered QTLs have concentrated on secondary drought resistance features (Lanceras et al., 2004). In the present research, yield and physiological variable phenotypic data were coupled with SSR-based genotyping data from 150 RILs to identify quantitative trait loci. This was done in order to get a deeper understanding of the genetic architecture underlying the trait. Across all the markers, the allelic frequency of the CT9993 parental type was found to be negatively skewed (-0.72731), whereas that of the Samba Mashuri parental type was positively skewed (0.39916) (Fig. 3). A composite interval mapping study conducted under circumstances of drought stress and irrigation found a total of four quantitative trait loci in the dry season and four QTLs in the wet season. Because of the high level of genetic diversity present in the population that was mapped, we were able to conduct an analysis on this for the purpose of trait mapping. The vast majority of the QTLs that were discovered throughout the dry season and the wet season of the research were unique, and some of them explained the high PVE, which was higher than what had been reported in the past.

On chromosome 6, a significant quantitative trait locus for grain yield under stress was identified, and QTL Q_{GY-7-1} related to grain yield found in the wet season was in accordance with the previous findings of QTLs contributing to grain yield in rice (Baghyalakshmi et al., 2016; Mahalle et al., 2021; Rajurkar et al., 2021). A comparable quantitative trait locus for grain yield on chromosome 3 influences this area did not demonstrate any QTL for any of the variables that were

tested under conditions when there was no stress. Unexpectedly, the parent that is more vulnerable to the impacts of drought is also the source of the gene that improves yield at this particular QTL. Based on these findings, it would seem that this locus engages in epistatic interaction with other loci originating from the genetic background CT 9993. There are more instances of grain yield under drought stress QTLs being inherited from parents who are vulnerable to drought than any other kind of inheritance. On the other hand, the influence of these instances is often rather small, and they are more closely associated with yield potential than with drought tolerance per se (Lafitte et al., 2004; Lanceras et al., 2004). Many quantitative trait loci that are associated with high grain output despite the presence of drought have been discovered as a consequence of the success of breeding for drought resistance with grain yield serving as the selection criteria. This has resulted in better varieties of drought-resistant plants (Venuprasad et al., 2009; Vikram et al., 2011; Rajurkar et al., 2021).

A delay in blooming, a drop in plant height, and a loss in grain yield are all negative impacts that may occur on plants when they are subjected to the stress of drought (Lafitte et al., 2004; Zhao et al., 2010; Vikram et al., 2011; Kumar et al., 2014). In experiments where stress was introduced to populations, the degree to which stress produced a loss in grain production was much larger than in studies where stress was not given to populations. This was the case in both two types of research. When performing studies, it is usually ideal to submit the plants to changing degrees of stress to reduce the influence of yield potential and to choose genotypes with greater drought resistance. In addition, it is always better to subject the plants to varying levels of stress (Bernier et al., 2007). Because CT 9993 performed better than Samba Mashuri when subjected to drought stress during the reproductive stage, this demonstrates that breeding operations, including CT 9993, may be used as a source of genetic loci that boost grain production when subjected to drought stress. Rice cultivars that have deep roots and a larger root diameter can create more biomass above ground, which in turn increases the plant's tolerance to the negative effects of water stress. Since roots are crucial to a plant's capacity to absorb water and nutrients from the soil, it was postulated that attributes associated with roots should be given substantial implication. Improved physical strength, root system design, nutrient/soil moisture absorption from deeper soil layers, penetration capacity, hydraulic conductivity, rhizosphere volume, and spreading density lead to less likelihood of inadequate water balance in plant tissues and greater drought tolerance via an avoidance mechanism when combined with increased root numbers, deep root length, and deep root volume. The root density, root length, and root volume of a plant may all be increased, which should result in an enhancement in the plant's vitality (Venuprasad et al., 2009). During the course of this research, the quantitative trait loci Q_{RL-6-1} and Q_{RL-8-1} for deep root length on chromosomes 6 and 8 under stressful circumstances, as well as $Q_{RL-10-1}$ on chromosome 10 during the wet season, were discovered. The quantitative trait locus known as root length, Q_{RL-6-1} , was found to be located on chromosome 6 at the most distant place possible. Deep root length quantitative trait loci were found by Qu et al. (2008) at the very end of chromosome 6 at marker location RM454 and very near marker position RM520. Both of these positions are in close proximity to each other. According to Kamoshita et al. (2002), the locus for deep root length may be found on chromosome 11 adjacent to the RM167 marker. This marker is also close to the discovered QTL Q_{DRL11} , which can be found in the range RM202-RM229. Yue et al. (2005) found a quantitative trait locus that was equivalent to RM 229 on chromosome 11 at the same marker position. Several scholars have already looked at a variety of quantitative trait loci for root length (Price et al., 1999; Price et al., 2002; Uga et al., 2010; Sandhu et al., 2013). Regardless of whether a QTL has an overall positive or negative additive impact, each one is significant. Sometimes a QTL's favourable allele might be found in a poor parent. Since flanking markers in such case are connected to the chromosomal regions of both parents, respectively, inde-

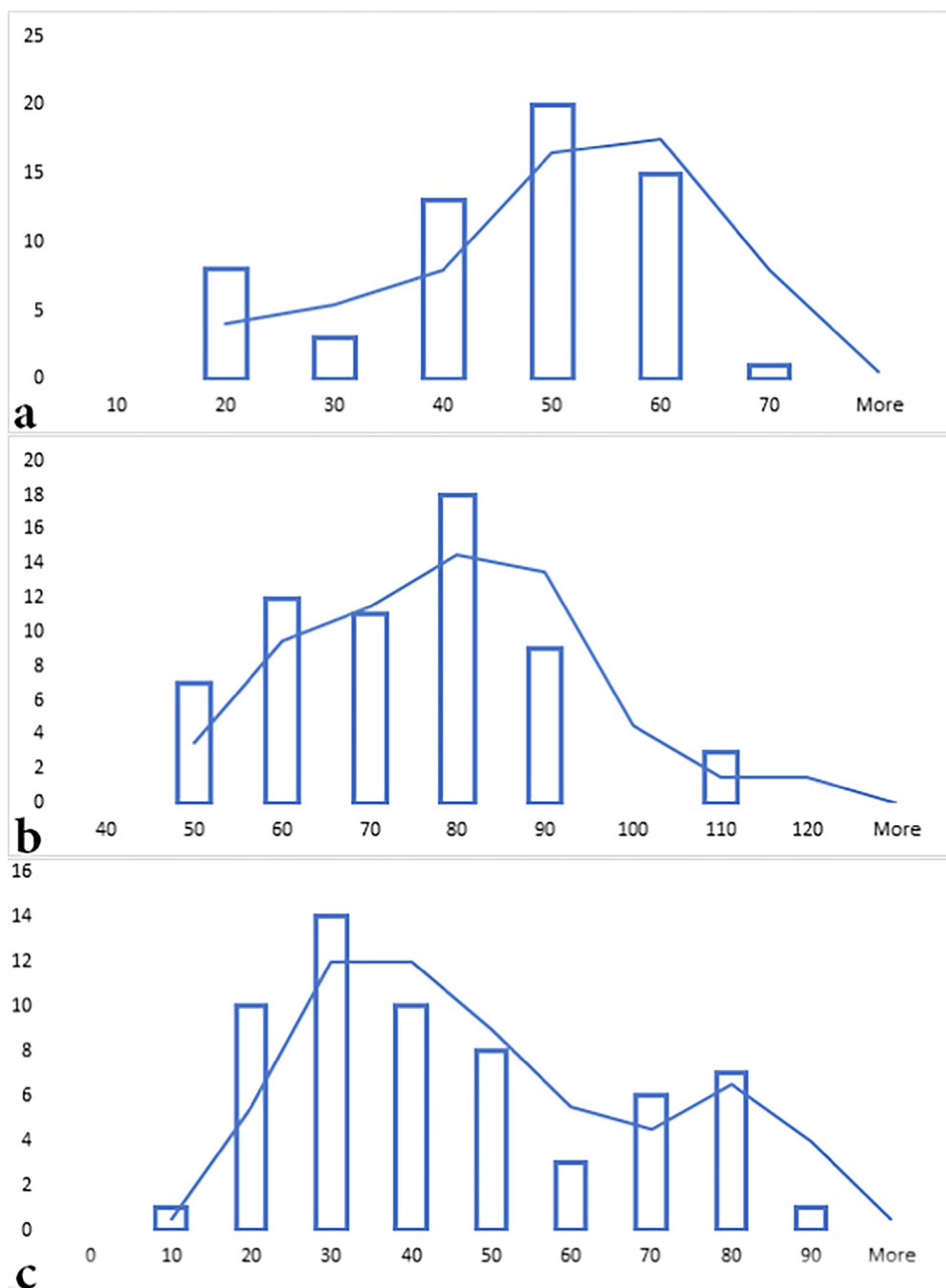


Fig. 3. Distribution of SSR markers in RIL populations based on their banding pattern. a) Allelic Frequency of the parental type CT-9993 among the RIL population. b) Allelic Frequency of Samba Mashuri paternal type in RIL populations. c) Frequency of absent or distorted bands in RIL populations.

pendent of the sign of the values. Here, “-” indicates flanking markers are linked to the chromosomal region of Samba Mashuri (Balakrishnan et al., 2020).

Our investigation identified a quantitative trait locus, q_{PH-4-1} , on chromosome 4 that was associated with plant height in both non-stressed conditions. q_{PH-4-1} loci was discovered between RM16341 and RM16251 and were shown to be unaffected by either stress or lack of stress. Additional quantitative trait loci that have an effect on plant height have previously been identified by other studies (Septiningsih et al., 2003; McNally et al., 2009; Rajurkar et al., 2021). It has been shown that plant height is reduced when plants are subjected to drought stress during the vegetative stage. This results in a relative yield penalty (Ahmadikhah and Marufinia, 2016). During the wet sea-

son, a quantitative trait locus for root dry weight was discovered on chromosome 3 of the chosen extremes. This $q_{RDW-3-1}$ was revealed to be responsible for the variation in root dry weight. The pace at which water was absorbed globally led to the establishment of this position. Qu et al. (2008) used SSR markers located on chromosome 4 in order to identify a QTL that was responsible for the root volume. Another quantitative trait locus for deep root volume under drought conditions was found by Yue et al. (2005) on chromosome 4 at marker point RM470, which is the same as RM451. We were able to identify eight stable QTLs that were linked with agronomic parameters throughout both the dry and wet seasons. The PVE for each of the major QTLs was found to be larger than 10.8% in most cases. These eight QTLs, which were found on Chr 04, Chr 08, Chr 3, Chr 6, Chr

7, and Chr 11, have shown their value in the breeding program for drought tolerance by showing impacts in the background of high-yielding recipient parents. While certain QTLs were found across all seasons, others were found in either a wet or a dry environment. Therefore, it is suggested that the genomic areas mediating drought tolerance are QTLs that have been proven to be stable throughout seasons. These QTLs need to be adequately characterized and validated before they can be utilized for molecular breeding.

Conclusions

In the course of this investigation, a number of genomic regions responsible for a wide range of phenotypes have been identified, and these findings apply to both the dry and the rainy seasons. In addition, some of those genomic loci for quantitative traits were located that were revealed to be stable over both seasons. Identifying genetic areas related to grain yield and associated attributes, and root establishment features under reproductive stage drought stress may aid future marker-assisted-pyramiding or introgression breeding initiatives aimed at increasing rice production amid drought circumstances. Furthermore, the identified potentially candidate lines may aid in the facilitation of these efforts. Fine mapping, meticulous introgression of genetic regions with positive interactions, and evaluation of long-term success across a wide range of environments and genetic contexts could be used to increase grain yield and gain a deeper understanding of QTL functionality on both a morpho-physiological and genetic level.

CRedit authorship contribution statement

Tapas Paul: Conceptualization, Investigation, Supervision, Data curation, Formal analysis, Resources, Writing – original draft, Writing – review & editing. **Sandip Debnath:** Conceptualization, Investigation, Supervision, Data curation, Formal analysis, Methodology, Project administration, Resources, Software, Validation, Writing – original draft, Writing – review & editing. **S.P. Das:** Conceptualization, Investigation, Supervision, Data curation, Project administration, Resources. **Shanthi Natarajan:** Manuscript preparation and reviewing. **Kahkashan Perveen:** Manuscript preparation and reviewing. **Najla A. Alshaikh:** Manuscript preparation and reviewing. **Kavindra Kumar Kesari:** Manuscript preparation and reviewing. **Sarbani Banik:** Data analysis. **Mallar Nath:** Data analysis. **Biswajit Pramanik:** Data analysis.

Data availability

Data will be made available on request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

The first author would like to thank Visva-Bharati University for all the help and resources offered to conduct his doctoral thesis, “**Identification and validation of major QTLs for drought tolerance in Rice (*Oryza sativa* L.)**.” K.P. and N.A.A. would like to acknowledge the support provided by Researchers Supporting Project Number RSP2023R358, King Saud University, Riyadh, Saudi Arabia

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.crbiot.2023.100125>.

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