Transcription factors involved in abiotic stress responses in maize (*Zea mays* L.) and their roles in enhanced productivity in the post genomics era

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Background: Maize (*Zea mays* L.) is a principal cereal crop cultivated worldwide for human food, animal feed, and more recently as a source of biofuel. However, as a direct consequence of water insufficiency and climate change, frequent occurrences of both biotic and abiotic stresses have been reported in different regions around the world, and recently, this has become a major threat in increasing global maize yields. Plants respond to abiotic stresses by utilizing the activity of transcription factors, which are families of genes coding for specific transcription factor proteins whose target genes form a regulon which is involved in the repression/ activation of genes associated with abiotic stress responses. Therefore, it is of uttermost importance to have a systematic study on each family of the transcription factors, the downstream target genes they regulate, and the specific transcription factor genes which are involved in multiple abiotic stress responses in maize and other main crops.

Method: In this review, the main transcription factor families, the specific transcription factor genes and their regulons which are involved in abiotic stress regulation will be momentarily discussed. Great emphasis will be given on maize abiotic stress improvement throughout this review, although other examples from other plants like rice, Arabidopsis, wheat, and barley will be used.

Results: We have described in detail the main transcription factor families in maize which take part in abiotic stress responses together with their regulons. Furthermore, we have also briefly described the utilization of high-efficiency technologies in the study and characterization of TFs involved in the abiotic stress regulatory networks in plants with an emphasis on increasing maize production. Examples of these technologies include next-generation sequencing, microarray analysis, machine learning and RNA-Seq technology.

Conclusion: In conclusion, it is hoped that all the information provided in this review may in time contribute to the use of TF genes in the research, breeding, and development of new abiotic stress tolerant maize cultivars.

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Abstract

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Keywords: Abiotic stress, transcription factors, regulons, maize, response

Introduction

Abiotic stresses for instance drought, salinity, cold, high temperatures and mineral toxicity are the main cause of major crop yield reductions worldwide, reducing expected average yields for the major crops by more than 50% (Prasad et al., 2011; Mahalingam, 2015). Plants are sessile beings which are constantly and continuously exposed to various changes in the environmental conditions. Variations in the environment consisting of both biotic and abiotic stresses have a detrimental effect on the economically important crops such as maize (Ramegowda and Senthil-Kumar, 2015). Evolutionary changes have helped many plants adapt to different adverse conditions. Some species show a marked increase in tolerance to these mentioned stresses compared to others (Phukan et al., 2014). Due to global warming and climatic abnormalities accompanying it, the number of combined biotic and abiotic stresses have significantly increased leading to reduced growth and yields of the major crops worldwide (Mittler., 2006; Pandy et al., 2015; Ramegowda and Senthil-Kumar, 2015). The Continuous manifestation of abiotic stresses such as heat and drought together, has led to a severe reduction in crop yields as opposed to when these stresses take place separately at diverse times during the crop growth stages (Mittler., 2006; Prasad et al., 2011).

Maize (Zea mays ssp. Mays L) is one of the most important cereal crops worldwide (particularly in Africa and South America) utilized as a chief nutrient source for food and animal feed industries. It occupied 156 million hectares, producing 809 million tons in the year 2009 (http://www.fas.usda.gov/psdonline/). This production has increased significantly and in the year 2012, production of 870 million tons per hectares was achieved based on a report by FAOFTAT, with its production enlarging in both the developing countries and the developed countries (Wang et al., 2013). Recently, there has been a major focus on the utilization of C4 grasses as a suitable source of ligno-cellulosic biomass for use in the production of biofuels. Maize has been identified as a potential sustainable feedstock, as well as a model system for research in bioenergy and biofuel technologies (Perlack et al., 2005). Moreover, continuous research in maize genetics can lead to further understanding of other related C4 grasses such as miscanthus (*Miscanthus gigantus*) and switchgrass (*Panicum virgatum*) as we aim to develop and domesticate these plants (Perlack et al., 2005). For the last 100 years, maize has been utilized as a model system in the research and study of various biological events and systems including paramutation, transposition, allelic diversity, and heterosis (Bennetzen and Hake., 2009). However, maize belts around the world which range from the latitude 40^{o} South to the latitude 58^{o} North are exposed to continuous effects of both biotic and abiotic stresses (Gong et al., 2014). Abiotic stresses, such as salinity, drought, nutrient deficiency, and high and low temperatures are the predominant environmental factors that negatively influence maize production. In particular, intense waterlogging, extreme temperatures, and droughts have significantly affected maize yields (Ahuja et al., 2010).

A variety of abiotic stresses in plants including extreme temperatures, heavy metals, osmotic stresses, and high light intensity, lead to an overproduction of reactive oxygen species (ROS). Reactive oxygen species such as hydrogen peroxide (H_2O_2) and superoxide ($\bullet O^-_2$) which are produced due to oxidative stresses inhibit photosynthesis and cause vast cellular destruction

(Allan and Fluhr, 2007). ROS are normally removed rapidly by antioxidative mechanisms, although this removal can be hurt by the stresses themselves leading to an increase of ROS concentration inside the cells, further increasing the damage caused (Allan and Fluhr, 2007). Plants do not respond to multiple stresses by way of a linear pathway, the responses involve complex circuits involving various pathways in tissues, cellular specific compartments and the interactions of signaling molecules and/ or additional cofactors to control a particular response to a stimulus (Dombrowski, 2003). Abiotic stresses are known to alter numerous proteins and transcripts through the regulation of both protein turnover and gene expression (Jiang et al., 2007; Wong et al., 2006).

In this review, we will briefly describe regulons including the TFs of the main families and the interactions of these TFs with the *cis*-acting elements (CREs) which are present in the promoter regions of genes which are responsive to different abiotic stresses. Even though (Gahlaut et al 2016; Joshi et al., 2016) have described TFs regulons recently, this review will focus on TFs which are involved in abiotic stress tolerance with a specific focus on maize. We will also focus on new ways of increasing production of maize by utilizing currently available genomic information, tools and data.

Survey methodology

All published manuscripts cited in this review were obtained from different databases including Pubmed, Web of Science, EBSCO, Google Scholar and many others. We have critically analyzed articles, which aim to provide an in-depth and comprehensive research trend focusing on the TFs involved in abiotic stress tolerance in maize.

Transcription Factors

Abiotic stress-induced genes are divided into two main groups based on the protein products produced. One type includes the genes coding for products which directly allow cells to resist environmental stresses such as osmotic regulatory protein, late embryogenesis abundant (LEA) protein, enzymes synthesizing proline, betamine, malondialdehyde (MDA) and other osmotic regulators and anti-freezing proteins (Loredana et al., 2011). The second type of genes are regulatory proteins which operate in the signal transduction networks, for example, molecular chaperones, functional proteins, and transcription factors (TFs) or kinases (Song et al., 2013; Loredana et al., 2011).

Transcriptional regulation of plant genes is directly controlled by networks of transcription factors together with transcription factor binding sites (TFBS) (Chaves and Oliveira, 2004). Transcription factors are proteins containing a DNA domain which binds to *cis*-acting elements which are present in the upstream region of all gene promoters (Loredana et al., 2011). A large percentage of genes in the plant genome (nearly 10%) essentially encode for transcription factors (Franco-Zorrilla et al., 2014). Additionally, TFs activate or repress the activity of RNA polymerase, leading to gene regulation. TFs can be categorized into various families in regard to their DNA binding domains (Riechmann et al., 2000). Since abiotic stresses are quantitative traits which might require regulation of several genes including the TF genes, and due to the fact that a single transcription factor may regulate several genes which are involved in abiotic stress

tolerance responses, a detailed study of all TFs associated with abiotic stress regulatory mechanisms in maize will be significantly rewarding. For example, Xu et al. (2006) successfully converted flood sensitive rice genotypes into flood-tolerant varieties by introgression of the *sub1* locus which encodes an (ethylene response factor) TF, leading to the induction of about 900 stress-responsive genes.

TF DNA-binding domains are strongly conserved between species, to the extent of using these characteristics to classify the TFs into various families (Fig. 1). These families differ between plant species in that different plant systems have between 26 to 83 TFs families (Jin et al., 2014). In *Arabidopsis*, for instance, approximately 34 families consisting of 1533 TFs have so far been classified (Riechmann et al., 2000). Additionally, in *Arabidopsis* and many other plants, transcriptome data has revealed a number of pathways which respond to abiotic stresses independently, pointing to the possibility that susceptibility or tolerance of both biotic and abiotic stresses are controlled by a sophisticated gene regulatory network at the transcriptome level (Umezawa et al., 2006).

Abscisic acid (ABA) is the principal hormone involved in the coordination of abiotic stress in plants (Fig. 1). This hormone regulates an intricate gene regulatory system which enables plants to handle decreased moisture availability (Cutler et al., 2010). ABA-dependent gene activation pathways have been identified as pathways which determine stress tolerance by the induction of a minimum of two separate regulons: the first one is the myeloblastosis oncogene (MYB)/ myelocytomatosis oncogene (MYC) regulon and the second one, is the ABA-responsive element binding protein/ ABA-binding factor (AREB/ ABF) (Abe et al., 1997; Saibo et al., 2009) (Fig. 1). ABA- independent regulons include; the NAC (CUC, NAM and ATAF) and the zinc-finger homeodomain (ZF-HD) regulon (Nakashima et al., 2009; Saibo et al., 2009) (Fig. 1). The different stress tolerance responsive TFs normally function independently, although there is a possibility that some level of cross-link occurs between these TFs. The above TF families have been studied in detail in a number of important food crops and also in model plant systems including; *Arabidopsis thaliana*, *Oryza sativa*, *Triticum aestivum*, *Sorghum bicolor*, *Vitis vinifera*, *Hordeum vulgare*, *Solanum tuberosum,* and *Brassica napus.* Recent studies have shown the roles abiotic stress-responsive TFs play, and their potential to be used in future for purposes of molecular breeding and improvement of different crop varieties.

Much progress has been achieved in our understanding of transcriptional regulation, signal transduction, and gene expression in plant responses to abiotic stresses (Zhu et al., 2010). In rice for example, overexpression of a NAC TF encoding gene, *SNAC1* resulted in increased yields and increased tolerance to drought in transgenic plants (Hu et al., 2006). Overexpression of a *Glycine soja* NAC TF designated as *GsNAC019* in transgenic Arabidopsis resulted in plants that were tolerant to alkaline stress at both the seedling and mature stages although the transgenic plants had reduced sensitivity to ABA (Cao et al., 2017). Similarly, functional analysis of a *Pyrus betulifolia* NAC TF gene designated *PbeNAC1*, revealed that this gene is involved in the regulation of cold and drought tolerance (Jin et al., 2017). Additionally, a chickpea (*Cicer arietinum*) stress associated TF, *CarNAC4* was found to be linked with reduced MDA content and water stress rates in response to salt and drought stress respectively (Yu et al., 2016).

Ramakrishna et al. (2018) showed that overexpression of a finger millet bZIP TF gene *EcbZIP17*, in tobacco plants resulted in higher germination rate, increased biomass, and increased survival rate in the transgenic plants. Furthermore, the transgenic tobacco plants also

showed increased seed yields compared to the control plants. Similarly, Xu et al. (2016) showed that transgenic Arabidopsis and soybean seedlings overexpressing a soybean bZIP TF designated as *GmbZIP110* had improved salt tolerance, suggesting that *GmbZIP110* functions as a positive regulator involved in salt stress tolerance. Additionally, functional analysis of *GmbZIP110* in transgenic Arabidopsis revealed that this gene can bind to the ACGT motif and regulate many downstream target genes (Cao et al., 2017). Elsewhere, overexpression of an Arabidopsis bZIP TF designated as *ABF3* in transgenic alfalfa (*Medicago sativa*) under the command of a sweet potato oxidative stress-inducible promoter *SWPA2,* resulted in improved growth under drought stress (Wang et al., 2016c). In hot pepper (*Capsicum annuum*), overexpression of a bZIP encoding gene *CaBZ1* in transgenic potato significantly improved dehydration stress tolerance without any detrimental effects on plant growth or yield (Moon et al., 2015).

In maize, overexpression of a rice MYB encoding gene *OsMYB55* in transgenic maize resulted in improved plant growth as well as decreased negative effects of drought and high temperature (Casaretto et al., 2016). Wei et al. (2017) demonstrated that *CiMYB3* and *CiMYB5* cloned from *Cichorium intybus* are both involved in the fructan pathway degradation in response to various abiotic stresses. In banana (*Musa paradisiaca*), overexpression of an MYB TF gene designated as *MpMYBS3* significantly improved tolerance to cold stress in transgenic plants (Dou et al., 2015). Recently, a *Medicago truncatula* MYB TF gene, *MtMYBS1* was able to enhance salt and drought tolerance in transgenic Arabidopsis by improving the primary root growth (Dong et al., 2017). In cotton (*Gossypium arboreum*), overexpression of *GaMYB62L* in transgenic Arabidopsis resulted in enhanced drought tolerance (Butt et al., 2017).

Exogenous expression of the Arabidopsis DREB TF gene, *AtDREB1A* in transgenic *Salvia miltiorrhiza* resulted in plants displaying higher antioxidant activities and photosynthetic rates under drought stress (Wei et al., 2016). Elsewhere, overexpression of *SbDREB2A* from *Salicornia brachita* in transgenic tobacco resulted in improved growth and seed germination under hyperionic and hyperosmotic stresses (Gupta et al., 2014). Zhang et al. (2015) cloned SsDREB protein from *Suaeda salsa* and showed that this protein enhances the photosynthesis rate in transgenic tobacco plants under drought and salt stresses.

In the WYKY TF gene family, *OsWRKY71* from rice was found to act as a positive regulator of cold stress tolerance by regulating several downstream genes such as *WSI76* and *OsTGFR* (Kim et al., 2016). VIGS (Virus-induced gene silencing) of *GhWRKY6* gene from cotton (*Gossypium hirsutum*) led to increased sensitivity to various abiotic stresses in the silenced plants (Ullah et al., 2017). Elsewhere, *SIDRW1* and *SLWRKY39* WRKY TFs were found to confer both abiotic and biotic stress tolerance in tomato (*Solanum lycopersicum*) by activating both abiotic stress and pathogenesis-related downstream genes (Liu et al., 2014; Sun et al., 2015).

TFs and regulons involved in abiotic stress regulation from other TF families have also been identified and described. For instance in *Populus euphratica*, exogenous expression of *PeHLH35* which belongs to the bHLH TF family resulted in significant improvement in water deficit tolerance through changes in several physiological processes such as stomatal density and transcription rate (Dong et al., 2014). In tomato, overexpression of a cycling Dof factor (CDF) TF designated as *CDF3* resulted in increased biomass production and higher yields in transgenic tomato plants under salt stress (Renau-Morata et al., 2017).

Regulons involved in abiotic stress tolerance in maize; TFs and the specific target genes

TFs usually consists of two domains (1) a DNA binding domain (DB) and (2) an activation domain (AD). A TF binds to the *cis*-acting element (TF binding site) located in the promoter region of a stress-induced gene with the support of a DB domain (Yamasaki et al., 2013). This event brings the AD close to the target gene leading to repression or activation of this gene. A regulon consists of a number of genes carrying a similar *cis*-acting element, thus these particular set of genes are induced by the same TF(s), this has been described in detail by (Singh and Laxmi, 2015; Nakashima et al., 2014). In this review, we will briefly discuss several of the widely studied and researched TF families involved in abiotic stress regulation mechanisms, together with their regulons with a special focus given on maize.

MYC/ MYB regulon

The MYC (myelocytomatosis)/ MYB (myeloblastosis) families of TF proteins have diverse functions and are found in both animals and plants (Abe et al., 2003). Both MYB/ MYC TFs participate in the ABA-dependent pathway involved in abiotic stress signaling for the control of stress-responsive genes. The first MYB TF gene in plants was identified as *C1* in *Zea mays*, it codes for a c-MYB like TF which takes part in the biosynthesis of anthocyanin (Paz-Ares et al., 1987). In the MYB family, each TF consists of an MYB domain containing 1 to 3 imperfect repeats and is made up of around 52 amino acid residues that have a helix-turn-helix (HTH) conformation which interposes inside the major grooves of DNA (Yanhui et al., 2006). MYB and MYC TFs are usually both involved in making up the common regulons which are known as the MYB/ MYC regulons (Gahlaut et al., 2016).

In the maize genome, a total of 72 MYB related proteins have been reported (Du et al., 2013). Chen et al. (2017) analyzed the expression data of 46 MYB genes from maize, in response to various abiotic stresses. A total of 22 genes responding to the different stress conditions were found, 16 of which displayed responses to a minimum of two stresses. The above results pointing to a strong indication that these genes could be taking part in signal transduction pathways involved in abiotic stress responses. Of all the genes analyzed, *ZmMYB30* was exceptionally up-regulated under drought, salt, and ABA stresses, and its functions were analyzed further (Table. 1). Exogenous expression of *ZmMYB30* in *Arabidopsis* stimulated tolerance to salt and elevated the expression of eight abiotic stress corresponding genes (*ABF3*, *ATGolS2, AB15, DREB2A, RD20, RD29B, RD29A,* and *MYB2*) enabling transgenic plants to be more tolerant to adverse environmental conditions (Table. 1). Moreover, another six genes (*RD22*, *RbohD*, *P5CS1, RAB18, RbohF,* and *LEA14*) were either unchanged or slightly elevated in the transgenic *Arabidopsis* plants.

Another maize MYB TF, *ZmMYB31* was found to repress the biosynthesis of sinopoylmalate leading to increased sensitivity to UV irradiation and dwarfism in transgenic plants (Fornale et al., 2010). Furthermore, *ZmMYB31* activated a number of stress-responsive genes in maize (*ZmF5H*, *C3H*, *ZmActin* and *ZmCOMT*) in vivo and *A. thaliana 4CL1* and *A. thaliana COMT* genes in transgenic *Arabidopsis*. The roles of maize MYB related genes in response to drought stress were examined by (Du et al., 2013) based on microarray data obtained by (Dash et al., 2012). On the maize 18k GeneChip, 26 probe sets were shown to correspond to 32 MYB-related genes (whereby one gene was represented by five probes). Further analysis of this highly similar

sequence data revealed that the majority of the MYB-related genes were expressed at low levels, although their expression was in response to a specific stress. Du et al., (2013) analyzed gene expression between two maize varieties, a drought sensitive (Ye478) variety, and a drought tolerant (Han21) variety. Gene expression was found to be very similar. For example, amidst all the genes analyzed, four CCA1-like/ R-R genes (*ZmMYBR49*, *ZmMYBR19, ZmMYBR56,* and *ZmMYBR28*), six TBP-like genes (*ZmMYBR55, ZmMYBR45, ZmMYBR47, ZmMYBR31, ZmMYBR26,* and *ZmMYBR07*) and a single TRF-like gene (*ZmMYBR41*) were all elevated in response to drought stress. Expression analysis of *ZmMYBR37* an I-box-like gene, and five CCA1-like/ R-R genes (*ZmMYBR63, ZmMYBR44, ZmMYBR27, ZmMYBR18,* and *ZmMYBR03*), showed that these genes were highly down-regulated in response to drought stress, however, recovery of all these genes was observed after re-watering (Table. 1). Liu et al. (2012) analyzed a maize R1-type TF which is encoded by *ZmMYB-R1* gene and found that this gene was activated by cold, exogenous ABA, drought, heat and high salinity. Functional analysis of *ZmMYB-R1* in different tissues indicated that it first reaches its maximum levels in the leaves and later it is detected in the roots and stems.

In the model plant *Arabidopsis,* MYB and MYC TFs were found to only accumulate in plant tissues following accumulation of ABA (Lata et al., 2007). Seven *Arabidopsis* MYB TF genes namely *AtMYBCDC5, AtMYB77, AtMYB73, AtMYB44, AtMYB6, AtMYB7,* and *AtMYB4* were all found to be strongly expressed in all organs, during exposure to several abiotic stresses (Yanhui et al., 2006). Functional analysis of two MYB/ MYC genes, (*AtMYC2* and *AtMYB2*) in transgenic *Arabidopsis* revealed that the TF proteins encoded by these two genes can bind to the promoter regions of several ABA or jasmonic-acid (JA) inducible genes, for example, *AtADH1* and *RD22,* making the transgenic plants ABA-responsive and more tolerant to both drought and osmotic stress *(*Abe et al., 2003).

Taken together, the above findings suggest that MYB genes could be engineered in crops leading to activation of general pathways involved in abiotic stress responses in plants. For example, overexpression of a rice R2R3-MYB TF *OsMYB55,* significantly improved rice plants tolerance to extreme temperature, which was directly associated with improved amino acid metabolism (El-kereamy et al., 2012). Additionally, these findings will also facilitate our understanding of gene regulation by MYB TFs leading to the development of new abiotic stress tolerant crop varieties. Finally, these findings will be useful in crop improvement by providing a basis for identification and functional characterization of individual MYB TF genes involved in abiotic stress tolerance in food crops and other commercially important plants.

The DREB/ CBF regulons

The dehydration responsive element binding proteins (DREBs) are vital TFs found only in plants and take part in the induction of abiotic stress-associated genes, resulting in abiotic stress tolerant plants (Lata et al., 2007). They constitute a massive subfamily of TFs which belong to the AP2/ERF (A2/ ethylene-responsive element binding protein) or AP2/EREBP. DREBs play a significant part in the ABA-independent pathways which are responsible for the activation of abiotic stress-regulatory genes (Lata et al., 2007). DREB TFs are made up of one AP2/ERF DNA binding region, which binds to the *cis*-acting element DRE composed of TACGACAT (a 9bp core sequence) and which is present in the promoters of Abiotic stress-responsive genes (Gahlaut et al., 2016). The existence of this *cis*-acting element (CRE) has been recorded in several abiotic

stress-responsive genes (e.g *RD29B* and *RD29A*) in *Arabidopsis* (Yamaguchi-Shinozaki and Shinozaki, 1994). C-repeat (CRT) *cis*- acting elements consisting of the A/GCCGAC motif and which are similar to DREBs have been identified in the promoter regions of cold-responsive genes in *Arabidopsis*, whereby the CRT elements bind to the TF CBF (CRT binding factor) in response to cold stress (Saleh et al., 2005). In *Arabidopsis* for example, exogenous overexpression of *AtDREB1/CBF* led to cold, drought, and high salinity tolerance in transgenic plants. These findings clearly suggest that DREBs/CBFs TFs have the potential to target multiple stress-responsive candidate genes in the major plant genomes (jaglo-Ottosen et al., 1998; Kasuga et al., 1999).

In maize, the role of DREB TFs has been investigated using both molecular and genetic analyses. For example, *ZmDREB1A* was activated by cold stress and moderately elevated by high-salinity stress in maize seedlings (Qin et al., 2004) (Table. 1). Over-expression of *ZmDREB1A* in transgenic *Arabidopsis* led to induced over-expression of abiotic stress-activated genes giving rise to plants with enhanced tolerance to extreme drought and freezing stresses (Table. 2). Investigations were done to ascertain whether *ZmDREB1A* could induce other genes in the dehydration and/or cold pathways of wild-type plants. The results revealed that expression levels of *KIN1, KIN2*, and *COR15A* were all highly up-regulated in the 35S:ZmDREB1Aa transgenic line under normal conditions when compared to the wild-type plants. Expression analysis of *RD17, ERD10* and *RD29A* showed that these genes were slightly up-regulated in the 35S:ZmDREB1Aa transgenic line. The above results suggest that since *ZmDREB1A* induces both ABA-independent genes (*COR15A, KIN1,* and *KIN2*) and ABA-dependent genes (*RD17, ERD10,* and *RD29A*), it might affect the expression of dehydration and cold-responsive genes in both the ABA-independent and ABA-dependent pathways. Another maize DREB TF gene *ZmDBP3,* was highly induced by cold stress and moderately induced by salt (Wang and Dong, 2009) (Table. 1). Over-expression of this gene in transgenic *Arabidopsis* led to improved tolerance to both cold and drought stresses (Table. 2).

Natural variation present in the promoter region of another maize DREB TF gene *ZmDREB2,* lead to drought tolerance in maize (Liu et al., 2013) (Table. 1). In transgenic *Arabidopsis,* over-expression of *ZmDREB2* resulted in plants with enhanced tolerance to drought. Similarly, qRT-PCR analysis of maize leaves revealed that expression of *ZmDREB2A* was induced by dehydration, heat and cold stress (Qin et al., 2007). Additionally, over-expression of *ZmDREB2A* in transgenic *Arabidopsis* resulted in dwarf plants which exhibited increased tolerance to drought and heat stresses. Microarray analysis of these transgenic *Arabidopsis* plants identified a number of genes associated with detoxification and heat shock for example *RD29B* and *At5G03720*. Moreover, five genes coding for late embryogenesis abundant (LEA) proteins (*LEA14, At1g52690, At3G53040, At3G15670,* and *At2G36640*) in addition to a metabolism associated gene *AtGoIS3*, were all up-regulated under different stress treatments in the transgenic lines (Table. 1). Elsewhere, functional analysis of *ZmDBF3* showed that this TF gene was activated by drought, high temperature, salt, cold and abscisic acid (ABA), although no significant differences were noted under methyl jasmonate (MeJA) and salicylic acid (SA) (Zhou et al., 2015). Ectopic expression of *ZmDBF3* in yeast (*Saccharomyces cerevisiae*) resulted in a higher survival rate during exposure to KCl, Na_2CO_3, $NaHCO_3$, NaCl, PEG 6000, sorbitol, and freezing temperatures. Moreover, exogenous expression of *ZmDBF3* in transgenic *Arabidopsis* considerably improved tolerance to drought, freezing and salt stresses (Table. 2). These findings, suggest that *ZmDBF3*, a novel maize DREB TF may have similar functions to a regulatory factor

taking part in abiotic stress response pathways. Another maize DREB TF gene *ZmDBP4* was shown to be involved in drought and cold stress responses (Wang et al., 2011). Over-expression of *ZmDBP4* in *Arabidopsis* resulted in transgenic plants with improved cold and drought stress tolerance (Table. 2). Analysis of the promoter region of *ZmDBP4* identified *cis*-acting elements which respond to abiotic stresses, suggesting that *ZmDBP4* encodes a functional factor that plays an important role in the control of multiple abiotic stress responses in maize. Similarly, mRNA accumulation analysis profiles of two DRE-binding proteins (*DBF1* and *DBF2*) in maize seedlings revealed that *DBF1* was induced during embryogenesis and in response to drought, ABA, and NaCl treatments (Kizis and Investigacio, 2002). However, *DBF2* was not induced by any abiotic stress treatment.

In conclusion, it has been known that DREB/CBF target genes, including genes coding for KIN (cold-inducible) proteins, LEA (late embryogenesis abundant) proteins, protease inhibitors, and osmoprotectant biosynthesis proteins are all involved in abiotic stress regulatory pathways (Gahlaut et al., 2016). A minimum of 40 such genes composed of DRE/CRT or other different core motifs present in their promoters have been identified thus far (Maruyama et al.,2004; Seki et al., 2001). So far, 164, 167 and 147 AP2/ERF genes have been identified in rice, maize, and Arabidopsis, respectively (Zhuang et al., 2010).

NAC TFs and regulons

The TF members in the NAC family, (ATAF, CUC, and NAM) represent one of the largest plant-specific TFs (Ooka et al., 2003). In the main crop species, a large number of NAC TFs have been analyzed and sequenced at the genome-wide level, this includes 151 members in rice and 117 in *Arabidopsis* (Nuruzzaman et al., 2010), 204 members in the Chinese cabbage (Liu T.K et al., 2014) and 152 members in maize (Shiriga et al., 2014). NAC TFs are specific to plants since they have not been identified in animals. The TFs belonging to the NAC family share a greatly conserved N-terminus made up of between 150-160 amino acid residues, a DNA-binding domain which carries five sub-domains (A-E) and a varying C-terminal (Hu et al., 2008; Ooka et al., 2003). NAC genes and their constituent *cis*-acting elements (NARCs) make up the NAC regulons, which further provide vital examples of finely characterized collaboration between a single TF and one or more *cis*-acting elements which associate in response to multiple stresses (Christianson et al., 2010). The roles of NAC TFs in plants have been extensively studied in rice and *Arabidopsis*. In *Arabidopsis,* for example, an *ERD1* (early dehydration stress 1) gene was activated by a number of NAC TFs including *ANAC055*, *ANAC019,* and *ANAC072* (Tran et al., 2007). A rice NAC TF designated as *OsNAM,* was found to regulate the activation of five genes (*OsAH*, *OsCESA*, *OsMtN3*, *OsGdpD,* and *OsGDP*) in response to drought (Dixit et al., 2015). Several NAC TFs utilize the NACRS motif in plants, some examples include *SNAC2* and *ENAC1* found in rice (Sun et al., 2012) and *ANAC055*, *ANAC072* and *ANAC019* found in *Arabidopsis* (Tran et al., 2004).

In maize, several NAC TFs that are involved in abiotic stress regulatory pathways have been isolated, cloned and characterized. Recently, expression analysis of *ZmSNAC1* in maize seedlings revealed that this TF gene was strongly induced by high salinity, drought, abscisic acid (ABA) treatment, and low temperature, although it was down-regulated in response to salicylic acid (SA) treatment (Lu et al.,2012). Over-expression of *ZmSNAC1* in transgenic *Arabidopsis* led to increased hypersensitivity to osmotic stress and ABA and enhanced tolerance to dehydration

stress at the germination phase (Table. 2). These results suggest that *ZmSNAC1* acts as a multiple stress responsive TF, positively modulating abiotic stress tolerance in maize. Elsewhere, Shiriga et al. (2014) identified 11 NAC TF genes in maize, which were predicted to be induced by various abiotic stresses. This prediction was confirmed when these genes were differentially expressed in response to drought stress. Four genes, *ZmNAC45, ZmNAC72, ZmNAC18,* and *ZmNAC51* were all found to be up regulated in the drought-tolerant maize genotypes and down-regulated in the drought susceptible genotypes. Recently, seven ZmNTL, NAC TFs genes (*ZmNTL1, ZmNTL2, ZmNTL3, ZmNTL4, ZmNTL5*, *ZmNTL6*, and *ZmNTL7*) were analyzed in maize seedlings and all seven genes were found to be strongly expressed in the stem and roots and down-regulated in the leaves when the plants were exposed to hydrogen peroxide and/ or abscisic acid (ABA) treatments. Exogenous expression of *ZmNTL1, ZmNTL2,* and *ZmNTL5* in transgenic *Arabidopsis* led to increased tolerance to hydrogen peroxide in transgenic plants (Wang et al., 2016a). Overexpression of *ZmNAC55* in transgenic *Arabidopsis* resulted in plants which were hypersensitive to abscisic acid (ABA) at the seedling stage but showed enhanced resistance to drought when compared to the wild-type control seedlings (Mao et al., 2016). Additionally, twelve stress-responsive genes (*RD20, NCED3, ZAT10, ANAC019, LEA14, RD29B, RD29A, DREB2A, RD17, RD26, RAB18,* and *PP2CA*) were all up regulated in response to drought stress in the transgenic lines during qRT-PCR analysis (Table. 1). Expression profiles of *ZmNAC55* in maize revealed that this gene was induced by high salinity, drought, abscisic acid (ABA) and cold stress.

Elsewhere, seven NAC TF genes analyzed in maize seedlings (*Zma001259*, *Zma000584*, *Zma029150*, *ZmSNAC052*, *Zma003086*, *Zma054594,* and *Zma0064*93) were all found to be up regulated in response to salt stress in all tissues (Lu et al., 2015). In response to PEG treatment, three of the above genes *Zma0064*93, *Zma003086* and *Zma000584* were significantly up regulated in the roots only, while *Zma001259*, *Zma029150*, *Zma000584*, and *Zma054594* were all strongly expressed in both the roots and shoots. Five genes, *Zma054594*, *Zma000584*, *Zma001259*, *Zma003086,* and *ZmSNAC052* were activated by cold stress although in varying degrees. In conclusion, due to the strong expression in response to ABA treatments, the sevens genes above might play a vital role in the ABA-dependent signaling network in maize.

Finally, numerous studies have demonstrated the use of stress-responsive NAC TFs in the improvement of abiotic stress tolerance in crops by genetic engineering. In view of the specificity of NAC TF in multiple stress responses, NAC TFs that are induced by multiple abiotic stresses are promising candidates in the engineering of plant varieties with improved multiple stress tolerance (Shao et al., 2015). Moreover, field evaluation of engineered crops containing NAC TF genes and efficient promoters, for reducing detrimental effects triggered by overexpression of some NAC genes must be considered (Rushton et al., 2008).

bZIP TFs: AREB/ABF regulon

The ABA-responsive element (ABRE; PyACGTGG/TC), is a conserved *cis*-acting element subjugated by the basic Leucine Zipper Domain (bZIP) TFs (Loredana et al., 2011). The ABRE was first established on the promoter region of ABA-activated genes by (Giraudat et al., 1994). The bZIP TFs, belong to one of the most immense and diversified TF families in plants (Perez-Rodrigues et al., 2010). bZIP TFs have been categorized into ten subfamilies based on the

presence of extra conserved motifs and the basic region sequence similarities. AREB/ABF TFs are characterized by a strongly conserved bZIP domain which is made up of two structural components [a leucine (Leu) zipper and a basic region], the leucine (Leu) zipper is composed of heptad repeats of Leu and/ or other heavy hydrophobic amino acid residues and controls hetero- and or homodimerization of the bZIP proteins. Whereas the basic region is composed of 16 amino acids with the indistinguishable N-x7-R/K-x9 motif and is responsible for DNA binding and nuclear localization (Jakoby et al., 2002). bZIP TFs which are part of the AREB/ABF regulons give an excellent example of interactions involving stress-responsive genes and TFs carrying the *cis*-acting element (ABRE). In maize, a bZIP TF gene *ABP9* that has the ability to bind to the AREB2 motif located in the *Cat1* promoter region was activated by drought, salt, H_2O_2, and ABA (Zhang et al., 2011). Exogenous expression of *ABP9* in *Arabidopsis* led to significant tolerance to freezing, salt, oxidative stress and drought in transgenic plants. Transgenic *Arabidopsis* plants also showed enhanced sensitivity to exogenously supplied ABA during stomatal closure, seed germination, and root growth. Furthermore, transgenic plants expressing *ABP9* showed reduced levels of oxidative cellular damage, reduced cell death and reduced levels of ROS.

More recently, Wang et al. (2017) demonstrated that *ABP9* enhanced salt and osmotic stress tolerance in transgenic cotton plants. Overexpression of *ABP9* resulted in elevated transcripts of several stress responsive-genes (*GhNCED2*, *GhDBP2*, *GhZFP1*, *GhHB1*, *GhSAP1,* and *GhERF1*) in the transgenic cotton plants in response to salt stress (Table. 2). Additionally, transgenic plants were also observed to have higher germination rates, and improved root systems in a greenhouse setting and reduced stomatal density and stomatal aperture in a growth room. Finally, the relative water content (RWC) and survival rate of the transgenic plants was significantly higher compared to the control plants in response to drought. Wang et al. (2012) demonstrated that expression of *ZmbZIP60* was highly activated by a wide range of stresses including ABA, high salinity, tunicamycin treatment and dehydration (Table. 1). In the wild-type *Arabidopsis*, over-expression of *ZmbZIP60* resulted in plants with enhanced tolerance to dithiothreitol (DDT) stress. Additionally, Li et al. (2018) discovered a major QTL governing heat-induced *ZmbZIP60* expression. They deduced that the upstream region of *ZmbZIP60* plays a vital role in regulating responses to heat stress in maize.

Similarly, Ying et al. (2011) cloned and characterized a maize bZIP TF gene designated as *ZmbZIP72,* which was induced by drought, abscisic acid (ABA) and high salinity stress (Table. 1). Moreover, *ZmbZIP72* was differentially expressed in various organs in maize. Overexpression of *ZmbZIP72* in transgenic *Arabidopsis* led to enhanced tolerance to drought, partial tolerance to salinity and hypersensitivity to osmotic stress and abscisic acid (ABA) treatment. Furthermore, the transgenic *Arabidopsis* plants also showed enhanced expression of several ABA-inducible genes including (*RAB18*, *HIS1-3,* and *RD29B*). Elsewhere, microarray analysis of two specific maize inbred lines, a drought-sensitive Ye478 line, and a drought tolerant Han21 line revealed that 22 ZmbZIP genes might play a critical role in drought tolerance (Wei et al., 2012a). In the same report, *ZmbZIP37* an orthologous gene of two rice genes *OsbZIP72* and *OsbZIP23* which both play vital roles in drought tolerance and ABA response in rice was found to be up-regulated in response to drought stress in maize. Similarly, cloning and characterization of a bZIP TF gene *ZmbZIP17* from the Han21 maize inbred line revealed that this gene was up regulated in response to drought (Jia et al., 2009). Real-time PCR analysis revealed that *ZmbZIP17* was highly up regulated in response to heat, salinity, drought, and ABA

stresses immediately, suggesting that this gene is an early responsive gene that reacts to various abiotic stresses. Elsewhere, expression analysis of two maize bZIP TF genes *ZmbZIP107* and *ZmbZIP54* revealed that these two genes were highly elevated in a lead tolerant maize line when compared to a lead sensitive line in response to different treatments of lead (Zhang et al., 2017) (Table. 1). Recently, Ma et al. (2018) demonstrated that *ZmbZIP4* was induced by drought, cold, high salinity, ABA, and heat in maize seedlings. Overexpression of *ZmbZIP4* led to an improved root system, increase in the number of lateral roots, and longer primary roots. Additionally, genome-wide analysis of *ZmbZIP4* target genes by immunoprecipitation sequencing, unearthed a number of downstream stress response genes that were positively regulated by *ZmbZIP4*. These downstream target genes included *ZmRD21, ZmLEA2, ZmRD20, ZmGEA6, ZmNHX3,* and *ZmRAB18.* Collectively, these results suggest that *ZmbZIP4* is a positive regulator of abiotic stress response and it takes part in root development in maize.

In conclusion, the promoter region of each abiotic stress responsive gene might carry a single or several proximal or distal coupling elements (CE), for example, CE 3 and CE1 which activate expression of abiotic stress-responsive genes. Shen et al. (1996) for example identified CEs in *Hordeum vulgare* which forms an abscisic acid response complex (ABRC). This complex can be a necessary component conferring ABA response or triggering ABA-mediated gene expression. Collectively, the above reports confirmed the participation of bZIP TFs in the ABA signaling pathway. These findings could be useful in the future development of better genotypes with improved tolerance to various abiotic stresses (Todaka et al., 2015). An accurate understanding of the functions of bZIP TFs in crops will require an accurate mapping of the location of bZIP genes in the different plant organs.

WRKY TFs and WRKY regulons

WRKY proteins represent the largest superfamily of TFs, which are only found in plants. WRKY TFs control plant growth and development and spur tolerance against both abiotic and biotic stresses (Tripathi et al., 2014). WRKY TFs are usually identified by a WRKY domain made up of 60 amino acid residues, and contains a highly conserved WRKYGQK sequence which is followed up by a zinc- finger motif. The WRKY domain shows a strong binding affinity for a *cis*-acting element known as W-box (TTGACC/T), which is present in a number of abiotic stress responsive genes (Rushton et al., 2010; Ulker and Somssich, 2004).

Several WRKY TFs involved in abiotic stress tolerance have recently been reported in maize. For example, functional analysis of *ZmWRKY33* under different abiotic stresses, revealed that this gene is activated by cold, dehydration, ABA and salt treatments (Li et al., 2013). Over-expression of *ZmWRKY33* in transgenic *Arabidopsis* led to the activation of two stress-activated genes (*RD29A* and *DREB1B*), which were both up-regulated leading to enhanced salt tolerance in the transgenic plants (Table.1). The above results strongly point to the fact that this maize WRKY TF plays a vital role in abiotic stress regulation in maize. Wang. (2013) demonstrated that exogenous over-expression of *ZmWRKY44* in transgenic *Arabidopsis* resulted in plants that were moderately sensitive to NaCl stress. In maize seedlings, *ZmWRKY44* was induced by high temperature, salt stress, ABA, and hydrogen peroxide treatments. Recently, *ZmWRKY17* was cloned, characterized and its expression analyzed in maize seedlings (Cai et al., 2017) (Table. 1). The results determined that *ZmWRKY17* was induced by ABA, salt and drought stresses. Additionally, constitutive expression of this gene in transgenic *Arabidopsis* led to a striking

reduction in tolerance to salt stress, as confirmed by the physiological assays performed on relative electrical leakage, malondialdehyde (MDA) content, cotyledons greening rate and root growth. Still in the same study, RNA-Seq analysis showed that eight stress-related genes (*DREB1F, KIN1, bHLH92*, *RD29A, RD29B, NAC019, RD22,* and *MYB101*) were significantly increased in the wild-type plants when compared to the transgenic plant lines in response to salt stress. However, expression of *NCED5* was higher in transgenic plants under the same stress. Together, these results give a strong indication that *ZmWRKY17* may function as a negative regulator in response to drought stress in maize. This could be due to elevated levels of ABA ensuing as a direct response to salt stress through the ABA signaling system. Wei et al. (2012b) compared the expression profiles of 31 WRKY genes between two maize lines, a drought-sensitive Ye478 line and a drought tolerant Han21 line. The results showed that the expression of the WRKY genes in the drought-tolerant Han21 line changed less, and the seedlings recovered faster when re-watered, as opposed to the drought-sensitive Ye478 seedlings. In the same study, the expression of *ZmWRKY115* was decreased as a direct result of drought stress. Elsewhere, qRT-PCR expression analysis showed that *ZmWRKY58* was activated by salt, drought and abscisic acid (ABA) treatments (Cai et al., 2014) (Table. 1). Constitutive expression of *ZmWRKY58* in transgenic rice led to delayed germination and constrained post-germination growth and development. However, transgenic seedlings over-expressing *ZmWRKY58* reported increased tolerance to both salt and drought stresses (Table. 2). Wang et al. (2018a) identified a WRKY TF gene named *ZmWRKY40* (Table. 1). A number of stress-related transcriptional regulatory factors were located in the promoter region of this gene. In maize, *ZmWRKY40* was induced by high salinity, drought, abscisic acid (ABA) and high temperature. Overexpression of *ZmWRKY40* in *Arabidopsis* led to enhanced drought tolerance in the transgenic plants. Additionally, overexpression of *ZmWRKY40* induced the expression of three stress-responsive genes *DREB2A*, *STZ* and *RD29A* in transgenic *Arabidopsis*. Recently, the expression of *ZmWRKY106* a member of the WRKYII group was found to be induced by high temperature, drought, and exogenous ABA treatment, but was weakly induced by salinity (Wang et al., 2018c). Overexpression of *ZmWRKY106* in transgenic Arabidopsis led to improved tolerance to heat and drought. Additionally, *ZmWRKY106* positively regulated the expression of several stress response genes including *RD29A*, *CuZnSOD*, *DREB2A,* and *NCED6.* The above results strongly indicate that *ZmWRKY106* may play an important role in the abiotic stress response pathways in maize by regulating stress-related genes.

In the model plant *Arabidopsis,* two WRKY genes WRKY 60 and WRKY 18 were found to regulate ABA signaling positively. However, one WRKY gene WRKY40 was negatively regulating ABA signaling. The three WRKY genes mentioned above, bind to the promoter region of several genes including some TFs genes for example (*DREB1A/CBF3, ABI5,* and *DREB2A*), and several stress-regulated genes for example (*COR47* and *RD29A*) in the process controlling their expression (Shang et al., 2010; Chen et al., 2010).

WRKY TFs have been identified as promising candidates for crop improvement due to the strict regulations involved in the identification and binding of these TFs to the downstream target promoter regions (Phukan et al., 2016). Taken together, all the above insights highlight the multiple stress responses and diverse regulation of WRKY TFs in maize and other crops.

Other TFs and there Regulons

Apart from the five main TF families described above, other TF families take part in diverse roles in plants including, regulating responses to both abiotic and biotic stresses, and various growth and development processes. Recently, extensive research has uncovered stress mitigating roles of a number of TFs whose responses to abiotic stressors was previously unknown in maize. Three of these TF families are briefly described below.

Homeodomain-leucine zipper I (HD-ZIP) I

HD-Zip proteins represent a large TF family which is specific to plants. HD-Zip proteins have been cloned and characterized in several important crops and some model plants such as rice, *Arabidopsis*, tomato and sunflower (Johannesson et al., 2003; Lin et al., 2008; Agalou et al., 2008; Manavella et al., 2006). HD-Zip proteins are characterized by a DNA-binding homeodomain (HD) and a neighboring leucine zipper (Zip) motif whose function is to mediate protein dimerization (Ariel et al., 2007). HD-Zip proteins belonging to the subfamily I are believed to take part in the majority of plant responses to abiotic stresses (Ariel et al., 2007). In *Arabidopsis* for example, analysis of four HD-Zip TFs (*ATHB6*, *ATHB7*, *ATHB5* and *ATHB12*) revealed that these genes were up-regulated or repressed by either ABA or drought stress (soderman et al., 1996; Lee et al., 2001; Soderman et al., 1999; Johannesson et al., 2003). Suggesting that these four genes may play a vital role in the regulation of abiotic stress regulatory networks in plants.

In maize, *Zmhdz10* was the first HD-Zip TF to be isolated and characterized (Zhao et al., 2014). Expression of this gene was activated by abscisic acid (ABA) treatment and salinity stress (Table. 1). Exogenous over-expression of *Zmhdz10* in transgenic rice resulted in improved tolerance to salt and drought stress and enhanced sensitivity to abscisic acid (ABA). Furthermore, the transgenic plants had elevated levels of proline and reduced malondialdehyde (MDA) content when compared to the wild-type plants (Table. 2). Transgenic *Arabidopsis* plants over-expressing *Zmhdz10* exhibited strong tolerance to salt and drought stresses, at the same time, expression patterns of several ABA-responsive genes namely (*ABI1, RD29B, P5CS1,* and *RD22*) were altered. The above results give a strong indication that *Zmhdz10* serves as a transcriptional regulator which can positively regulate both salt and drought stress tolerance in the ABA-dependent pathway in plants. Recently, Qing and Wei. (2018) isolated and characterized a maize HD-ZIP TF designated as *Zmhdz12*. Tissue expression analysis revealed that this TF was strongly expressed in the leaves compared to other tissues. In transgenic *Arabidopsis*, *Zmhdz12* was activated by drought as observed when the transgenic lines which were drought resistant were compared to the wild-type lines. Similarly, expression status of 17 *Zmhdz* I genes from maize (*Zmhdz1* to *Zmhdz17*) revealed that all these genes were either repressed or up-regulated due to drought stress (Zhao et al., 2011). Additionally, the majority of the genes above belonging to the same subgroup in the phylogenetic tree, showed similar patterns of expressions.

In conclusion, it is worth noting that HD-Zip proteins play crucial roles in cuticle formation, thus they might be involved in abiotic stress tolerance and protection against plant pathogens (Chew

et al., 2013). In addition, the roles described above make HD-Zip TFs ideal candidates for genetic engineering of maize and other major crops. More in-depth studies are needed in order to ascertain the function of individual HD-Zip family members in response to various abiotic stresses.

Heat Shock Proteins (HSPs)

All organisms are composed of an evolutionarily conserved, fast cellular defense system known as heat shock (HS) response, which regulates various reactions associated with heat stress and a variety of chemical stressors (Lin et al., 2011). HSPs were first discovered in the salivary glands of *Drosophila* in response to heat shock (Ashburner and Bonner, 1979). HSFs family members function by binding to the promoter of chaperones referred to as heat shock proteins. HSF TFs have a 3 N-terminal section and a C-terminal section in addition to leucine amino acid (Schuetz et al., 1991). HSPs are categorized into six main families, (Hsp90, Hsp40, Hsp90, Hsp60, Hsp70, and Hsp110) based on their molecular sizes (Wang et al., 2004). HSPs in plants were first characterized in tomato (Scharf et al., 1990), and since then more HSFs have been reported in other plants such as *Arabidopsis*, rice, sunflower and wheat (Hubel and Schoffl, 1994; Yamanouchi et al., 2002; Almoguera et al., 2002; Shim et al., 2009). A survey recently reported that there are at least 24 HSFs in *Brachypodium*, 21 in *Arabidopsis*, 30 in maize, 25 in rice, 52 in soybeans and 27 in tomatoes (Scharf et al., 2012). In the model plant *Arabidopsis*, a HsfA2 mutant displayed tolerance to osmotic stress, salt, and heat stresses, suggesting that this gene is involved in several abiotic stress response networks and pathways (Ogawa et al., 2007).

Few HSPs gene have been isolated and characterized in maize. Jinhui et al. (2015) isolated and characterized a Hsp70 gene named *ZmERD2* (Early Responsive to Dehydration 2) from maize (Table. 1). Expression patterns of *ZmERD2* revealed that this gene was induced by cold, high salinity, dehydration, heat stress, and PEG but was not induced by abscisic acid (ABA). Further expression analysis revealed that *ZmERD2* was instantly activated at 42^{o}C and its peak was reached after 1 hour of exposure to heat stress. This results lead to the prediction that this gene could be a stress-responsive gene in maize. Elsewhere, expression patterns of 22 Hsf genes from maize showed that these genes were differentially expressed when subjected to heat stress (Lin et al., 2011). Further analyses from this study revealed that *ZmHsfA2* subclass in maize has close relations with heat shock response. This is after three HsfA2 genes (*ZmHsf-17*, *ZmHsf-01,* and *ZmHsf-04*) were strongly expressed in response to heat stress. Additionally, six more genes were highly up-regulated in response to heat stress (*ZmHsf-03*, *ZmHsf-01*, *ZmHsf-23*, *ZmHsf-24*, *ZmHsf-04, and ZmHsf-25*). These results pointing to the specific roles these genes play in maize in response to heat stress. Li et al. (2015) recently cloned a maize HSF designated as *ZmHsf06* from maize and transformed it in *Arabidopsis thaliana*. Expression analysis of the transgenic plants over-expressing *ZmHsf06* revealed that this gene was induced by drought and heat stress (Table. 2). The above results were confirmed by biochemical and physiological evidence which showed that the transgenic plants displayed longer axial root length, higher seed germination rate, elevated levels of chlorophyll in leaves as well as reduced osmotic potential (OP) and malondialdehyde (MDA) content when compared to the wild-type plants. Based on the above

results, it's evident that *ZmHsf06* could have future potential use in molecular breeding in maize as well as other crops for improved drought and heat stress tolerance.

Collectively, it is important to mention that HSPs have been shown to have a close association with reactive oxygen species (ROS), meaning that plants have gained a stronger level of ROS regulation throughout the course of evolution (Banti et al., 2010). Therefore, understanding the roles played by HSPs in plant responses to abiotic stresses will be useful in the engineering of abiotic stress tolerant crop varieties. HSP have been studied and characterized in a number of important crop varieties as mentioned above, although their functional plasticity and genome sequence data is still limited (Echevarria-Zomeno et al., 2016).

NF-Y Transcription Factors

Nuclear factor Y also referred to as CBF (CCAAT binding factor) or heme activator protein (HAP), is a complex made up of three subunits NF-YB (CBF-A or HAP3), NF-YA (CBF-B or HAP2) and NF-YC (CBF-C or HAP5) (Nardini et al., 2013; Wang et al., 2018b). The NF-Y TF family has been comprehensively studied in animal systems, and it was found that each subunit is encoded by a single gene in yeast and mammals (Mantovani., 1999). NF-Y transcription factors interact with other factors in the regulatory network to induce or inhibit the expression of downstream target genes (Benatti et al., 2008). Unlike mammals and yeast, plants have many NF-Y subunit genes (Wang et al., 2018b). For example, in *Arabidopsis* 13 genes encoding NF-YB, 10 genes encoding NF-YA and 13 genes encoding NF-YC have been reported (Siefers et al., 2009). Individual NF-Y subunits have been shown to play vital roles in plant abiotic stress tolerance (Sato et al., 2014; Ma et al., 2015).

Even though maize has numerous NF-Y subunits, very few studies have been done to investigate the roles these subunits play in response to abiotic stress (Wang et al., 2018b). Nelson et. (2007) demonstrated that transgenic maize plants with elevated levels of *ZmNF-YB2* showed increased tolerance to drought stress based on responses from various stress-related parameters which included stomatal conductance, chlorophyll content, reduced wilting and leaf temperature (Table. 2). Recently, overexpression of an NF-YB transcription factor complex member designated as *ZmNF-YB16* resulted in improved drought and dehydration resistance in transgenic inbred maize line B104 during reproductive and vegetative stages (Wang et al., 2018b) (Table 1). Analysis of gene expression in the photosynthesis system between the WT and transgenic plants revealed that several genes were up-regulated in the transgenic plants when compared to the WT plants. Examples of genes up-regulated included GRMZM2G117572 (encoding the photosystem II PsbZ protein), GRMZM2G414660 (encoding the photosystem II cytochrome b599 subunit) and GRMZM5G831399 (encoding the photosystem II PsbH protein) among others.

Analysis of the co-expression between miR169 miRNA family and ZmNF-YA TFs in transgenic *Nicotiana bethamiana* revealed that mutations in deletion sites terminate the regulation of zma-miR169 (Luan et al., 2014). The levels of expression of *zma-miR169l, zma-miR169i,* and *zma-miR169a* were all inversely correlated with *ZmNF-YA11, ZmNF-YA6,* and *ZmNF-YA7* over the short term. However, over the long term, the expression levels of all the NF-YA genes and miR169s decreased, revealing that *ZmNF-YA11, ZmNF-YA6,* and *ZmNF-YA7*

could not have been regulated by zma-miR169 in response to PEG stress after 15 days. Majority of the zma-miR169s were up-regulated by external ABA and down-regulated by drought stress but showed an early increase in expression and later a decline in response to salinity stress. Recently, Su et al. (2018) identified an NF-Y TF designated as *ZmNF-YA3*. Genome-wide analysis revealed that *ZmNF-YA3* was linked to more than 6000 sites in the maize genome, 2259 of which are linked with genic sequences. Moreover, it was shown that *ZmNF-YA3* could significantly improve high temperature and drought tolerance in maize by binding to the promoter region of three downstream genes (*ZmMYC4, ZmbHLH92,* and *ZmFAMA*).

In conclusion, all of the insights obtained above suggest that NF-Y TFs play an important role in abiotic stress tolerance in maize by regulating several vital downstream genes involved in important aspects of abiotic stress responses, and plant growth and development, for example, photosynthesis and ER stress response. Therefore, NF-Y TF genes could be engineered in maize and other crops in order to improve their abiotic stress tolerance, leading to improved production.

Engineering the activity of TFs

The recent discovery of TFs as potential tools in the manipulation and engineering of quantitative traits such as drought and salinity has ignited the development of novel technologies based on TFs and benefiting not only gene discovery but also crop improvement. Engineering of TF activity has been a major target in these efforts, a direction that offers future promises in modulating metabolic pathways. For example, over-expression of DREB2 resulted in no stress tolerance improvement due to the fact that proteins are composed of domains which limit the induction of their target genes downstream (Liu et al., 1998). Sakuma et al. (2006) obtained drought-tolerant plants by removing this repressor function through the engineering of point mutations. An undesirable effect of overexpressing stress-related TFs is that sometimes it negatively affects the growth and development of a plant leading to stunted growth or toxicity (Hussain and Amjad, 2011). Li et al. (2018) analyzed the expression of *ZmDREB4.1* and found that overexpression of this gene in transgenic tobacco led to repressed stem elongation and petiole, hypocotyl and leaf extension. In maize, Overexpression of this gene suppressed growth and regeneration of the calli. However, *ZmDREB4.1* was not induced by any abiotic or biotic stress treatments. Moreover, over-expression of *ZmDREB2A* under a stress-activated promoter in the transgenic plants led to significant improvement in drought tolerance (Qin et al., 2007).

Transcriptional down regulators which repress gene expression in response to various abiotic stresses are also important tools in manipulating drought tolerance. For example, over-expression of a yeast transcription repressor *CaZPF1* in *Arabidopsis* led to drought tolerance in transgenic plants (Kim et al., 2004). In the model plant *Arabidopsis*, systematic analysis of TF families resulted in the discovery of target genes which have the potential to enhance abiotic stress tolerance in major crops (Reichmann et al., 2000). A good example is the discovery of *AtNF-YB1* gene which belongs to the Nuclear factor Y TF family (Nelson et al., 2007). The orthologue of (*AtNF-YB1*) gene in maize, (*ZmNF-YB2*) when over-expressed in transgenic maize, resulted in drought-tolerant crops (Table. 2). These findings emphasize the significance of TFs, especially when used in the engineering of plants.

The abiotic stress response networks in plants are very complex due to the large number of gene families involved and the complicated associations between the *cis*-acting elements and the TFs.

In addition, a single TF may regulate a large number of target genes with similar *cis*-elements whereas TFs from different families may regulate a single target gene with different types of *cis*-acting elements (Hussain and Amjad, 2011). Therefore, abiotic stress regulating TFs not only function independently but also co-regulate abiotic stress responses between each other (Wang et al., 2016b). As mentioned throughout this review, genetic engineering of TF genes will be much more significant than manipulating a single functional gene. Thereafter, validation of the identified genes should be performed in model crops as well as the main crops by utilizing a stress-inducible promoter in order to reduce the detrimental effects brought about as a result of over-expression of certain TFs (Lan et al., 2017). Moving forward, all of these advances will help elucidate the detailed regulatory channels taking part in multiple abiotic stress responses in plants, leading to the acquisition of target TF genes for enhanced breeding of abiotic stress-tolerant plants with improved desirable qualities and yields.

Current and post genomics approaches

Abiotic stresses represent a combination of various individual traits consisting of a quantitative pattern of inheritance. Thus, to efficiently understand the plants response to the different abiotic stresses at the molecular level, a deeper understanding of the systems involved in transcription regulation is required. Trait mapping, functional characterization, genomic selection, rapid RNA and DNA high-throughput SNP genotyping tools, sequencing technologies, and other platforms are currently used to analyze the genetic mechanisms of different abiotic stresses including drought, salinity, and cold in an effort to speed up the breeding process in maize (Nepolean et al., 2018).

Genome editing techniques are the most recent technologies used in gene function analyses and manipulations. RNA interference (RNAi) is a rapid and inexpensive technique used to analyze gene function in targeted gene knockdown analyses (Rabara et al., 2014). However, a disadvantage of this technique is that the inhibition of gene function is not complete and this could lead to unintended off-target effects leading to misinterpretation of results (Gaj et al., 2013). Of the targeted genome editing approaches currently available, clustered regulatory interspaced short palindromic repeats ‘CRISPR’ is the most effective system used in editing plant genomes (Cong et al., 2013). CRISPR artificial transcription factors (CRISPR-ATFs) are gaining popularity as an effective system for regulating in vivo plant gene expression (Lowder et al., 2018). In the same study, two novel systems (CRISPR-Act2.0 and mTALE-Act) were developed that could be used to study gene regulatory networks and the control mechanisms involved in plants.

The other systems are transcription activator-like effectors nucleases (TALENS) (Boch et al., 2009) and Zinc-finger nuclease (ZFNs) (Kim et al., 1996). Another approach with huge potential in the functional genomics in plants is targeting-induced local lesions in genomes (TILLING). For example, a TILLING approach known as ecotilling, which is used to identify variations in natural populations, was successfully used to identify TFs in rice associated with drought tolerance (Yu et al., 2012). These techniques are vital in the selection of better quality genotypes and target genes in the abiotic stress tolerance breeding of maize hybrids.

Another approach currently being explored is the use of machine learning in the study of TFs gene regulatory networks. Predictions of TF binding sites (TFBSs) and their corresponding

transcription factor target genes (TFTGs) using machine learning approaches has made substantial contributions to the study of gene regulatory networks (Cui et al., 2014). Understanding the interplay between TFs, TFBSs and TFTGs is vital in understanding the mechanisms involved in the gene regulatory processes taking place during biotic and abiotic stress responses in plants. Various computational algorithms are available in form of software packages. Additionally, expansive use of these software packages has revealed that even though some techniques were developed for one species, the same techniques can be used to analyze the dataset from other species (Cui et al., 2014). For example, a combination of Context Likelihood of Relatedness algorithm analyzed on *Escherichia coli* (Faith et al., 2007), Double Two-way t-tests algorithms analyzed on *Escherichia coli* and Learning Module Networks algorithm tested on yeast (Joshi et al., 2009) was used to identify the presence of oxidative stress regulatory transcription factors in Arabidopsis (Vermeirssen et al., 2014). Moreover, The Algorithm for the Reconstruction of Gene Regulatory Networks (ARACNE) (Margolin et al., 2006) was established to deduce transcriptional regulations in human immune B cells, but was later used to deduce transcriptional interactions regulating root physiological and developmental processes in Arabidopsis (Chavez et al., 2014).

Gene regulatory networks (GRNs) provide insights into the relationships between TFs and their corresponding target genes (Koryachko et al., 2015). For instance, network component analysis (NCA), a computational method developed for analysis of TF-gene interactions in microbial TF-GRNs, was employed to quantitatively analyze TF-GRNs critical in floral development in Arabidopsis (Misra and Sriram, 2013). The results showed that the NCA model adequately accounted for the total gene expression analysis in a TF-GRN of seven TFs (AG, HY5, SEPALLATA3, AP3/P1, AG, AP2, and AGL15) and 55 genes. Strong interactions were present between different TF- gene pairs, for example, *LFY* and *MYB17, AG* and *CRC, AP2* and *RD20, AGL15* and *RAV2* and finally *HY5* and *HLH1*. In maize, a machine learning algorithm GENIE3 was used together with numerous RNA-Seq expression data to establish a four tissue (root, SAM, seed, and leaf) specific GRNs (Huang et al., 2017). The results showed that even though many TFs were expressed in multiple tissues, a multi-level examination predicted regulatory roles for many TFs. Additionally, 76.6% (30,028/39479) of the genes were found to be expressed in all the maize tissues. Out of the total of 2587 TFs annotated by GRASIUS in maize (Chen et al., 2013), 54.46% were expressed in all the four tissues while 86.63% of the total TFs were expressed in at least one of the four tissues.

Understanding the mechanisms of gene regulatory networks (GRNs) is vital in gaining insights on how TFs control gene expression in response to various abiotic stresses. Wet lab experiments are technically demanding, time-consuming and financially demanding (Penfold and Wild, 2011). Many machine learning approaches have been proposed with an aim of reducing costs and time spent in the prediction of GRNs. Adaptation of available crop databases such as Gramene (Tello-Ruiz et al., 2018) in machine learning approaches, as well as developing and adopting new databases for example the Wheat Information System (WheatIS) will help in the storage of data at the same time making it more accessible to scientists (Hu et al., 2018).

Traditional breeding techniques for selecting desirable traits depend on the observed phenotypic traits which can be misleading sometimes during selection, this has led to low success in such strategies. Genomic selection is an accurate and efficient approach when it comes to the prediction of genotypic performance in crops. In maize, utilization of genomic techniques in the manipulation and analyses of TFs has been reported in few studies. Mittal et al. (2017) utilized

genomic selection techniques on 240 subtropical maize lines during exposure to drought by selecting 29,619 SNPs. The study found that 77 out of 1053 SNPs were linked with 10 drought associated TFs located inside a 150 kb area. For example, MYB (149Kb), WRKY (125Kb), NAC (149Kb), bZIP (92Kb), and AP-ERF (148 Kb) among others. Similarly, transcriptome analysis of two maize inbred lines using RNA-Seq showed that a total of 2558 and 555 genes responded to drought in both the sensitive and the tolerant lines respectively (Zhang et al., 2017a). TFs were found to be enriched in the genotype-specific responsive genes, and the genotypic differentially expressed genes. It was postulated that the differential expression of 22 TF genes and the genotype-specific response of 20 TFs in the tolerant line might play an important role in drought tolerance enhancement in maize. Zhang et al. (2017b) utilized RNA-Seq platform to analyze the expression of TFs in response to Lead stress in a maize 178 Lead-tolerant line. In this study, a total of 464 genes were expressed, among which 262 differentially expressed TFs (DETs) which responded to Pb treatment were identified. More recently, (Zhao et al., 2018) mapped several abiotic stress responsive TFs to QTLs. The results showed that *MYB78* and *hsp70* were mapped to mQTL1-5. On chromosome 6, *pep7* and *mlip15* were both mapped on mQTL6-1. Additionally, two more genes, a *APx1* (cystolic ascorbate peroxidase 1) and *hsp101* were mapped on mQTL6-3. Kusano et al. (1995) demonstrated that *mlip15* was a low-temperature activated gene which encodes a bZIP protein composed of 135 amino acid.

Approaches involving genome-editing techniques create possibilities allowing for gene knockouts, point mutations, epigenetic changes, and the activation or repression of genes (Kamburova et al., 2017). Svitashev et al. (2016) reported the use of biolistic delivery of Cas9-gRNA ribonucleoproteins in maize cells, this approach resulted in plants with both edited and mutated alleles. This marks a major leap in plant transformation opening new opportunities in accelerated breeding in other main crops such as wheat, soybeans, sorghum, and rice. Recently, (Cox et al., 2017) reported the use of single-effector programmable RNA guided RNases Cas13. By using the RNA editing tools, the DNA structure is left intact but the function of the TF genes is manipulated. Utilization of genome editing techniques is still in its infancy and its yet to be fully explored for abiotic stress tolerance in maize.

Future outlook

Recent advances in genomics, molecular biology, metabolomics and proteomics have yielded fresh insights into the plant gene regulatory network, composed mainly of regulatory elements (*trans*-elements and *cis*-elements) , inducible genes (developmental and environmental cues), varying signal factors and complementary biochemical pathways (Tang et al., 2003; Wang et al., 2003; Zhu., 2002). Sequencing of the whole maize genome has provided a basis for the functional characterization and identification of genetic networks and genes for maize improvement (Schnable et al., 2009). Moreover, the recent availability of transcriptome profiling technologies, including genome sequencing and DNA microarrays, has opened new doors for understanding the patterns of transcription in the area of plant growth and development (Sekhon et al., 2011).

Understanding the genetic architecture of the molecular networks involved in maize, by utilizing current “OMICS” technologies is urgently needed in order to unravel the drought, heat and salt tolerance mechanisms in maize. Numerous genetic studies have shown that abiotic stress tolerance traits are usually polygenic making the selection of such traits extremely difficult

(Loredana et al., 2011). With the recent whole-genome sequencing of the B73 maize line, it's now feasible to identify most maize TFs and to systematically estimate their contribution to abiotic stress tolerance. Maize has an increased level of genetic disequilibrium linkage (LD) and genetic diversity making it an ideal plant species since the LD and genetic diversity have been predicted to be within a number of kilobases (kbs) in maize landraces (Tenaillon et al., 2003). This characteristic makes genome-wide association studies (GWAS) at the gene level more accurate when compared to plant species which are self-pollinated, as long as genome-wide and high-density DNA markers are present (Yan et al., 2011; Li et al., 2012). For example, using a Bayesian-based genome-wide association method in which RNA-seq-based systems of transcript buildup were utilized as explanatory variables (eRD-GWAS), genes linked to 13 traits were discovered from a group of 369 inbred maize lines (Lin et al., 2017). Additionally, TFs were found to be considerably enriched among the trait associated genes discovered with eRD-GWAS. Similarly, genome-wide analyses carried out on the maize B73 inbred line to identify all the Hsf genes identified 25 non-redundant Hsf genes designated as *ZmHsfs* (Lin et al., 2011). In soybean, an all-inclusive phylogenetic study revealed 58 dehydration responsive genes from the *GmNAC* TF family (Le et al., 2011). RNA sequencing performed on 14-day old maize seedlings of inbred lines Mo17, B73, PH207, B37 and Oh43 under heat, cold and control treatments, revealed a large number of genes which responded differentially between parental inbred lines (Waters et al., 2017). Moreover, 20 of the 57 annotated TF families in maize were enriched for elevated genes in heat and /or cold stress in at least three of the five inbred genotypes. Finally, TF families with TFs that were enriched for up-regulated genes in response to heat stress included MYB and HSF TF families, while 18 TF families with TFs enriched for up-regulated genes in response to cold stress included APETALA2/ (AP2/EREB).

A new approach currently gaining rapid popularity is the field of phenomics. By utilizing high-throughput phenotyping, various physiological parameters such as biomass, internode length, leaf area, chlorophyll content, plant width and height, and growth rate can be accurately determined in real time and noninvasively (Rabara et al., 2014). Large amounts of quality phenomics data can be generated for many transgenic plants. Currently, field phenotyping systems are being developed with the capacity to determine whether the engineering of TFs in plants can improve abiotic stress tolerance (Rabara et al., 2014). For instance, Awlia et al. (2016) demonstrated that the phenotyping of polygenic traits in one experimental study could provide new insights into the mechanisms of plant responses to different abiotic stresses. Establishment of new phenomics technologies will further strengthen the use of forward genetics in the identification of novel TF genes regulating plant responses to different abiotic stress.

Since TFs tend to regulate multiple pathways as opposed to a majority of the structural genes, they offer a powerful and unique system for use in the control of complex regulatory networks in plants. Over-expression of genes regulating the transcription of several down-stream abiotic/ drought stress regulatory genes is a much better approach in the engineering of drought tolerant/ resistant plants as opposed to the development of specific functional genes (Bartels and Hussain, 2008). Development of transgenic plants with enhanced abiotic stress tolerance by regulating TFs has become an important aspect of abiotic stress tolerance. Members of the WRKY, MYB, AREB, and bZIP, TF families have recently been utilized in the regulation of abiotic stress responses in major crops (Singh et al., 2002). Many of the members belonging to these TF families have been identified and characterized in *Arabidopsis*, whose genome has been analyzed using microarray analysis, leading to the discovery of potential genes (Shinozaki., 2003; Bray.,

2004; Denby and Gehring, 2005). Thus TF families offer important targets for use in gene manipulation and regulation which could be vital in understanding responses involved in abiotic stress tolerance. An increasing trend has seen the engineering of TFs involved in stress-signaling networks using biotechnology tools in order to generate transgenic stress tolerant plants. (Abe et al., 2003; Sakuma et al., 2006).

Conclusion

Our population is projected to rise to 9 billion by the year 2050 (Hussain., 2006), together with the rapid change in climate there is an urgent need to speed up the productivity of major crops. Understanding molecular mechanisms and mining stress-responsive genes that control plant responses to different abiotic stresses is a major prerequisite in the development of stress-resistant and high yielding crop varieties (Khan et al., 2018).

To safe guard the global food production, crops (for example maize) which are well adapted to adverse environmental conditions should be established (Vinocur and Altman, 2005).

Maize is highly affected by abiotic stresses especially drought throughout its growth cycle, with the most damage being seen during the developmental stage and prior to flowering (Claassen and Shaw,1970). TF mediated research in plants has recently shown progressive improvement since most of the TF encoding genes are early stress-responsive genes which control the expression of various downstream target genes (Lan et al., 2017). This has in turn led to a deeper understanding of the involvement and functions of TFs in plant responses to different abiotic stresses (Bartels and Sunkar, 2005). With the fact that up to 10% of the total plant genomes encode TFs, deeper studies on the roles of TFs play in response to multiple abiotic stresses will prove to be very useful in the near future. In order to further understand the functions of TFs in imparting abiotic stress tolerance in plants, it is of vital importance to not only identify TFs but also discover the downstream genes which are targets for the TFs (Rabara et al., 2014). Development of abiotic stress tolerant maize varieties will be of immense importance considering that maize feeds in excess of 350 million people in sub-Saharan Africa alone (M'mboyi et al., 2010). Understanding the molecular mechanisms and systems involved in abiotic stress responses is vital in the development of multiple stress tolerant maize varieties.

Incorporation of abiotic stress response pathways in the vital reproductive and vegetative development stages in crops is an efficient strategy to effectively improve productivity in field conditions (Nelson et al., 2007). TFs can be used to simulate a variety of developmental and biochemical networks which take part in the regulation of abiotic stresses, thus increasing the performance of crops in response to multiple plant abiotic stresses. Joshi et al. (2016) noted that over-expression of several TF genes significantly enhanced abiotic stress tolerance but at the same time caused a number of negative effects including lower yields, late flowering and dwarfing in transgenic plants. This should be considered in future studies in order to maximize the effectiveness of TF engineering in responses to different abiotic stresses.

Moving forward, identification and characterization of multiple stress regulatory genes should be given more focus not only in maize but in other major crops in order to target the most effective genes which can be universally used in developing abiotic stress tolerant crop varieties. Machine learning algorithms can be integrated with transcriptome data and high-throughput phenotyping

data to further increase automation of the gene discovery processes such as genome annotation and gene regulatory networks (GRNs) predictions.

Genetic engineering of multiple stress regulatory TF genes is a strong candidate for the enhancement of stress tolerance in plants when compared to focusing on a single individual gene. Nevertheless, recent advances in maize breeding, genomics and functional analysis of genes combined with high-throughput sequencing technologies have significantly increased the chances of achieving multiple stress tolerance. Since maize is a major crop in many countries, there is need for more collaboration in both applied and theoretical genomics in order to improve the production of maize. The rapid advancements in TFs genome analysis currently being witnessed are mostly on temperate maize varieties. It is hoped that these technologies can be transferred to subtropical and tropical maize varieties which are an essential food security crop in developing countries.

Acknowledgment

The authors would like to sincerely thank the Center for Agricultural Resource Research, Institute of Genetics and Developmental biology (CAS) for availing the facilities.

Conflict of Interest

The authors authoritatively declare that no conflict of interest exists.

Funding

This work was generously supported by The National Key Research and Development Program of China (2016YFD0100102-11) and (2016YFD0100605).

Author Contributions

RNK conceived and wrote the paper. ZZ provided the framework and also revised the final draft. EHB revised the final paper. All the authors read and reviewed the final draft.

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Table 1(on next page)

Abiotic stress- related TF families, together with the specific TFs in Maize.

Abiotic stress- related TF families, together with the specific TFs, their characteristics, the regulons they control and their regulatory functions in the abiotic stress responses in Maize.

Table 1 Abiotic stress- related TF families, together with the specific TFs, their characteristics, the regulons they control and their regulatory functions in the abiotic stress responses in Maize.

Family	TFs in Maize	Cis-element recognition	Stress response	Downstream genes	References
DREB/CBF	*ZmDREB2A*	(DRE) TACCGACAT	Salt, Heat, Drought, Cold	*rd29A*, *rd29B,ZmGOLS2*	Qin et al., 2007
	ZmDBP3	(DRE) TACCGACAT	Cold, salt	U	Wang and Dong., 2009
	ZmDREB1A	(DRE/CRT) G/ACCGAC	Drought, cold	*KIN1*, *KIN2*,*COR15A* etc	Qin et al., 2004
	ZmDBF3	N/A	Salt, drought, freezing	U	Zhou et al., 2015
	ZmDBP4	(DRE/CRT) G/ACCGAC	Cold, drought	U	Wang et al., 2011
	ZmDREB2.7	(DRE) A/GCCGAC	Drought	U	Liu et al., 2013
MYB/ MYC	*ZmMYB30*	(MYBR) TAACNA/G	Salt, drought, ABA	*RD20*, *RD29A*, *RbohD* e.t.c	Chen et al., 2015
	ZmMYB36	N/A	Salt, drought, ABA	U	Chen et al., 2015
	ZmMYB95	N/A	Salt, drought, ABA	U	Chen et al., 2015
	ZmMYB53	N/A	Cold	U	Chen et al., 2015
	ZmMYB31	N/A	Sensitivity to UV radiation	*ZmF5H*, *ZmCOMT, C3H*, and *ZmActin*	Fornale et al., 2010
	ZmMYB-R1	N/A	Cold, high salinity, drought, ABA and heat	U	Liu et al., 2012
bZIP	*ZmbZIP60*	(ABRE) ACGTGGC	Dehydration, high salinity, ABA	U	Wang et al., 2012
			Heat stress	U	Li et al., 2018
	ZmbZIP17	N/A	Drought, ABA, heat, Salt	U	Jia et al., 2009
	ZmbZIP54 and *ZmbZIP107*	(ABRE) ACGTGGC	Lead (Pb)	U	Zhang et al., 2017
	mlip15	(ABRE) ACGTGGC	Low temperature, salt, ABA	U	Kusano et al., 1995
	ZmbZIP72	(ABRE)	ABA, drought,	*Rab18*, *rd29B*,	Ying and Jing .,

		ACGTGGC	high salinity,	*HIS1-3* e.t.c	2012
	ABP9	(ABRE) (C/T) ACGTGGC	ABA, drought, H_2O_2, salt	*KIN1, COR15A, PP2C, AZF2* e.t.c	Zhang et al., 2011
	ZmbZIP4	(ABRE) (C/T) ACGTGGC	Heat, cold, salinity and ABA	*ZmLEA2, ZmRD20, ZMRab18, ZmGEA6* e.t.c	Ma et al., 2018
NAC	*ZmSNAC1*	N/A	Low temperature, ABA, high salinity, drought	U	Lu et al., 2012
	ZmNAC55	N/A	High salinity, cold, drought, ABA	*RD29B*, *LEA14*, *RD17*, *ZAT10* e.t.c	Mao et al., 2016
	Zma006493	N/A	Drought	U	Min et al., 2015
	Zma000584	N/A	Drought, cold	U	Min et al., 2015
	Zma001259	N/A	Drought, salt, cold	U	Min et al., 2015
	ZmSNAC052	N/A	Drought, cold	U	Min et al., 2015
	Zma029150	N/A	Drought, salt	U	Min et al., 2015
WRKY	*ZmWRKY17*	(W-box) TTGACC/T	Drought, salt, ABA	*bHLH92, KIN1, DREB1F* e.t.c	Cai et al., 2017
	ZmWRKY33	(W-box) TTGACC/T	High salinity, dehydration, cold, ABA	*RD29A* and *DREB1B*	Li et al., 2013
	ZmWRKY44	(W-box) TTGACC/T	Salt, high temperature, ABA, H_2O_2	U	Wang., 2014
	ZmWRKY58	(W-box) TTGACC/T	Drought, ABA, Salt	U	Cai et al.,2014
	ZmWRKY106	(W-box) TTGACC/T	Drought, high temperature, ABA, Salt	*CuZnSOD, DREB2A, NCED6* and *RD29A*	Wang et al., 2018c
	ZmWRKY40	(W-box) TTGACC/T	Drought, High salinity, High temperature, ABA	*DREB2B, STZ* and *RD29A*	Wang et al., 2018a
Others					
HD-Zip	*Zmhdz10*	CAATAATTG	Salt, ABA	*ABI1, RD22, P5CS1*e.t.c	Zhao et al., 2018
HSP	*ZmERD2*	N/A	Heat, salinity, cold, PEG, dehydration	U	Jinhui et al., 2015

NF-Y	*ZmNF-YB16*	CCAAT	Dehydration, Drought	*P5CS*, *Atj3*, *AtDJC82*, *HSP70* e.t.c	Wang et al., 2018b
	ZmNF-YB2	CCAAT	Drought	*U*	Nelson et al., 2007
	ZmNF-YA3	CCAAT	Drought, high temperature	*ZmbHLH92, ZmMYC4* and *ZmFAMA*	Su et al., 2018

N/A- The *cis*-acting element is unknown, U- unknown

Figure 1

A diagrammatic representation of gene expression and abiotic stress signal perception in plants via ABA-independent and ABA-dependent pathways.

A diagrammatic representation of gene expression and abiotic stress signal perception in plants via ABA-independent and ABA-dependent pathways (Modified from Gahlaut et al., 2016; Khan et al., 2018).

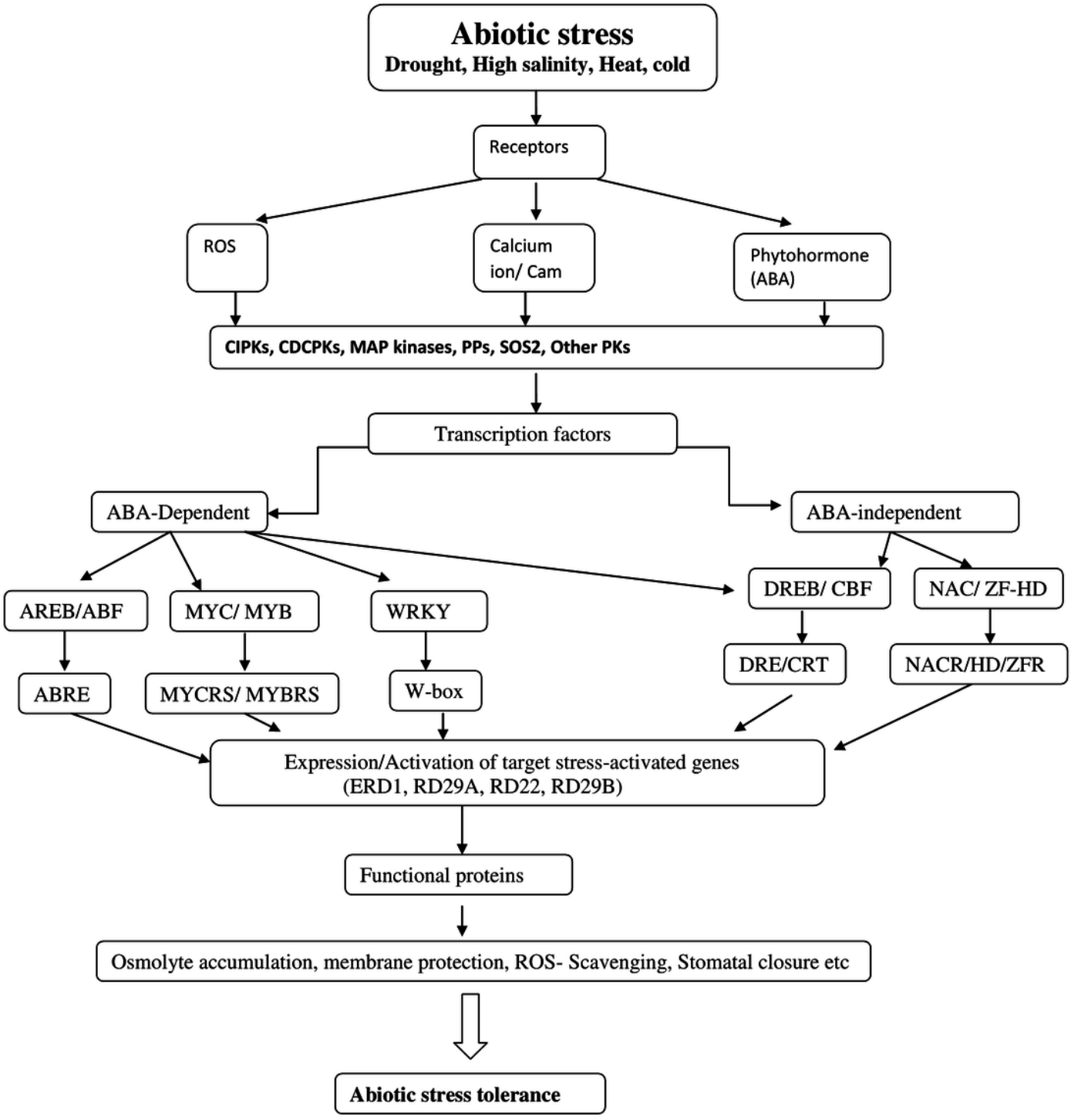
Abiotic stress
Drought, High salinity, Heat, cold
Receptors
ROS
Calcium ion/ Cam
Phytohormone (ABA)
CIPKs, CDCPKs, MAP kinases, PPs, SOS2, Other PKs
Transcription factors
ABA-Dependent
ABA-independent
AREB/ABF
MYC/ MYB
WRKY
DREB/ CBF
NAC/ ZF-HD
ABRE
MYCRS/ MYBRS
W-box
DRE/CRT
NACR/HD/ZFR
Expression/Activation of target stress-activated genes
(ERD1, RD29A, RD22, RD29B)
Functional proteins
Osmolyte accumulation, membrane protection, ROS- Scavenging, Stomatal closure etc
Abiotic stress tolerance

Table 2(on next page)

Abiotic stress responses of over-expressing Maize TFs in transgenic plants.

Represents the abiotic stress responses of over-expressing Maize TFs in transgenic plants.

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Family	Gene	Stress Tolerance	Transgenic Plant	References
MYB/ MYC	*ZmMYB30*	Salt	*Arabidopsis*	Chen et al., 2015
	ZmMYB31	Sensitivity to UV irradiation	*Arabidopsis*	Fornale et al., 2010
DREB/CBF	*ZmDREB2A*	Drought, heat	*Arabidopsis*	Qin et al., 2007
	ZmDBP3	Cold, salt	*Arabidopsis*	Wang and Dong., 2009
	ZmDBF3	Salt, freezing	yeast (*Saccharomyces cerevisiae*)	Zhou et al., 2015
	ZmDREB1A	Drought, Freezing	*Arabidopsis*	Qin et al., 2004
	ZmDREB2.7	Drought	*Arabidopsis*	Liu et al., 2013
	ZmDBP4	Drought, cold	*Arabidopsis*	Wang et al., 2011
bZIP	*ZmbZIP60*	Dithiothreitol (DDT)	*Arabidopsis*	Wang et al., 2012
	ZmbZIP72	Drought, partial salinity	*Arabidopsis*	Ying and Jing ., 2012
	Abp9	Salt, osmotic stress	Cotton (*Gossypium hirsutum*)	Wang et al., 2017
		Drought, ABA, Salt	*Arabidopsis*	Zhang et al., 2011
NAC	*ZmSNAC1*	Sensitivity to ABA, osmotic stress	*Arabidopsis*	Lu et al., 2012
		Tolerance to dehydration		
	ZmNAC55	Sensitivity to ABA	*Arabidopsis*	Mao et al., 2016
		Tolerance to drought		
	ZmNAC111	Drought	Maize (*Zea mays*)	Mao et al., 2015
WRKY	*ZmWRKY17*	Sensitivity to salt	*Arabidopsis*	Cai et al., 2017
		Tolerance to ABA		

	ZmWRKY33	Salt	*Arabidopsis*	Li et al., 2013
	ZmWRKY44	Sensitivity to salt	*Arabidopsis*	Wang., 2014
	ZmWRKY58	Enhanced tolerance to drought, salt	Rice (*Oryza sativa*)	Cai et al., 2014
	ZmWRKY106	Drought, heat stress	*Arabidopsis*	Wang et al., 2018c
	ZmWRKY40	drought	Arabidopsis	Wang et al., 2018a
Others				
HSF	*ZmHsf06*	Drought, thermotolerance	*Arabidopsis*	Li et al., 2015
HD-Zip	*Zmhdz10*	Drought, salt Sensitivity to ABA	Rice (*Oryza sativa*)	Zhao et al., 2018
		Drought, salt	*Arabidopsis*	
	Zmhdz12	Drought	*Arabidopsis*	Qing and Wei., 2018
NF-Y	*ZmNF-YB2*	Drought	Maize (*Zea mays*)	Nelson et al., 2007
	ZmNF-YB16	Drought, Dehydration	Maize (*Zea mays*)	Wang et al., 2018b

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