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Original Article

# Computational Analysis of Responsive Transcription Factors Involved in Drought and Salt Stress in Rice

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**Abstract**

**Introduction:** Rice is one of the most important crops to more than half the world's population. The reduction of rice yield has been severely influenced by drought and salt stress. The main purpose of this survey was to detect Transcription Factors (TFs) involved in drought and salt stress in rice.

**Materials and Methods:** In this study, microarray data in PlnTFDB and DRTF were taken to evaluate the expression of responsive TFs to drought and salt stress in the growth stages. A comprehensive analysis of responsive TFs were performed containing gene network, expression analysis in different tissues, and detection of Transcription Factor Binding (TFBs) sites.

**Results:** A total of 80 TFs were found differentially expressed (DEGs) under drought and salt stress in rice. Gene Ontology (GO) revealed that biological processes included transcription, regulation of transcription, regulation of RNA metabolic, and RNA metabolic. In addition, some molecular functions such as organic cyclic compound binding, heterocyclic compound binding, DNA binding, and cellular component are enriched in intracellular and nucleus. To survey selection pressure in responsive TFs under drought and salt conditions, Tajima's and Fu test analysis revealed balancing selection. Analysis of TFBs illustrated that several TFBs namely AP2, bZIP, and MYB/SANT act as basic TFBs linked to abiotic stress responses as well as different growth stages in rice. The current study revealed that most TFs related to histone modification were up-regulated whereas, TFs associated with regulation of repression/ activation transcription were down-regulated.

**Conclusions:** Our results can provide an insight into the regulatory mechanisms involved in response to drought and salt stress which can aid to improve rice varieties.

**Keywords:** Rice, TFBs, Balancing Selection, Salt, Drought, Gene Ontology

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## Introduction

Rice (*Oryza Sativa*) is a monocotyledonous plant and a main staple food for one-third of the world's population.[1] Rice can provide up to 80% of a population daily calories. However, rice is exposed to drought and salinity conditions which are estimated to decrease global rice yield by 50%.[2] Salinity and drought are considered as major constraints to rice production. Based on past reports, rice production is extremely influenced to salt, drought, heat, and other environmental stresses during the seedling and reproductive stages.[3,4] Plants respond to abiotic and biotic stresses by exhibiting many physiological and developmental changes. Both salinity and drought stress can affect every stage of rice growth; seedling, flowering, tillering, spikelet filling, and shoot and root growth and hence can highly reduce grain yield.[5] Gene expression studies can provide an insight to activity of expressed genes and can provide an overall picture of cell function.[6] Over the last three decades, many technologies for transcriptome analysis have been introduced however, microarray could yet be utilized to investigate and integrate the responsive genes under stresses providing a more clear insight to an integrated view of the intricacies of cellular life.[7] Both salinity and drought transcriptome studies on rice leaves at seedling stage showed a largely common response involving similar pathways and genes.[8] Patterns of gene expression in response to drought or high-salinity stress showed significant overlap within a particular organ type and unique patterns among different organs.[6] The TFs are critical molecules in the regulation of gene expression, directly regulating when, where and the rate to which genes are expressed. Their functional characterization has categorized them in growth, transcription, biotic, and abiotic stresses.[9] TF, as a group of genes, are stimulated by abiotic stress which in turn regulate the stress signal transduction and as a result change gene expression and thus possibly function in stress response.[9] The plant TFs and NAC regulate multiple processes associated to plant growth and development as well as biotic and abiotic stresses in tomato.

In *A. thaliana* and in other numerous plants it is stipulated that there are several pathways independently responding to environmental stresses, suggesting that resistance or sensitivity

is regulated at the transcriptional level by complex gene regulatory networks.[10] Li et al., (2020) showed that TFs as key messengers activated under drought and salt stress in potato. These results demonstrated that *StZEP*, *StNAC*, *StERF*, and *StDREB* are up-regulated under drought and salt stress. In soybean, DREB1 is important for transcriptional activator under drought, salt, and cold stresses, encoding an ABA receptor family protein in tolerance mechanism. *OsMYB6* may protect cell membrane integrity of plants in response to drought and salinity stresses, enriching different tissues namely, roots, leaves, stems, panicles, and seed. The OsNAC72 is activated by another TF in the ABA pathway to maintain moisture and enhance drought resistance in maize.

TFs are candidates for engineering stress tolerant plants in such a way that a single TF modulates a large set of genes. Microarray technology can provide expression profiles of thousands of TFs involved in abiotic stress responses.[11] The objectives of this study were to detect TFs which are responsive to drought and salinity stresses, to evaluate TFBs, co-expression patterns, and developmental relationships. Evaluation of molecular mechanisms of salt and drought tolerance in rice can be useful for breeders for the development of tolerant varieties.

## Materials and Methods

### *Data Mining and in silico Analysis of TFs Expression*

Nucleotide sequences of TFs were retrieved from Plant Transcription Factor Database (PlnTFDB, http://plntfdb.bio.uni-potsdam.de/v3.0/) and Database of Rice Transcription Factors (DRTF) (http://drtf.cbi.pku.edu.cn/). The data were normalized using RMA algorithm implemented in R software (affy) and the intensity values were transformed into log2 scale.[12] To evaluate the responsive TFs expression, microarray data required for control and stress conditions was taken from 18 different drought and salt treatments to identify stress-responsive TFs. Analysis of data were performed using fold change which is based on log2 ratio and differentially expressed TFs were determined to fold change ≤ (-2) (down regulated TFs) and ≥ 2 (up regulated TFs). In addition, TFs were selected by $p<0.05$ as statistical significant. Probe sets were mapped to MSU Rice Genome Annotation Project gene set. To convert probe set to ID genes, DAVID sites was utilized. One-way ANOVA revealed significantly different TFs among the surveyed genotypes at a 5% significant level. Furthermore, the corrected *O*-value of Benjamin-Hookberg allowed a more stringent selection of up-regulated TFs showing less than 5% significance level.

In order to identify the DEGs (TFs) expression, Genevestigator program was used (Figure 2). In addition, the perturbations tool was used to find out the differential gene expression under drought and salt stress. Compendium-wide analysis in the Genevestigator program show the fold changes in the expression of DEGs under different tissue. The DEGs (TFs) under drought and salt stress conditions were used to generate TFs expression heatmap using Red/Green color scheme where "Red" color shows up-regulation and "Green" color shows down-regulation of respective TFs. The anatomy tool was subjected to evaluate the expression potential of each TF using microarray OS-AFFY-RICE-0 dataset. The interaction among all the 80 TFs were determined using the "The Rice Interactions Viewer" web based on the publicly available Botany Array Resource (BAR) expression browser tool (http://bar.utoronto.ca/welcome.htm).[13]

### *Gene Ontology (GO) Enrichment Analysis and Characterization of TFs*

Classification of differentially expressed TFs by agriGO indicates probable pathways captured by the responsive TFs involved in drought and salt stress. This tool generated functional classification of a list of AGI IDs based on the GO database used to identify the biological processes, molecular functions, and cellular component.

### *Selection Pressure and TFBs Analysis*

The nucleotide diversity, Tajima's D test, and Fu test were carried out using DNASP4.10. The number of non-synonymous substitutions per non-synonymous site (dN) to the number of synonymous substitutions per synonymous site (dS) were calculated using the Nei and Gojobori method in SNAP software. This ratio measures evolutionary pressures on protein-coding region. Promoter regions of 80 TFs were analyzed using PlantPAN software (http://plantpan2.itps.ncku.edu.tw/). For each gene, 1500 bp upstream of the transcription initiation region was considered as a promoter sequence. Investigation of TFBs was performed using the PlantPAN database.

## Results and Discussion

### *Analysis of Differentially Expressed TFs under Drought and Salt Stress*

Heat map is representative of differentially expressed TFs. The expression of the TFs under 18 different drought and salt experiments are represented in the heat map in the color scale of -2 to 2 in red-green color scheme. The conditions are represented in columns while TFs are shown in rows. As seen in Figure 1, the genevestigator profile shows a tightly-specified expression pattern, with the highest transcript abundance in seedling 10-d after germination-salt (CSR27 genotype), 7-d-old seedling-drought (Indica genotype), root-panicle-elongation-stage-drought (IR64 genotype), and root-tillering-stage-drought (IR64). The transcripts were up-regulated during all developmental stages in rice in response to salinity and drought. Our results showed that most of the differentially expressed TFs were responsive to drought and salinity stress, with down-regulation exceeding the up-regulation of TFs. The number of down-regulated TFs in

leaves was higher than the up-regulated TFs, while the opposite occurred in roots under drought stress. However, the number of up-regulated TFs in seedling was higher than the down-regulated TFs, whereas the opposite occurred in roots under salt stress. In contrast with previous studies, up-regulation occurred in roots and seedling, while down-regulation observed in leaves was associated to TFs in multiple signal pathways to drought and salt in *Populus davidiana*.[14]

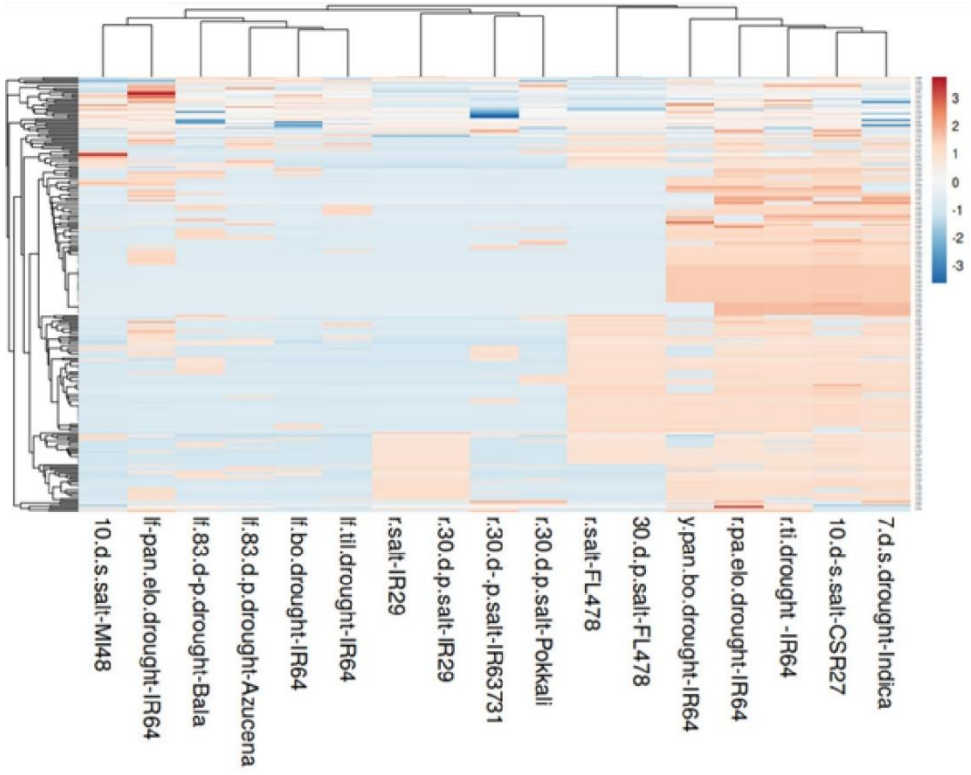


**Figure 1**. Heat Map Analysis of Tolerance-responsive TFs in Response to Drought and Salt Stress.

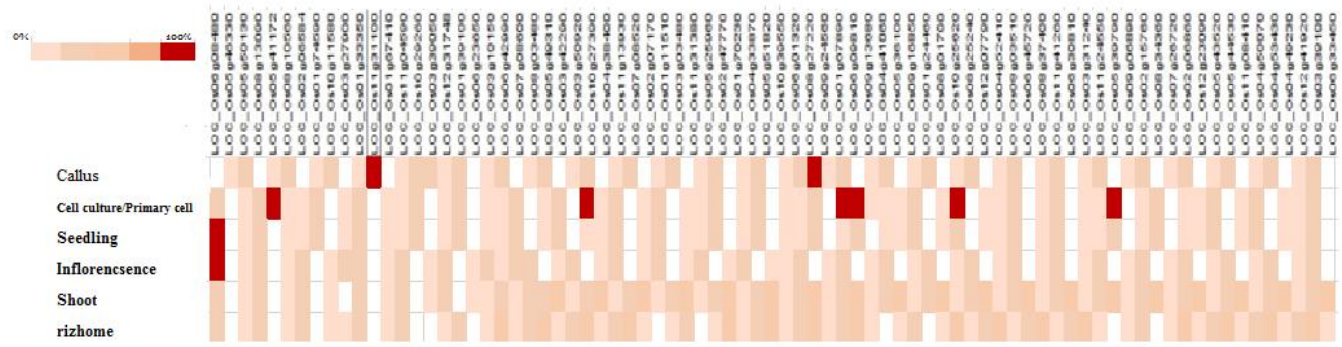


**Figure 2**. Anatomy Expression Profiles of Responsive TFs at Different Developmental Stages of Rice.

### *In silico Analysis of TFs Expression under Drought and Salt Stress*

Meta-analysis of Genevestigator microarray dataset was performed on rice under drought and salt stress. The corresponding TFs, *LOC_Os06g08480 (*CHD3-type chromatin remodeling factor PICKLE), *LOC_Os05g46330 (*MYB family transcription factor), *LOC_Os08g10560* (NF-YC family protein), *LOC_Os08g13090* (BTB/POZ domain containing protein), *LOC_Os05g41172* (histone-lysine N-methyltransferase), *LOC_Os02g06584* (zinc finger C-x8-C-x5-C-x3-H type family protein), and *LOC_Os05g50130* (HB-other family protein) are strongly expressed in cell culture under drought and salt stress conditions (Figure 2). A pervious study demonstrated that BTB domain and zinc finger genes play a critical role in many biological processes by changing the transcriptional activities of some downstream genes.[15] BTB domain is up-regulated under drought and salinity thereby making them highly flexible and involved

in methylation of lysine residues in histones, nucleosomes and other proteins.[16] It was supported that histone methylation was the largest epigenetic regulatory in response to abiotic stress. Significantly, the MYB family transcription factor (*LOC_Os01g74590*), NF-YC12 (*LOC_Os10g11580*), and ZIM motif family protein (*LOC_Os03g27900*) are strongly down-regulated in seedling and shoot. Also, the MYB family transcription factor (*LOC_Os01g74590*), NF-YC12 (*LOC_Os10g11580*), and zinc-binding protein (*LOC_Os01g33350*) are down-regulated in shoot and rhizome under drought and salt stress conditions. The most of NF-Y genes are highly expressed under drought, however, it has been shown that they can be down-regulated in response to limited water availability.[17] Other genes down regulated included the ZIM domain which acts as a mediator among JAZ proteins. The ZIM domain caused to recruit general transcriptional repressors. Since plants are influenced by abiotic and biotic stresses, ZIM can be introduced as key regulators of defense signaling pathways.[18] In this study, *PICKLE* is up-regulated in drought and salt stress in rice. This gene plays critical roles in the repression of genes that are involved in the growth and development in *A.thaliana*. *PICKLE* encodes ATP-dependent chromatin remodeler that limit the expression of developmental regulators. According to findings it can be stated that transcriptional changes in response to stress are often accompanied by modifications in nucleosome occupancy. Accordingly, *PICKLE* is one of several ATP-dependent chromatin-remodeling complexes that are required for adapting against environmental stresses in various organisms. MYB as key components regulates and modulates adaptive pathways in response to ABA, drought, salinity, and cold.

### *Analysis of TFBs in Responsive TFs under Drought and Salt Stress*

In rice, TFBs (AP2, bZIP, Mby/SANT, bHLH, Homeodomain, GATA, B3, AT-Hook, EIN3, C2H2, CG-1, and LEA-5) have been identified on the promoter regions of both strands, and are mostly located in the upstream region of 1000 bp. The description of the first three most frequently occurring TFBs of the total detected elements is provided in Figure 3. Our analysis revealed that among TFs, AP2 had the highest number of TFBs whereas, the lowest number of TFBs was observed in LEA-5 genes under drought and salinity stresses. Previous study showed that several families of stress-responsive TFs have been characterized under drought and salt stress such as, NAC, bZIP, WRKY, MYB, and AP2/ERF that formed stress regulation network in *Arabidopsis*. Our findings are in agreement with study on Arabidopsis that AP2, bZIP, MYB induced under drought and salt stress. In Sorghum, LEA-5 is induced due to its increased tolerance under drought conditions.[19] Based on reports, down-regulated TFs, e.g. AtMYB60, are related to drought. MYB is down-regulated and as a result causes a considerable reduction of stomatal opening to increase tolerance against drought stress.[20] However, other reports have revealed that MYB enhanced tolerance to drought and salt stress and higher survival rates in maize.[21] AP2 is up-regulated and is involved in a wide range of stress tolerance, enabling it to form an interconnected stress regulatory network. Our results showed that bZIP was activated in both salinity and drought stresses. Previous studies have accurately revealed that bZIP was induced under stress conditions like heat, salinity, and dehydration.[22] In accordance with previous studies, transcription down regulated which repressed gene expression in response to diverse abiotic stresses are also important tools in managing drought tolerance.[23]

### *Gene Ontology Enrichment Analysis*

To identify the differentially expressed TFs associated with drought and salt TFs, gene ontology analysis was performed in the biological processes including regulation of RNA metabolic, RNA metabolic, and developmental processes. The cellular component encompasses intracellular and nucleus and the molecular function is related to DNA binding, organic cyclic compound binding, heterocyclic compound binding, ion binding, and metal binding (Figure 4). In cotton, the GO term showed that TFs are involved in plant hormone signal transduction and metabolic pathways enrichment under drought and salt stresses.[24] Based on a recent report, TFs were identified in major metabolic pathways such as the biosynthesis of amino acid, lipid, and carbohydrate.[25] Our results suggested that further investigation into the functions of responsive TFs and metabolic pathways can aid researchers to gain a better understanding of stress tolerance.

### *Analysis of Co-expressed TFs in Network*

The interactive network analysis of all the significant TFs revealed a co-expressed TFs network (Figure 3). In network, *LOC_Os06g08480* and *LOC_Os05g46330* seemed to be the central proteins encoding for "CHD3-type chromatin remodeling factor PICKLE and MYB family transcription factor". In addition, a few co-expressed TFs were also observed in our network which included histone acetylation/deacetylation and chromatin remodeling events in nucleus and mitochondria. Other TFs were involved in editing mitochondria. Most of the co-expressed TFs pretend to be localized mostly in mitochondria (light blue), cytoplasm (purple) and nucleus (blue) and encode mainly for the homeobox proteins such as *LOC_Os08g19650* and *LOC_Os10g28040* (histone acetyltransferase GCN5) (Figure 3). In analysis network, only few proteins are located in the chloroplast (green) and plasma membrane (orange). The proteins localized in the chloroplast (green) are mainly translation proteins such as *LOC_Os11g08080* (SWIRM domain containing protein) and *LOC_Os06g08480* (Phosphatidylinositol kinase and FAT containing domain protein). Based on our results, most of the TFs encoding

proteins are involved in histone acetylation/deacetylation and homeobox protein in nucleus (Figure 5). A recent study indicated that chromatin change mediated by histone modification can be managed dynamically to conserve gene and genome activities.[26] According to another report, H3K3me3 modification is involved in the activation of *NCED3* which encodes a key enzyme in the ABA biosynthesis under drought stress conditions. In accordance with our finding, the expression of *HvGCN5* was induced by ABA treatment in barely (*Hordeum vulgare L.*).[27] However, another researcher suggested that *HD2* genes play important roles in resistance to environmental stress in both monocot and dicot plants.[28] A Pervious study suggests that nucleosome modification may occur under drought and salt stress. For example, *PICKLE* exhibited under drought, salt, and cold stress which is required for the deposition and maintenance of the repressive chromatin mark H3K27me3. H3K27me3 plays a key role in prolonged cold stress memory during vernalization. *PICKLE* acts in an epigenetic pathway that examines H3K27me3 homeostasis in *Arabidopsis*.

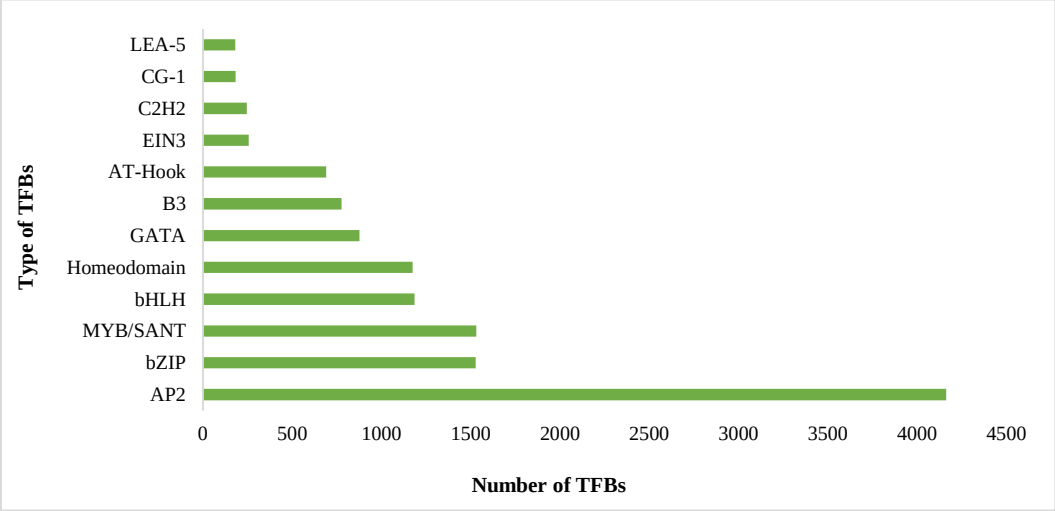


**Figure 3**. Histogram Showing the Frequencies of Responsive TFs of TFBs under Drought and Salt Stress in rice.

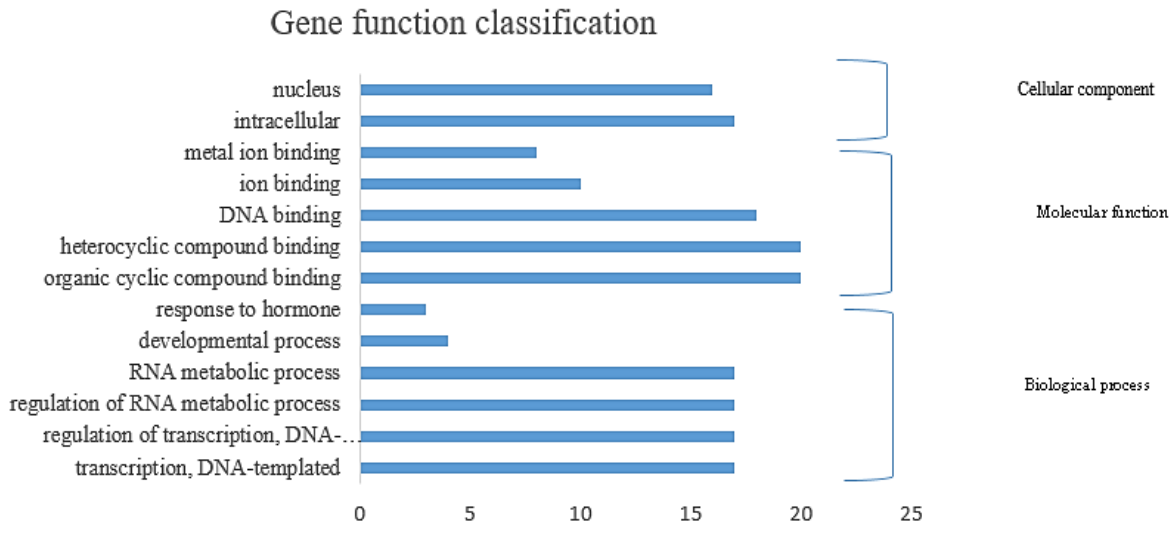


**Figure 4.** Gene Ontology (GO) Distributions for the Responsive TFs in Drought and Salt Stress. AgriGO database defined GO under three categories, (a) biological processes, (b) molecular functions and (c) cellular component.

### *Selection Pressure in Tolerance-responsive TFs under Drought and Salt Stress*

Two approaches (Tajima's D test, Fu and Li's D*) were utilized to execute the neutrality test. Analysis of 110 nucleotide sequences showed that Tajima's test was significant (D = 8.95 where, D = Tajima test statistic). Tajima's test indicated the presence of balancing selection in expressed TFs under drought and salt stress conditions (Table 1). These results were in agreement with other researchers who reported that the drought-tolerance TFs are expected to have evolved under

**Table 1.** Results from Tajima's Neutrality Test in Responsive TFs

| *m* | *π* | *D* | *dS/dS* | Fu's Fs statistic |
|---|---|---|---|---|
| **110** | 0.72 | 8.95 | 1.03 | -13.84 |

balancing selection.[29,30] Our results support this perception because of a higher genetic diversity observed in drought-responsive than non-responsive genes.[29,31] Another neutrality test in Table 1 showed that Fu and Li's test gave a significant value of -13.84. These results revealed that there is an excess of rare mutations in the expressed genes under drought and salt stress conditions.[32] The ratios of dN/dS, indicating protein evolution, were computed within and among the defined groups for rice (Table 1). Synonymous and nonsynonymous ratio and nucleotide diversity levels were highly significant.[33,34] A ratio higher than one indicates a balancing selection. Results showed that a balancing selection occurred on drought and salt stress responsive TFs, adapting to the extreme abiotic and biotic stresses. Other reports have clearly revealed that balancing selection has occurred on drought and salinity tolerance responsive genes due to the maintenance of adaptive polymorphism through multi-locus balancing selection in this heterogeneous environment.[35,36]

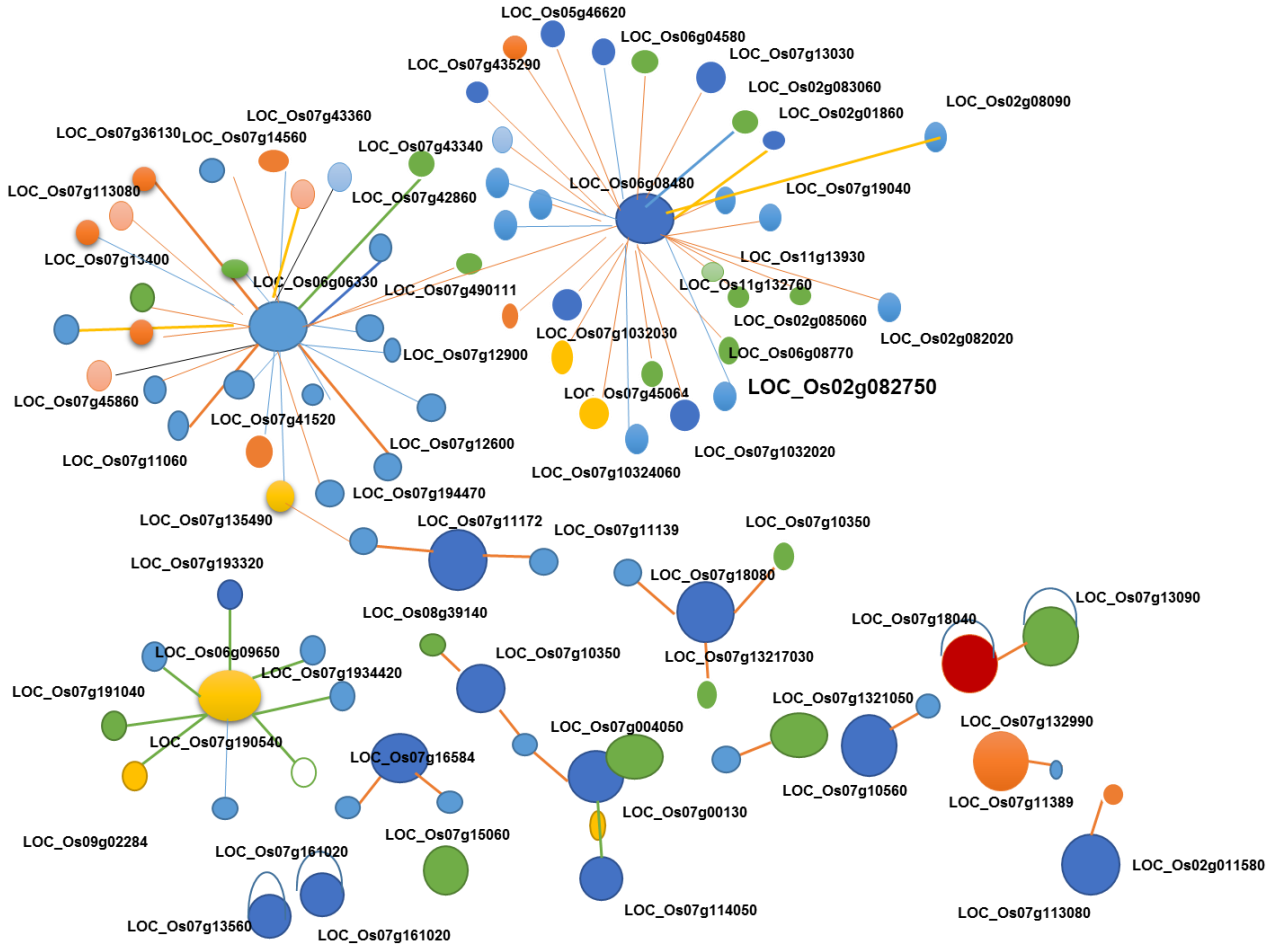


**Figure 5**. Co-expressed Network of All 110 TFs in Rice Genotypes. The "Rice Interactions Viewer" (http://bar.utoronto.ca/interactions/cgi-bin/rice_interactions_viewer.cgi) web was used to predict the interactions.

## Conclusion

This study presents a comprehensive overview of transcriptome modifications of responsive TFs under drought and salt stress which can help insight the molecular basis of drought and salt tolerance in rice. Analysis of responsive TFs to drought and salt stress conditions using TFBs, network of co-expressed TFs, expression patterns in different tissues were performed based on bioinformatics tools. Based on our results, some TFs are down-regulated to reduce photosynthesis rates related to stomatal control under drought and salt stress. However, some TFs conserve cell components through decreasing transcription using methylation residues in histones under drought and salt stresses. Gene expression data showed that regulated PICKLE and MYB family transcription factor were up-regulated and controlled nucleosome modification was limited under drought and salt conditions. Modification of histones are affected by up regulation of BTB, PICKLE and MYB while down

regulation of ZIM domains regulated repression or activation of transcription. TFs associated with chromatin-based modifications can be considered as important proteins for increasing drought/salt tolerance in plant genetic engineering improvements. Understanding the above mentioned mechanisms can enable us to improve stress tolerance in rice.

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## Authors' Contributions

AS carried out literature search, designing and editing of the manuscript. ZH and AA wrote and drew all the figures of the manuscript. All authors contributed to the final manuscript. All authors have read and approved the manuscript.

## Conflict of Interest Disclosures

The authors declare that they have no conflicts interest.

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