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RESEARCH ARTICLE

Study on submergence tolerance of rice (*Oryza sativa* L.) in a core panel of North-East India using GWAS

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Abstract

Rice (*Oryza sativa* L.) being the major food crop of the north-eastern region, combating floods in rice fields for higher economic yield is a major challenge. A core panel, consisting of local rice landraces that have been cultivated in the flood-prone areas of this region for years, was used for this GWAS study to uncover possible genetic resistance sources to submergence. A study on GWAS was conducted to understand the mechanism of resistance of rice under water-submerged conditions through higher expression of genes. The GWAS analysis of a core panel of 400 rice landraces generated 38,723 filtered SNPs. The result showcased nine loci across the 12 rice chromosomes, one locus each in chromosome 2 and 4, five loci in chromosome 6, and two loci in chromosome 9. The two promising loci among these nine identified loci codes for zinc fingers, C3HC4 type domain-containing proteins, with FDR adjusted *p-values* of 0.04 each and allele effect of 4.60 and 4.57, respectively. These GWAS-identified association signals are a valuable source for allele mining and can be validated and introgressed into elite germplasms to decipher submergence tolerance in future breeding programs.

Keywords: GWAS, submergence, SNPs identification, rice landraces

Introduction

Rice (*Oryza sativa* L.) requires a huge amount of water for its growth and development, but prolonged submergence causes a hypoxia environment, which affects the growth and productivity of rice plants. Approximately 15 mha area under rice cultivation is affected by flash floods in Asia alone (Sarkar et al. 2014). The change in the climate affects rainfall patterns and may result in heavy rain and causing heavy floods. About 4 lakh ha of *sali* paddy areas are affected due to floods in Assam (Bujarbaruah 2015). However, other than the natural occurrence of floods experienced in the rice growing season, intermittent flooding with various degrees of submergence is also observed for a duration ranging from 1 to 17 days (Neog et al. 2016). Understanding the tolerance mechanism of rice under submergence is an important requirement for managing flood stress in rice during the crop season. *Indica* and *japonica* ecotypes of rice confer flood tolerance by adapting to *SUB1A* gene-regulated process of quiescence. Deepwater and most of the lowland rice genotypes usually adapt different escape strategies to combat the stress. Ethylene-mediated SNORKEL1 and SNORKEL2 genes were identified, which can withstand submergence through internode elongation (Bailey-Serres et al. 2010; Nagai et al. 2010; Nishiuchi et al. 2012). The variation among the *bao* genotypes (deepwater rice) of Assam is due to elongation ability and kneeing ability as an adaptation mechanism for submergence tolerance (Neog et al. 2016). After the identification of a QTL for submergence tolerance SUBMERGENCE 1 (SUB1) from FR13A landrace, remarkable progress has been achieved in the last 10 years in the development of flood-tolerant varieties through marker-assisted backcrossing (Khalil et al. 2024).

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Being the secondary centre of origin, the areas in the North-East states of India is a hotspot of genetic variation and endowed with a huge diversity of rice germplasm due to the presence of various ethnolinguistic groups, variation in altitude and diverse climatic conditions (Sharma et al. 1971; Choudhury et at. 2013). The germplasms available in this region have been the sources of resistance against biotic stresses (Umakanth et al. 2017), abiotic stresses (Sharma et al. 1971; Patra et al. 2018; Verma et al. 2019) and nutrition (Vanlalsanga et al. 2019; Chattopadhyay et at. 2019). North-East India harbors diverse ecotypes of rice, namely, *sali* (coarse-grained, photosensitive), *lahi* (slender-grained), ahu (aus), *asra* (semi-deepwater rice), *bao* (deepwater rice), *bora* (waxy), *chakua* (intermediate amylase content) and aromatic (scented). Many wild species of rice are also found in the region (Choudhury et al. 2013). The rice germplasms being cultivated in this region have been selected based on its adaptation to the diverse topography and agro-climatic conditions of North-East India. The rice germplasms that do well in submergence conditions are categorized into three groups, namely, *sali, bao* and *asra*. The *sali* rice varieties are tall and are cultivated during *kharif* season under rainfed lowland conditions. The *bao* rice varieties are cultivated in deepwater areas and these varieties can escape submergence by elongating themselves with the strength of their kneeing ability as the water level rises. The *asra* rice varieties can withstand stagnant water conditions by elongating their internodes. With the available germplasm adapted to the submergence environment can be assured that these rice cultivars are excellent genetic reserves for tolerance to submergence.

Although various mechanisms of submergence tolerance have been uncovered among different germplasms, only SUB1 has been extensively used for introgression by the breeders and the SUB1 introgressed varieties have expressed tolerance for about 12 days under submergence (Nishiuchi et al. 2012). However, practically in the farmers' field, these varieties didn't perform well in varying degrees of flood duration (Neog et al. 2016). This happened due to the short height of almost all *Sub1* introgressed genotypes, which were not suitable for lowland areas with water levels of more than 100 cm and flood exits for more than 21 days. This made the researchers discover other genes and genotypes showing tolerance to submergence from the early vegetative stage to the panicle initiation stage, which could withstand intermittent flooding ranging from 1 to 21 days (Chattopadhyay et al. 2018).

Genome-wide association study (GWAS) is a powerful technique to determine genomic regions by linking phenotypic and genotypic information using a diverse set of germplasms. GWAS is useful in the identification of QTLs for specific traits in rice, such as for agronomic traits (Huang et al. 2010) and anaerobic germination of deepwater rice (Rohila et al. 2020). The GWAS study also has the potential to understand the mechanism of resistance of rice under water-submerged conditions through higher expression of certain genes or due to specific QTL effects. Considering the above factors, the GWAS approach was used in the present study to dissect the genetic architecture and mechanisms for tolerance to submergence using a diverse rice panel to determine the genetic elements underlying the response.

Materials and methods

Plant material and experimental layout

The rice plants were grown in an experimental area at Assam Rice Research Institute, Assam Agricultural University (AAU-ARRI), Titabor, Assam, during *kharif* season in the year 2021. A panel of 400 landraces selected from over 6,000 available germplasm at Assam Rice Research Institute, Assam Agricultural University, Titabor was grown in a concrete tank for submergence treatment. These landraces consisted of 12 different groups, namely, aromatic, *asra*, *bao*, black rice, *bora*, new *bora*, *chakua*, *joha*, *lahi*, *khamti lahi*, *sali* and new *sali* (Supplementary Table S1). Augmented-randomised complete block design was used for designing the experiment. Each germplasm was planted with seven plant hills per row, in a total of 5 rows, 35 plants per block, and with a planting density of 20 cm x 30 cm (plant x row). The submergence tank used was 2.5 m deep. The protocol described by Xu et al. (2000) was followed for screening for submergence survival percentage of the plants. About 30 days old seedlings were submerged for a continuous ten days and de-submerged. The de-submerged plants were kept undisturbed for ten days for full recovery from submergence shock. The survival percentage after recovery was recorded visually based on the rice submergence tolerance standard evaluation system (SES). The total number of lines before submergence and after de-submergence were recorded and survival was calculated in percentage.

Sampling and genome sequencing

For leaf sampling, the youngest mature leaf was collected from one-month-old plants grown in a tank before submergence in the morning and kept in an ice box during the sampling time. The genomic DNA was isolated using the CTAB method and sequencing was performed using V4 sequencing chemistry in Illumina HiSeq™ X10. The *Oryza sativa* reference genome which was downloaded from Ensembl Genomes (http://ftp.ensemblgenomes.org/pub/ plants/release-51/fasta/oryza_sativa/). The sequence reads were mapped to the downloaded reference genome using the MEM algorithm version 0.7.5 of BWA. The mapped reads were realigned using RealignerTargetCreator and IndelRealigner inversion v3.6 of GATK (https://gatk.broadinstitute.org/hc/en-us). The vcftoolsversion0.1.17 was used for filtering the variants and removal of indels (http://

vcftools.sourceforge.net/). A minor allele frequency of 5% MAF and a missing rate of 10% were applied to filter the SNPs to target a total of 39,045 SNPs, with a minimum of 90% of samples having that particular SNPs. A total of 38,723 SNPs were mapped in the 12 rice chromosomes across the 399 samples and were further used for downstream analysis. BAM format was used in all the mapping results, and SAMtools version 0.1.18 was used to filter out the non-unique and unmapped reads.

Diversity study, population structure and PCA

The SniPlay (https://sniplay.southgreen.fr/cgi-bin/home.cgi) was used for the diversity study. With a 200 kb window in the genome, the transition-transversion ratio was calculated and plotted in VCFtools (Danecek et al. 2011). SNP density was plotted within a range of 250 kb using SNIPlay (Dereeper et al. 2011). LD plotting was done using Tomahawk software (Klarqvist 2018). LD plots were illustrated in ggplot of R. Structuring was plotted in PGDSpider, version 2.1.1.5 (Lischer and Excoffier 2018) using the 1,472 filtered SNPs with no missing data within 250 kb and filtered with the best SNP with the highest DP. STRUCTURE (version 2.3.4) was used to estimate population structure using Bayesian Markov Chain Monte Carlo model (MCMC). Each population (k) set 1-10 was run three times. The burn-in time was set to 100000 and MCMC replication number was set to 300000 for each run. Structure Harvester was used to determine the most probable K-value. PLINK (version 1.9) was used to calculate the PCA and the plot was made in R.

Genome-wide association studies

GAPIT (version 3) within R was used in the compressed mixed linear model (CMLM) to perform a genome-wide association study (GWAS) and genome prediction. Unified mixed model, EMMA, CMLM and P3D/ EMMAx were used to study statistical genetics. An association study was performed using 38,723 chromosomal SNPs by CMLM method along with kinship and population file. The significance of the SNPs was considered with a cut-off of $\log_{10}$ [P] <1e-4 threshold.

The qqman within R was used for the Manhattan plots and quantile-quantile (Q-Q) plots. A *P*-value along with a false discovery rate (FDR) was set to $P < 0.05$ to reduce any false positives and to keep the higher associations. The threshold level was set based on Q-Q plots and chromosomal positions of known loci using Bonferroni correction for submergence resistance. The polymorphism within 50kb region, flanking the highly associated SNPs with the target trait was included to identify the SNPs in intergenic regions or gene promoters (putative). Variations within the flanking region of the coding sequence were considered to keep the SNPs in open reading frames (ORFs). Nucleotide diversity was calculated and deviations from neutral equilibrium (Tajima's *D*) were studied using DnaSP (v5.10.01) (Rozas 2009) to look for the significant signals for each candidate gene.

Results

Phenotyping and GWAS overview

The plants in the submergence tank were screened for recording the degree of tolerance under submerged conditions. The submergence survival percentage of the plants was with a minimum of 10% and a maximum of 100% (Supplementary Table S1). A GWAS analysis was performed for the plants to uncover the tolerance factors in the genetic sequence. The analysis has extracted 38,723 filtered SNPs. SNPs density across the 12 chromosomes ranged from 2,252 to 4,332 SNPs with the lowest in chromosome 12 and the highest in chromosome 1 (Fig. 1). Highest number of significant SNPs was mapped in chromosome 6 (5 SNPs).

SNP identification

A number of SNPs significantly associated with submergence tolerance were detected to be nine, with 1 SNP in chromosome 2, 1 SNP in chromosome 4, 5 SNPs in chromosome 6, and 2 SNPs in chromosome 9. The SNPs have been studied for their functional role under submergence conditions. The SNP mapped to chromosome 2 is annotated as retrotransposon protein (SNP ID 2:9208802, Accession LOC_Os02g16200); in chromosome 4 as ZOS4-03 - C2H2 zinc finger protein (SNP ID 4:4296750, Accession LOC_Os04g08060); in chromosome 6 as zinc finger (SNP ID 6:20412681, Accession LOC_Os07g06560), zinc finger (SNP ID 6:20412682, Accession LOC_Os07g06560), MYB family transcription factor (SNP ID 6:20454821, Accession LOC_Os06g35140), MYB family transcription factor (SNP ID 6:20455307, Accession LOC_Os06g35140) and exostosin family protein (SNP ID 6:28365560, Accession LOC_Os06g46690); in chromosome 9 as OsFBX315 - F-box domain containing protein (SNP ID 9:9511779, Accession LOC_Os09g15570) and proteasome/ cyclosome repeat containing protein (SNP ID 9:9620587, Accession LOC_Os09g15750) (Table 1). A summary of the association mapping for submergence with data for allelic variations, minor allele frequencies (ranged 0.09–0.35), *p*-values (ranged 1.34E-05–9.58E-06), FDR Adjusted P-values (0.04 - 0.30), effect (-6.01–6.73) and R^2 (0.24–0.25) are presented in Table 2.

Population structure and LD estimation

The population structure of the 400 germplasms have been analyzed using PCA and the result showed three distinct sub-groups, with group 1 containing aromatic, *joha* and *sali*; group 2 containing *asra, bao* and new *bora*; group 3 containing aromatic, *joha*, black rice, *sali*, new *sali*, *asra*, *bao*, *bora*, new *bora*, *chakua*, *lahi* and *khamti lahi*. A decrease in the LD value from its maximum has been observed within 120-350 kb across the twelve chromosomes (Fig. 2). In the present study, the pairwise squared correlation coefficient (r2) decreased to half of its maximum value, with LD decay value of 0.6 in Chromosome 1, 0.62 in Chromosome 2, 0.62 in Chromosome 3, 0.63 in Chromosome 4, 0.6 in Chromosome

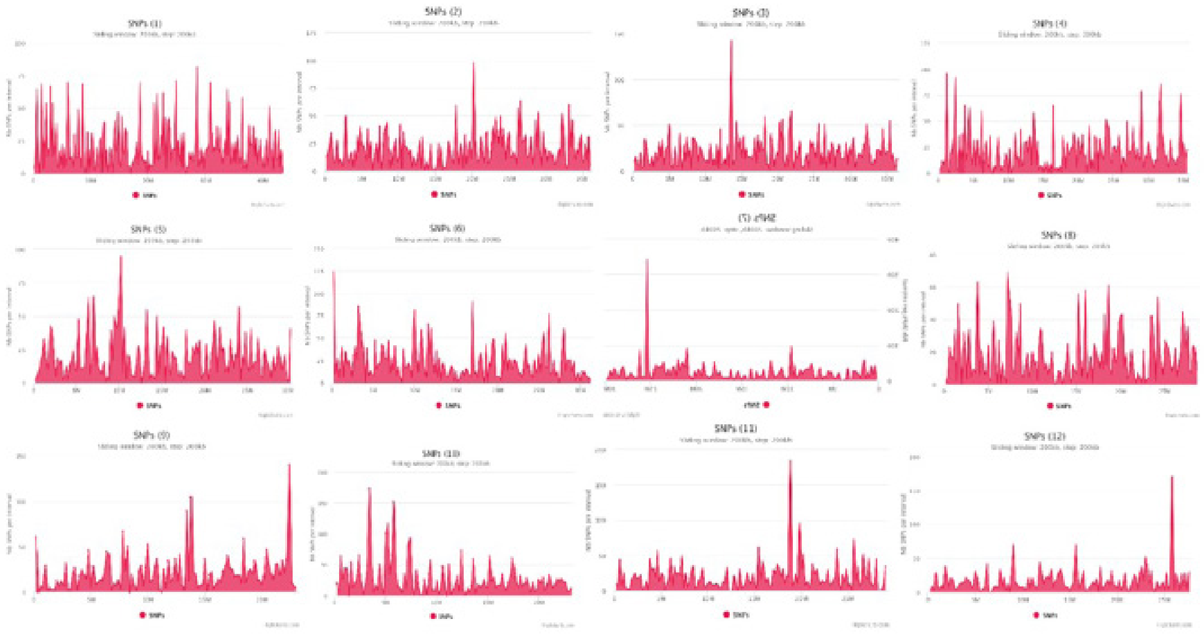

Fig. 1. SNP density variation across the twelve chromosomes. 'SNPs (1)' is SNPs in chromosome

Table 1. List of significant SNPs with gene annotation for submergence

S. No.	Trait	Chromosome	Location	Accession	Allelic variation	Description (IRGSP)
1	Submergence Survival (%)	2	9208802	LOC_Os02g16200	G/G	retrotransposon protein, putative, Ty3-gypsy subclass
2	Submergence Survival (%)	4	4296750	LOC_Os04g08060	C/T	ZOS4-03 - C2H2 zinc finger protein
3	Submergence Survival (%)	6	20412681	LOC_Os07g06560	T/T	zinc finger, C3HC4 type domain containing protein
4	Submergence Survival (%)	6	20412682	LOC_Os07g06560	C/C	zinc finger, C3HC4 type domain containing protein
5	Submergence Survival (%)	6	20454821	LOC_Os06g35140	C/CT	MYB family transcription factor, putative
6	Submergence Survival (%)	6	20455307	LOC_Os06g35140	C/C	MYB family transcription factor, putative
7	Submergence Survival (%)	6	28365560	LOC_Os06g46690	G/A	exostosin family protein, putative
8	Submergence Survival (%)	9	9511779	LOC_Os09g15570	G/A	OsFBX315 - F-box domain containing protein
9	Submergence Survival (%)	9	9620587	LOC_Os09g15750	G/T	proteasome/cyclosome repeat containing protein

5, 0.6 in Chromosome 6, 0.58 in Chromosome 7, 0.64 in Chromosome 8, 0.59 in Chromosome 9, 0.58 in Chromosome 10, 0.6 in Chromosome 11 and 0.63 in Chromosome 12.

GWAS for submergence

To analyse genome-wise association signals for submergence tolerance, 3,808,730 SNPs were used and analysed through the SUPER method of GAPIT package within R. Ten highly significant association signals were found which were with *p*-value of < 0.05 (Table 2). The detected loci were further studied for their gene annotation to understand their role in the physiological pathways to combat submergence. The nine candidate SNPs detected in the GWAS analysis for submergence tolerance were retrotransposon protein (LOC_Os02g16200, chromosome 2), ZOS4-03–C2H2 zinc finger protein (LOC_Os04g08060, chromosome 4), zinc

Table 2. Summary of association mapping for submergence

S. No.	SNP ID	Trait	Chromosome No.	Genome Position	Major allele	Minor allele	Minor allele frequency	P Value	FDR Adjusted P-values	effect	R^{2a}	Significant loci^{b}
1	2:9208802	Submergence Survival	2	9208802	G	GA	0.18	3.33E-05	0.16	4.86	0.24	LOC_Os02g16200
2	4:4296750	Submergence Survival	4	4296750	C	T	0.09	1.61E-05	0.09	6.73	0.25	LOC_Os04g08060
3	6:20412681	Submergence Survival	6	20412681	T	C	0.33	4.00E-06	0.04	4.60	0.25	LOC_Os07g06560
4	6:20412682	Submergence Survival	6	20412682	C	A	0.34	4.53E-06	0.04	4.57	0.25	LOC_Os07g06560
5	6:20454821	Submergence Survival	6	20454821	C	CT	0.35	9.58E-06	0.07	-4.28	0.25	LOC_Os06g35140
6	6:20455307	Submergence Survival	6	20455307	C	T	0.34	1.76E-06	0.04	-4.56	0.25	LOC_Os06g35140
7	6:28365560	Submergence Survival	6	28365560	G	A	0.17	4.39E-06	0.04	-4.63	0.25	LOC_Os06g46690
8	9:9511779	Submergence Survival	9	9511779	G	A	0.09	1.34E-05	0.09	-6.01	0.25	LOC_Os09g15570
9	9:9620587	Submergence Survival	9	9620587	G	T	0.09	6.99E-05	0.30	5.68	0.24	LOC_Os09g15750

^{a}R^{2} represents the genetic variations explained by the significant SNPs; ^{b}Gene ID of MSU rice genome annotation project (http:/rice.plantbiology.msu.edu/)

finger (LOC_Os07g06560, chromosome 6), zinc finger (LOC_Os07g06560, chromosome 6), MYB family transcription factor (LOC_Os06g35140, chromosome 6), MYB family transcription factor (LOC_Os06g35140, chromosome 6), exostosin family protein (LOC_Os06g46690, chromosome 6), OsFBX315-F-box domain-containing protein (LOC_Os09g15570, chromosome 9), proteasome/cyclosome repeat-containing protein (LOC_Os09g15750, chromosome 9) (Figs. 3a and 3b).

Discussion

Practical approaches through deep molecular studies such as GWAS and QTL identification are the ways to answer the challenges due to climate change (Oladosu et al. 2020). Abiotic stresses have always reduced plant yield worldwide. The plants have been fighting to grow well under adverse conditions and the need for adaptation has made a way to evolve new mechanisms to grow and develop under stressed environments. A large set of transcriptional factors and stress-responsive proteins are extensively involved in response mechanisms to stresses such as low temperature, high temperature, salinity, high light, drought, and submergence.

Based on the morpho-physiological and grain quality traits such as growth traits, yield traits, and biotic and abiotic resistance traits, the best 400 rice landraces were selected from over 6,000 landraces. This new panel of 400 landraces was used in the present GWAS analysis. Several studies on agronomically important traits in rice have reported similar findings previously (Huang et al. 2015; Zhang et al. 2019). In the present analysis, the SNP density was found to be higher in chromosome 1 and chromosome 8 among all the chromosomes. However, more significant SNPs were found in chromosome 6 and chromosome 9 (Fig. 1). Population structure analysis showed three sub-groups within the population. Subgroup 1 has scented aromatic and *joha,* and coarse-grained kharif *sali*; subgroup 2 has semi-deep water *asra,* deep water *bao* and glutinous new *bora*; and subgroup 3 has scented aromatic and *joha*, pigmented black rice, coarse-grained kharif *sali* and new *sali*, semi-deep water *asra*, deep water bao, glutinous bora and new bora, semi-glutinous chakua, and fine-grained kharif *lahi* and *khamti lahi*. In GWAS, LD estimation is crucial in understanding the identifying genetic markers because the quality of the GWAS analysis using SNPs also relies on LD while studying population genetics (Joiret et al. 2019). In the present study, LD has decreased (Fig. 2) and the distant relatedness has increased among the landraces. The results of population structure analysis and LD decay indicate that the core panel of 400 landraces used in the present study is suitable for studies on association mapping studies.

This GWAS study was analyzed using 3,808,730 SNPs to identify any new submergence-tolerant loci using the panel of 400 rice accessions under submergence conditions.

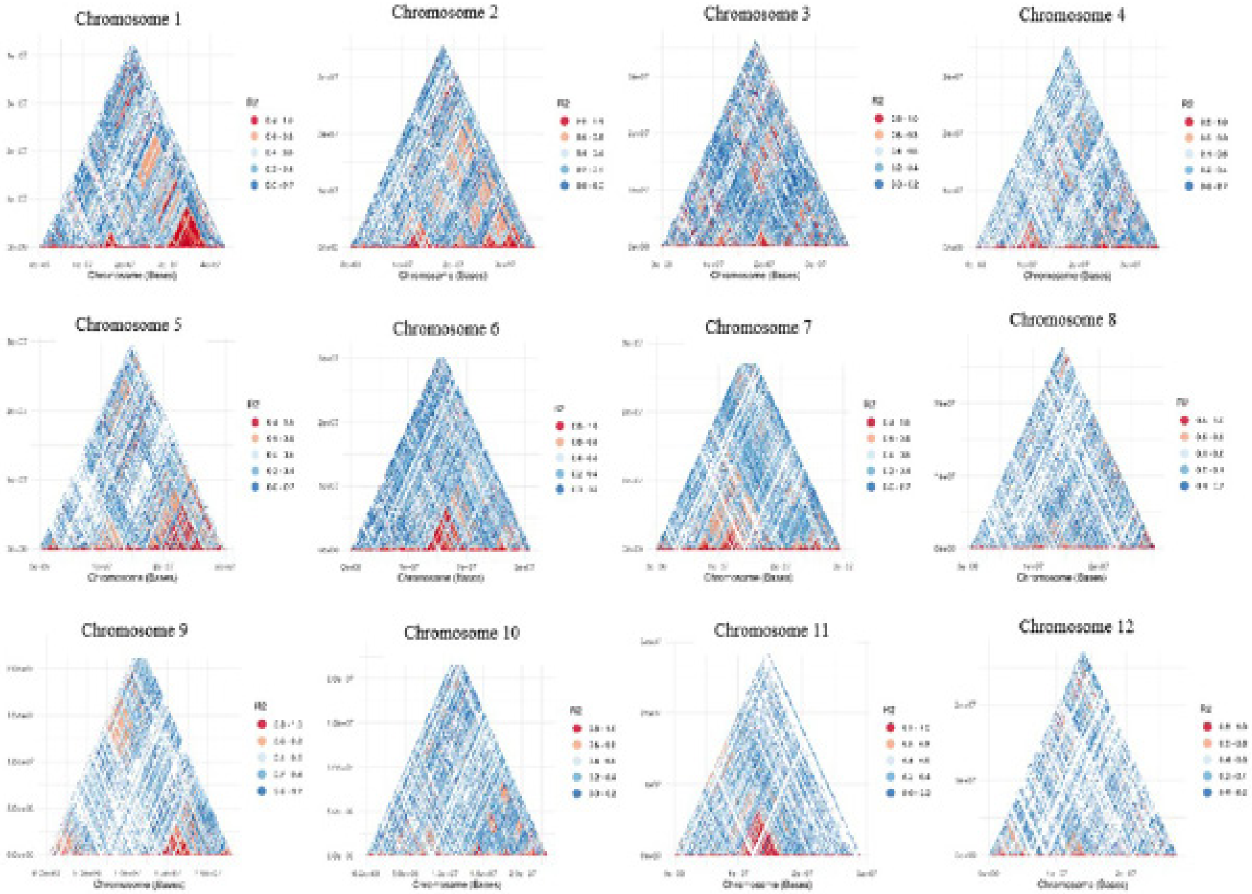

Fig. 2. LD heatmap for twelve chromosomes

The analysis employed a mixed linear model. The highly significant loci that are associated with the submergence trait were selected with a *p-value* cut-off of 0.05. The SNPs positioned within a length of 350 kb of a gene are considered close to that particular gene (Zhang et al. 2019). The nine SNPs found to be associated with submergence tolerance were mapped across twelve chromosomes (Fig. 3; Table 2). The loci uncovered in the present investigation, LOC_Os02g16200, LOC_Os04g08060, LOC_Os07g06560, LOC_Os07g06560, LOC_Os06g35140, LOC_Os06g35140, LOC_Os06g46690, LOC_Os09g15570 and LOC_Os09g15750, are believed to be involved in submergence tolerance mechanism in rice (Table 1).

The identified SNP LOC_Os02g16200 (SNP ID 2:9208802, Table 1), which annotates Ty3-gypsy subclass retrotransposon protein showed significantly high expression under submergence, indicating its involvement under the stress. Retrotransposons are transposable elements that are abundant in plant genomes and they gets activated under environmental stimuli such as microbial excretion, pathogen infection, physical injury, and other environmental stresses (Galindo-González et al. 2017). The LOC_Os04g08060 with SNP ID 4:4296750 has been predicted to be a ZOS4-03-C2H2 zinc finger protein (Table 1) which belongs to C2H2 family. This protein is involved in adaptive pathways to withstand submergence stress directly or indirectly (Wang et al. 2019). The zinc finger, C3HC4 type domain-containing proteins (SNP ID 6:20412681, Accession LOC_Os07g06560; SNP ID 6:20412682, Accession LOC_Os07g06560; Table 1) helps in plant growth and development and might have a role in submergence which is yet to be validated. MYB family has four groups of transcription factors (1R-MYB, 2R-MYB, 3R-MYB and 4R-MYB) that play a role in the overall development of plants, signal transduction, secondary metabolic pathways, biotic and abiotic stress (Katiyar et al. 2012). In the present study, two highly significant loci were found (SNP ID 6:20454821, Accession LOC_Os06g35140; SNP ID 6:20455307, Accession LOC_Os06g35140; Table 1), which encodes MYB family transcription factor, suggesting that this protein might has a role in submergence tolerance mechanism. An identified SNP LOC_Os06g46690 in this study (SNP ID 6:28365560) has been annotated exostosin family protein. Exostosin protein interacts with and influences growth molecules, morphogens and proteases and thereby regulates cell to cell crosstalk events (Busse-Wicher et al. 2014). The exact function of Exostosin proteins not yet known, and the role of this important locus in rice under submergence are yet to be validated. The identification

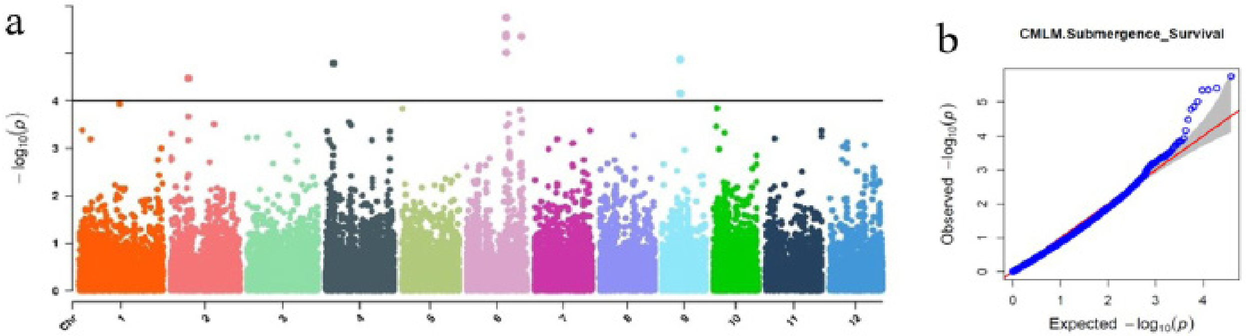

Fig. 3. Manhattan plot of EMMAX for submergence survival in genome-wide association studies. Negative log 10 p-values from a genome-wide scan are plotted against position on each of 12 chromosomes. (a) Manhattan plots of EMMAX (MLM-SUPER model). Black horizontal solid line indicates the genome-wide significant threshold; (b) Quantile-quantile (Q-Q) plot of the EMMAX (MLM-SUPER model)

of OsFBX315 - F-box domain-containing protein (SNP ID 9:9511779, Accession LOC_Os09g15570; Table 1) in the present GWAS study suggests that this protein might have a strong role in submergence tolerance in rice. The F-box encoded proteins are involved in developmental pathways in plants such as floral development, signal transduction through hormones, secondary metabolic pathways, biological clock, and biotic and abiotic stresses (Zhang et al. 2019). Proteasome/cyclosome repeat-containing protein (SNP ID 9:9620587, Accession LOC_Os09g15750; Table 1) might be connected to the maintenance and degradation of cells during submergence. In eukaryotes, proteasomes regulate the degradation of intracellular proteins (Sorokin et al. 2009). Cyclosome or APC/C responds to protein-damaging stress (Ahlskog et al. 2010). The functions of proteasome and cyclosome under submergence are yet to be confirmed.

The escape mechanism in rice under a submerged environment includes stem elongation, modification in plant architecture, internal aeration, metabolism and control in growth (Oladosu et al. 2020). The discovery of SUB1 gene has facilitated faster development of flood-tolerant varieties. The SUB1 rice varieties cannot respond to biotic and abiotic stresses simultaneously (Sharma et al. 2013). Breeding efforts have been made in recent years to combat this challenge. A simple trait governed by a single gene can be handled effectively through marker-assisted backcrossing; it would not be possible for a complex trait. A diverse set of landraces that responds well to flood and deep water can be a good set of germplasms for gene discovery other than SUB1. The landraces expressing genes for anaerobic germination will be a good source for yield stability in areas with intermittent and stagnant floods. This kind of breeding strategy can support the development of varieties for cultivation in the rainfed rice ecosystem through higher yield by preventing loss during heavy rainfall season (Oladosu et al. 2020). Identification of nine loci given in Table 1, which are highly significant under a submerged environment, can be a valuable source for submergence tolerance in rice. Among nine, two promising loci are LOC_Os07g06560 and LOC_Os07g06560 in chromosome 6. Validation of the function of these loci in the three landraces, namely Kheron (90% submergence survival percentage), Kala birain (90%) and Dhupa Bao (100%), showing maximum tolerance along with appropriate breeding efforts, can lead to new variety development with submergence tolerance as well as increase yield.

The present study used GWAS to understand and explore genic regions significantly expressed under submergence. A total of nine strong genome-wide association signals were identified across the twelve rice chromosomes in a set of 400 landraces, including observed submergence tolerance in Kheron (90% submergence survival percentage), Kala birain (90%) and Dhupa Bao (100%). Screening for new tolerant loci other than the well-acquainted SUB1 gene treated with 10 days of submergence is an important achievement. These identified loci can be tested for different durations of flood ranging from 10 to 21 days of extended submergence. Among the nine loci, the two promising loci are LOC_Os07g06560 and LOC_Os07g06560 in chromosome 6 which encodes zinc fingers, C3HC4 type domain-containing proteins. The identified loci can be validated and utilized through marker-assisted backcrossing with appropriate breeding strategies for submergence-tolerant variety development.

Supplementary material

Supplementary Table S1 contains the list of 400 landraces used in the GWAS, at www.isgpb.org

Authors' contribution

Conceptualization of research (SKC, MP); Designing of the experiments (SKC, MP); Contribution of experimental materials (SKC); Execution of field/lab experiments and data collection (MP, JD, PB, SR); Analysis of data and interpretation

(MP, SKC); Preparation of the manuscript (MP, JD, PB,SKC, MKM, AB, RKV, SR).

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Supplementary Table S1. A list of 400 landraces used in the GWAS study for submergence tolerance along with their submergence survival percentage

Sample No.	Group	Germplasm	Origin	Features	Submergence survival (%)
1	AROMATIC	IC-596590	Assam	Scented Rice	10
2	AROMATIC	IC-596559	Assam	Scented Rice	10
3	AROMATIC	IC-596560	Assam	Scented Rice	10
4	AROMATIC	IC-596580	Assam	Scented Rice	10
5	AROMATIC	IC-596562	Assam	Scented Rice	10
6	AROMATIC	IC-596563	Assam	Scented Rice	10
7	AROMATIC	IC-596564	Assam	Scented Rice	10
8	AROMATIC	IC-596565	Assam	Scented Rice	10
9	AROMATIC	IC-596566	Assam	Scented Rice	10
10	AROMATIC	IC-596567	Assam	Scented Rice	10
11	AROMATIC	IC-596568	Assam	Scented Rice	10
12	AROMATIC	IC-596569	Assam	Scented Rice	10
13	AROMATIC	IC-596570	Assam	Scented Rice	10
14	AROMATIC	IC-596571	Assam	Scented Rice	10
15	AROMATIC	IC-596572	Assam	Scented Rice	10
16	Black rice 4	AAU-1347-7	Assam	Black Rice	10
17	Black rice 6	AAU-1491-3	Assam	Black Rice	10
18	Black rice 13	AAU-1491-1	Assam	Black Rice	10
19	Black rice 8	AAU-1491-6	Assam	Black Rice	10
20	Black rice 3	AAU-1347-6	Assam	Black Rice	10
21	Black rice 9	AAU-1354	Assam	Black Rice	10
22	Black rice 12	AAU-1347-4	Assam	Black Rice	10
23	Black rice 15	AAU-1491-5	Assam	Black Rice	10
24	Black rice 5	AAU-1347-8	Assam	Black Rice	10
25	Black rice 2	AAU-1347-5	Assam	Black Rice	10
26	Black rice 1	AAU-1347-3	Assam	Black Rice	10
27	Black rice 7	AAU-1491-4	Assam	Black Rice	10
28	Black rice 11	AAU-1347-2	Assam	Black Rice	10
29	Black rice 10	AAU-1347-1	Assam	Black Rice	10
30	Black rice 14	AAU-1491-2	Assam	Black Rice	10
31	Joha	Manipuri Joha	Assam	Scented Rice	10
32	Joha	Kola Joha	Assam	Scented Rice	10
33	NEW SALI	BIRAZ	Assam	Coarse-grained kharif rice	10
34	NEW SALI	BIYOLI SALI	Assam	Coarse-grained kharif rice	10
35	ASRA	Sail Badal	Assam	Semi-deep water rice	10
36	ASRA	Laki Badal	Assam	Semi-deep water rice	10
37	ASRA	Ekar Chali	Assam	Semi-deep water rice	10
38	ASRA	Kali Mekri	Assam	Semi-deep water rice	10

39	ASRA	Lal Bora	Assam	Semi-deep water Glutinous Rice	10
40	ASRA	Bagdar	Assam	Semi-deep water rice	10
41	ASRA	Hashbadal	Assam	Semi-deep water rice	10
42	ASRA	Sunamuki	Assam	Semi-deep water rice	10
43	ASRA	Kachbadal	Assam	Semi-deep water rice	10
44	ASRA	Dud Laki	Assam	Semi-deep water rice	10
45	ASRA	Gutak	Assam	Semi-deep water rice	10
46	ASRA	Naliuri	Assam	Semi-deep water rice	10
47	ASRA	Mukbadal	Assam	Semi-deep water rice	10
48	ASRA	Hoopani	Assam	Semi-deep water rice	10
49	ASRA	ChitriKachu	Assam	Semi-deep water rice	10
50	ASRA	Joal banga	Assam	Semi-deep water rice	10
51	ASRA	Birpak	Assam	Semi-deep water rice	10
52	ASRA	Karkati	Assam	Semi-deep water rice	10
53	ASRA	Bogaamon	Assam	Semi-deep water rice	10
54	ASRA	Boga amon	Assam	Semi-deep water rice	10
55	ASRA	SunaBirain	Assam	Semi-deep water rice	10
56	ASRA	Lal Badal	Assam	Semi-deep water rice	10
57	ASRA	Garia amon	Assam	Semi-deep water rice	10
58	ASRA	Hopani	Assam	Semi-deep water rice	10
59	ASRA	Laki Asra	Assam	Semi-deep water rice	10
60	ASRA	Asra	Assam	Semi-deep water rice	10
61	ASRA	Parinoli	Assam	Semi-deep water rice	10
62	ASRA	Badal	Assam	Semi-deep water rice	10
63	ASRA	Laiva Juta	Assam	Semi-deep water rice	10
64	ASRA	Sachi amon	Assam	Semi-deep water rice	10
65	ASRA	Bir kajal	Assam	Semi-deep water rice	10
66	ASRA	Chote guta	Assam	Semi-deep water rice	10
67	ASRA	Takurbhog	Assam	Semi-deep water rice	10
68	ASRA	Baraguta	Assam	Semi-deep water rice	10
69	ASRA	Bethi Chikan	Assam	Semi-deep water rice	10
70	ASRA	Kala birain	Assam	Semi-deep water rice	**90**
71	ASRA	Parichok	Assam	Semi-deep water rice	10
72	ASRA	Jarabadal	Assam	Semi-deep water rice	10
73	ASRA	Fupari	Assam	Semi-deep water rice	10
74	ASRA	Laki	Assam	Semi-deep water rice	10
75	ASRA	Borabadal	Assam	Semi-deep water rice	10
76	ASRA	Borbadal	Assam	Semi-deep water rice	10
77	ASRA	Bung badal	Assam	Semi-deep water rice	10
78	ASRA	Madan Jaria	Assam	Semi-deep water rice	10
79	ASRA	Bazailamon	Assam	Semi-deep water rice	10

80	ASRA	Champar Koli	Assam	Semi-deep water rice	10
81	ASRA	Shona Birain	Assam	Semi-deep water rice	10
82	ASRA	Bura badal	Assam	Semi-deep water rice	30
83	ASRA	Parchan	Assam	Semi-deep water rice	60
84	ASRA	Khame	Assam	Semi-deep water rice	10
85	ASRA	Motia Badal	Assam	Semi-deep water rice	10
86	ASRA	Jora badal	Assam	Semi-deep water rice	10
87	ASRA	Ghila Kach	Assam	Semi-deep water rice	10
88	ASRA	Sukni Sail	Assam	Semi-deep water rice	20
89	ASRA	Paninoliamon	Assam	Semi-deep water rice	10
90	ASRA	Khaibadal	Assam	Semi-deep water rice	10
91	ASRA	Bura amon	Assam	Semi-deep water rice	10
92	ASRA	Muribadal	Assam	Semi-deep water rice	10
93	ASRA	Asra beroin	Assam	Semi-deep water rice	10
94	ASRA	Dholabadal	Assam	Semi-deep water rice	10
95	ASRA	Khai asra	Assam	Semi-deep water rice	10
96	ASRA	Asra Sail	Assam	Semi-deep water rice	10
97	ASRA	Ghatak Sail	Assam	Semi-deep water rice	60
98	ASRA	Boal gadda	Assam	Semi-deep water rice	60
99	ASRA	Paninoli	Assam	Semi-deep water rice	10
100	ASRA	Kheron	Assam	Semi-deep water rice	**90**
101	ASRA	Kanla	Assam	Semi-deep water rice	10
102	ASRA	Latibadal	Assam	Semi-deep water rice	10
103	ASRA	Tenga Badal	Assam	Semi-deep water rice	10
104	ASRA	Baurash	Assam	Semi-deep water rice	10
105	ASRA	Khud badal	Assam	Semi-deep water rice	10
106	ASRA	Jaol Gadda	Assam	Semi-deep water rice	10
107	ASRA	Dhari	Assam	Semi-deep water rice	10
108	ASRA	Mukh Badal	Assam	Semi-deep water rice	10
109	ASRA	Boralaki	Assam	Semi-deep water rice	10
110	ASRA	Chotolaki	Assam	Semi-deep water rice	10
111	ASRA	Khoi asra	Assam	Semi-deep water rice	10
112	ASRA	Asra Variant	Assam	Semi-deep water rice	10
113	ASRA	Kola Amon	Assam	Semi-deep water rice	60
114	ASRA	Sangar Paddy	Assam	Semi-deep water rice	10
115	ASRA	Jaisiya	Assam	Semi-deep water rice	10
116	ASRA	Turhiya	Assam	Semi-deep water rice	10
117	ASRA	Kariywa	Assam	Semi-deep water rice	10
118	ASRA	Koloingi	Assam	Semi-deep water rice	30
119	ASRA	Lahata	Assam	Semi-deep water rice	30
120	Bao	Sunamukhi Bao	Assam	Deep Water Rice	10

121	Bao	Kakua Bao	Assam	Deep Water Rice	10
122	Bao	Raiji Bao	Assam	Deep Water Rice	20
123	Bao	Sonamoti Bao	Assam	Deep Water Rice	10
124	Bao	Nepali Bao	Assam	Deep Water Rice	10
125	Bao	Batha Bao	Assam	Deep Water Rice	10
126	Bao	Dhupa Bao	Assam	Deep Water Rice	**100**
127	Bao	Biria bhanga Bao	Assam	Deep Water Rice	30
128	Bao	Basjok Bao	Assam	Deep Water Rice	10
129	Bao	Daffa Bao	Assam	Deep Water Rice	10
130	Bao	Sonajul Bao	Assam	Deep Water Rice	10
131	Bao	Kolomi Bao	Assam	Deep Water Rice	10
132	BAO	Mothonga Bao	Assam	Deep Water Rice	10
133	BAO	Sursuri Joha	Assam	Scented Rice	10
134	BAO	Amona Bao	Assam	Deep Water Rice	10
135	BAO	Negheri Bao	Assam	Deep Water Rice	10
136	BAO	Mem Bao	Assam	Deep Water Rice	10
137	BAO	Kola Amona Bao	Assam	Deep Water Rice	10
138	BAO	Koladah Bao	Assam	Deep Water Rice	10
139	BAO	Rongadah Kokua	Assam	Deep Water Rice	10
140	BAO	Bogadah Bao	Assam	Deep Water Rice	10
141	BAO	Kumoli Bao	Assam	Deep Water Rice	10
142	BAO	Gujari Bao	Assam	Deep Water Rice	10
143	BAO	Koli Bao	Assam	Deep Water Rice	10
144	BAO	Tulsi Bao	Assam	Deep Water Rice	10
145	BAO	Tora Bao	Assam	Deep Water Rice	10
146	BAO	Sona Bao	Assam	Deep Water Rice	10
147	BAO	Kon Bao	Assam	Deep Water Rice	10
148	BAO	Ronga Bao	Assam	Deep Water Rice	10
149	BAO	Dewri Bao	Assam	Deep Water Rice	10
150	BAO	Duat Kalam	Assam	Deep Water Rice	10
151	BAO	PaniKakua	Assam	Deep Water Rice	10
152	BAO	Adolia Bao	Assam	Deep Water Rice	10
153	BAO	Sona Mukhi	Assam	Deep Water Rice	10
154	BAO	Kahijul	Assam	Deep Water Rice	10
155	BAO	Rangoon	Assam	Deep Water Rice	10
156	BAO	Ranga Balam	Assam	Deep Water Rice	10
157	BAO	Boga Balam	Assam	Deep Water Rice	10
158	BAO	At Bao	Assam	Deep Water Rice	10
159	BAO	Buruli Bao	Assam	Deep Water Rice	10
160	BAO	Maimansinga	Assam	Deep Water Rice	10
161	BAO	Dhepa Bao	Assam	Deep Water Rice	10

162	BAO	Lal Dhepa	Assam	Deep Water Rice	10
163	BAO	Saru Raj	Assam	Deep Water Rice	10
164	BAO	Rangchali	Assam	Deep Water Rice	10
165	BAO	Basikalam	Assam	Deep Water Rice	10
166	BAO	Rupohi	Assam	Deep Water Rice	30
167	BAO	Bogi Bao	Assam	Deep Water Rice	30
168	BAO	Rangagutia	Assam	Deep Water Rice	10
169	BAO	Naya Kadam	Assam	Deep Water Rice	10
170	BAO	Bao 325	Assam	Deep Water Rice	10
171	BAO	Bil Badam	Assam	Deep Water Rice	10
172	BAO	Kokua-1	Assam	Deep Water Rice	10
173	BAO	Ranga Bao	Assam	Deep Water Rice	10
174	BAO	Jul Bao	Assam	Deep Water Rice	10
175	BAO	Kajoli Bao	Assam	Deep Water Rice	10
176	BAO	Tara Bao	Assam	Deep Water Rice	10
177	BAO	ASRA Bao	Assam	Deep Water Rice	10
178	BORA	Abor Bora	Assam	Glutinous Rice	10
179	BORA	Ahu Bora	Assam	Glutinous Rice	10
180	BORA	Alohi Bora	Assam	Glutinous Rice	10
181	BORA	Bor Bora-1	Assam	Glutinous Rice	10
182	BORA	Bao Bora	Assam	Glutinous Rice	10
183	BORA	Beji Bora-1	Assam	Glutinous Rice	10
184	BORA	Begun Bora	Assam	Glutinous Rice	10
185	BORA	Boga Bora-1	Assam	Glutinous Rice	10
186	BORA	Boka Bora	Assam	Glutinous Rice	10
187	BORA	Bakul Bora	Assam	Glutinous Rice	10
188	BORA	Bhat Bora	Assam	Glutinous Rice	10
189	BORA	Bora-1	Assam	Glutinous Rice	10
190	BORA	Botia Bora	Assam	Glutinous Rice	10
191	BORA	BorMalbhog	Assam	Glutinous Rice	10
192	BORA	hakua Bora-1	Assam	Glutinous Rice	10
193	BORA	Chansep Bora	Assam	Glutinous Rice	10
194	BORA	Chandra Bora	Assam	Glutinous Rice	10
195	BORA	Danbori Bora	Assam	Glutinous Rice	10
196	BORA	Dudh Bora	Assam	Glutinous Rice	10
197	BORA	Durodia Bora	Assam	Glutinous Rice	10
198	BORA	Fakial Bora	Assam	Glutinous Rice	10
199	BORA	Gela Bora	Assam	Glutinous Rice	10
200	BORA	Garu Chakua Bora-1	Assam	Glutinous Rice	30
201	BORA	Gomiri Bora	Assam	Glutinous Rice	10
202	BORA	Noldang Bora	Assam	Glutinous Rice	30

203	BORA	Helochi Bora-1	Assam	Glutinous Rice	10
204	BORA	Hurupi Bora	Assam	Glutinous Rice	10
205	BORA	Hoki Bora	Assam	Glutinous Rice	10
206	BORA	Khurupi Bora	Assam	Glutinous Rice	10
207	BORA	Jota Bora	Assam	Glutinous Rice	10
208	BORA	kankhua Bora	Assam	Glutinous Rice	10
209	BORA	Kanchi Bora	Assam	Glutinous Rice	10
210	BORA	Khaldhora Bora	Assam	Glutinous Rice	10
211	BORA	Koni Bora	Assam	Glutinous Rice	10
212	BORA	Kuki dhan Bora	Assam	Glutinous Rice	10
213	BORA	Kola Bora-1	Assam	Glutinous Rice	10
214	BORA	Kola Ampakhi	Assam	Glutinous Rice	30
215	BORA	Lothow Bora	Assam	Glutinous Rice	10
216	BORA	Mon Bora-1	Assam	Glutinous Rice	10
217	BORA	Memon Bora	Assam	Glutinous Rice	10
218	BORA	Mikir Bora	Assam	Glutinous Rice	30
219	BORA	Monipuri Bora	Assam	Glutinous Rice	30
220	BORA	Mouguti Bora	Assam	Glutinous Rice	10
221	BORA	Noga Joha Bora	Assam	Glutinous Rice	10
222	BORA	Narul Bora	Assam	Glutinous Rice	10
223	BORA	Nashingget Bora	Assam	Glutinous Rice	30
224	BORA	Neoli Bora	Assam	Glutinous Rice	10
225	BORA	Nolchuti Bora	Assam	Glutinous Rice	60
226	BORA	Paro chakua	Assam	Glutinous Rice	30
227	BORA	Pokor Kola Bora	Assam	Glutinous Rice	10
228	BORA	Pangari Bora	Assam	Glutinous Rice	10
229	BORA	Pakhi Loga Bora	Assam	Glutinous Rice	10
230	BORA	Rajat Bora	Assam	Glutinous Rice	10
231	NEW SALI	DINESH	Assam	Coarse-grained kharif rice	10
232	BORA	Sikora Bora	Assam	Glutinous Rice	10
233	BORA	Soru Bora	Assam	Glutinous Rice	10
234	BORA	Sorai Bhanu Bora	Assam	Glutinous Rice	60
235	BORA	SungalGhew Bora	Assam	Glutinous Rice	10
236	NEW SALI	Jal dubi Sali	Assam	Coarse-grained kharif rice	10
237	BORA	Sontuki Bora	Assam	Glutinous Rice	10
238	BORA	Saudang Bora-1	Assam	Glutinous Rice	10
239	BORA	Sukoni Bora-1	Assam	Glutinous Rice	10
240	BORA	Saukha Bora	Assam	Glutinous Rice	10
241	BORA	Sorai Nakhia Bora	Assam	Glutinous Rice	10
242	BORA	Singphow Bora	Assam	Glutinous Rice	10
243	BORA	Tengun Bora-1	Assam	Glutinous Rice	10

244	BORA	Titaphulia Bora-1	Assam	Glutinous Rice	10
245	BORA	Thopa Bora	Assam	Glutinous Rice	10
246	BORA	TilKochu Bora	Assam	Glutinous Rice	10
247	BORA	Tulokhi Bora	Assam	Glutinous Rice	10
248	BORA	Kuki Bora	Assam	Glutinous Rice	10
249	NEW BORA	Ronga Bora	Assam	Glutinous Rice	10
250	NEW BORA	Kawari Bora	Assam	Glutinous Rice	10
251	NEW BORA	Nol Bora	Assam	Glutinous Rice	10
252	NEW BORA	Jengoni Bora	Assam	Glutinous Rice	10
253	NEW BORA	Nac Lace Bora	Assam	Glutinous Rice	10
254	NEW BORA	Chakua Bora	Assam	Glutinous Rice	10
255	NEW BORA	Ghew Bora	Assam	Glutinous Rice	10
256	NEW BORA	Rupohi Bora	Assam	Glutinous Rice	10
257	NEW BORA	Khamti Bora	Assam	Glutinous Rice	10
258	NEW BORA	Til Bora	Assam	Glutinous Rice	10
259	NEW BORA	Bokul Bora	Assam	Glutinous Rice	10
260	NEW BORA	Dhigol Bora	Assam	Glutinous Rice	10
261	NEW BORA	Tanguna Bora	Assam	Glutinous Rice	10
262	NEW BORA	Pakhiloga Bora	Assam	Glutinous Rice	10
263	NEW BORA	Poita Bora	Assam	Glutinous Rice	10
264	NEW BORA	KoKua Bora	Assam	Glutinous Rice	10
265	NEW BORA	Soro Chakua Bora	Assam	Glutinous Rice	10
266	NEW BORA	Dadhora Bora	Assam	Glutinous Rice	10
267	NEW BORA	Moulabi Bora	Assam	Glutinous Rice	10
268	NEW BORA	Misiri Bora	Assam	Glutinous Rice	10
269	NEW BORA	Jangoni Bora	Assam	Glutinous Rice	10
270	NEW BORA	Kanhuli Bora	Assam	Glutinous Rice	10
271	NEW BORA	Pakhori Bora	Assam	Glutinous Rice	30
272	NEW BORA	Solpona Bora	Assam	Glutinous Rice	30
273	NEW BORA	NamborMising Bora	Assam	Glutinous Rice	10
274	NEW BORA	Tulsi Bora	Assam	Glutinous Rice	10
275	NEW BORA	Nolia Bora	Assam	Glutinous Rice	20
276	NEW BORA	Makhi Bora	Assam	Glutinous Rice	10
277	NEW BORA	Kati Donga Bora	Assam	Glutinous Rice	10
278	NEW BORA	Chakhao (Black Rice)	Manipur	Glutinous Rice	10
279	CHAKUA	Boga Chakua	Assam	Semi-glutinous rice	10
280	CHAKUA	Boka Chakua-1	Assam	Semi-glutinous rice	10
281	CHAKUA	BorChakua	Assam	Semi-glutinous rice	10
282	CHAKUA	Bora Chakua	Assam	Semi-glutinous rice	10
283	CHAKUA	Chakua	Assam	Semi-glutinous rice	10
284	CHAKUA	Haru Chakua	Assam	Semi-glutinous rice	10

285	CHAKUA	KajoliChakua	Assam	Semi-glutinous rice	10
286	CHAKUA	KalamdaliChakua	Assam	Semi-glutinous rice	10
287	CHAKUA	Kola Boka Chakua	Assam	Semi-glutinous rice	10
288	CHAKUA	Lahi Chakua	Assam	Semi-glutinous rice	10
289	CHAKUA	Maju Chakua-1	Assam	Semi-glutinous rice	10
290	CHAKUA	MalbhogChakua	Assam	Semi-glutinous rice	10
291	CHAKUA	MisiriChakua	Assam	Semi-glutinous rice	10
292	CHAKUA	Nepali Chakua	Assam	Semi-glutinous rice	10
293	CHAKUA	Sam Chakua	Assam	Semi-glutinous rice	10
294	CHAKUA	Saru Chakua	Assam	Semi-glutinous rice	10
295	CHAKUA	Pozo Chakua	Assam	Semi-glutinous rice	10
296	JOHA	Arab Joha	Assam	Scented Rice	10
297	JOHA	Badsabhog	Assam	Scented Rice	10
298	JOHA	Bengoli Joha	Assam	Scented Rice	10
299	JOHA	Bhoboli Joha	Assam	Scented Rice	10
300	JOHA	Bokul Joha	Assam	Scented Rice	10
301	JOHA	Boga Joha	Assam	Scented Rice	10
302	JOHA	Bhungri Joha	Assam	Scented Rice	10
303	JOHA	Bor Joha	Assam	Scented Rice	10
304	JOHA	Bogi Joha	Assam	Scented Rice	10
305	JOHA	Boga ManikiMadhuri Joha	Assam	Scented Rice	10
306	JOHA	Boga Tulsi	Assam	Scented Rice	10
307	JOHA	Borsal Joha	Assam	Scented Rice	10
308	JOHA	Cheniguti	Assam	Scented Rice	10
309	JOHA	Chufon	Assam	Scented Rice	10
310	JOHA	Goalporia Joha-1	Assam	Scented Rice	10
311	JOHA	Gobinda Bhog	Assam	Scented Rice	10
312	JOHA	Jaha	Assam	Scented Rice	10
313	JOHA	Joha Bora	Assam	Scented Rice	10
314	JOHA	Koli Joha	Assam	Scented Rice	10
315	JOHA	Konjoha-1	Assam	Scented Rice	10
316	JOHA	Kunkuni Joha	Assam	Scented Rice	10
317	JOHA	Kopow Joha	Assam	Scented Rice	10
318	JOHA	Konbogi Joha	Assam	Scented Rice	10
319	JOHA	Kaljira	Assam	Scented Rice	10
320	JOHA	Khorika Joha	Assam	Scented Rice	10
321	JOHA	Krishna Joha	Assam	Scented Rice	10
322	JOHA	Kotari Bhog	Assam	Scented Rice	10
323	JOHA	Kamini Joha	Assam	Scented Rice	10
324	JOHA	ManikiModhuri Joha	Assam	Scented Rice	10
325	JOHA	Monipuri Joha	Assam	Scented Rice	10

326	JOHA	Nepali Joha	Assam	Scented Rice	10
327	JOHA	Ronga Joha-1	Assam	Scented Rice	10
328	JOHA	Rampal Joha	Assam	Scented Rice	10
329	JOHA	Tulsi Joha	Assam	Scented Rice	10
330	JOHA	Tulsi Bhog	Assam	Scented Rice	10
331	JOHA	Joha	Assam	Scented Rice	10
332	JOHA	Bokul (Colour)	Assam	Scented Rice	10
333	JOHA	Bur Joha	Assam	Scented Rice	10
334	JOHA	KDML	Assam	Scented Rice	10
335	KHAMTI LAHI	Khamti Lahi-1	Arunachal Pradesh	Fine-grained kharif rice	30
336	KHAMTI LAHI	Khamti Lahi-2	Arunachal Pradesh	Fine-grained kharif rice	30
337	KHAMTI LAHI	Khamti Lahi-3	Arunachal Pradesh	Fine-grained kharif rice	30
338	KHAMTI LAHI	Khamti Lahi-4	Arunachal Pradesh	Fine-grained kharif rice	10
339	KHAMTI LAHI	Khamti Lahi-5	Arunachal Pradesh	Fine-grained kharif rice	10
340	KHAMTI LAHI	Khamti Lahi-6	Arunachal Pradesh	Fine-grained kharif rice	10
341	KHAMTI LAHI	Khamti Lahi-7	Arunachal Pradesh	Fine-grained kharif rice	60
342	KHAMTI LAHI	Khamti Lahi-8	Arunachal Pradesh	Fine-grained kharif rice	10
343	KHAMTI LAHI	Khamti Lahi-9	Arunachal Pradesh	Fine-grained kharif rice	10
344	KHAMTI LAHI	Khamti Lahi-10	Arunachal Pradesh	Fine-grained kharif rice	10
345	LAHI	Kataribhog	Assam	Fine-grained kharif rice	10
346	LAHI	BOR JAHINGA	Assam	Fine-grained kharif rice	10
347	LAHI	Cheni Lahi	Assam	Fine-grained kharif rice	10
348	LAHI	Beji Jung	Assam	Fine-grained kharif rice	10
349	SALI	Kalamdani	Assam	Coarse-grained kharif rice, Blast Resistant	10
350	SALI	Sial Sali	Assam	Coarse-grained kharif rice, Blast Resistant	10
351	NEW SALI	KAWARIJUL BAO	Assam	Coarse-grained kharif rice	10
352	SALI	FR13A	Odisha	Coarse-grained kharif rice, Submergence Resistant	30
353	SALI	Andrew Sali-1	Assam	Coarse-grained kharif rice, Blast Resistant	10
354	SALI	Behari Sali	Assam	Coarse-grained kharif rice	10
355	SALI	Dholamula-1	Assam	Coarse-grained kharif rice	10
356	SALI	Ikora Sali-1	Assam	Coarse-grained kharif rice, Blast Resistant	10
357	SALI	Jopora Sali	Assam	Coarse-grained kharif rice	10

358	SALI	Manohar Sali	Assam	Coarse-grained kharif rice, Blast Resistant	10
359	SALI	BorSolpona	Assam	Coarse-grained kharif rice, Blast Resistant	10
360	SALI	Hati Sali	Assam	Coarse-grained kharif rice	10
361	SALI	BorGathi	Assam	Coarse-grained kharif rice	10
362	SALI	Basbor	Assam	Coarse-grained kharif rice	10
363	SALI	Behoni Sali	Assam	Coarse-grained kharif rice	10
364	SALI	Batkopahi-1	Assam	Coarse-grained kharif rice	10
365	SALI	Chatuki Sali-2	Assam	Coarse-grained kharif rice	10
366	SALI	Dhoma Sali	Assam	Coarse-grained kharif rice	10
367	SALI	Doria Dhan	Assam	Coarse-grained kharif rice	10
368	NEW SALI	KRISHNA HAMSA	Andhra Pradesh	Coarse-grained Boro rice	10
369	Basmati	Pusa Basmati -1121	IARI, Pusa	Long graing Scented Basmati rice	10
370	NEW SALI	MALBHOG	Assam	Coarse-grained kharif rice	10
371	SALI	Mahsuri	Assam	Medium slender kharif rice, Blast Resistant	10
372	SALI	Dhola Suplish	Assam	Coarse-grained kharif rice	10
373	SALI	Genow	Assam	Coarse-grained kharif rice	10
374	SALI	Gua Sari-1	Assam	Coarse-grained kharif rice	10
375	SALI	Herai Powa Sali	Assam	Coarse-grained kharif rice	10
376	SALI	Haldhor	Assam	Coarse-grained kharif rice	10
377	SALI	HinutomaBordhan	Assam	Coarse-grained kharif rice	10
378	SALI	Jaimasi	Assam	Coarse-grained kharif rice	10
379	SALI	Kachui Kumari	Assam	Coarse-grained kharif rice	10
380	SALI	Kuncheng Foe	Assam	Coarse-grained kharif rice	10
381	SALI	Kola Sakhoru	Assam	Coarse-grained kharif rice	10
382	NEW SALI	SARAJU	Assam	Coarse-grained kharif rice	10
383	SALI	Konidhan	Assam	Fgrained kharif rice	10
384	SALI	Kamaltara	Assam	Coarse-grained kharif rice	10
385	SALI	Kulki Sali	Assam	Coarse-grained kharif rice	10
386	SALI	Lal-Chatkora Sali	Assam	Coarse-grained kharif rice	10
387	SALI	Leo-mom Sali	Assam	Coarse-grained kharif rice	10
388	SALI	Motia Soru	Assam	Coarse-grained kharif rice	10
389	SALI	Sonkosi	Assam	Coarse-grained kharif rice	10
390	SALI	Monila	Assam	Coarse-grained kharif rice	10
391	SALI	MohisungiaRupohi	Assam	Coarse-grained kharif rice	10
392	SALI	Rupohi Sali	Assam	Coarse-grained kharif rice	10
393	SALI	Son Bor Sali	Assam	Coarse-grained kharif rice	10
394	NEW SALI	Teraboli	Assam	Coarse-grained kharif rice, Blast Resistant	10
395	NEW SALI	NCM-7-Solpona	Assam	Coarse-grained kharif rice	10
396	NEW SALI	AMPAKHIA	Assam	Coarse-grained kharif rice	10

397	NEW SALI	AMULYA	Assam	Coarse-grained kharif rice	10
398	NEW SALI	Saru jahinga-1	Assam	Coarse-grained kharif rice	10
399	NEW SALI	Hati Dotia	Assam	Coarse-grained kharif rice	10
400	NEW SALI	Beto Bao	Assam	Coarse-grained kharif rice	10