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RESEARCH

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Meta-analysis of microarray and RNAseq data reveal OsbZIP52 to mediate salt stress responses in sensitive, tolerant and halophyte rice varieties

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Abstract

The development of salt-tolerant rice has become urgent due to climate change and rising global rice consumption. A large-scale analysis using different but related platforms has become imperative to filter out candidate genes responsible for salinity tolerance and salinity stress-responsive pathways. Such genes can be used to find prospective candidate salt resistance genes in donor rice genotypes and transfer them to high-yielding rice varieties. We performed a meta-analysis to screen out candidate genes using stress-related three microarray and one RNASeq datasets from NCBI. As different genotypes of rice and different salinity stress conditions were considered in our analysis, the sensitivity of the results is expected to be multi-fold higher. Our analysis revealed the differentially expressed genes (DEGs) OsbZIP52 and OsLTP2.5 to be common between leaf and root tissues. These genes were further compared with those of the wild halophytic rice *Oryza coarctata* expression data in stress conditions to understand the significance of these genes. The OsbZIP52 gene homolog of *Oryza coarctata* was the only one found to be differentially expressed. The expression level of OsbZIP52 was quantified using RT-qPCR and observed downregulated expression in salt stress in root and leaf tissues of four rice cultivars (2 salt-tolerant and 2 salt-sensitive). Promoter and motif analysis revealed a high number of variations in promoter and motif regions of the gene in IR29 salt-sensitive rice. Expression correlation analysis and Gene Ontology study suggested that OsbZIP52 interacts with genes that are engaged in stress response and participate in stress-responsive pathways. Collectively this study increases our understanding of the differential gene expression in various stress conditions in root and leaf tissues. It also helped identify a critical regulatory transcription factor in assisting the plant in combating salinity stress.

Keywords Salinity, Rice, Microarray, RNASeq, Salt-stress, OsbZIP52

Introduction

Rice is one of the most important food crops globally, with 154 million hectares under cultivation and humans consuming 85% of the total rice produced. Rice is the primary diet of Asia, where 70% of the world's 1.3 billion people live (Anon 1997). Around 1.0 billion hectares of salt-affected soils are predicted to exist globally, which significantly hampers rice productivity (Singh 2022). While rice (*Oryza sativa* L.) is by far the most important crop and the most practical alternative for starting crop production in saline soil (Ismail et al. 2007; Singh et al. 2010), it is projected to suffer the most from salt stress, especially in nations with extensive coastlines (Swaminathan and Kesavan 2012). Rice is one of the most

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vulnerable crop species to salt stress (Steduto et al. 2012), and often a small amount of 50 mM NaCl can have a negative impact (Hairmansis et al. 2014; Munns and Tester 2008; Yeo and Flowers 1986).

By 2025, the global total rice consumption would be 800 mT, whereas rice demand in Asia is predicted to rise further by about 70% in the next 30 years due to population expansion (Kubo and Purevdorj 2004; Muthayya et al. 2014). This is likely to produce a double blow to producers and consumers alike with the expected rise in salinity stress and a loss in production per unit area. Salinity remediation has its set of constraints, and so rice genetic modification for higher salinity tolerance is critical (Goff 2002).

Salt stress has two critical effects: ionic imbalance and osmotic stress. Membrane damage, increased lipid peroxidation, and the formation of reactive oxygen species are all consequences of these effects (Kumar et al. 2013). Excess Na^+ accumulation results in nutritional imbalance, which ultimately reduces the growth and development of plants (Li et al. 2017). However, some plants have evolved methods to cope with the salty environment. The accumulation of suitable osmolytes in the cytosol, the reduction of osmotic potential to maintain water intake, and the increased activity of enzymes that detoxify reactive oxygen species (ROS) (Schmidt et al. 2013) are some of the key mechanisms. The type of downstream response to abscisic acid (Kurotani et al. 2015), Ca^{2+} binding proteins (Garg et al. 2015), photosynthesis apparatus damage prevention and preservation (Gill et al. 2013), and energy production and compartmentalization also influence the tolerance or sensitivity of a rice genotype. In stress-tolerant cultivars, several catalytic, DNA binding, transcription regulator activities (Hirayama and Shinozaki 2010; Yamaguchi-Shinozaki and Shinozaki 2006), carbon fixation, glycolysis, and metabolic pathways have been reported to be enriched (Walia et al. 2005), and genes encoding enzymes related to these systems are promising targets to improve stress tolerance in economically important crops (Pardo 2010; Umezawa et al. 2006).

Gene response and the relative importance of those in combating salinity stress must be prioritized to perform the candidate gene approach method. Over a thousand research publications on salinity stress in rice and other crops have been published worldwide in the previous decade, and data on differential gene expression studies have been stored in several public databases. This availability of data opens up a plethora of opportunities to screen out candidate gene list responses to salinity stress and use them further for gene editing or modification. There are no environmental, food, or feed safety concerns with the candidate gene strategy because the donor and receivers are both from the rice gene pool. Through meta-analysis, a group of possible candidate salinity tolerance-linked genes can be identified, validated, and used in rice improvement strategies.

A meta-analysis combines multiple scientific studies followed by statistical validation (Normand 1999; Raudenbush et al. 1991). The challenges of identifying essential salinity tolerance-linked genes and prioritizing them can be resolved using a meta-analysis approach. While meta-analysis regarding abiotic stress such as drought (Khowaja et al. 2009; Shaik and Ramakrishna 2013; Swamy et al. 2011; Trijatmiko et al. 2014), cold or heat stress (Raza et al. 2020), and biotic stresses like rice blast (Ballini et al. 2008) and bacterial blight (Shaik and Ramakrishna 2013) of rice has been implemented, a meta-analysis of salinity stress of rice has not. A platform for rice meta-analysis is now available (McLaren et al. 2005), and thus the available datasets need to be investigated appropriately to find out the candidate genes responsible for salinity tolerance. There are not many studies that performed a wide range of meta-analyses considering different tissue types and different stress conditions for rice. This research used an integrated meta-analysis approach and discovered crucial genes implicated in salinity response. Both microarray and RNASeq analysis methods were implemented, which made the analysis more robust and sensitive. This study considered different tolerant and sensitive rice varieties and various salt stresses to pinpoint the most potent genes expressed in leaf and root tissues responding to salt stress. Various bioinformatics analyses were performed to analyze the effect of potential genes in response to salt stress. The result of this novel study will aid in understanding the salt stress tolerance mechanism by looking at the different rice varieties and stress conditions and coming to a common ground regarding the genes that are likely responsible for stress tolerance.

Materials and methods

Data mining

Salinity stress data were retrieved from GEO: Gene Expression Omnibus (Barrett et al. 2012) (www.ncbi.nlm.nih.gov/geo/). GSE76613 (Kong et al. 2019), GSE58603 (Wang et al. 2016), and GSE21651 (Mishra et al. 2018) datasets of salt stress experiments were chosen for Microarray data analysis. The RNASeq data (Illumina and 454) of rice salinity were retrieved from Sequence Retrieval Archive (SRA) at NCBI, and their accessions were GSE109341 (Formentin et al. 2018). The count data obtained from NCBI were all already preprocessed and directly utilized for differential expression analysis. These datasets were employed in a rice salinity meta-analysis

where independent differential expression analysis was performed on each dataset.

Dataset categorization

Datasets were categorized into two types: leaf and root. Root data includes 3 japonica varieties (TCN1: salt-sensitive, Baldo: salt-tolerant, and Vialone Nano: salt-sensitive) and 3 indica varieties (TNG67: salt-tolerant, PL177: salt-tolerant, and IR64: salt-sensitive), whereas leaf data encompasses of 4 indica varieties (PL177: salt-tolerant, IR64: salt-sensitive, CSR11: salt-tolerant, and VSR156: salt-sensitive) and 2 japonica varieties (Baldo: salt-tolerant, and Vialone Nano: salt-sensitive). The datasets, along with genotypes, treatment, and stress concentration, were recorded in Table 1.

Identification of differentially expressed genes (DEGs) using microarray datasets

Microarray data analysis for leaf tissue was performed by GEO2R, an available interactive web tool at NCBI. Using the Bioconductor project's GEOquery and limma R packages (Ritchie et al. 2015), GEO2R compares original submitter-supplied processed data tables. Bioconductor is an open-source software project of R programming language that provides tools for analyzing high-throughput genomic data. GEOquery parses GEO data into R data that other R tools can use. The limma (Linear Models for Microarray Analysis) package is one of the most widely used statistical tests for identifying differentially expressed genes. It can handle a wide range of experimental designs and data sources, as well as apply multiple-testing corrections to P-values to assist in eliminating false-positive results. GEO2R analysis was performed using default parameters where Benjamini–Hochberg procedure controls false discovery rate (FDR) and GEO2R automatically performs log2-transformation on the values in log space and quantile normalization on expression data to have an identical distribution of all samples. The rank of differentially expressed genes was based on log fold change >1 or <-1 and with a threshold P-value <0.05. So, genes with a log fold change greater than 1 or less than -1 were considered differentially expressed genes (Hong and Breitling 2008). Independent expression analysis was performed on each dataset and different numbers of DEGs were identified in each experiment of the microarray data. They were combined to identify the most significant genes between all microarray data experiments.

Identification of differentially expressed genes (DEGs) using RNASeq datasets

The raw read count data was collected for the RNASeq dataset from Sequence Retrieval Archive (SRA) at NCBI. Differentially expressed genes (DEGs) identification analyses were then performed using the DESeq2 method in R programming language by comparing the read counts

Table 1 Microarray and RNASeq datasets with plant names and salinity stress conditions

Tissue	GEO_ACC	Platform	Genome	Stress	Treatment time	Plant	Cultivar	Type	Analysis
Root	GSE76613	Phalanx Rice OneArray® v1	MSU Rice Genome Annotation Project release 6.1, BGI 93-11, GenBank Oryza sativa Japonica Group mRNA	250 mM NaCl	3 h	TNG67	Indica	Tolerant	Microarray
						TCN1	Japonica	Sensitive	
	GSE58603	Affymetrix Rice Genome Array	Affymetrix rice genome array containing 48,564 japonica and 1260 indica sequences	140 mM NaCl	11 days	PL177	Indica	Tolerant	
						IR64	Indica	Sensitive	
Leaf	GSE58603	Affymetrix Rice Genome Array	Affymetrix rice genome array containing 48,564 japonica and 1260 indica sequences	140 mM NaCl	11 days	PL177	Indica	Tolerant	Microarray
						IR64	Indica	Sensitive	
	GSE21651	Affymetrix Rice Genome Array		150 mM NaCl	24 h	CSR11	Indica	Tolerant	
						VSR156	Indica	Sensitive	
Root	GSE109341	Illumina HiSeq 2000 (Oryza sativa Japonica Group)	Oryza sativa v. Nipponbare genome	100 mM NaCl, 10 mM Na_2SO_4, 20 mM $MgCl_2$, and 10 mM $CaCl_2$	3 days	Baldo	Japonica	Tolerant	RNASeq
						Vialone Nano	Japonica	Sensitive	
Leaf	GSE109341	Illumina HiSeq 2000 (Oryza sativa Japonica Group)	Oryza sativa v. Nipponbare genome	101 mM NaCl, 10 mM Na_2SO_4, 20 mM $MgCl_2$, and 10 mM $CaCl_2$	3 days	Baldo	Japonica	Tolerant	RNASeq
						Vialone Nano	Japonica	Sensitive	

of the transcripts of the control and salt-treated samples. DESeq2 analysis performs three consecutive steps to identify differentially expressed genes, such as size factor estimation, dispersion estimation, and FDR statistics. DESeq2 uses the median of ratios method to normalize the count data and employ Benjamini–Hochberg FDR (Benjamini and Hochberg 1995) statistics to screen out differentially expressed genes. DESeq2 analysis was performed in a default setting where default normalization method, size factor, wald test and a negative binomial generalized linear model (GLM) were used to assess differential expression. For differentially expressed genes, a log fold change greater than 1 or less than −1 and adjusted P-value < 0.05 were considered as cut-off values to preserve consistency over the whole experiment.

Differentially expressed genes in leaf and downstream analysis

Microarray and RNASeq analysis under leaf category were performed, and the genes of the two analyses were compared. Genes from both microarray and RNASeq analysis that passed the cut-off value were considered as significantly differentially expressed genes. The shared genes between the two analyses were selected for further analysis. To predict the relationship between differentially expressed genes, protein–protein interactions were analyzed in Cytoscape software using the STRING v11.0 database (Shannon 2003; Szklarczyk et al. 2019). The RAP (Rice Annotation Project) ID of DEGs in leaf was submitted, and a PPI network was constructed with the default confidence level of 0.4 utilizing STRING database. Gene ontology enrichment study was performed to identify the enriched "Biological process" in response to salt stress. The analysis was also performed using the STRING web tool which utilizes rank-based enrichment detection algorithms and visualized through the R programming language and Cytoscape software.

Differentially expressed genes in root and downstream analysis

Differentially expressed genes from microarray and RNASeq analysis of root were compared, and the shared genes between the two studies were filtered out. These shared genes were then subjected to a protein–protein interaction network (PPI) and gene ontology (GO) enrichment analysis. Cytoscape software was used to perform PPI network analysis by using the STRING database (https://version-11-0b.string-db.org/), and the GO Biological process was also observed from the STRING v11.0 web tool. A default condifence score of 0.4 was used for GO analysis. For clear visualization, R and Cytoscape tools were used.

DEGs between leaf and root, and their significance

Resultant differentially expressed genes from leaf and root were examined to distinguish the shared genes between the two tissues. In addition, log fold changes of common genes in different rice varieties from the experiments, as well as their involvement in protein networks and biological processes through the STRING database, were observed.

Comparison of DEGs with halophyte *Oryza coarctata*

Oryza coarctata (Oryza coarctata) is a wild halophyte that has adapted to high salinity (20–40 dS ml^{-1}) and can withstand long periods of complete submersion in saline water. The differential genes for *Oryza* were obtained from a previously performed transcriptomic (Garg et al. 2014). The study provides DEGs from different stress conditions with at least twofold changes. A comparison between the differential expression of genes obtained from the above analysis and the differential expression of genes from *Oryza coarctata* was performed.

Real-time qPCR and data anlaysis

RT-qPCR analysis was carried out to confirm that the bZIP52 gene is differently expressed between salt-stressed and control samples in both salt-sensitive and salt-tolerant genotypes. Two salt-sensitive cultivars (BR28 and IR29) and two salt-tolerant cultivars (Horkuch and Pokkali) were selected for this purpose. The experiment was performed in the net house of the Plant Biotechnology Laboratory, University of Dhaka. Seeds from these cultivars were incubated at 50 °C for 5 days to break their dormancy. Seeds soaked in distilled water were then placed in a 37 °C incubator for germination for 3 days. The seeds were then transferred to Styrofoam sheets floating in two trays containing Yoshida's solution. Yoshida's solution was changed every 2d. After 14 days, 60 mM salt stress was applied to one tray; no salt was applied to an identical control tray. Then the salt concentration of the salt stress treatment tray was increased by 20 mM each day until it reached 100 mM salt concentration. Seedlings were randomly taken from both trays after 24 h of 100 mM salt application. Samples were washed and dried with tissue paper. Shoot and root tissues were collected separately in liquid nitrogen. Therefore, the total number of samples was [4 cultivars × 2 treatments × 3 biological replicates × 2 tissues = 48].

Total RNA was isolated from the collected tissues using TRIZOL following the manufacturer's protocol (Invitrogen, USA) and quantified using Qubit™ 4 Fluorometer (Thermo Fisher Scientific Inc.). Total RNA purity and degradation were again evaluated on 1% agarose gels before proceeding to the RT-qPCR step. 1.5 µg samples of purified total RNA from all four

cultivars were reverse transcribed into cDNA using SuperScript™ III First-Strand Synthesis System for RT-qPCR (Invitrogen, USA). RT-qPCR was performed in triplicate using SYBRTM Select Master Mix for CFX on CFX Opus 96 Real-Time PCR System (Bio-Rad) according to the manufacturer's recommendations. The primers were designed using the Primer3Plus program and are listed in Additional file 6: Table S6. The thermal cycling conditions were as follows: 95 °C for 3 min followed by 40 cycles of 95 °C for 10 s and 62 °C for the 30 s. The specificity of amplification was verified at the end of each PCR run using the melting curve data. To determine the relative fold differences for each sample, the Ct value for each gene was normalized to the Ct value of the sno gene, and the difference between cultivars was calculated using the $2-\Delta\Delta Ct$ method (Livak and Schmittgen 2001). Data analysis was performed in R using multiple T-test statistical analysis where P-value < 0.05 was considered significant against control.

Genetic variant analysis

The variant analysis was performed on the promoter and motif regions of the OsbZIP52 gene between salt-tolerant (Horkuch and Pokkali) and salt-sensitive varieties (IR29). A Meme suite server was utilized to find the transcription factor binding regions within the promoter of the gene and examined the variations between tolerant and sensitive varieties. It utilizes an expectation–maximization algorithm to iteratively build position-specific probability matrices (PSPMs) representing the motifs. The MEME algorithm also incorporates background models to estimate motif significance (Bailey et al. 2015). For this analysis, promoter sequence of OsbZIP2 was entered into the Meme suite server and as a result, the server provided with transcription factor binding regions within the promoter. Later, multiple sequence alignment was used to those particular binding sites from both tolerant and sensitive varieties in order to see how the transcription factor binding sequences varied. Moreover, motif regions from coding sequences of the gene from tolerant and sensitive varities were sreached using the Tomtom algorithm and subjected to multiple sequence alignment between varieties. Tomtom employs a similarity measure, such as the Pearson correlation coefficient or the Kullback–Leibler divergence, to assess the similarity between motifs and identify potential matches. (Gupta et al. 2007). Tomtom allows to compare a query motif against a database of known motifs to find potential matches and infer functional annotations.

Co-expression analysis

The significant differentially expressed gene was then subjected to co-expression analysis. The co-expression analysis was performed in the genevestigator software. Genevestigator (Hruz et al. 2008) application contains gene expression databases and tools for analyzing expression data. The co-expression analysis was conducted by analyzing samples of stress-related microarray datasets for tolerant plants with a maximum threshold value of 0.9 and P-value < 0.05. Using the euclidian distance approach, the Hierarchical clustering algorithm depicted pattern similarities of co-expressed genes in different stress expression data based on log fold change in transcript abundance with the largest difference from control.

Expression analysis in different plants

The expression pattern of the most significant gene was then observed in different plants, such as *Arabidopsis thaliana* (Accession number: GSE27548, GSE27550, and GSE53990), *Medicago truncatula* (Accession number: E-MTAB-2681, and GSE13907), *Glycine max* (Accession number: PRJNA516324, E-MTAB-4352, and PRJNA306380), and *Zea mays* (Accession number: PRJNA556806, PRJNA657262, and E-MTAB-4258), under different stress conditions using genevestigator software. The software selects samples from all available microarray or RNASeq datasets from different databases, including NCBI, array express, and many others, for each plant based on different stress conditions and performs expression analysis using a log fold change cut-off of 1.

Result

The analysis focused on identifying genes consistently regulated across different studies, providing insights into the shared molecular mechanisms underlying salt stress response in rice. The complete structure of the research is represented in Fig. 1.

Microarray and RNASeq analysis result of leaf tissue

The expression analysis was performed on two leaf microarray dataset and obtained 767 statistically significant DEGs. One leaf RNASeq analysis revealed 650 statistically significant DEGs. The comparison between microarray and RNASeq analysis results provided 106 DEGs (Additional file 1: Table S1) common in both leaf tissue analyses in different rice varieties (Fig. 2A). The expression pattern of these 106 genes was investigated through a heatmap (Fig. 2B), and two clusters of genes were observed across the pattern expressing in the opposite manner. The general differential expression pattern appeared to be quite similar between tolerant and sensitive plants, but the heat map revealed a small variation

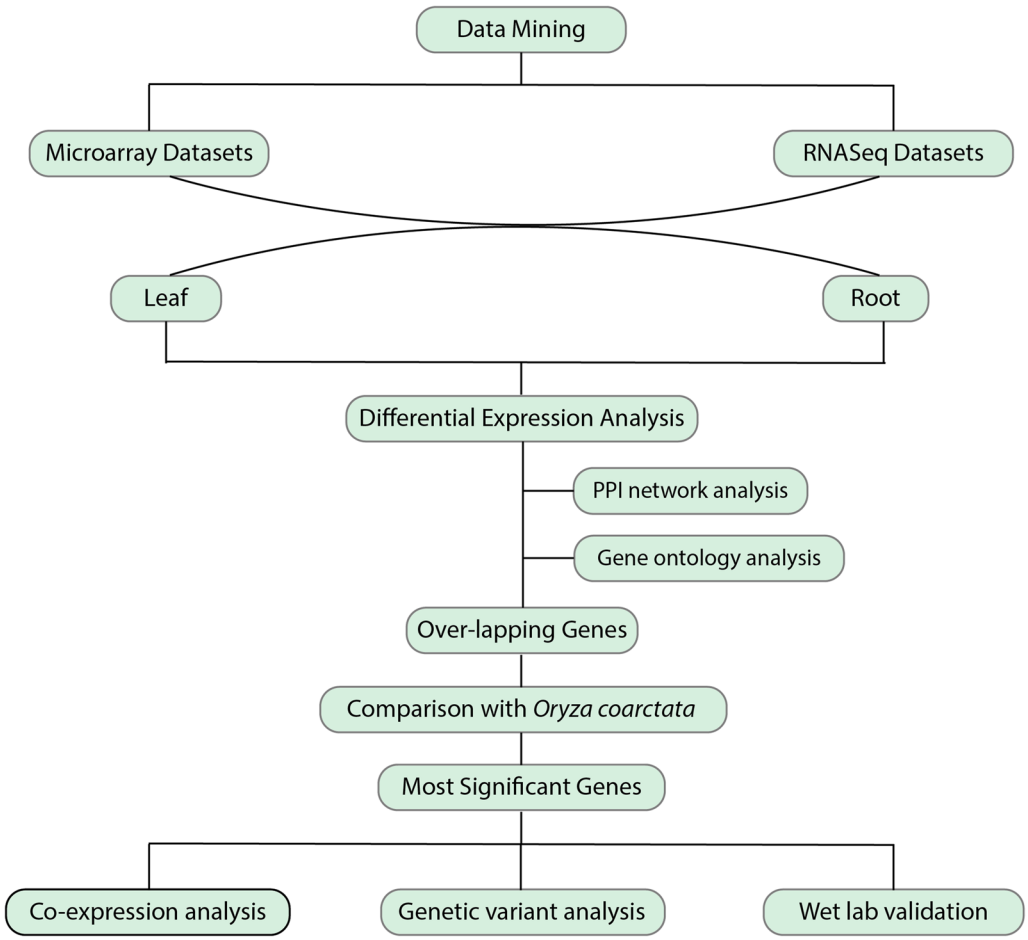

Fig. 1 Workflow of the analysis

that could be attributable to the stress treatment time, as each data set employed varied treatment periods such as 3 h, 24 h, 3 days, and so on. Also, some salt stress genes were found expressed differently in tolerant and sensitive plants, including OsTPS2 (improve tolerance under cold and salinity stress), OsLEA14A (improve tolerance against dehydration, salinity, $CuSO_4$, and $HgCl_2$) (Hu et al. 2019), OsMST6 (enhances membrane integrity and stability under salt stress) (Monfared et al. 2020), OsHsfB2b (acts as a negative regulator in response to salinity stress) (Xiang et al. 2013), and many others.

Protein–Protein network and gene ontology analysis of leaf DEGs

The interactions between the predicted 106 differentially expressed leaf proteins were investigated through the STRING web tool. 33 proteins were depicted in the network that showed interaction with one or more proteins (Fig. 2C). OsJ_04024 (putative heat shock protein 70 kDa) protein was identified to interact with the highest number of proteins (8 proteins) in the network. The network also includes some other salt stress-related genes, including OsPYL4, Os01g0337500, OsBZ8, OsTPS2, OsSRFP1, and many others. Gene ontology analysis to explore enriched biological processes revealed that these DEGs were significantly enriched in 15 biological processes (Additional file 2: Table S2) terms (FDR < 0.04) (Fig. 2D), including terpenoid metabolic process (GO:0006721)(4 genes), primary metabolic process (GO:0044238)(16 genes), cellular metabolic process (GO:0044237)(15 genes), and organic substance biosynthetic process (GO:1901576)(10 genes).

Microarray and RNASeq analysis result of root tissue

The GEO2R analysis of two root microarray datasets provided 82, and DESeq2 analysis of one root RNASeq studies unraveled 754 DEGs. Further observation of the results of these two analyses identified 29 common (Fig. 3A) DEGs (Additional file 3: Table S3). The expression pattern of these 29 genes was observed via heatmap, and the dendrogram divided all the genes into 2 clusters (Fig. 3B). The overall differential expression pattern looked quite similar between tolerant and sensitive, but

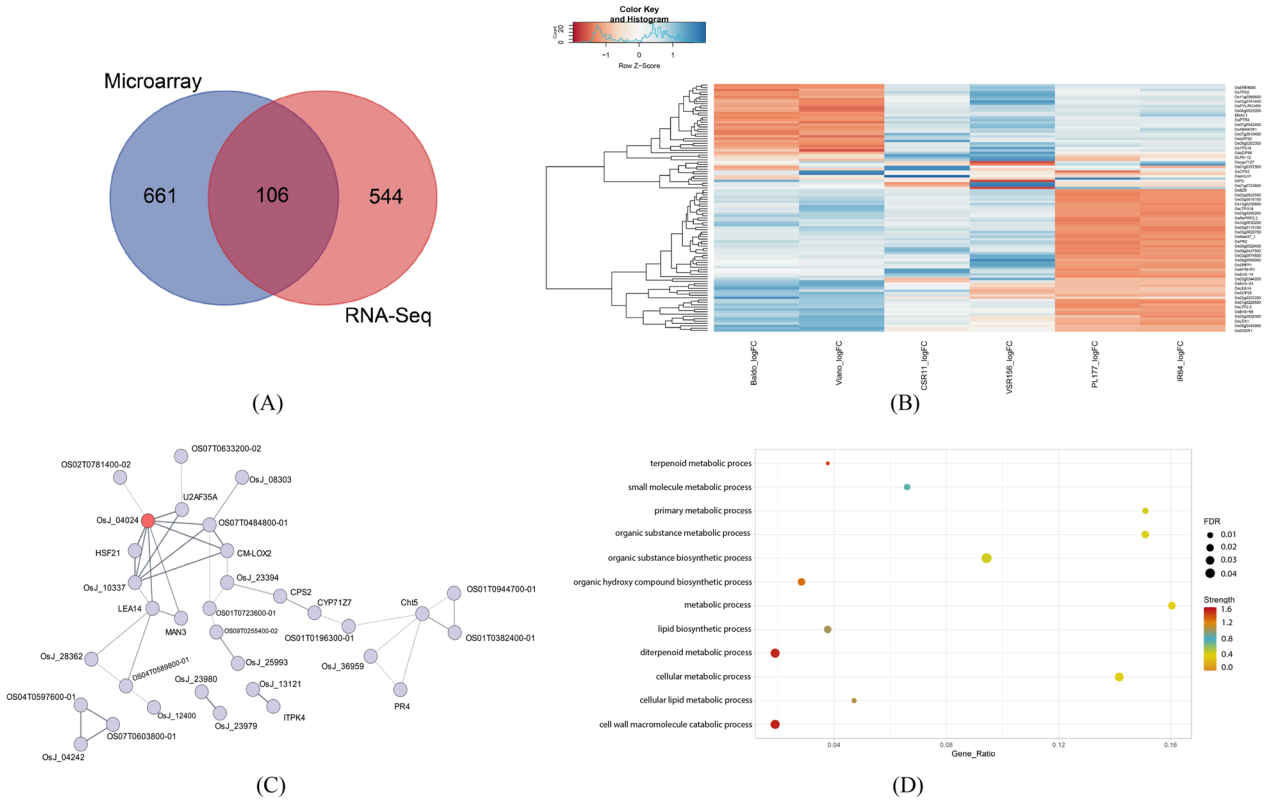

Fig. 2 DEGs in leaf and downstream analysis. **A** Common genes in the leaf between microarray and RNASeq analysis, and **B** visualization of the expression pattern. **C** Protein–protein interaction (PPI) network and **D** enriched GO Biological process of leaf differentially expressed genes

the subtle difference that was observed from the heat map are due to stress response genes and different stress treatment procedure as each data used different treatment periods and conditions (Table 1). Various salt stress genes were discovered from the analysis that expressed differentially in root tissue, such as OsHOX24 (enhances susceptibility to abiotic stresses through fine-tuning salt-responsive gene expression in rice) (Bhattacharjee et al. 2017), OsHOX22 (functions as a negative regulator in salt and drought tolerance in rice) (Zhang et al. 2012b), OsPP2C30 (regulates abiotic stress via ABA signaling pathways) (Singh et al. 2015), and Os03g0757600 (response to abiotic stress through glycosylation of flavonoids) (Dong et al. 2020).

protein–protein network and gene ontology analysis of root DEGs

The relationship between predicted DEGs in root tissue, protein–protein interaction network was constructed using the STRING database. Only 5 of the genes were depicted in the network that interacts with one another (Fig. 3C), and OsJ_009875 (probable protein phosphatase 2C 30) interacts with the highest (2 proteins) number of proteins in the network. Gene ontology analysis showed that the predicted DEGs were enriched in 29 biological process terms (FDR < 0.04) (Fig. 3D), among them, regulation of cellular process (GO:0050794) (5 genes), cellular response to acid chemical (GO:0071229) (2 genes), carbohydrate derivative metabolic process (GO:1901135) (3 genes), cellular response to chemical stimulus (GO:0070887) (3 genes), and nitrogen compound metabolic process (GO:0006807) (9 genes) were included (Additional file 4: Table S4).

Significant DEGs in leaf and root tissues and downstream analysis

Differential expression analysis revealed 106 and 29 dysregulated genes, respectively, from leaf and root experiments. Among these genes, two genes (OsbZIP52: b-ZIP transcription factor 52 and OsLTP2.5: non-specific lipid transfer protein 2.5) were shared between the leaf and root that were differentially expressed. Log fold change of OsbZIP52 gene in different rice varieties across the analysis was observed (Fig. 4A). The dysregulation of OsbZIP52 was found to vary based on the plant's geographical distribution and salt response in different tissues. STRING network analysis showed that OsbZIP52 forms a

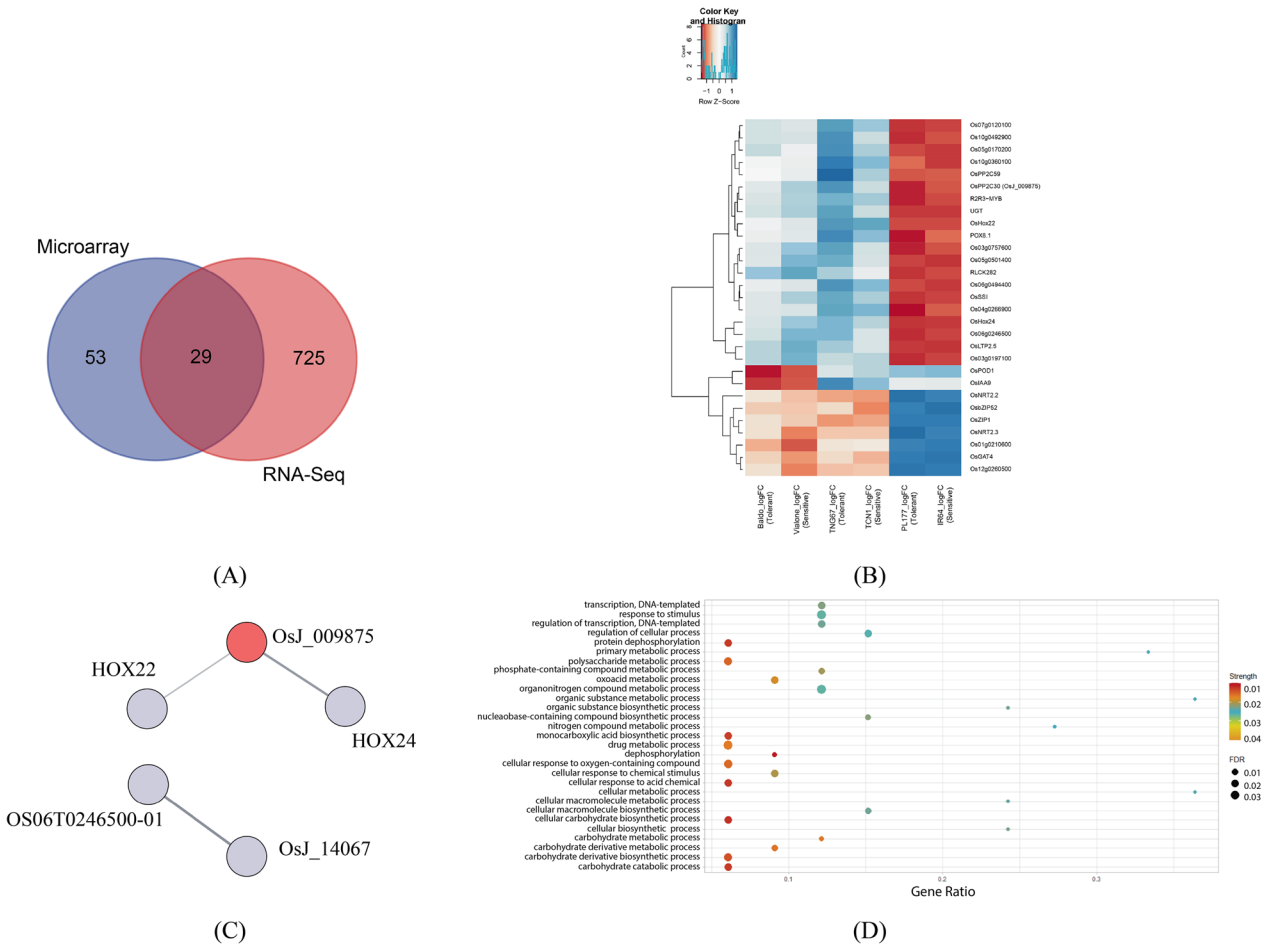

Fig. 3 DEGs in root and downstream analysis. **A** Common genes in the root between microarray and RNASeq analysis and **B** visualization of the expression pattern. **C** Protein–protein interaction (PPI) network and **D** enriched GO Biological process of root differentially expressed genes

protein–protein network composed of 11 significant proteins (Fig. 4B). These proteins were enriched in 13 critical biological processes (Additional file 5: Table S5) terms (FDR < 0.03) (Fig. 4C), including signal transduction (GO:0007165) (2 genes), cellular response to an organic substance (GO:0071310) (2 genes), response to abscisic acid (GO:0009737) (2 genes), response to stress (GO:0006950) (3 genes), and response to oxygen-containing compound (GO:1901700) (4 genes). On the other hand, OsLTP2.5 was also found to be dysregulated based on the regional distribution of plants and tissues (Fig. 5A). OsLTP2.5 formed a network of 9 proteins (Fig. 5B), but no significant GO terms have been found. However, recent studies found that the involvement of nsLTP in abiotic stress responses may aid plant adaptation to change environmental circumstances (Liu et al. 2015). Therefore OsbZIP52 and OsLTP2.5 were of great significance in tolerating stress conditions.

Analysis of resultant DEGs with *Oryza coarctata* expression analysis

The significant genes were then compared with *Oryza* differential expression analysis in different stress conditions. Transcriptomic analysis in different stress conditions of *O. coarctata* has been performed in past experiments (Garg et al. 2014). The expression data of that experiment revealed that the bZIP9 gene of *Oryza* with the 'Arabidopsis' annotation of basic leucine zipper 9 and a homolog to the OsbZIP52 rice gene (HomoloGene:116482) was found to be differentially expressed in submergence plus salt stress condition. Such a response of a specific gene to salt stress in a highly salt-tolerant plant clearly depicted the significance of the gene.

Expression analysis of OsbZIP52 genes by RT-qPCR

The expression profile of the OsbZIP52 gene in the root and shoot of tolerant and sensitive plants was studied to determine the physiological and functional importance of the gene during salt stress. It was observed that the

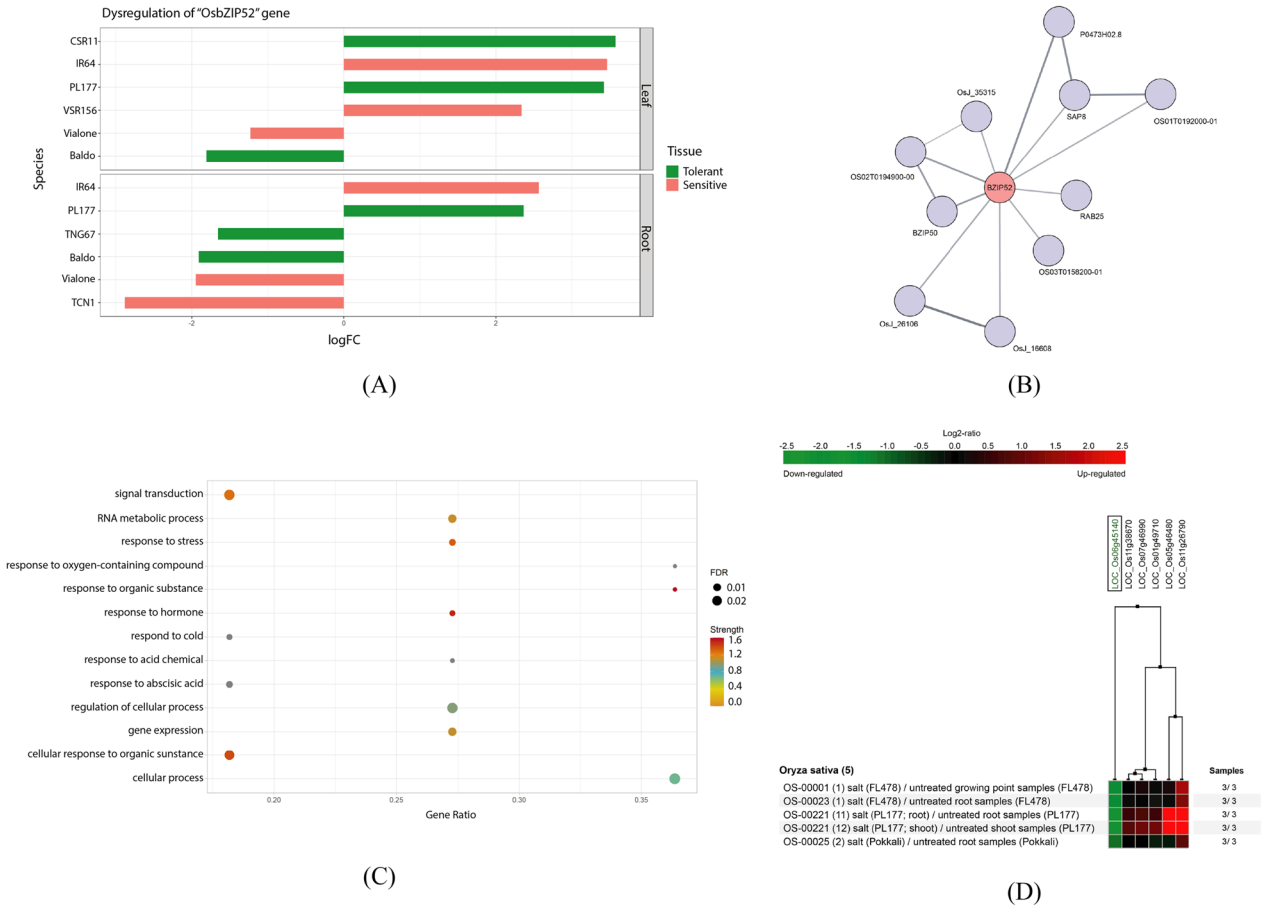

Fig. 4 OsbZIP52 gene characterization. **A** Log fold change observation in different plants used in the analysis and **B** protein–protein network of OsbZIP52 gene. **C** Enriched GO biological process of OsbZIP52 gene network. **D** Correlation analysis of OsbZIP52 (LOC Os06g45140) gene with other salt response genes

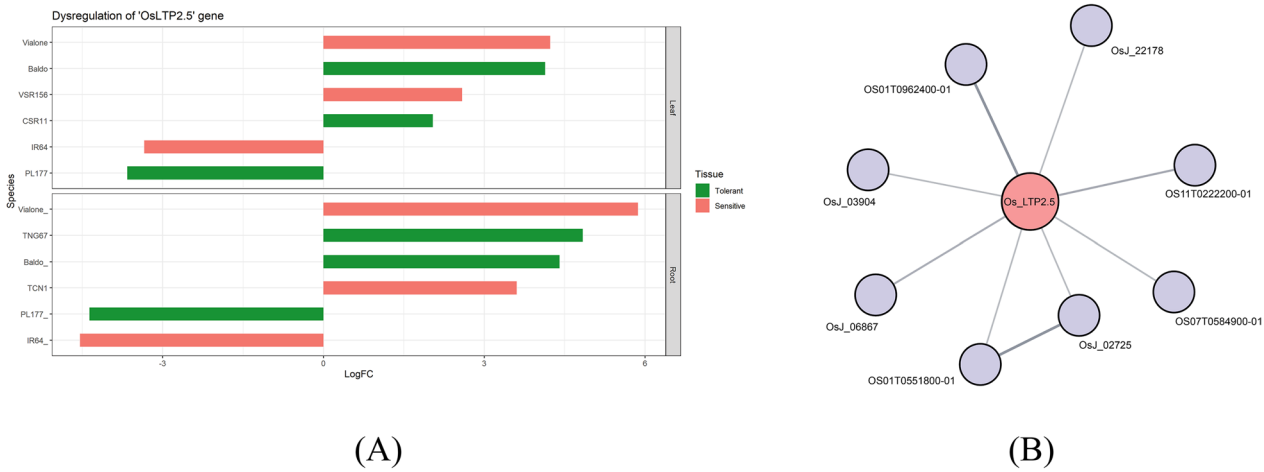

Fig. 5 OsLTP2.5 gene characterization. **A** Log fold change observation in different plants used in the analysis and **B** protein–protein network of OsLTP2.5 gene

gene was significantly downregulated under salt stress compared to control conditions in roots of both salt-tolerant (Horkuch, Pokkali) and salt-sensitive cultivars (BR28, IR29) (Fig. 6A). A similar result was found for shoot tissue but the decrease in expression of the gene was only significant for Horkuch but not in Pokkali, IR29, and BR28 (Fig. 6B). So there appeared to be no difference in the response of OsbZIP52 to salt stress between salt sensitive and tolerant geneotypes.

Variant analysis between tolerant and sensitive varities

Promoter and gene sequence of OsbZIP52 gene of two salt-tolerant and one salt-sensitive genotypes were obtained from Plant Biotechnology Laboratory, University of Dhaka. After analyzing the OsbZIP52 promoter regions of two salt-tolerant verities (Horkuch and Pokkali) and one salt-sensitive verity (IR29), a greater number of variations was observed in IR29 where different abiotic stress-responsive transcription factors bind which act by increasing expression of genes involved in ion channel (AP2-ERF family) (Xie et al. 2019), by regulating alternative splicing (ARF family) (Ye et al. 2020), and by controlling Na^+ and K^+ transport systems (bHLH and WRKY) (Rajappa et al. 2020) (Fig. 7 and Additional file 7: Table S7). The differences in sequence variation between tolerant and sensitive varieties was also visualized in Fig. 7 As a result, regulation in the expression of the OsbZIP52 gene in salt-sensitive varieties may be altered due to these variations in the promoter regions during abiotic stress including salt stress.

Using the MEME suit 7 motif regions were predicted for the salt-tolerant varieties. These motifs correspond to a number of domains of different transcription factor families which play a role in response to abiotic stresses. There were many variations in the genomic motif regions of salt-sensitive verity (IR29) found by performing multiple sequence alignment using horkuch, pokkali and IR29 varieties, which may indicate a lack in sensitivity of the functionality of OsbZIP52 TF during abiotic stresses (Additional file 8: Table S8).

Co-expression analysis of the significant gene

To further assess the significance of the OsbZIP52 gene, a co-expression analysis using the genevestigator software was performed. Tolerant plants (FL478, PL177, and Pokkali) expression data were used from GSE13735, GSE58603, and GSE14403 experiments to perform co-expression analysis. Co-expressional analysis showed different salt stress-response genes were negatively co-related with OsbZIP52 (LOC_Os06g45140) gene, including OsLEA3:Late Embryogenesis Protein (LOC_Os05g46480) (Duan and Cai 2012), RAB16A protein (LOC_Os11g26790) (Ganguly et al. 2012), glutathione-S-transferase (LOC_Os01g49710) (Sharma et al. 2014), copper/zinc superoxide dismutase like protein (LOC_Os07g46990) (Prashanth et al. 2008), and DEAD-box helicase ATP-binding protein (LOC_Os11g38670) (Macovei et al. 2012). The expression pattern of these genes, along with OsbZIP52, was visualized using the Hierarchical clustering method (Fig. 4D). OsbZIP52 (LOC Os06g45140) was found to be down-regulated, whereas the other salt response genes were found to be up-regulated, according to the heatmap. Thus, downregulation of OsbZIP52 in tolerant plants may lead to increased

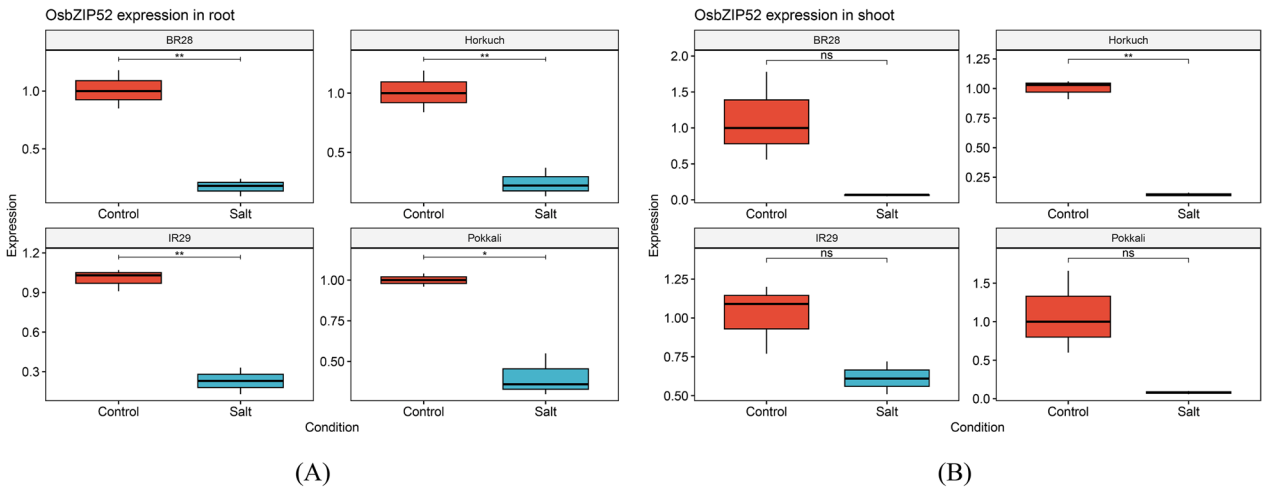

Fig. 6 OsbZIP52 expression analysis using RT-qPCR**.** The relative expression levels of OsbZIP52 in root (**A**) and shoot (**B**) tissues of BR28, Horkuch, IR29 and Pokkali under 100 mM NaCl after 24 h. * and ** denoted significance at p 0.05, p 0.01 and ns means no significance respectively as compared to control

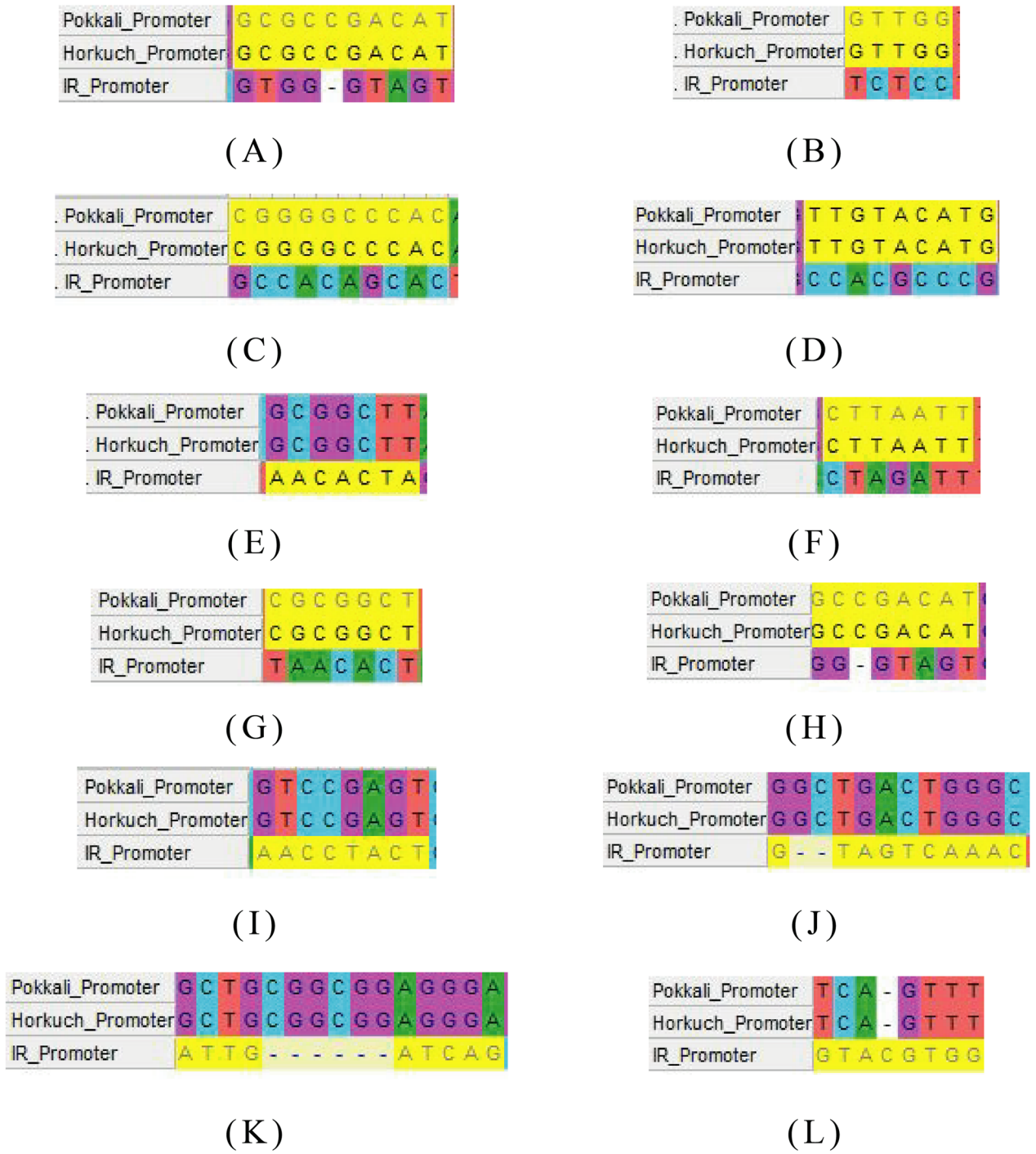

Fig. 7 Comparison of promoter sequence between salt-sensitive and tolerant varieties. Visualization of variations in promoter between tolerant (Horkuch and Pokkali) and sensitive (IR29) varieties for the binding of **A** AP2, **B** NF-YB, **C** TCP, **D** SBP, **E** C2H2, **F** Alpha-amylase, **G** ERF, **H** ARF, **I** Myb/SANT, **J** WRKY, **K** GATA, and **L** bHLH transcription factors

expression of other salt response genes, resulting in salt tolerance.

Expression pattern observation in different plants

The expression of the OsbZIP52 gene in rice and other plants was studied under various stress conditions. BZIP9 gene from *Arabidopsis thaliana*, GLYMA_17G188500

gene from *Glycine max*, MTR_1g008990 gene from *Medicago truncatula*, and Zm00001d003529 gene from *Zea mays* were selected for expression analysis as they are similar to OsbZIP52 gene. Genevestigator software was used in order to analyze the expression pattern of these genes, and the software used available stress-related microarray experiments for each plant. The analysis revealed that genes from each plant were differentially expressed with a log fold change greater than 1. Therefore, each gene responds to abiotic stresses and may be engineered to observe its role in the corresponding plants (Fig. 8).

Discussion

Salinity stress is a major agricultural limitation that has a global impact on the food supply. Much research has been carried out to decipher the complex systems that operate under stress, but more work is required due to the differences and complexities of the species, genotype, and type of tissue involved. In this study, a meta-analysis was performed using available microarray and RNASeq datasets of root and leaf tissues to find the association of various genes or factors that responds to salt stress. The objective was to find common genes between these two tissues, which may enable us to work on both tissues and overall enhance tolerance. This research considered different tolerant (TNG67, PL177, CSR11, and Baldo) and sensitive (TCN1, IR64, VSR156, and Vialone Nano) rice species with varying salt stresses, which broadened the scope of possible solutions to the salinity problem globally. 106 and 29 differentially expressed genes were discovered in leaf and root tissues, respectively, from the analysis.

In the network of leaf DEGs, OsJ_04024 (heat-shock protein 70, HSP70) was found to have the highest interactions in the network of leaf DEGs, which is a key regulator in response to heat stress (Hu et al. 2009). This protein also responds to cold stress (Lee et al. 2009), dehydration stress (Choudhary et al. 2009), salt stress (Hoang et al. 2015), and some more abiotic stresses (Chankova et al. 2014; Qi et al. 2011). The HSPs family are essential in cell homeostasis, transport of synthesized proteins through cell organelles, and folding, preventing misfolded, denatured, and aggregated proteins induced by stress (Balchin et al. 2016; Ratajczak et al. 2009; Tyedmers et al. 2010). Some essential genes were also discovered from the leaf DEGs. OsPYL4 (abscisic receptor PYL4) is a PYLs family protein that promotes the activation of ABA-regulated genes and results in the acquisition of abiotic stress resistance (Ma et al. 2009; Melcher et al. 2009; Tian et al. 2015). OsBZ8 (Abscisic acid Responsive Element (ABRE)-binding factor) is an important trans-acting factor that regulates NaCl-stress-induced gene expression. This protein strongly interacts with an ABRE-based promoter and regulates abiotic stress-inducible genes (Mukherjee et al. 2006). Ring-type E3-Ubiquitin Ligases (such as OsSRFP1) were reported to interact with the transketolase enzyme to induce NADPH production under salinity stress, which is important in combating ROS-induced damage under abiotic stresses. OsSRFP1 is an unusual ligase protein that acts as a negative regulator under cold stress and a positive regulator under heat stress (Melo et al. 2021; Tunc-Ozdemir et al. 2009). Monosaccharide transporters (OsMST6) are proteins that transport xylose, glucose, and galactose across the hydrophobic membrane and contribute to abiotic stress tolerance (Monfared et al. 2020; Wang et al. 2008). Germin-like proteins (OsGLP8-12) have been reported to function as auxin receptors (Yin et al. 2009) and superoxide dismutase activity which defends against various stresses (Breen and Bellgard 2010). GLPs have the ability to convert superoxide to H_2O_2 and CO_2 while also strengthening the cell wall through protein coupling and glycosylation (Li et al. 2016; Rietz et al. 2012). Therefore

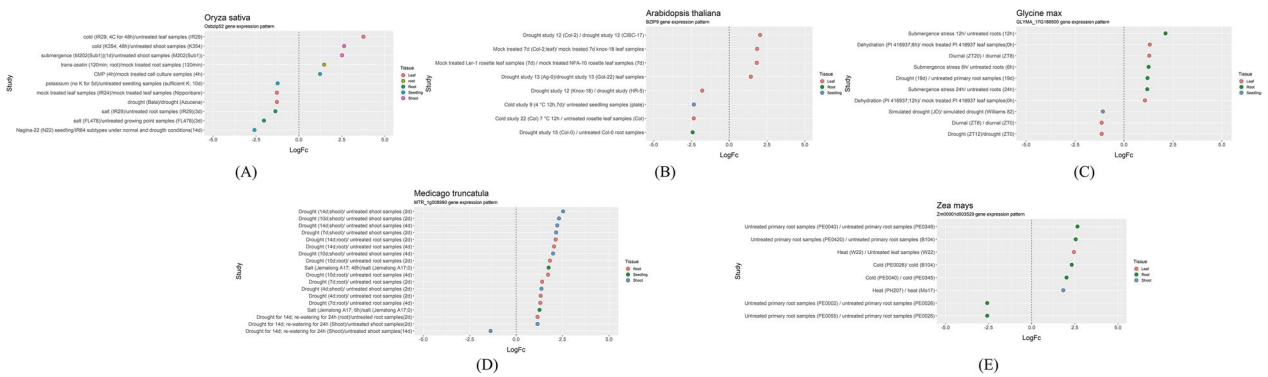

Fig. 8 OsbZIP52-like gene Expression analysis in different plants. Expression pattern of OsbZIP52-like gene in different stress conditions for **A** *Oryza sativa*, **B** *Arabidopsis thaliana*, **C** *Glycine max*, **D** *Medicago truncatula*, and **E** *Zea mays*

differential expression analysis of leaf tissue unravels several crucial genes that actively respond to abiotic stresses and regulate various stress-related pathways. Leaf DEGs were also enriched in important GO biological process terms, such as GO:0006721 (terpenoid metabolic process) (Qiu et al. 2008), GO:1901576 (organic substance metabolic process) (Li et al. 2020), GO:0016998 (cell wall macromolecule catabolic process) (Kim et al. 2015), and many others that are responsive to stress.

OsJ_009875 (probable protein phosphatase 2C 30; OsPP2C30) was the most interacted protein in the Root DEGs network, and a previous study revealed that the protein involves in the ABA-signaling pathway as well as response to abiotic stresses (Singh et al. 2015). Several root DEGs were found that play a crucial role in salinity stress and stress-responsive pathways. Nitrate transporters (OsNRT2.3) form a bridge between hormones such as abscisic acid, ethylene, cytokines, etc., which respond to stress conditions (Krouk 2016). These transporters are also involved with nitrate and k^+ or cl^- shuttling, and loss of its function prevents plant growth under salinity stress (Drechsler et al. 2015; Fan et al. 2017; Hsu and Tsay 2013; Taochy et al. 2015). OsHox22 and OsHox24 genes that were found to be differentially expressed in root tissue have been reported to have a crucial role in response to abiotic stresses (Bhattacharjee et al. 2016; Jain and Khurana 2009; Zhang et al. 2012b). The network proteins were also seen enriched in salt-responsive GO biological process terms, including GO:0005975 (carbohydrate metabolic process), GO:0050794 (regulation of cellular process), GO:0006807 (nitrogen compound metabolic process) (Jadamba et al. 2020; Wang et al. 2012; Yan et al. 2005; Zhang et al. 2012a). By observing GO terms of both leaf and root tissues, 4 GO Biological processes were found common, such as the primary metabolic process (GO:0044238), organic substance metabolic process (GO:0071704), cellular metabolic process (GO:0044237), and organic substance biosynthetic process (GO:1901576).

After analyzing differentially expressed genes from leaf and root tissues, OsbZIP52 and OsLTP2.5 genes were common. To assess the significance of these genes, downstream bioinformatics analyses were undertaken. The OsbZIP52 logFC observation revealed that gene expression might vary based on tissue types and geographic distribution. The action mechanism of this gene, response to salt, may differ between tissues as we observed relative difference in expression between tissues from Fig. 6, and the regional distribution of the plants (such as Baldo and Vialone Nano are small-grained risotto rice from Europe (Cirillo et al. 2009), whereas CSR11 and VSR156 rice genotypes are from Asia (Mishra et al. 2018) may also contribute to this variation of expression. PPI network analysis of the OsbZIP52 gene revealed the association with essential genes (RAB25, BZIP50, Os03g0158200) that are highly responsive to stress, and the proteins of the network were enriched in GO Biological pathways such as response to stress (GO:0006950), response to abscisic acid (GO:0009737), response to hormone (GO:0009725), signal transduction (GO:0007165), and many other stress-responsive biological processes. OsbZIP52 gene was greatly induced by low temperatures and responded to drought, heat, and other abiotic stresses (Liu and Chu 2015; Liu et al. 2012; Zhang et al. 2013). A PPI network was also constructed for OsLTP2.5, a non-specific lipid transfer protein, but no enriched GO terms were found. A previous study suggested that non-specific lipid transfer proteins were crucial in resisting biotic and abiotic stresses (Choi et al. 2008; Jang et al. 2002; Jung et al. 2003; Kielbowicz-Matuk et al. 2008; Liu et al. 2012; Molina and Garcia-Olmedo 1993). They are also vital to plant growth and development. Therefore, OsLTP2.5 may play an essential role in response to salt stress and become a target for further genetic research to resist salinity.

Oryza coarctata expression analysis with resultant DEGs revealed that the basic leucine zipper 9 annotated gene, a homolog of the OsbZIP52 gene, was differentially expressed in submergence and stress conditions. *Oryza coarctata* is a plant of high salinity tolerance which can tolerate up to 40 dS ml^{-1} salt stress (Garg et al. 2014). Differential expression of basic leucine zipper 9 in *Oryza coarctata* under stress conditions explains the significance of the gene to tolerate salinity stress. Consequently, the OsbZIP52 gene is anticipated to play an important role in response to salt stress. The dysregulation of the OsbZIP52 gene in different rice varieties considered by the analysis was examined, and it was observed that the up and down-regulation varied based on species and tissue types.

bZIP transcription factors are key regulators in plant salt stress responses. They perceive and signal salt stress, regulating the expression of stress-responsive genes. These transcription factors control ion homeostasis by modulating ion transporters and channels (Liu et al. 2023). They also regulate osmotic adjustment by influencing the synthesis and accumulation of compatible solutes (Yang et al. 2019). Additionally, bZIP factors play a role in antioxidant defense by regulating genes involved in scavenging reactive oxygen species (Dvořák et al. 2021). They interact with hormone signaling pathways, particularly abscisic acid, affecting stomatal closure and other hormonal responses (Schlögl et al. 2008). There isn't any clear indication about the regulation mechanism of bzip transcription factor under salt stress and so further analysis is required to understand the complex mechanism of

this family protein under salt stress. The OsbZIP52 gene expression and promoter sequence differences between tolerant and sensitive types were found to be significantly altered in this study, which highlights the need for deeper characterization and understanding of proteome interactions for salt-tolerant crop development.

OsbZIP52 expression was found to be downregulated in root and shoot tissues of salt-tolerant and salt-sensitive verities under salt stress in the RT-qPCR analysis. There were no differences in the response between tolerant and sensitive varieties in terms of gene expression. Since the RT-qPCR analysis was done for only a one-time point of 24 h, it is not enough to get a comprehensive understanding. In addition, the variant analysis showed a significant alteration in the promoter and motif regions of the OsbZIP52 gene in salt-sensitive varieties. Although there wasn't a significant difference observed between salt-tolerant and salt-sensitive varieties in a time point of 24 h, extensive analysis may be performed to perceive the behaviour of the gene expression under salt stress at different time points in order to understand the role of the OsbZIP52 gene in defending against salt stress in tolerant genotypes.

The co-expression analysis of OsbZIP52 genes was performed to identify the co-expressing genes associated with salt stress response using tolerant plant data in genevestigator software. In comparison to the down-regulation of OsbZIP52, multiple salt response genes were up-regulated, such as OsLEA3 and RAB16A, genes that enhance salt tolerance, copper/zinc superoxide dismutase, glutathione S transferase, and DEAD-box helicase ATP-binding protein are such salt response proteins that play a critical role in response to salinity stress. This result was also found consistent with the previously performed test (Liu et al. 2012), where it was observed that OsbZIP52 over-expression cell lines showed a significant decrease in the expression of several salt-stress genes, including OsLEA3, LOC_Os05g39250, Rab25, etc. Therefore, OsbZIP52 down-regulation may enhance salinity tolerance.

Expression pattern observation in *Oryza sativa*, *Arabidopsis thaliana*, *Medicago truncatula*, *Glycine max*, and *Zea mays* plants for OsbZIP52 revealed that the gene was differentially expressed in each plant in different tissues and stress conditions. As this gene was found to respond to different abiotic stresses in various plant species, this gene may become a common point to increase the tolerance of a wide range of plant species.

Following substantial expression investigation employing Microarray and RNASeq analytical techniques, the OsbZIP52 gene was found to be the most crucial gene, having important interactions with other essential genes and participating in salt-responsive pathways. Compared to OsbZIP52, which is downregulated, the co-expression analysis found that salt stress-responsive genes up-regulated in tolerant plants. The study considered a wide range of rice plants along with different salt concentrations, which helped to understand the significance of the OsbZIP52 gene better. Altering the expression of this gene may control the growth of different rice varieties in any saline condition. Gene-specific study of the OsbZIP52 gene may establish potential evidence behind its role against salt stress. The findings of the study can become a stronghold in future research studies and assist in the development of the salt-tolerant transgenic breed.

Conclusion

The research performed meta-analyses on several salinity-related microarray and RNASeq datasets and filtered out the OsbZIP52 gene to be the most significant gene for salinity response shared between root and leaf. Differences in the response of OsbZIP52 to 24 h of salt stress were not observed among the salt-tolerant and sensitive genotypes. However, there is further scope in fine-tuning this response at different times and levels of stress. The research also showed that OsbZIP52 responds to other abiotic stresses and is differentially expressed in other plant species. Therefore, this gene can be used as a potential target for genetic engineering or mutant analysis for future investigation and will serve as a valuable genetic resource for the development of salt-tolerant rice.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s43170-023-00173-3.

Additional file 1: Table S1. Differentially expressed genes in leaf tissue.

Additional file 2: Table S2. List of enriched GO terms from leaf DEGs.

Additional file 3: Table S3. Differentially expressed genes in root tissue.

Additional file 4: Table S4. List of enriched GO terms from root DEGs.

Additional file 5: Table S5. List of enriched GO terms from OsbZIP52 protein network.

Additional file 6: Table S6. Primer used in real-time qPCR.

Additional file 7: Table S7. Promoter region variation analysis by comparing salt-tolerant (Horkuch and Pokkali) and salt-sensitive (IR29) rice varieties.

Additional file 8: Table S8. Motif region variation analysis by comparing salt-tolerant (Horkuch and Pokkali) and salt-sensitive (IR29) rice varieties.

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Author contributions

Conceptualization: MUSS; Formal analysis and investigation: DC, MUSS; Lab Experiment: NT; Writing—original draft preparation: DC; Writing—review and

editing: DC, MUSS, ZIS; Supervision: ZIS. All authors approved the submitted version.

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Data Availability
Not applicable.

Declarations

Ethics approval and consent to participate
Not applicable.

Competing interests
The authors have no competing interests to declare that are relevant to the content of this article.

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