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An Update of STIFDB Database: Insight into Additional Plant Stress–Responsive Genes and Stress-Specific Transcription Factors

Mahantesha Naika
Department of Plant Biotechnology
University of Agricultural Sciences GKVK Campus
National Centre for Biological Sciences (TIFR)
India

Khader Shameer
Division of Biomedical Statistics and Informatics
and Division of Cardiovascular Diseases
USA

Oommen Mathew
National Centre for Biological Sciences (TIFR)
India

Ramanjini Gowda
Department of Plant Biotechnology
University of Agricultural Sciences, GKVK Campus
India

R. Sowdhamini
National Centre for Biological Sciences (TIFR)
India

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Athens Institute for Education and Research
8 Valaoritou Street, Kolonaki, 10671 Athens, Greece
Tel: + 30 210 3634210 Fax: + 30 210 3634209
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An Update of STIFDB Database: Insight into Additional Plant Stress–Responsive Genes and Stress-Specific Transcription Factors

Mahantesha Naika
Department of Plant Biotechnology
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National Centre for Biological Sciences (TIFR)
India

Abstract

Major worldwide agricultural losses occur due to biotic and abiotic stress conditions affecting plant growth and development which prevents them from reaching their complete genetic potential. They overcome this by reprogramming metabolism and differential gene expression by gaining a new equilibrium between growth, development and survival. This is controlled by the binding of transcription factors to their promoter sites. Various genes get upregulated in plants during adverse environmental conditions, which alter the metabolic functions to mitigate the stress effects for adaptation. Therefore, it is important to know the regulatory motifs of stress-induced genes for given stress tolerance. Stress-responsive upregulated genes from different microarray experiments were reported by us earlier and HMM-based models were used to identify binding sites for the transcription factors belonging to these stress-inducible genes. We now provide updated and more comprehensive

information for abiotic stress responsive genes and their transcription factors, with addition of one agriculturally important model plant *Oryza sativa* and options to identify probable transcription factor binding sites in their promoters. In the response to abiotic stresses like heat, osmotic, UV-B, heavy metals *etc*., additional stress-responsive genes have been accumulated. We refer to this update as STIFDB2 (Stress Responsive Transcription Factor Database version 2). We trust STIFDB2 would be a very useful database, particularly to understand abiotic transcriptome and the regulatory positions of abiotic stress genes in *Arabidopsis* and rice. STIFDB2 is available from the URL: http://caps.ncbs.res.in/stifdb2

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Contact Information of Corresponding author: R. Sowdhamini:
mini@ncbs.res.in

Introduction

In agriculture, achieving sustainability has emerged as a major goal to fulfil the requirements of food. The ever-increasing world population is expected to reach about 10 billion by 2050, and will witness serious food shortage. Out of 13.4 billion hectares, only about 3 billion hectares of land is suitable for crop production (Smith *et al.,* 2010). In modern agriculture, maintaining crop yield under adverse environmental conditions is the major challenge. Abiotic stresses like ABA, drought, cold, high salinity, oxidative stress, heat, UV-B, dehydration and heavy metals are the primary cause of crop loss worldwide, reducing average yield for most major crop plants by more than 50% (Boyer 1982; Bray *et al.,* 2000). Plants are exposed to adverse environmental conditions and integrated in a complex way depending on the timing and length that allows them to adapt to the existing constraints. Plant stress tolerance involves a variety of changes at the physiological level. These changes are crucial for their survival during stress conditions (Farooq *et al.,* 2009). This affects plant growth and development which prevent them from reaching their complete genetic potential. Plants, however, overcome this by activating distinct signal transduction pathways when exposed to environmental stresses. This is achieved by altering the expression of a variety of genes, ultimately leading to transcriptional reprogramming of metabolism, physiology, morphology and survival (please see Figure 1; Xiong *et al.,* 2002). Therefore, efforts to develop improved stress-tolerant crop plants require understanding of molecular mechanisms and selective regulation of stress-responsive genes. The downstream signalling process is initially triggered by stress-responsive signal transduction cascades and is controlled by transcription factors directly binding to their discrete *cis*-regulatory elements to either activate or repress target genes (Rhee *et al.,* 2006). Many genes induced by stress challenges, including those encoding transcription factors have been identified and some of them have been shown to be essential for stress tolerance. Transcription factors are proteins which are involved in either upregulation or downregulation of single or multiple genes. They are reported in imparting abiotic stress tolerance (Agarwal and Jha, 2010). Their manipulation can be used to develop transgenics for conferring multiple stress tolerance (Pardo, 2010; Xu *et al.*, 2011). A number of transcription factor families have been implicated in abiotic stress tolerance, such as MYB, MYC, bZIP, NAC, AP2/EREBP, HB, DREB1/CBF, DREB2, AREB/ABF, NAC, and WRKY (Umezawa *et al.,* 2006; Bhatnagar-Mathur *et al.,* 2008) (see Table 1). Microarray technology is a powerful tool that has been intensely used to investigate plant transcriptomes to address many biological questions involved at different developmental stages. Moreover, microarray analyses are proving to be useful for identifying, understanding and deciphering various novel *cis*-elements and group of stress-responsive gene expression profiles exposed to abiotic stresses in various plant species such as *Arabidopsis thaliana* and *Oryza sativa* L. (Seki *et al.,* 2001; Kreps *et al.,* 2002; Chen *et al.,* 2002; Rabbani *et al.,* 2003; Kilian *et al.,* 2007; William R. Swindell, 2006; Ray *et al.,* 2011). The completion of *Arabidopsis*

thaliana and *Oryza sativa* L. genome sequence offered a good opportunity to determine putative transcription factor binding sites at the whole genome level. Most of the regulatory sequences in genes occur upstream of the transcription and translation start site (*i.e.*, 5′UTR). Exceptions are reported in earlier studies (Dean *et al.,* 1989; Sieburth *et al.,* 1997; Chung *et al.,* 2006). In plant biology, a detailed knowledge of the mechanisms of transcriptional regulation of genes in response to abiotic stresses is one of the most important areas. Identification and validation of individual gene response in abiotic stress by experimental methods is a laborious and time-consuming process. To overcome this, computational approaches would be of great help to acquire information by integrating diverse available datasets and algorithms. Collection of large-scale data from different available sources would provide a robust platform to understand the major molecular activities involved in stress response. Stress-responsive transcription factor database, STIFDB (Shameer *et al.,* 2009), contains information on stress-responsive transcription factor binding sites and stress-induced genes for abiotic stress conditions, where transcription factors are grouped into families based on the presence of conserved domains and following prior classification criteria. The latest version of the database, STIFDB2, contains stress induced genes in *Arabidopsis*, *Oryza sativa* L. spp. *indica* and *Oryza sativa* L. spp. *Japonica*, representing transcription factor families known to be involved in stress. Here, we updated the previous version of STIFDB to STIFDB2 with additional features like, addition of more stress responsive genes from microarray experiments and including stress-upregulated genes from the genome *Oryza sativa* L. The expression data were retrieved from gene expression omnibus (GEO) database maintained at NCBI (Tanya Barrett and Ron Edgar, 2006). Differentially expressed genes and promotor regions (1000 and 100 basepair upstream sequences and the 5′UTR sequence) were analysed to predict all probable abiotic stress-responsive Transcription Factor Binding Sites (TFBS). We have used a previously-developed, efficient, context-specific, stress-responsive transcription factor binding site prediction algorithm called STIFAL (Sundar *et al.,* 2008). We have also integrated Gene Ontology associations, gene descriptions from TAIR (Lamesch *et al.,* 2011), TIGR (Ouyang *et al.,* 2006), RAPDB (Ohyanagi *et al.,* 2006) and transcription factor related information from DATF (Guo *et al*., 2005) and DRTF (Gao *et al*., 2006). Stress profiles have been created for each gene to indicate stress signals associated with it.

Material and Methods

STIFDB2 offers an integrated and curated repository of experimentally characterized and reported stress-responsive genes for abiotic stress condition. The list of 527, 1487 and 3420 genes in *Arabidopsis thaliana*, *Oryza sativa* L. spp. i*ndica* and *Oryza sativa* L. spp. *japonica* have been compiled from abiotic stress-related microarray experiments. Genes are curated from gene expression database NCBI-GEO (Tanya Barrett and Ron Edgar., 2006) based on literature

survey using PubMed. Genes that are consistently upregulated (in at least three replicates) in microarray experiments, in response to various stress treatments like ABA, cold, drought, dehydration, osmotic stress, high salinity, heat, UV-B, oxidative stress, wounding, water deficit and heavy metals across various microarray experiments, have been considered as stress-responsive genes and have been included in the database. In cases where fold increase in expression levels are available, genes with a 2.5 and more fold expression change are also considered as 'stress-upregulated' and as probable candidates for STIFDB2. Gene sequences for 1000 bp, 100 bp and 5′ UTR are collected from TAIR (Version 10), TIGR and RAPDB (MSU6). The collected sequences are scanned further to identify potential abiotic stress responsive TFBS using the STIF algorithm (Sundar *et al.,* 2008). In response to all abiotic stresses considered, 10 specific families of transcription factors are known to be involved in *Arabidopsis thaliana* and five in *Oryza sativa* L. 19 and eight HMM-based models (Eddy 1998) of these 10 and five specific families (including subfamilies) are used in STIFAL algorithm to scan for TFBS (Table 1). We have also consulted literature to cross-validate the transcription factor binding sites predicted by the STIFAL for 48 genes. STIFDB provides upstream of 1000 bp and 100bp promoter regions, along with their 5′ UTR sequences, extracted from TAIR, TIGR, and RAPDB and identifies known transcription factor binding sites bound by abiotic stress responsive transcription factors. The logistics based on which STIFDB2 has been created is shown schematically in Figure 2.

Results and Discussion

Increasing crop productivity to keep up with the growing human population, diminishing cultivable land and natural resources has become more a matter of urgency and agriculture has become more of a 'struggle against nature'. Modern agriculture is adversely affected by abiotic stresses like drought, cold, heat, high light, high salinity, ABA, UV-B, oxidative conditions, dehydration, wounding and presence of heavy metals. Abiotic stress is the primary cause of crop loss worldwide, causing average yield losses of more than 50% for major crops (Boyer, 1982; Bray *et al* ., 2000). Sustainable agriculture in adverse environmental conditions requires an understanding of the manner in which plant genes respond to abiotic factors. Therefore, development of agriculturally important crops with high tolerance to various abiotic stresses should be developed to feed the growing world population. Better understanding of the genetic and molecular mechanisms underlying plant abiotic stress responses and application of knowledge obtained from different experimental and computational approaches are gaining importance. Hence, an explicit data organisation and a clearer understanding of the regulation of abiotic stress-responsive genes have become crucial. With genomic sequence data available, bioinformatics tools have been valuable for large scale analyses of genes (Rhee *et al.,* 2006) and understanding gene regulation (see Ochsner *et al.,* 2008 for a

review). Their examination of data-sharing statements revealed that 186 (only 47%) of these studies had made their datasets publicly available. Our STIFDB2 is a database of abiotic stress-responsive genes, identified as responsive to various abiotic stress signals, based on publicly available and genome-wide stress microarray data. It would be an useful resource to analyse the promoters of abiotic stress-induced genes for potential stress-specific transcription factor binding sites, which would provide insights into the regulatory mechanisms. It also provides clues towards the stress signal that affects the transcription of this gene, which might offer clarity about signal-specific regulation of these genes. List of genes in STIFDB2 indicate that abiotic stress-responsive genes differ in numbers on all chromosomes. Chromosome-wise distribution of abiotic stress-responsive genes in STIFDB2 is provided in the database. Distribution of genes responsive to specific abiotic stress signals indicates that numerous genes are regulated in response to ABA, cold, drought, light, salinity, oxidative, and new subset of genes that respond to UV-B, heat, osmotic, heavy metals and wounding. We have further analysed the number of TFBS on the promoters of these abiotic stress-responsive genes and have identified varying numbers of stress-specific TFBS. Frequency of individual transcription factor binding sites on 527 genes in *Arabidopsis* (Figure 3), and 1487, 3420 genes of *Oryza sativa* L. spp. *indica and Oryza sativa* L. spp. *japonica* in STIFDB 2 is provided in STIFDB2, respectively.

Conclusion

Worldwide, the plant productivity is affected due to various abiotic stresses including the global warming. On the other hand, the demand for food is expected to grow as a result of population growth. According to FAO, the World needs 70% more food by the year 2050. Therefore, it is necessary to obtain stress-tolerant varieties to cope with this huge demand and upcoming problem of food security. The identification of specific binding sites for transcription factors involved in regulating gene transcription is one of the most important and challenging problems in molecular and computational biology. The field of gene expression regulation brings together researchers from several disciplines, in particular from biology, statistics and informatics. It also needs to be determined if a greater number of stress-specific TFBS on the promoter, a particular gene, means a greater role of that particular TF in its regulation. It would also be worthwhile to analyse the promoters of subsets of genes that are regulated by specific stresses, to identify patterns of TFBS, which would have potential roles in the regulation of downstream genes responsive to a particular stress. STIFDB2 provides a unique platform to investigate the stress-regulome of abiotic stress-responsive genes in *Arabidopsis* and rice genomes. STIFDB2 will be a highly useful resource for a researcher working on abiotic stress responses in plants. The web interface of the STIFDB2 was re-designed to provide users with more flexible search

functionality. All resources in STIFDB2 can be browsed, retrieved and downloaded freely.

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Figure 1. The flow of signal transduction pathway activated in response to abiotic stresses.

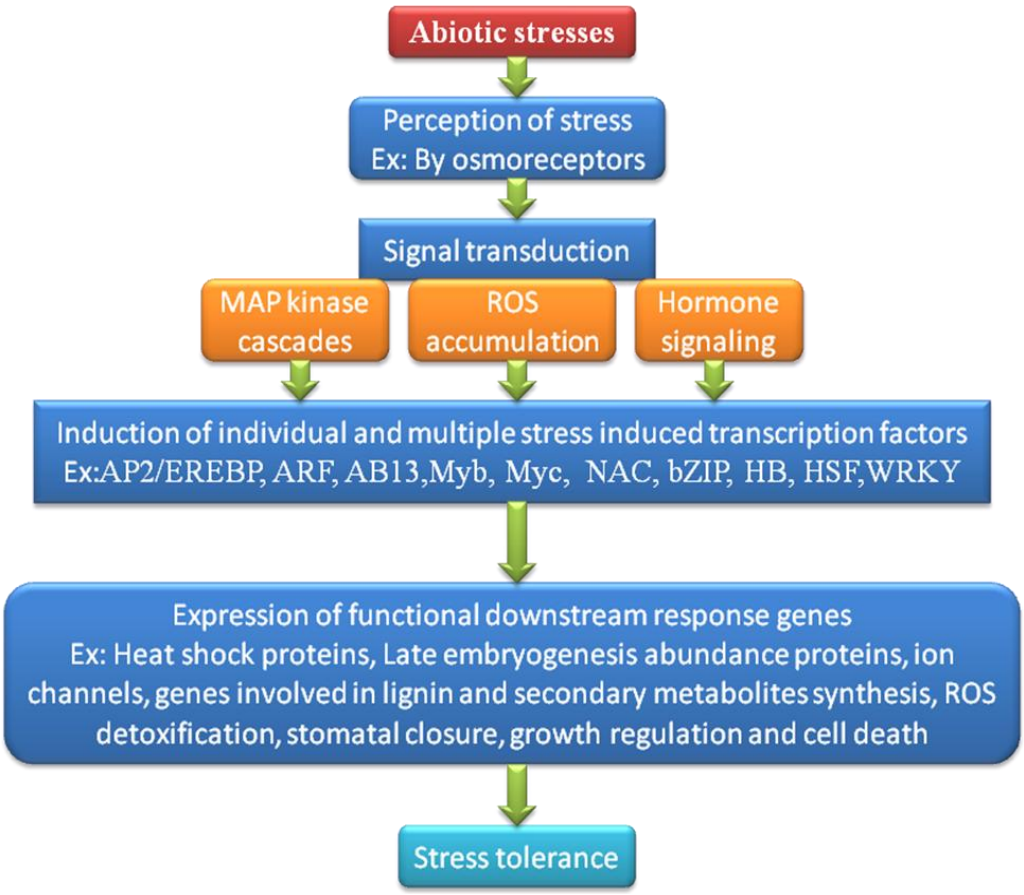

Figure 2. Flow chart of steps involved in the development of STIFDB 2

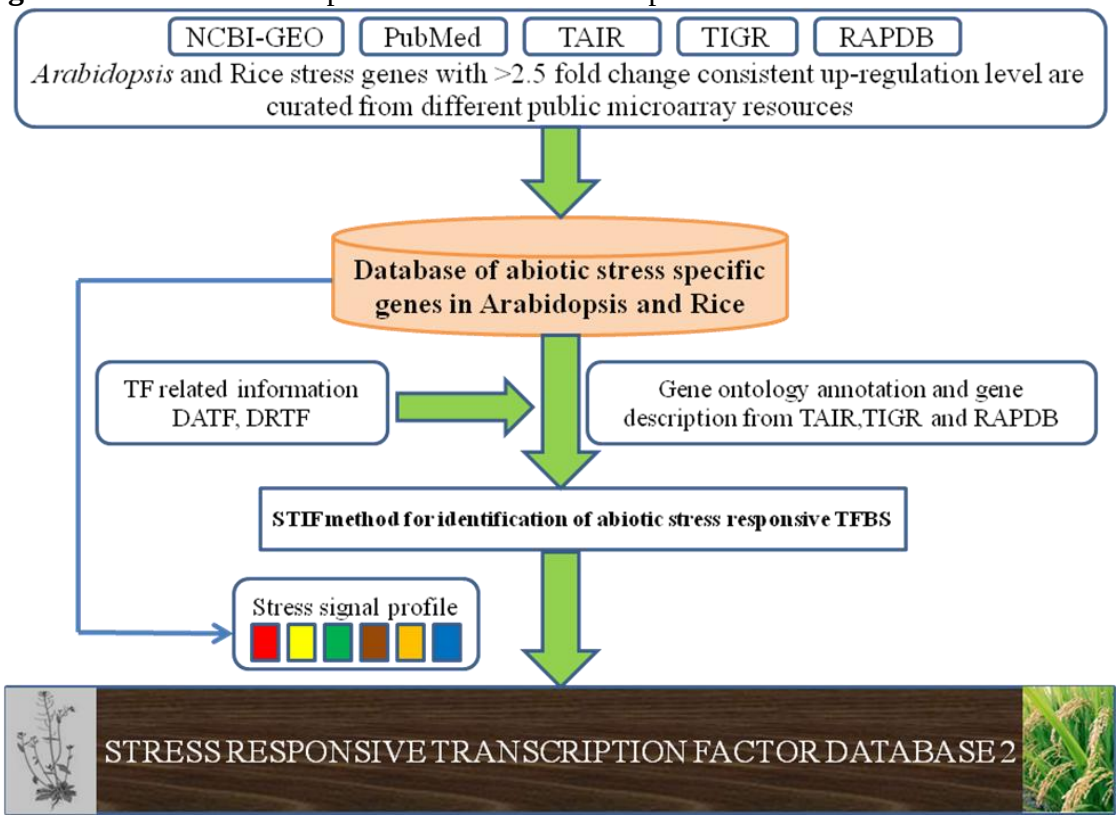

Figure 3. Frequency of transcription factors binding sites in STIFDB2

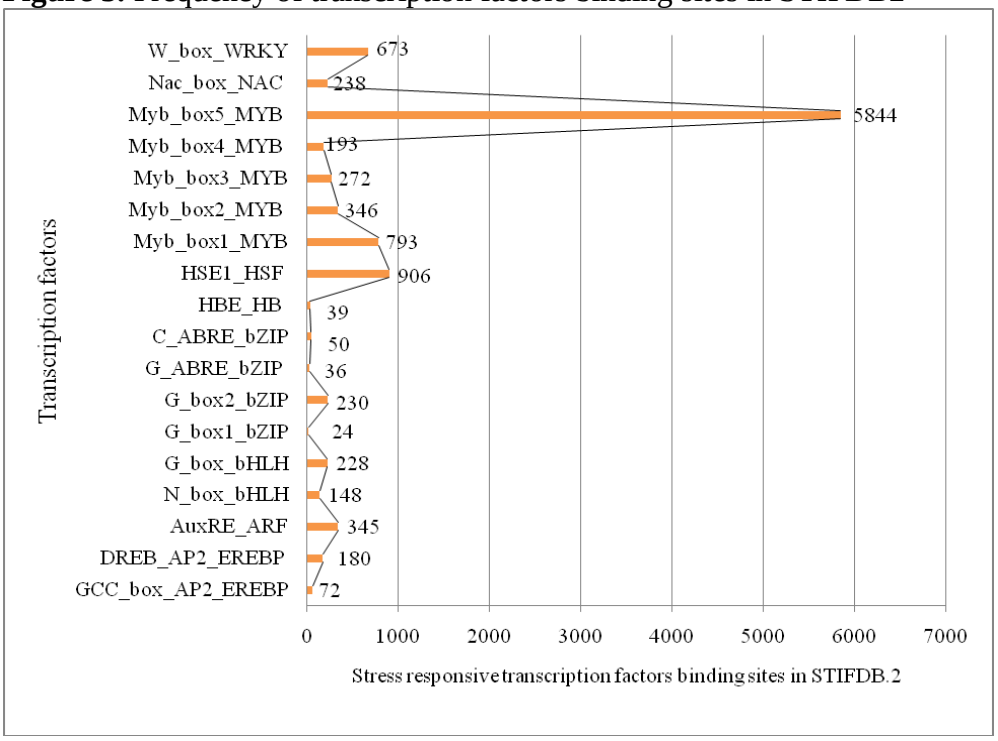

Table 1: Table of transcription factors considered.

No.	Family name	Stress signal	Reference (Stress signal) PMID:	Name of the Cis-element	Cis-element	Reference (Cis-element) PMID:
1	ABI3/VP1	ABA	11029704	distB ABRE	GCCACTTGTC	11029704
2	AP2/EREBP	Cold, Drought	9707537 9023378	CRT/DRE	(A/G)CCGAC	9707537 9023378
3	ARF	Auxin	10318972	AuxREs	TGTCTC	10318972
4	BHLH/myc	NaCl, ABA, Drought	12509522	N box Gbox	CACG(G/A)C CACGTG	12509522 12897250
5	bZIP,	ABA, Drought	10837265	G box1 G box2 G/ABRE C/ABRE	CCACGTGG TGACG(T/C) (C/T)ACGTGGC CGCGTG	1446171 1446171 10636868 10636868
6	HB	ABA, Drought	9617808		CAATNATTG	10331875
7	HSF	Drought, Cold, Heavy-metal and oxidative stress	9701569	HSE	TTCNNGAAGAANNTTC	10331875
8	MYB	Dehydration, Wounding	8312738		(T/C)AAC(G/T) G CC(T/A)ACC TAACTG CC(TA)AACC (C/T)AACN(A/G)	2279697 9611167 9011094 9611167 12535340
9	NAC	Drought, high salinity and ABA	15319476		CATGTG	12175016
10	WRKY	Biotic stress (pathogen attack) Abiotic stress	12068110	W box	(T)TGAC(C/T)	12602888
Oryza sativa L.						
1	ERF/AP2 CBF/DREB	Cold, Dehydration and high-salinity	12609047 18470484	DRE sequence	RCCGAC	12609047
2	bHLH	Fe deficiency	16887895		CACGTGG	16887895

3	bZIP	ABA, Salt, Drought, Heat, dehydration	11828032 10636868 18236009 20132733	ABRE G-box ABRE ABRE	ACGTG G/T C CACGTG ACGTGCC CGACGTGGC	11828032 18236009 20132733 10636868
4	MYB	Water stress responsive	19357984		TAACTG	19357984
5	NAC	Drought, cold, high salinity, abscisic acid	20632034	NACRS	CACG	20632034