# Chapter 6
# Effect of Climate Change on Abiotic Stress Response Gene Networks in *Arabidopsis thaliana*

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## 6.1 Introduction

Climate change threatens future food security, and, in turn, societal welfare since changing climatic conditions has been changing agricultural production and is expected to worsen in coming decades. Climate change decreases crop yield by intensifying the environmental stress duration or strength on plants. Environmental stresses such as drought, high/low temperature, salinity, and flooding put extensive pressure on plant growth and development (Fahad et al. 2021a).

Plants respond to environmental stress conditions in some conserved regulatory networks, whereas there are minute unique differences between the stresses (Fahad et al. 2021b). These global stress response pathways are essential to determine the stress tolerance level of a species. Among global stress response pathways, generally, genes coding for antioxidants and/or reactive oxygen species (ROS)-scavenging enzymes stand out. Additionally, there is a vast majority of different proteins, including transporters, aquaporins, heat shock proteins, freeze proteins, and secondary metabolites, integrated into stress response pathways. Taken together, all these responses act in synchrony to develop a tolerance response in the organism. Integration of different stress response pathways is a difficult task and needs precise control. The pathways are controlled at transcriptional, post-transcriptional, translational, and post-translational levels. Transcriptional control is performed with the help of transcription factors (TFs) that bind to the cis-elements at the promoter regions of the genes. TFs can induce or suppress the transcription, thereby affecting the mRNA abundance of target genes. This suggests that TFs are the most important regulators in stress response pathways. According to one report, there are more than 1533 TFs in the *Arabidopsis* genome (Riechmann et al. 2000), whereas this number is over 1789 according to another report (Guo et al. 2005). Transcription factors are organized into 49 families and constitute 6% of *Arabidopsis* genes (Riechmann 2008).

In addition to a high number of transcription factors encoded in the *Arabidopsis* genome, they can be induced or repressed by other TFs or other ways of stress signaling such as divalent metal binding, phosphorylation, or receptor–protein interactions. Moreover, the same transcription factor can induce a downstream gene while repressing another one. A TF gene can also be induced or suppressed by different stress conditions. Therefore, stress signaling triggers a massive network of genes to be activated and leads to the interaction of their products to develop the proper tolerance response (Song et al. 2016). This suggests that the understanding of abiotic stress response gene networks is essential to develop food crops resilient to climate change.

Recent bioinformatics analyses have identified a core gene network that is essential in abiotic stress tolerance in plants. These genes include various TFs with essential roles in regulating the downstream tolerance mechanisms. However, a more detailed analysis is required to understand the core transcriptional regulatory network of stress-responsive genes in the model plant *Arabidopsis thaliana*. Here, we explain the identification of a core transcriptional regulatory network of stress-responsive genes in *Arabidopsis* by bioinformatic analyses under several abiotic

stress conditions. These TFs are grouped in different families with previously known functions in stress tolerance in plants while some families need further studies to investigate the potential roles in the network.

## 6.2   Bioinformatic Analyses

To identify the gene networks affected by different abiotic stresses, extensive bioinformatic studies have already been done in *Arabidopsis thaliana* (Shinozaki et al. 2003; Fujita et al. 2006; Seki et al. 2007; Shinozaki and Yamaguchi-Shinozaki 2007; Tran et al. 2007; Nakashima et al. 2009; Urano et al. 2010; Nakashima et al. 2014), rice (Cooper et al. 2003; Yun et al. 2010; Seo et al. 2011; Zhang et al. 2012; Sharma et al. 2013), and wheat (Tardif et al. 2007). Here, we analyzed the differentially expressed genes in *A. thaliana* from a total of eight abiotic stress conditions that were deposited under the AtGenExpress global stress expression dataset (accession numbers: TAIR-ME00325, TAIR-ME00327, TAIR-ME00328, TAIR-ME00329, TAIR-ME00338, TAIR-ME00339, TAIR-ME00340, TAIR-ME00345) (Kilian et al. 2007; Goda et al. 2008; Wanke et al. 2009). First, differentially expressed gene lists were developed from individual stress microarray data by GeneSpring GX software (Agilent), then the list of overlapping genes that are differentially expressed in all stress conditions was generated. In all stress conditions, 11 or 9 genes were upregulated or downregulated, respectively. To understand the stress regulatory networks that function in all stress conditions, transcription factors or proteins that show putative DNA-binding function have been screened out from the list of all differentially expressed genes. Eleven genes in nine transcription factor families were found to be upregulated, whereas eight genes in eight transcription factor families were downregulated under all stress conditions (Tables 6.1 and 6.2). These genes are defined as the core gene cluster differentially expressed in various abiotic stresses, and the details about their known functions are provided in the following sections.

To elucidate the potential functions of the core gene cluster, network interactions of these core genes were identified via Atted II (Obayashi et al. 2017) and String software (Szklarczyk et al. 2016). According to these analyses, the co-expressed network of genes included very well-known abiotic stress response genes, such as late embryogenesis-abundant proteins, aquaporins, kinases, phosphatases, and chaperons. The extended gene networks included several transcription factors that are co-expressed with the core transcription factor gene clusters, suggesting that the abiotic stress response and tolerance is a complex phenomenon that integrates different signaling pathways (Fig. 6.1). Upregulated core genes were grouped in three gene clusters. The biggest of the three, the first cluster, included *SAP12*, *SCL11*, *WRKY25*, *CPDK32*, *EDF2/RAV2*, *RD26,* and *ZAT6*. The other two clusters were centered separately around *MYB44* and *NDB2*. Downregulated core genes, on the other hand, were separated into four groups. *BZIP61*, *BBX27*, *HAT1,* and *MYB30* were clustered in the largest group of clusters, whereas *MYB59* and *DEWAX* generated separate clusters of their own. *SOS3* and *ARR5* were clustered together.

**Table 6.1** Core gene cluster upregulated in various abiotic stresses

| AGI | Gene abbreviation | Gene name | Family name |
|---|---|---|---|
| AT3G21890 | *BBX31* | *B-BOX DOMAIN PROTEIN31* | C2C2-CO-like |
| AT3G57530 | *CPDK32* | *CALCIUM-DEPENDENT PROTEIN KINASE32* | EF-hand-containing protein |
| AT4G05020 | *NDB2* | *NAD(P)H DEHYDROGENASEB2* | |
| AT5G67300 | *MYB44* | *MYB DOMAIN PROTEIN44* | MYB |
| AT2G30250 | *WRKY25* | *WRKY DNA-BINDING PROTEIN25* | WRKY |
| AT4G27410 | *RD26 / NAC72* | *RESPONSIVE TO DESICCATION26 / NAC DOMAIN-CONTAINING PROTEIN72* | NAC |
| AT3G28210 | *SAP12* | *STRESS-ASSOCIATED PROTEIN12* | C2H2 |
| AT5G04340 | *ZAT6* | *ZINC FINGER OF ARABİDOPSİS THALIANA6* | |
| AT4G36990 | *HSF4/TBF1/ HSFB1* | *HEAT SHOCK FACTOR4 / TL1-BINDING TRANSCRIPTION FACTOR1 / HEAT SHOCK FACTORB1* | Heat shock factor |
| AT5G59450 | *SCL11* | *SCARECROW-LIKE11* | GRAS |
| AT1G68840 | *TEM2/EDF2/ RAV2* | *TEMPRANILLO2 / ETHYLENE RESPONSE DNA BINDING FACTOR2 / RELATED TO ABI3/VP1 2* | B3 DNA binding |

**Table 6.2** Core gene cluster downregulated in various abiotic stresses

| AGI | Gene abbreviation | Gene name | Family name |
|---|---|---|---|
| AT1G34760 | *GRF11* | *GENERAL REGULATORY FACTOR11* | 14-3-3 |
| AT1G68190 | *BBX27* | *B-BOX DOMAIN PROTEIN27* | C2C2-CO-like |
| AT3G48100 | *ARR5* | *ARABİDOPSİS THALIANA RESPONSE REGULATOR2* | aRR-B |
| AT3G58120 | *BZIP61* | *BASIC LEUCINE ZIPPER* | bZIP |
| AT4G17460 | *HAT1* | *HOMEOBOX-LEUCINE ZIPPER PROTEIN HAT1* | EaR repressome |
| AT5G24270 | *CBL4/SOS3* | *CALCINEURIN B-LIKE PROTEIN4 / SALT OVERLY SENSITIVE3* | EF-hand-containing protein |
| AT5G61590 | *DEWAX* | *DECREASE WAX BIOSYNTHESIS* | AP2/ERF |
| AT5G59780 | *MYB59* | *MYB DOMAIN PROTEIN59* | MYB |
| AT3G28910 | *MYB30* | *MYB DOMAIN PROTEIN30* | |

Interestingly, *GRF11* was not clustered with any other genes, suggesting that the gene requires more attention in understanding its functions in general stress response networks.

Cluster analysis of proteins that are identified in our core gene network indicated a large group of proteins interacting with each other (Fig. 6.2). The proteins in the network included the majority of the transcription factors affected by all abiotic stresses. Only some proteins, including HAT1, BZIP61, ARR5, BBX31, MYB59, DEWAX, and SCL11, were not identified in this network. Interestingly, some other
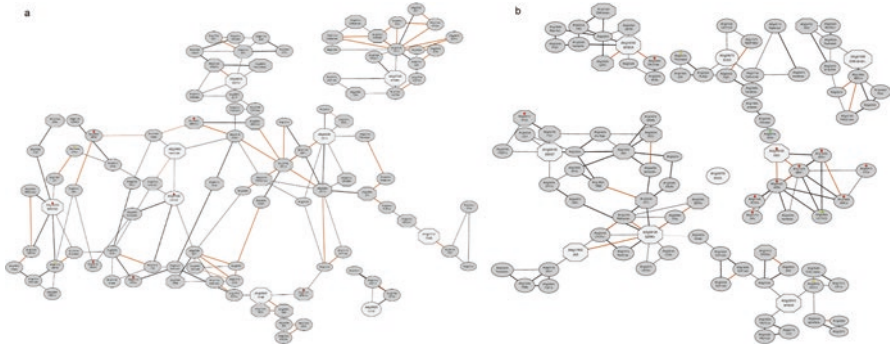
**Fig. 6.1** Abiotic stress response gene networks in *Arabidopsis thaliana*. (**a**) Co-expression gene network of upregulated core genes (**b**) Co-expression gene network of downregulated core genes. The gene networks were drawn with Atted II software (Obayashi et al. 2017)
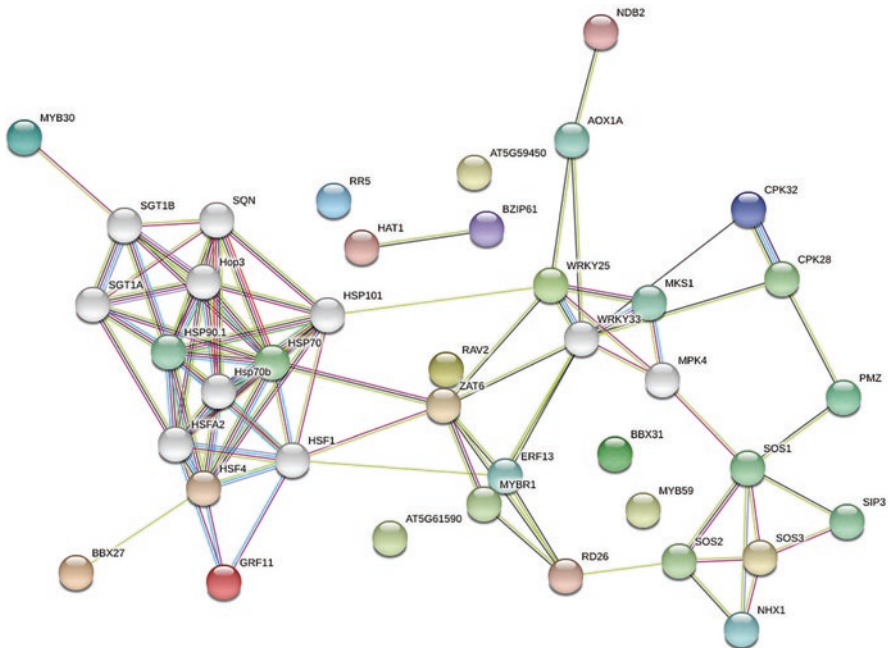


**Fig. 6.2** Abiotic stress response protein networks in *Arabidopsis thaliana*. The networks were drawn with String software (Szklarczyk et al. 2016)

stress-related proteins were also clustered in this network, including heat shock proteins and salinity tolerance pathway proteins. Protein cluster analysis represented significantly more interactions than expected (with a protein–protein interaction enrichment p-value of $2.22 \times 10^{-16}$), suggesting that the interactions in the protein network are theoretically significant. Therefore, further wet laboratory

experiments are needed for their verification. Blast2GO software (Conesa et al. 2005) was used to determine gene ontologies (GOs) that the protein network is representing (Fig. 6.3). As can be seen in the figure, the majority of the GOs were related to abiotic stress responses and hormonal signaling, indicating the necessity
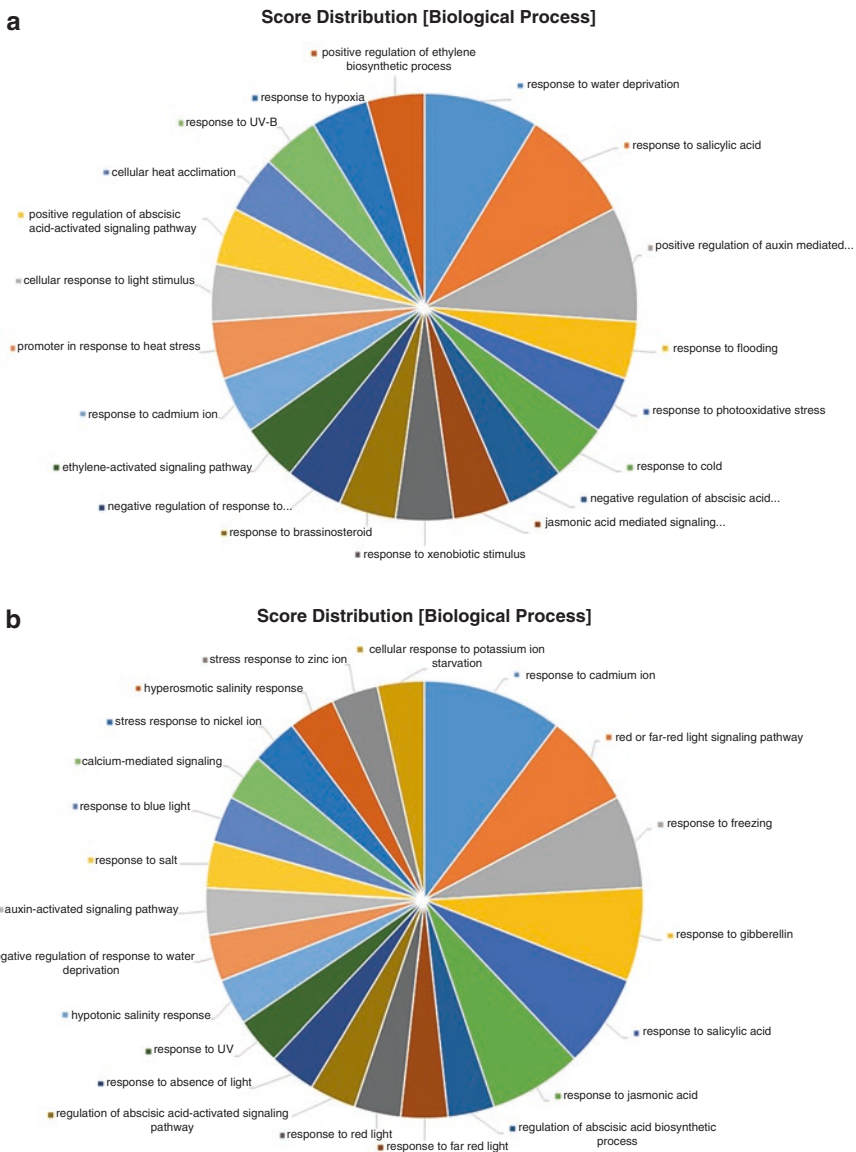


**Fig. 6.3** Gene ontology analysis according to the biological processes. (**a**) GO analysis of upregulated genes. (**b**) GO analysis of downregulated genes. The analysis was done with Blast2GO (Conesa et al. 2005)

of hormonal control on abiotic stress tolerance signaling. To confirm the Blast2GO analysis results, GO enrichment analysis was performed by using String software (Table 6.3). Accordingly, the top 10 biological processes GO terms enriched in abiotic stress response protein networks were related with environmental or chemical stress responses, further indicating the identified list of transcription factor genes and proteins that are functionally involved in stress response signaling networks.

Finally, four entities were shared between the networks identified in Atted II and String software, except for the transcription factors identified in our core gene list (Table 6.4). Since Atted II only compares the co-expressed genes whereas String compares any potential protein–protein interactions (even including the text mining), the entities that are identified in the intersection of both software specifically indicate the most striking genes in the entire dataset. Among these genes, *DREB26* and *WRKY33* have been shown to function in abiotic stress signaling and tolerance (Jiang and Deyholos 2009; Kazama et al. 2013). EXORDIUM (EXO) was identified as a probable intermediary protein that functions in brassinosteroid-promoted leaf and root growth (Schröder et al. 2009). Its mutants show several morphological deficiencies. However, its potential functions under abiotic stress tolerance have not been studied yet. Finally, CALCIUM-DEPENDENT PROTEIN KINASE28 (CPK28) was identified as a functional negative regulator of the BIK1 innate immune response pathway via regulating cytosolic calcium ($Ca^{2+}$) levels (Monaghan et al. 2015). It contains a 14-3-3-binding motif and was shown to phosphorylate 14-3-3 proteins (Swatek et al. 2014) as well as itself (Bender et al. 2017) for regulation of calcium signaling via the $Ca^{2+}$-calmodulin pathway. Although no reports prove the integration of CPK28 in abiotic stress response signaling networks, through the $Ca^{2+}$-calmodulin pathway and activation of 14-3-3 proteins, CPK28 shows a high potential to have an important function in stress signaling in the cells.

**Table 6.3** Functional enrichments in abiotic stress response protein networks

| GO term | Description | Gene count | | False discovery rate |
|---------|-------------|------------|------------|------|
| | | Observed | Background | |
| GO:0009628 | Response to abiotic stimulus | 23 | 1699 | 1.51e-15 |
| GO:0050896 | Response to stimulus | 33 | 5064 | 1.51e-15 |
| GO:0006950 | Response to stress | 26 | 2932 | 2.60e-14 |
| GO:1901700 | Response to oxygen-containing compound | 19 | 1398 | 1.00e-12 |
| GO:0042493 | Response to drug | 14 | 533 | 1.16e-12 |
| GO:0042221 | Response to chemical | 23 | 2654 | 4.73e-12 |
| GO:0009408 | Response to heat | 10 | 184 | 8.44e-12 |
| GO:0009266 | Response to temperature stimulus | 12 | 505 | 1.23e-10 |
| GO:0010200 | Response to chitin | 8 | 113 | 1.44e-10 |
| GO:0046677 | Response to antibiotic | 9 | 253 | 1.84e-09 |

**Table 6.4** Genes identified by Atted II and String software in abiotic stress response network

| AGI | Gene abbreviation | Gene name |
|-----|-------------------|-----------|
| AT1G21910 | DREB26 | *DEHYDRATION RESPONSE ELEMENT-BINDING PROTEIN26* |
| AT2G38470 | WRKY33 | *WRKY DNA-BINDING PROTEIN33* |
| AT4G08950 | EXO | *EXORDIUM* |
| AT5G66210 | CPK28 | *CALCIUM-DEPENDENT PROTEIN KINASE28* |

## 6.3   Basic Region/Leucine Zipper Family

The *Arabidopsis* genome includes 77 members of the basic region/leucine zipper family (bZIP) (Riechmann et al. 2000; Corrêa et al. 2008). Genetic and molecular studies of these AtbZIP factors demonstrated that they have key functions on diverse biological processes such as abiotic stress, biotic stress, light signaling, phytohormone response, seed maturation, and other developmental processes (Dröge-Laser et al. 2018). During the evolution of plants, early recruitment of bZIP TFs may contribute to this diversity, which is in contrast to apparently more bounded functions of the plant-specific R2R3-MYB and WRKY TFs (Eulgem et al. 2000). The ABFs or AREBs are bZIP TFs regulating ABA-dependent gene expression by binding to the ABRE motifs. ABA and abiotic stresses such as drought, cold, or salinity activate gene expression through cis-elements that consist of the ABA-responsive elements (ABRE) in vegetative tissues. Based on the in vitro and yeast assays, ABA-responsive element-binding proteins (AREBs) and ABRE-binding factors (ABFs) can bind to different ABRE-containing promoters (Choi et al. 2000). ABA and relevant stresses therefore possibly activate both transcriptional and post-translational regulation of several groups of bZIPs (Jakoby et al. 2002). One of the members of the bZIP transcription factor family, *AtbZIP61*, was downregulated under relevant stress conditions in our bioinformatic analyses. The bZIP34 and bZIP61 are two putative *Arabidopsis* E group bZIP transcription factors that can form heterodimers through their N-terminal regions for transcriptional activation. AtbZIP34 and AtbZIP61 have eight close homologs in *Arabidopsis,* and they contain a proline residue in the third heptad of the zipper region, which is a common property for physiological responses in plants to various abiotic stress (Kaur and Asthir 2015). In *Arabidopsis* mutants of *bZIP34* and *bZIP61*, heterodimer formation was not observed by yeast two-hybrid assay or electrophoretic mobility shift assay (EMSA), and interestingly mutated forms of AtbZIP34m and AtbZIP61m, where the proline residue was replaced by an alanine residue in the zipper region, could form a homodimer and bind G-box element instead of ABRE (Shen et al. 2007). Both bZIPs are highly expressed in the pollen and interact with bZIP18, which is required for proper pollen development (Gibalová et al. 2017). AtbZIP34 was shown to be necessary for correct pollen wall development (Gibalová et al. 2009). Interestingly, there are no previous studies on the potential roles of these two bZIPs under abiotic stress tolerance.

## 6.4   Homeodomain Leucine Zipper Family

The homeodomain leucine zipper (HD-ZIP) family of TFs is special to the plants, indicating their roles in growth and developmental processes unique for plants. The HD-ZIP family includes four subfamilies containing leucine zipper domain (ZIP) adjacent to a homeodomain (HD), which can form homo- and heterodimers (Ariel et al. 2007). HD-ZIP II subfamily can be discriminated from HD-Zip I subfamily proteins by containing a conserved "CPSCE" motif, which is present downstream of the leucine zipper (Chew et al. 2013). *HOMEOBOX-LEUCINE ZIPPER PROTEIN1* (*HAT1*) encoding an EaR repressome family protein was found to be downregulated in relevant stress conditions based on our study. HAT1 and its close homologs belong to the class of HD-ZIP II transcription factors, with their roles as a repressor binding to promoters of their target genes, and are involved in plant development and abiotic and biotic stress responses (Tan et al. 2018). The HD-ZIP II family has many important roles in biological processes such as meristem determination, gynoecium and fruit development, auxin and other hormone responses, shade avoidance, and leaf polarity (Harris et al. 2011). Each of these roles suggests that this family is directly or indirectly connected to the environmental stress signaling (Zhang et al. 2014). Tan et al. (2018) demonstrated HAT1 and HAT3 as the important regulators of ABA signaling under drought stress since they suppressed ABA signaling and drought responses.

## 6.5   Zinc Finger Protein Family

Zinc finger proteins (ZFPs) possess one or more zinc finger(s) that bond zinc ion(s) by histidine (His) and cysteine (Cys) residues, playing several important regulatory roles in plant development and growth, stress responses, and phytohormone responses through four ZFP subfamilies, $C_2H_2$, CCCH, $C_3HC_4$, and $C_4$ (Li et al. 2013). The cysteine2/histidine2-type zinc finger proteins are one of the largest TF families, and some of its members have essential roles in abiotic and biotic stress responses. In our analysis, two members of the $C_2H_2$ transcription factor family have been identified among the core stress-related transcription factors. Both *SAP12* and *ZAT6* were upregulated under relevant stress conditions. STRESS-ASSOCIATED PROTEIN12 (SAP12) is a member of the stress-associated protein (SAP) family that is considered a novel regulator of abiotic stress responses (Ströher et al. 2009; Giri et al. 2013). Its expression is highly induced under several abiotic stress conditions, resulting in the accumulation of reactive oxygen species (ROS) (Gadjev et al. 2006). Similar to our study, the *SAP12* transcript level was highly increased with respect to the redox potential under salt and cold stresses (Ströher et al. 2009). Cysteine2/histidine2-type transcription factor *ZINC FINGER of ARABİDOPSİS THALIANA6* (*AtZAT6*) was transcriptionally induced under dehydration, cold, salt, osmotic stresses, as well as hydrogen peroxide ($H_2O_2$) treatment

and pathogen infection (Mito et al. 2011; Liu et al. 2013; Shi et al. 2018a). Exogenous melatonin application-enhanced freezing tolerance is largely relieved in *AtZAT6* knock-down mutant, but was improved in *AtZAT6*-overexpressing plants (Shi and Chan 2014). It was shown that *AtZAT6* overexpression lines could tolerate the cold more efficiently than the nontransgenic plants, and the enhanced tolerance was due to the upregulation of *CBF* genes. Additionally, ZAT6 was shown to have roles in increased cadmium (Cd) tolerance (Chen et al. 2016). It was shown that ZAT6 positively regulates the expression of genes involved in glutathione production such as *GSH1, GSH2, PCS1,* and *PCS2* under Cd treatment.

## 6.6    B3 Domain Family

Members of the plant-specific B3 transcription factor superfamily contain a B3 domain, and the superfamily is divided into four subfamilies: LAV (LEAFY COTYLEDON2 [LEC2]-ABSCISIC ACID INSENSITIVE3 [ABI3]-VAL), ARF (AUXIN RESPONSE FACTOR), REM (REPRODUCTIVE MERISTEM), and RAV (Related to ABI3/VP1), encoding 118 genes in *Arabidopsis* (Swaminathan et al. 2008). ABI3 binds with bZIP TF, ABI5, to regulate the seed and seedling development and growth (Finkelstein et al. 2005; Lumba et al. 2014). RAV superfamily in *Arabidopsis* includes 13 members. Six members of the RAV superfamily consist of the DNA-binding domain and AP2 domain. Due to the AP2 domain, they are classified in AP2/ERF transcription factors. One of the members of the B3 transcription factor family, TEMPRANILLO2/*ETHYLENE RESPONSE DNA BINDING FACTOR2/RELATED TO ABI3/VP1 2* (*TEM2/EDF2/RAV2*), was upregulated under relevant stress conditions in our study. RAV2 is required for the upregulation of genes involved in stress response pathways in various species (Li et al. 2011a, b). Fu et al. (2014) investigated the potential functions of three homologous proteins, RAV1, RAV1L, and RAV2, and prove that these three RAV transcription factors have functions in both growth and abiotic stress responses in *Arabidopsis*. They performed their analysis with the mutants (*rav1*, *rav1l,* and *rav2*) and overexpression lines (*35S-RAV1OE*, *35S-RAV1LOE,* and *35S-RAV2OE*) of these three RAV transcription factors. When drought stress was applied to the mutants and wild type, they both showed a similar pattern. However, water loss of the *35S-RAV1OE* and *35S-RAV2OE* transgenic plants was significantly higher than that of wild type. Under salt stress conditions, no differences were observed in seed germination of *rav* mutants in comparison with the wild type. *RAV* overexpression lines showed decreased seed germination rates compared with the wild type. These results indicate that RAVs negatively regulate drought and salinity tolerance in *Arabidopsis*. When *AtRAV1* and *AtRAV2* were overexpressed in cotton, it resulted in longer cotton fibers under drought in the field (Mittal et al. 2015). The overexpression lines showed delayed flowering and retained bolls at higher nodes. RAV2 was also identified to interact physically with a trihelix transcription factor GT-4 in salt tolerance (Wang et al. 2014).

## 6.7  APETALA2/ETHYLENE-RESPONSIVE FACTOR Family

APETALA2/ETHYLENE-RESPONSIVE FACTOR (AP2/ERF) family of transcription factors from several plant species have demonstrated that this TF family is involved in abiotic stress responses (Mizoi et al. 2012). Many of the transcription factors in AP2 and ERF/DREBP subfamilies are mostly involved in ethylene- and ABA-related responses (Zhu et al. 2010). DREB1/CBF and DREB2 subgroups have key roles in the acquisition of stress tolerance by controlling gene transcription sets via DRE/CRT sequences in stress-inducible gene promoters (Agarwal et al. 2006). By crosstalking with each other, AP2/ERF family transcription factors mostly regulate physiological, biochemical, and developmental responses to several environmental stress factors (Mizoi et al. 2012). *DECREASE WAX BIOSYNTHESIS* (*DEWAX*) encoding an AP2/ERF transcription factor (*ERF107*) was found to be downregulated in our study under relevant stress conditions. DEWAX is known as a negative transcriptional regulator that can repress the expression of genes included in cuticular wax biosynthesis in *Arabidopsis* (Go et al. 2014; Suh et al. 2014). It is specifically expressed in the epidermis and upregulated at dark. DEWAX is involved in resistance to *Botrytis cinerea* in *A. thaliana* and *Camelina sativa* by physically binding to the promoters and inducing the expression of genes involved in biotic stress tolerance such as *PRX37, IGMT1,* and *PDF1.2a* (Ju et al. 2017). Under abiotic stress conditions, there are no specific studies about the functions of DEWAX; therefore, there is a gap in the literature.

## 6.8  Myeloblastosis Family

Myeloblastosis (MYB) superfamily is the most abundant group of transcription factors in plants. In total, 198 genes in the *MYB* superfamily were discovered in the *Arabidopsis* genome. Among these, 5 are *R1R2R3-MYB,* 126 are *R2R3-MYB*, 64 are *MYB*-related, and 3 are atypical *MYB* genes (Cominelli and Tonelli 2009). Based on many studies about the MYB family, most of its members showed significant regulation by abiotic and biotic stresses (Persak and Pitzschke 2014). There are also some studies related to the hormonal regulation of MYB TFs (Roy et al. 2016). Based on our study, three members of the MYB TF family were included in the core gene set. *MYB DOMAIN PROTEIN59* (*MYB59*) and *MYB DOMAIN PROTEIN30* (*MYB30*) were downregulated, whereas *MYB DOMAIN PROTEIN44* (*MYB44*) was upregulated under stress conditions. MYB59 is identified as a negative regulator of nutrient stress signaling in plants. It is overaccumulated under Cd and regulates the cell cycle progression and root elongation. Moreover, it is a repressor of $Ca^{2+}$ homeostasis and signaling under $Ca^{2+}$ deficiency, thus regulating stress responses (Fasani et al. 2019). MYB59 also maintains the balance of $K^+$ and $NO_3^-$ distribution between roots and shoots by regulating the transcription of the nitrate transporter

*NRT1.5/NPF7.3* under low K⁺ stress (Du et al. 2019). Liao et al. (2017) have demonstrated that transcription factor MYB30 can bind and regulate *ANNEXIN* (*ANN)* genes and promote their expression at a functional level. *ANNs* have controls on oxidative and heat stress responses. Moreover, MYB30 participates in ABA responses via SUMO ligase SIZ1-mediated sumoylation, and the stability of MYB30 is disrupted by a RING-type ubiquitin E3 ligase RHA2b in ABA signaling (Zheng et al. 2018). According to a recent study, *MYB30* is highly upregulated under ROS treatment and controls a gene network, leading to the blockage of root cell elongation via hydrogen peroxide production (Mabuchi et al. 2018). *MYB44* over-expression lines showed elevated tolerance to salt stress compared with wild type (Persak and Pitzschke 2013). Moreover, AtMYB44 was shown to suppress the gene transcription of type 2C protein phosphatases (*PP2Cs*) involved in ABA signaling such as *ABI1, ABI2,* and *HAI1* (Nguyen et al. 2019a, b) or late embryogenesis-abundant protein *LEA4-5* (Nguyen et al. 2019a, b) through histone H3 acetylation (H3ac) and methylation (H3K4me3) around transcription start site under salinity and osmotic stresses.

## 6.9 WRKY Family

WRKY transcription factor family is one of the largest families that have comprehensive biological functions in plant biotic and abiotic stress responses, nutrient deprivation, hormone-controlled processes, seed and trichome development, senescence, and embryogenesis (Rushton et al. 2010). WRKYs can act as transcriptional activators or repressors in various homo- and heterodimer combinations (Ülker and Somssich 2004; Eulgem and Somssich 2007; Rushton et al. 2010; Agarwal et al. 2011). One of the WRKY members, *WRKY25*, was upregulated under all stress conditions in our analysis. In addition to our study, Castillo et al. (2018) studied high levels of nitric oxide (NO) combined with stress-triggered responses and development, analyzing early changes in the transcriptome for the identification of transcription factors involved in NO sensing. In that study, WRKY25 was found hypersensitive in ABA signaling in NO-triggered responses. Moreover, Zheng et al. (2007) have investigated the function of WRKY25 in plant defense responses against the bacterial pathogen *Pseudomonas syringae*. WRKY25 was found as a negative regulator of salicylic acid (SA)-mediated defense mechanism against *P. syringae.* According to Kilian et al. (2007), *WRKY25* was negatively regulated by heat and salt stresses. In contrast to Kilian et al. (2007), Jiang and Deyholos (2009) have shown that the transcript abundance of *WRKY25* and its close relative *WRKY33* were increased under salt stress. Additionally, the expression level of *WRKY25* was also induced by heat stress (Li et al. 2009, 2011a, b; Zhou et al. 2015).

## 6.10    NAM, ATAF, and CUC Families

One of the largest TF families, the plant-specific NAM, ATAF, and CUC transcription factor (NAC) family, has vital roles in plant growth, development, and abiotic plant responses (Nakashima et al. 2012; Nuruzzaman et al. 2013). Many studies reported that lots of the stress-responsive NAC factors have been used to develop stress-tolerant crops by genetic engineering (Nuruzzaman et al. 2013). There are more than a hundred NAC proteins included in *Arabidopsis* and rice (Olsen et al. 2005). Based on our study, one of the members of the NAC family belonging to the ATAF subfamily, *RD26/NAC72,* was positively regulated under all relevant stress conditions. Similar to our work, *RD26* was markedly upregulated by salt, drought, and abscisic acid (ABA) treatments (Chung et al. 2014; Fujita et al. 2004; Tran et al. 2004; Takasaki et al. 2015). However, Huang et al. (2018) showed that the transcript level of *RD26* was negatively regulated by sodium chloride (NaCl), but slightly increased under NaCl + ABA treatment. In addition, RD26 has been shown as a key regulator of starch degradation and the accumulation of mono- and disaccharides by directly enhancing the expression of *AMY1*, *SFP1,* and *SWEET15* that are involved in carbohydrate metabolism and transport under the control of dark-induced senescence (Kamranfar et al. 2018). Interestingly, heterologous expression of AtRD26 homolog in *Eutrema salsugineum*, NAC1, in *Arabidopsis* inhibited the vegetative growth of *Arabidopsis*, and the overexpression lines were more tolerant to salt and oxidative stresses than the wild type (Liu et al. 2018).

## 6.11    Heat Shock Factor Family

Heat shock transcription factors (HSFs) act as regulators of genes induced by thermal stress, coding heat shock proteins. Most eukaryotes have 1–3 heat shock factors; however, plants have more than 20 heat shock factors, classified as classes A, B, and C (Baniwal et al. 2004). HSFs are essential for plants to respond to adverse abiotic stress conditions by regulating stress-responsive genes (Nover et al. 2001; Klaus-Dieter 2012). In our analysis, we found that one of the HSFs, *HSF4/TBF1/ HSFB1* (*ARABİDOPSİS THALIANA HEAT SHOCK FACTOR4, TL1-BINDING TRANSCRIPTION FACTOR1, ARABİDOPSİS THALIANA HEAT SHOCK FACTOR B1*), is upregulated under adverse stress conditions. Normally, *HSF4* is shown to respond to heat stress (Charng et al. 2007; Tunc-Ozdemir et al. 2013; Weng et al. 2014), but its transcript level also increases under several biotic and abiotic stress conditions (Nover et al. 2001; Klaus-Dieter 2012). Genome-wide expression profiling showed that HSF4 has an essential role in the growth to defense transition (Pajerowska-Mukhtar et al. 2012). Additionally, *HSF4* expression is tightly regulated at both the transcriptional and translational levels. In vitro and in vivo experiments indicate that HSF4/TBF1 binds to TL1 cis-element (translocon 1; *GAAGAAGAA*), which is in the promoter regions of NPR1-dependent ER-resident

genes through the involvement of an unknown TF, regulating the genes associated with pathogen infection and salicylic acid (Wang et al. 2005; Pajerowska-Mukhtar et al. 2012). Additionally, HSFB1 and HSFB2b suppress the response of heat shock under nonheat stress conditions (Ikeda et al. 2011). *HsfB1* and *HsfB2b* are the necessary heat stress-inducible heat shock protein genes to acquire thermotolerance, and they are activated by histone chaperone ASF1 under heat stress conditions (Weng et al. 2014). Moreover, HSF4/TBF1 is associated with the unfolded protein response (UPR) (Nagashima et al. 2014).

## 6.12 GIBBERELLIC ACID INSENSITIVE (GAI), REPRESSOR OF GAI (RGA), and SCARECROW (SCR) Families

GRAS proteins are plant-specific proteins, which are found in higher angiosperms (Cenci and Rouard 2017). Thirty-three GRAS proteins are present in the *Arabidopsis* genome, and they are divided into eight groups according to their amino acid sequence similarities (Lee et al. 2008). Its name is derived after the three initially identified members GIBBERELLIC ACID INSENSITIVE (GAI), REPRESSOR OF GA (RGA), and SCARECROW (SCR) (Pysh et al. 1999). GRAS proteins have key roles in very diverse processes, including plant growth and development, signal transduction, meristem maintenance, and development (Hirsch and Oldroyd 2009; Sun et al. 2012). They are especially very critical for gibberellin and mycorrhizal signaling (Xue et al. 2015). GRAS proteins include several conserved regions at their N-terminus, two leucine-rich areas (LHRI and LHRII) flanking VHIID motifs, PFYRE and SAW (Pysh et al. 1999; Bolle 2004). Based on our study, one of the GRAS proteins *SCL11 (SCARECROW-LIKE11)* was upregulated under all relevant stress conditions. In addition to our study, Ma et al. (2006) investigated that *SCL11* was extensively upregulated under salt stress. However, the biological roles of SCL11 are largely unknown; therefore, it requires further studies.

## 6.13 C2C2-CO-Like Family

The *Arabidopsis* genome consists of 30 members of the C2C2-CO-like transcription factor family containing an atypical domain composition. These proteins have one response regulator receiver domain and two motifs that suggest a role in transcriptional regulation: an acidic domain and a basic motif within the CONSTANS family of transcription factors (Griffiths et al. 2003). Saibo et al. (2008) investigated that the C2C2-CO-like gene family was primarily involved in drought stress responses in *Arabidopsis* (Mun et al. 2017). Two of the members of the C2C2-CO-like transcription factor family were determined in our bioinformatic analyses.

*B-BOX DOMAIN PROTEIN31/MICROPROTEIN1A* (*BBX31/MIP1A*) was upregulated, whereas *B-BOX DOMAIN PROTEIN27* (*BBX27*) was downregulated under relevant stress conditions. In addition to our study, Gangappa and Botto (2014) investigated that BBX31 negatively regulated photomorphogenesis under visible light. It induced photomorphogenesis under UV-B and increased tolerance to high doses of UV-B radiation. BBX31 and HY5 oppositely and independently have control on seedlings to adapt to varying light intensities (Gangappa and Botto 2014). In another research, BBX31 was identified as a key signaling factor in visible and UV-B light signal transduction in *Arabidopsis* (Heng et al. 2019). *BBX31* expression is promoted by UV-B radiation in a fluorescence-dependent manner. HY5 can directly bind to the promoter of *BBX31* and increase its transcript levels (Heng et al. 2019). Gain-of-function and loss-of-function mutants of *BBX31* showed that it plays a negative role in photomorphogenesis under white light; however, it acts as a positive regulator of UV-B signaling. Genetic interaction studies investigated that BBX31 promotes photomorphogenesis apart from HY5. There was no evidence for direct BBX31-HY5 interaction, and they primarily induced different sets of genes in white light. Under the high intensity of UV-B radiation, BBX31 induced the accumulation of UV-protective flavonoids and phenolic compounds, resulting in tolerance to UV-B radiation by regulating genes involved in photoprotection. Under UV-B radiation, overexpression of BBX31 promoted transcript level of *HY5* in a UV RESISTANCE LOCUS8-dependent manner, indicating that BBX31 may regulate *HY5* transcription. Under low intensities of white light, BBX31 also controlled primary root elongation. Multiple primary and secondary metabolites were identified in *35S-BBX31* by GC-MS- and HPLC-based metabolite profiling, which may suggest their involvement in UV-B tolerance in plants (Yadav et al. 2019). *BBX27* was downregulated in our study; however, there is no study about its control under abiotic stress conditions in the literature. Therefore, further studies need to be conducted to understand the functions of members of the C2C2-CO-like family in plants under environmental stress conditions.

## 6.14 Type B *Arabidopsis thaliana* Response Regulator Family

There are 15 members of the aRR-B family in the *Arabidopsis* genome. Type B *Arabidopsis thaliana* response regulators (ARRs) are transcription factors having functions in the final step of signaling systems (Mason et al. 2005). ARR family members function as DNA-binding transcriptional regulators, whose activities are mostly seen as regulated by phosphorylation/dephosphorylation. The major subfamily of type B ARRs was investigated, resulting particularly in high expression in regions where cytokinin plays a key role (Yoshinori et al. 2004). Pavlů et al. (2018) studied that cytokinin is a plant hormone having major roles not only in plant growth and development processes but also in stress responses. Expression patterns of abiotic stress-related genes were overlapped with those of cytokinin metabolism and signaling genes (Pavlů et al. 2018). Based on our analysis, one of the members of

the aRR-B family, *RESPONSE REGULATOR5/ARABIDOPSIS THALIANA RESPONSE REGULATOR2/INDUCED BY CYTOKININ6* (*ARR5/ATRR2/IBC6*), was downregulated under relevant stress conditions; however, this transcription factor has not been characterized yet, and further research is needed to determine the function of ARR5 under abiotic stress conditions.

## 6.15   14-3-3 Family

The 14-3-3 family of proteins are not classified as transcription factors; however, they are phosphoserine-binding proteins that have key functions on targets via direct protein–protein interactions and play essential roles in metabolic pathways (De Lille et al. 2001). The 14-3-3s have important features in generating proton gradients through the plasma membrane and promoting $H^+$-ATPase in the plasma membrane (Jahn et al. 1997). Due to this specific feature of the 14-3-3 proteins, their genes can be regulated by several biotic and abiotic stresses such as low temperature (Jarillo et al. 1994), pathogen attack (Brandt and Neve 1992), salt stress (Xu and Shi 2006), hypoxia (De Vetten and Ferl 1995), and drought (Porcel et al. 2006). During plant growth and development, various members of the 14-3-3 family are involved in multiple stress and signaling pathways, suggesting their roles in crosstalk between abiotic and biotic stresses (Cao et al. 2007). In the *Arabidopsis* genome, 15 members of the 14-3-3 protein family are present (Rosenquist et al. 2001). This family is also called general regulatory factors (GRFs) in *A. thaliana* because of their potential roles in a wide range of cellular processes (Rooney and Ferl 1995). Based on our analysis, the transcript level of one member of the GRF protein family *GRF11* (*GENERAL REGULATORY FACTOR11*) was upregulated under all relevant stress conditions. In addition to our study, *GRF11* is frequently reported to be induced by Fe deficiency (Jian et al. 2013). There is no more study about GRF11 in the literature. Therefore, further studies need to be conducted under abiotic stress conditions to determine the functions of this protein in signal transduction.

## 6.16   Other Regulatory Proteins: Calcium Sensor Family

$Ca^{2+}$ sensors are known as $Ca^{2+}$-binding proteins, and most of the $Ca^{2+}$-binding proteins consist of EF-hand motifs having a conserved helix–loop–helix structure that can bind a single $Ca^{2+}$ ion (Day et al. 2002). The family of $Ca^{2+}$ sensors includes calmodulin (CaM), calcium-dependent protein kinases (CDPKs), and calcineurin B-like proteins (CBL). Most of the $Ca^{2+}$-binding proteins have been studied to involve in the transduction of signals related to biotic and abiotic stress (Wang et al. 2013). Based on our study, three members of EF-hand-containing protein family, namely, CALCINEURIN B-LIKE PROTEIN4/*SALT OVERLY SENSITIVE3* (CBL4/SOS3), *CALCIUM-DEPENDENT PROTEIN KINASE32* (*CDPK32*), and

*NAD(P)H DEHYDROGENASEB2* (NDB2), were differentially expressed under relevant stress conditions. SOS3 protein is mainly known to be associated with salinity responses (Gong et al. 2004). Salt stress responses in plants are being controlled mainly by the proteins involved in the salt overly sensitive (SOS) pathway, which have responses to ion homeostasis and salt tolerance in plants (Ji et al. 2013). *SOS1*, *SOS2*, and *SOS3* loci were first discovered by forward genetic screens through salt-hypersensitive growth. The calcium sensor *SOS3* promotes the kinase *SOS2*, which positively regulates *SOS1* under salt stress conditions (Ma et al. 2014). SOS1 is a $Na^+/H^+$ antiporter that transports $Na^+$ out of cells under salt stress (Shi et al. 2000; Qiu et al. 2002). High-affinity $K^+$ TRANSPORTER1 (HKT1) can limit the root-to-shoot sodium transportation and has been proven to be involved in the salt tolerance with SOS pathway in *A. thaliana* (Uozumi et al. 2000). Distinct physiological roles for HKT1 and SOS3 have been shown to protect plants against salinity (Horie et al. 2006). Salinity tolerance mechanisms have been studied a lot; therefore, the details of SOS3 functions are not detailed here. Recently, proteins that induce or suppress the SOS pathway have been shown (Yang et al. 2019a, b), suggesting that there are still missing steps in the salinity tolerance mechanisms. Another member, *CDPK32*, has been shown as the critical component of $Ca^{2+}$ homeostasis based on the overexpression and mutant studies (Zhou et al. 2014). AtCPK32 has autophosphorylation activity and can phosphorylate ABF4 in vitro, thereby regulating the ABA-responsive gene expression via ABF4 (Shi et al. 2018a). Nitrate triggers a unique $Ca^{2+}$–CPK signaling via CPK32 and its orthologs in *Arabidopsis* (Liu et al. 2017). The third member, NDB2, has been shown to regulate hormones such as auxin (through alternative oxidase *AOX1a*) and play important roles in salt and oxidative stresses (Elhafez et al. 2006). NDB2 and AOX1a cluster together as they are members of an alternative respiratory pathway in mitochondria (Van Aken et al. 2009). Together, these proteins can form a complete respiratory chain, dissipating energy as heat and not contributing to ATP synthesis (Clifton et al. 2005). The relation of *NBD2* with hormones suggests that it can also get involved in plant growth and development (Smith et al. 2011).

## 6.17 Conclusion and Future Prospects

As the climatic changes will lead to extensive environmental stress conditions in the future, sessile plants are expected to be affected the most. This eventually causes a drastic decrease in crop yield and food production. Technological advances in molecular plant breeding, hybrid breeding, plant genetic engineering, genomics, and genome editing have been deployed in the development of new crop species that can tolerate environmental stress conditions. Even though the genetics of abiotic stress tolerance mechanisms have been studied in the last 50 years, we now start to understand the real meaning of those mechanisms and the network of genes regulating them with the help of bioinformatics and systems biology. As transcription factors are located in the heart of abiotic stress signaling networks, our approach here

detailed a core cluster of 20 differentially regulated transcription factors in various abiotic stresses. Important functions of some of these transcription factors have already been demonstrated under different abiotic stresses. However, more extensive research is required to understand their roles in stress tolerance and regulation of downstream gene products. Since transcription factors can target several genes involved in various metabolic pathways, genetic engineering or molecular breeding of plants by using one or multiple of these identified transcription factors may eventually lead to the development of crop species with higher levels of stress tolerance.

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