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

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Introduction

70 Abiotic stresses for instance drought, salinity, cold, high temperatures and mineral toxicity are
71 the main cause of major crop yield reductions worldwide, reducing expected average yields for
72 the major crops by more than 50% (Prasad et al., 2011; Mahalingam, 2015). Plants are sessile
73 beings which are constantly and continuously exposed to various changes in the environmental
74 conditions. Variations in the environment consisting of both biotic and abiotic stresses have a
75 detrimental effect on the economically important crops such as maize (Ramegowda and Senthil-
76 Kumar, 2015). Evolutionary changes have helped many plants adapt to different adverse
77 conditions. Some species show a marked increase in tolerance to these mentioned stresses
78 compared to others (Phukan et al., 2014). Due to global warming and climatic abnormalities
79 accompanying it, the number of combined biotic and abiotic stresses have significantly increased
80 leading to reduced growth and yields of the major crops worldwide (Mittler., 2006; Pandy et al.,
81 2015; Ramegowda and Senthil-Kumar, 2015). The Continuous manifestation of abiotic stresses
82 such as heat and drought together, has led to a severe reduction in crop yields as opposed to
83 when these stresses take place separately at diverse times during the crop growth stages (Mittler.,
84 2006; Prasad et al., 2011).

85 Maize (Zea mays ssp. Mays L) is one of the most important cereal crops worldwide (particularly
86 in Africa and South America) utilized as a chief nutrient source for food and animal feed
87 industries. It occupied 156 million hectares, producing 809 million tons in the year 2009
88 (http://www.fas.usda.gov/psdonline/). This production has increased significantly and in the year
89 2012, production of 870 million tons per hectares was achieved based on a report by FAOFTAT,
90 with its production enlarging in both the developing countries and the developed countries
91 (Wang et al., 2013). Recently, there has been a major focus on the utilization of C4 grasses as a
92 suitable source of ligno-cellulosic biomass for use in the production of biofuels. Maize has been
93 identified as a potential sustainable feedstock, as well as a model system for research in
94 bioenergy and biofuel technologies (Perlack et al., 2005). Moreover, continuous research in
95 maize genetics can lead to further understanding of other related C4 grasses such as miscanthus
96 (*Miscanthus gigantus*) and switchgrass (*Panicum virgatum*) as we aim to develop and
97 domesticate these plants (Perlack et al., 2005). For the last 100 years, maize has been utilized as
98 a model system in the research and study of various biological events and systems including
99 paramutation, transposition, allelic diversity, and heterosis (Bennetzen and Hake., 2009).
100 However, maize belts around the world which range from the latitude 40° South to the latitude
101 58° North are exposed to continuous effects of both biotic and abiotic stresses (Gong et al.,
102 2014). Abiotic stresses, such as salinity, drought, nutrient deficiency, and high and low
103 temperatures are the predominant environmental factors that negatively influence maize
104 production. In particular, intense waterlogging, extreme temperatures, and droughts have
105 significantly affected maize yields (Ahuja et al., 2010).

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

110   (Allan and Fluhr, 2007). ROS are normally removed rapidly by antioxidative mechanisms,
111   although this removal can be hurt by the stresses themselves leading to an increase of ROS
112   concentration inside the cells, further increasing the damage caused (Allan and Fluhr, 2007).
113   Plants do not respond to multiple stresses by way of a linear pathway, the responses involve
114   complex circuits involving various pathways in tissues, cellular specific compartments and the
115   interactions of signaling molecules and/ or additional cofactors to control a particular response to
116   a stimulus (Dombrowski, 2003). Abiotic stresses are known to alter numerous proteins and
117   transcripts through the regulation of both protein turnover and gene expression (Jiang et al.,
118   2007; Wong et al., 2006).

119   In this review, we will briefly describe regulons including the TFs of the main families and the
120   interactions of these TFs with the *cis*-acting elements (CREs) which are present in the promoter
121   regions of genes which are responsive to different abiotic stresses. Even though (Gahlaut et al
122   2016; Joshi et al., 2016) have described TFs regulons recently, this review will focus on TFs
123   which are involved in abiotic stress tolerance with a specific focus on maize. We will also focus
124   on new ways of increasing production of maize by utilizing currently available genomic
125   information, tools and data.

126

127   **Survey methodology**

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

132

133   **Transcription Factors**

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

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

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

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

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

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

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

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

207 In maize, overexpression of a rice MYB encoding gene *OsMYB55* in transgenic maize resulted in
208 improved plant growth as well as decreased negative effects of drought and high temperature
209 (Casaretto et al., 2016). Wei et al. (2017) demonstrated that *CiMYB3* and *CiMYB5* cloned from
210 *Cichorium intybus* are both involved in the fructan pathway degradation in response to various
211 abiotic stresses. In banana (*Musa paradisiaca*), overexpression of an MYB TF gene designated
212 as *MpMYBS3* significantly improved tolerance to cold stress in transgenic plants (Dou et al.,
213 2015). Recently, a *Medicago truncatula* MYB TF gene, *MtMYBS1* was able to enhance salt and
214 drought tolerance in transgenic Arabidopsis by improving the primary root growth (Dong et al.,
215 2017). In cotton (*Gossypium arboreum*), overexpression of *GaMYB62L* in transgenic
216 Arabidopsis resulted in enhanced drought tolerance (Butt et al., 2017).

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

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

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

238

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

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

249

250   **MYC/ MYB regulon**

251   The MYC (myelocytomatosis)/ MYB (myeloblastosis) families of TF proteins have diverse
252   functions and are found in both animals and plants (Abe et al., 2003). Both MYB/ MYC TFs
253   participate in the ABA-dependent pathway involved in abiotic stress signaling for the control of
254   stress-responsive genes. The first MYB TF gene in plants was identified as *C1* in *Zea mays*, it
255   codes for a c-MYB like TF which takes part in the biosynthesis of anthocyanin (Paz-Ares et al.,
256   1987). In the MYB family, each TF consists of an MYB domain containing 1 to 3 imperfect
257   repeats and is made up of around 52 amino acid residues that have a helix-turn-helix (HTH)
258   conformation which interposes inside the major grooves of DNA (Yanhui et al., 2006). MYB
259   and MYC TFs are usually both involved in making up the common regulons which are known as
260   the MYB/ MYC regulons (Gahlaut et al., 2016).

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

274   Another maize MYB TF, *ZmMYB31* was found to repress the biosynthesis of sinopoylmalate
275   leading to increased sensitivity to UV irradiation and dwarfism in transgenic plants (Fornale et
276   al., 2010). Furthermore, *ZmMYB31* activated a number of stress-responsive genes in maize
277   (*ZmF5H*, *C3H*, *ZmActin* and *ZmCOMT*) in vivo and *A. thaliana 4CL1* and *A. thaliana COMT*
278   genes in transgenic *Arabidopsis*. The roles of maize MYB related genes in response to drought
279   stress were examined by (Du et al., 2013) based on microarray data obtained by (Dash et al.,
280   2012). On the maize 18k GeneChip, 26 probe sets were shown to correspond to 32 MYB-related
281   genes (whereby one gene was represented by five probes). Further analysis of this highly similar

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

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

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

315

316 **The DREB/ CBF regulons**

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

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

335   In maize, the role of DREB TFs has been investigated using both molecular and genetic
336   analyses. For example, *ZmDREB1A* was activated by cold stress and moderately elevated by
337   high-salinity stress in maize seedlings (Qin et al., 2004) (Table. 1). Over-expression of
338   *ZmDREB1A* in transgenic *Arabidopsis* led to induced over-expression of abiotic stress-activated
339   genes giving rise to plants with enhanced tolerance to extreme drought and freezing stresses
340   (Table. 2). Investigations were done to ascertain whether *ZmDREB1A* could induce other genes
341   in the dehydration and/or cold pathways of wild-type plants. The results revealed that expression
342   levels of *KIN1, KIN2,* and *COR15A* were all highly up-regulated in the 35S:ZmDREB1Aa
343   transgenic line under normal conditions when compared to the wild-type plants. Expression
344   analysis of *RD17, ERD10* and *RD29A* showed that these genes were slightly up-regulated in the
345   35S:ZmDREB1Aa transgenic line. The above results suggest that since *ZmDREB1A* induces
346   both ABA-independent genes (*COR15A, KIN1,* and *KIN2*) and ABA-dependent genes (*RD17,*
347   *ERD10,* and *RD29A*), it might affect the expression of dehydration and cold-responsive genes in
348   both the ABA-independent and ABA-dependent pathways. Another maize DREB TF gene
349   *ZmDBP3,* was highly induced by cold stress and moderately induced by salt (Wang and Dong,
350   2009) (Table. 1). Over-expression of this gene in transgenic *Arabidopsis* led to improved
351   tolerance to both cold and drought stresses (Table. 2).

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

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

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

388

389   NAC TFs and regulons

390   The TF members in the NAC family, (ATAF, CUC, and NAM) represent one of the largest
391   plant-specific TFs (Ooka et al., 2003). In the main crop species, a large number of NAC TFs
392   have been analyzed and sequenced at the genome-wide level, this includes 151 members in rice
393   and 117 in *Arabidopsis* (Nuruzzaman et al., 2010), 204 members in the Chinese cabbage (Liu
394   T.K et al., 2014) and 152 members in maize (Shiriga et al., 2014). NAC TFs are specific to
395   plants since they have not been identified in animals. The TFs belonging to the NAC family
396   share a greatly conserved N-terminus made up of between 150-160 amino acid residues, a DNA-
397   binding domain which carries five sub-domains (A-E) and a varying C-terminal (Hu et al., 2008;
398   Ooka et al., 2003). NAC genes and their constituent *cis*-acting elements (NARCs) make up the
399   NAC regulons, which further provide vital examples of finely characterized collaboration
400   between a single TF and one or more *cis*-acting elements which associate in response to multiple
401   stresses (Christianson et al., 2010). The roles of NAC TFs in plants have been extensively
402   studied in rice and *Arabidopsis*. In *Arabidopsis,* for example, an *ERD1* (early dehydration stress
403   1) gene was activated by a number of NAC TFs including *ANAC055*, *ANAC019,* and *ANAC072*
404   (Tran et al., 2007). A rice NAC TF designated as *OsNAM,* was found to regulate the activation of
405   five genes (*OsAH*, *OsCESA*, *OsMtN3*, *OsGdpD,* and *OsGDP*) in response to drought (Dixit et al.,
406   2015). Several NAC TFs utilize the NACRS motif in plants, some examples include *SNAC2* and
407   *ENAC1* found in rice (Sun et al., 2012) and *ANAC055*, *ANAC072* and *ANAC019* found in
408   *Arabidopsis* (Tran et al., 2004).

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

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

435 Elsewhere, seven NAC TF genes analyzed in maize seedlings (*Zma001259, Zma000584,*
436 *Zma029150, ZmSNAC052, Zma003086, Zma054594,* and *Zma006493*) were all found to be up
437 regulated in response to salt stress in all tissues (Lu et al., 2015). In response to PEG treatment,
438 three of the above genes *Zma006493, Zma003086* and *Zma000584* were significantly up
439 regulated in the roots only, while *Zma001259, Zma029150, Zma000584,* and *Zma054594* were all
440 strongly expressed in both the roots and shoots. Five genes, *Zma054594, Zma000584,*
441 *Zma001259, Zma003086,* and *ZmSNAC052* were activated by cold stress although in varying
442 degrees. In conclusion, due to the strong expression in response to ABA treatments, the sevens
443 genes above might play a vital role in the ABA-dependent signaling network in maize.

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

451

452 **bZIP TFs: AREB/ABF regulon**

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

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

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

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

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

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

525

WRKY TFs and WRKY regulons

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

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

547   reduction in tolerance to salt stress, as confirmed by the physiological assays performed on
548   relative electrical leakage, malondialdehyde (MDA) content, cotyledons greening rate and root
549   growth. Still in the same study, RNA-Seq analysis showed that eight stress-related genes
550   (*DREB1F, KIN1, bHLH92*, *RD29A, RD29B, NAC019, RD22,* and *MYB101*) were significantly
551   increased in the wild-type plants when compared to the transgenic plant lines in response to salt
552   stress. However, expression of *NCED5* was higher in transgenic plants under the same stress.
553   Together, these results give a strong indication that *ZmWRKY17* may function as a negative
554   regulator in response to drought stress in maize. This could be due to elevated levels of ABA
555   ensuing as a direct response to salt stress through the ABA signaling system. Wei et al. (2012b)
556   compared the expression profiles of 31 WRKY genes between two maize lines, a drought-
557   sensitive Ye478 line and a drought tolerant Han21 line. The results showed that the expression of
558   the WRKY genes in the drought-tolerant Han21 line changed less, and the seedlings recovered
559   faster when re-watered, as opposed to the drought-sensitive Ye478 seedlings. In the same study,
560   the expression of *ZmWRKY115* was decreased as a direct result of drought stress. Elsewhere,
561   qRT-PCR expression analysis showed that *ZmWRKY58* was activated by salt, drought and
562   abscisic acid (ABA) treatments (Cai et al., 2014) (Table. 1). Constitutive expression of
563   *ZmWRKY58* in transgenic rice led to delayed germination and constrained post-germination
564   growth and development. However, transgenic seedlings over-expressing *ZmWRKY58* reported
565   increased tolerance to both salt and drought stresses (Table. 2). Wang et al. (2018a) identified a
566   WRKY TF gene named *ZmWRKY40* (Table. 1). A number of stress-related transcriptional
567   regulatory factors were located in the promoter region of this gene. In maize, *ZmWRKY40* was
568   induced by high salinity, drought, abscisic acid (ABA) and high temperature. Overexpression of
569   *ZmWRKY40* in *Arabidopsis* led to enhanced drought tolerance in the transgenic plants.
570   Additionally, overexpression of *ZmWRKY40* induced the expression of three stress-responsive
571   genes *DREB2A*, *STZ* and *RD29A* in transgenic *Arabidopsis*. Recently, the expression of
572   *ZmWRKY106* a member of the WRKYII group was found to be induced by high temperature,
573   drought, and exogenous ABA treatment, but was weakly induced by salinity (Wang et al.,
574   2018c). Overexpression of *ZmWRKY106* in transgenic Arabidopsis led to improved tolerance to
575   heat and drought. Additionally, *ZmWRKY106* positively regulated the expression of several
576   stress response genes including *RD29A, CuZnSOD, DREB2A,* and *NCED6.* The above results
577   strongly indicate that *ZmWRKY106* may play an important role in the abiotic stress response
578   pathways in maize by regulating stress-related genes.

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

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

589

590   **Other TFs and there Regulons**

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

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598

599   **Homeodomain-leucine zipper I (HD-ZIP) I**

600   HD-Zip proteins represent a large TF family which is specific to plants. HD-Zip proteins have
601   been cloned and characterized in several important crops and some model plants such as rice,
602   *Arabidopsis*, tomato and sunflower (Johannesson et al., 2003; Lin et al., 2008; Agalou et al.,
603   2008; Manavella et al., 2006). HD-Zip proteins are characterized by a DNA-binding
604   homeodomain (HD) and a neighboring leucine zipper (Zip) motif whose function is to mediate
605   protein dimerization (Ariel et al., 2007). HD-Zip proteins belonging to the subfamily I are
606   believed to take part in the majority of plant responses to abiotic stresses (Ariel et al., 2007). In
607   *Arabidopsis* for example, analysis of four HD-Zip TFs (*ATHB6, ATHB7, ATHB5* and *ATHB12*)
608   revealed that these genes were up-regulated or repressed by either ABA or drought stress
609   (soderman et al., 1996; Lee et al., 2001; Soderman et al., 1999; Johannesson et al., 2003).
610   Suggesting that these four genes may play a vital role in the regulation of abiotic stress
611   regulatory networks in plants.

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

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

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

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639

640   **Heat Shock Proteins (HSPs)**

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

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

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

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

685

686

687   **NF-Y Transcription Factors**

688   Nuclear factor Y also referred to as CBF (CCAAT binding factor) or heme activator protein
689   (HAP), is a complex made up of three subunits NF-YB (CBF-A or HAP3), NF-YA (CBF-B or
690   HAP2) and NF-YC (CBF-C or HAP5) (Nardini et al., 2013; Wang et al., 2018b). The NF-Y TF
691   family has been comprehensively studied in animal systems, and it was found that each subunit
692   is encoded by a single gene in yeast and mammals (Mantovani., 1999). NF-Y transcription
693   factors interact with other factors in the regulatory network to induce or inhibit the expression of
694   downstream target genes (Benatti et al., 2008). Unlike mammals and yeast, plants have many
695   NF-Y subunit genes (Wang et al., 2018b). For example, in *Arabidopsis* 13 genes encoding NF-
696   YB, 10 genes encoding NF-YA and 13 genes encoding NF-YC have been reported (Siefers et al.,
697   2009). Individual NF-Y subunits have been shown to play vital roles in plant abiotic stress
698   tolerance (Sato et al., 2014; Ma et al., 2015).

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

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

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

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

731

732   **Engineering the activity of TFs**

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

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

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

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

773

774   Current and post genomics approaches

775   Abiotic stresses represent a combination of various individual traits consisting of a quantitative
776   pattern of inheritance. Thus, to efficiently understand the plants response to the different abiotic
777   stresses at the molecular level, a deeper understanding of the systems involved in transcription
778   regulation is required. Trait mapping, functional characterization, genomic selection, rapid RNA
779   and DNA high-throughput SNP genotyping tools, sequencing technologies, and other platforms
780   are currently used to analyze the genetic mechanisms of different abiotic stresses including
781   drought, salinity, and cold in an effort to speed up the breeding process in maize (Nepolean et al.,
782   2018).

783   Genome editing techniques are the most recent technologies used in gene function analyses and
784   manipulations. RNA interference (RNAi) is a rapid and inexpensive technique used to analyze
785   gene function in targeted gene knockdown analyses (Rabara et al., 2014). However, a
786   disadvantage of this technique is that the inhibition of gene function is not complete and this
787   could lead to unintended off-target effects leading to misinterpretation of results (Gaj et al.,
788   2013). Of the targeted genome editing approaches currently available, clustered regulatory
789   interspaced short palindromic repeats 'CRISPR' is the most effective system used in editing
790   plant genomes (Cong et al., 2013). CRISPR artificial transcription factors (CRISPR-ATFs) are
791   gaining popularity as an effective system for regulating in vivo plant gene expression (Lowder et
792   al., 2018). In the same study, two novel systems (CRISPR-Act2.0 and mTALE-Act) were
793   developed that could be used to study gene regulatory networks and the control mechanisms
794   involved in plants.

795   The other systems are transcription activator-like effectors nucleases (TALENS) (Boch et al.,
796   2009) and Zinc-finger nuclease (ZFNs) (Kim et al., 1996). Another approach with huge potential
797   in the functional genomics in plants is targeting-induced local lesions in genomes (TILLING).
798   For example, a TILLING approach known as ecotilling, which is used to identify variations in
799   natural populations, was successfully used to identify TFs in rice associated with drought
800   tolerance (Yu et al., 2012). These techniques are vital in the selection of better quality genotypes
801   and target genes in the abiotic stress tolerance breeding of maize hybrids.

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

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

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

836   Understanding the mechanisms of gene regulatory networks (GRNs) is vital in gaining insights
837 on how TFs control gene expression in response to various abiotic stresses. Wet lab experiments
838 are technically demanding, time-consuming and financially demanding (Penfold and Wild,
839 2011). Many machine learning approaches have been proposed with an aim of reducing costs
840 and time spent in the prediction of GRNs. Adaptation of available crop databases such as
841 Gramene (Tello-Ruiz et al., 2018) in machine learning approaches, as well as developing and
842 adopting new databases for example the Wheat Information System (WheatIS) will help in the
843 storage of data at the same time making it more accessible to scientists (Hu et al., 2018).

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

849   genomic selection techniques on 240 subtropical maize lines during exposure to drought by
850   selecting 29,619 SNPs. The study found that 77 out of 1053 SNPs were linked with 10 drought
851   associated TFs located inside a 150 kb area. For example, MYB (149Kb), WRKY (125Kb),
852   NAC (149Kb), bZIP (92Kb), and AP-ERF (148 Kb) among others. Similarly, transcriptome
853   analysis of two maize inbred lines using RNA-Seq showed that a total of 2558 and 555 genes
854   responded to drought in both the sensitive and the tolerant lines respectively (Zhang et al.,
855   2017a). TFs were found to be enriched in the genotype-specific responsive genes, and the
856   genotypic differentially expressed genes. It was postulated that the differential expression of 22
857   TF genes and the genotype-specific response of 20 TFs in the tolerant line might play an
858   important role in drought tolerance enhancement in maize. Zhang et al. (2017b) utilized RNA-
859   Seq platform to analyze the expression of TFs in response to Lead stress in a maize 178 Lead-
860   tolerant line. In this study, a total of 464 genes were expressed, among which 262 differentially
861   expressed TFs (DETs) which responded to Pb treatment were identified. More recently, (Zhao et
862   al., 2018) mapped several abiotic stress responsive TFs to QTLs. The results showed that *MYB78*
863   and *hsp70* were mapped to mQTL1-5. On chromosome 6, *pep7* and *mlip15* were both mapped on
864   mQTL6-1. Additionally, two more genes, a *APx1* (cystolic ascorbate peroxidase 1) and *hsp101*
865   were mapped on mQTL6-3. Kusano et al. (1995) demonstrated that *mlip15* was a low-
866   temperature activated gene which encodes a bZIP protein composed of 135 amino acid.

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

877

878   **Future outlook**

879   Recent advances in genomics, molecular biology, metabolomics and proteomics have yielded
880   fresh insights into the plant gene regulatory network, composed mainly of regulatory elements
881   (*trans*-elements and *cis*-elements) , inducible genes (developmental and environmental cues),
882   varying signal factors and complementary biochemical pathways (Tang et al., 2003; Wang et al.,
883   2003; Zhu., 2002). Sequencing of the whole maize genome has provided a basis for the
884   functional characterization and identification of genetic networks and genes for maize
885   improvement (Schnable et al., 2009). Moreover, the recent availability of transcriptome
886   profiling technologies, including genome sequencing and DNA microarrays, has opened new
887   doors for understanding the patterns of transcription in the area of plant growth and development
888   (Sekhon et al., 2011).

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

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

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

927   Since TFs tend to regulate multiple pathways as opposed to a majority of the structural genes,
928   they offer a powerful and unique system for use in the control of complex regulatory networks in
929   plants. Over-expression of genes regulating the transcription of several down-stream abiotic/
930   drought stress regulatory genes is a much better approach in the engineering of drought tolerant/
931   resistant plants as opposed to the development of specific functional genes (Bartels and Hussain,
932   2008).   Development of transgenic plants with enhanced abiotic stress tolerance by regulating
933   TFs has become an important aspect of abiotic stress tolerance. Members of the WRKY, MYB,
934   AREB, and bZIP, TF families have recently been utilized in the regulation of abiotic stress
935   responses in major crops (Singh et al., 2002). Many of the members belonging to these TF
936   families have been identified and characterized in *Arabidopsis*, whose genome has been analyzed
937   using microarray analysis, leading to the discovery of potential genes (Shinozaki., 2003; Bray.,

938 2004; Denby and Gehring, 2005). Thus TF families offer important targets for use in gene
939 manipulation and regulation which could be vital in understanding responses involved in abiotic
940 stress tolerance. An increasing trend has seen the engineering of TFs involved in stress-signaling
941 networks using biotechnology tools in order to generate transgenic stress tolerant plants. (Abe et
942 al., 2003; Sakuma et al., 2006).

943

944 Conclusion

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

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

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

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

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

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

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

992

996

997 **Conflict of Interest**

998 The authors authoritatively declare that no conflict of interest exists.

999

1003

1004 **Author Contributions**

1005 RNK conceived and wrote the paper. ZZ provided the framework and also revised the final draft.
1006 EHB revised the final paper. All the authors read and reviewed the final draft.

1007

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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.

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

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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

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

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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).
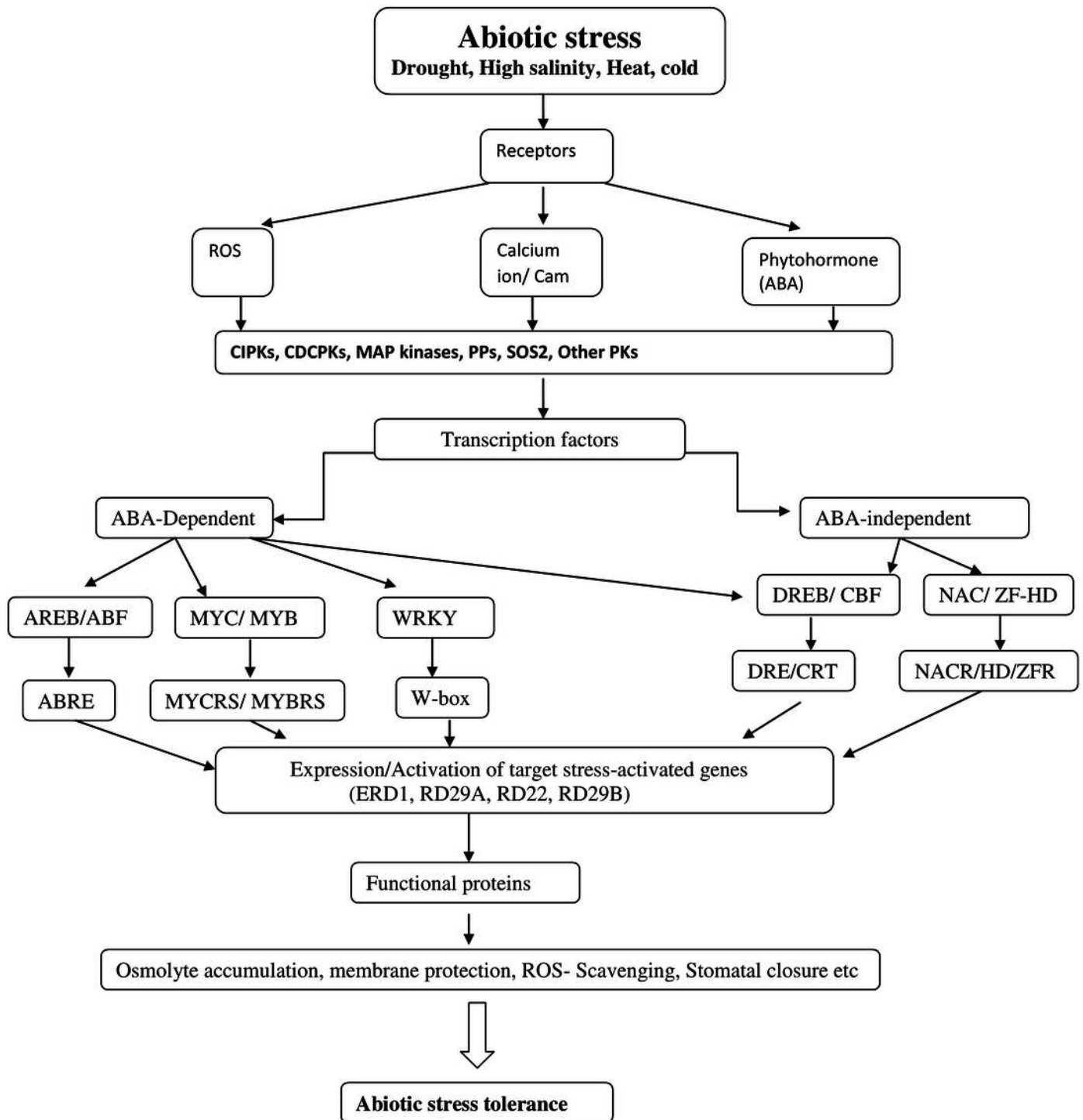
Table 2(on next page)

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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2 **Table 2** Represents the abiotic stress responses of over-expressing Maize TFs in transgenic
3 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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