

Transcription factors involved in drought tolerance and their possible role in developing drought tolerant cultivars with emphasis on wheat (*Triticum aestivum* L.)

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Abstract

Key message TFs involved in drought tolerance in plants may be utilized in future for developing drought tolerant cultivars of wheat and some other crops.

Abstract Plants have developed a fairly complex stress response system to deal with drought and other abiotic stresses. These response systems often make use of transcription factors (TFs); a gene encoding a specific TF together with -its target genes constitute a regulon, and take part in signal transduction to activate/silence genes involved in response to drought. Since, five specific families of TFs (out of >80 known families of TFs) have gained widespread attention on account of their significant role in drought tolerance in plants, TFs and regulons belonging to these five multi-gene families (AP2/EREBP, bZIP, MYB/MYC, NAC and WRKY) have been described and their role in improving drought tolerance discussed in this brief review. These TFs often undergo reversible phosphorylation to perform their function, and are also involved in

complex networks. Therefore, some details about reversible phosphorylation of TFs by different protein kinases/phosphatases and the co-regulatory networks, which involve either only TFs or TFs with miRNAs, have also been discussed. Literature on transgenics involving genes encoding TFs and that on QTLs and markers associated with TF genes involved in drought tolerance has also been reviewed. Throughout the review, there is a major emphasis on wheat as an important crop, although examples from the model cereal rice (sometimes maize also), and the model plant *Arabidopsis* have also been used. This knowledge base may eventually allow the use of TF genes for development of drought tolerant cultivars, particularly in wheat.

Introduction

Drought stress has an adverse impact on growth and productivity of plants including all major crops worldwide. Genetic variation for adaptation for drought tolerance is available in all plant species, and involves genes that express at multiple levels including physiology, morphology and cellular/molecular levels. In particular, the drought stress initiates transcription factor (TF)-mediated expression of a variety of genes in many plant species (Shinozaki et al. 2003; Bartels and Sunkar 2005; Lata et al. 2015; Singh and Laxmi 2015). It has also been shown that in plant genomes ~6–10 % genes encode TFs (Franco-Zorrilla et al. 2014). DNA-binding domains of these TFs are highly conserved among species, so that the characteristics of these domains have been used to classify TFs into families. The number of families of TFs differ in different plant species, so that in different plant systems the number of TF families ranges from 26 to 83 (Jin et al. 2014). For instance, as many as 34 families

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containing 1,533 TFs are known in *Arabidopsis thaliana*; about ~45 % of these TFs belong to families that are specific to plants (Riechmann et al. 2000). Some of the major families of TFs include the following: AP2/EREBP or AP2/ERF, ABI3VP1, ARF, bZIP/HD-ZIP, C2H2, GRAS, MYB/MYC, Zinc fingers, MADS, NAC and WRKY; of these, TFs belonging to five multi-gene families [bZIP (mainly AREB/ABF), DREB (AP2/EREBP), MYB/MYC, NAC and WRKY)] have been shown to be associated with drought tolerance (although there are exceptions; see later). Three of these five families (AP2/EREBP, NAC and WRKY) are also known to be unique to plants, although AP2/EREBP domain was also reported to be present in TFs of protists, cyanobacteria and phages (Wessler 2005). It is known that most TFs belonging to the above five families are key regulators of several developmental processes and are also involved in response to biotic and abiotic stresses including drought (Riechmann and Meyerowitz 1998; Uno et al. 2000; Jakoby et al. 2002; Abe et al. 2003; Fujita et al. 2004; Tran et al. 2004; 2007; Yan-hui et al. 2006; Lata and Prasad, 2011; Zhu et al. 2013; Huang et al. 2015). The above five families of TFs have been systematically studied in a number of plant systems including the following: *Arabidopsis thaliana*, *Arachis hypogea*, *Brassica napus*, *Cicer aritinum*, *Gossypium hirsutum*, *Glycine max*, *Hordeum vulgare*, *Oryza sativa*, *Pen-nisetum glaucum*, *Poncirus trifoliata*, *Solanum tuberosum*, *Sorghum bicolor*, *Triticum aestivum*, *Vitis vinifera* and *Zea mays* (Table 1; Table S1).

Since drought tolerance may require regulation of the expression of a number of genes including TF genes, and because some TFs may each regulate transcription of a number of genes involved in drought tolerance, a study of TFs in all major crops including wheat has been rewarding. A successful example of TFs used in breeding for abiotic stress is the conversion of flood sensitive rice varieties into flood-tolerant genotypes after introgression of *Sub1* locus that encodes a TF (ethylene response factor), which has been shown to induce transcription of ~900 genes (Xu et al. 2006; Septiningsih et al. 2009). There are also reports in several other crops including wheat, where the role of TFs in imparting tolerance against abiotic stresses including drought has been systematically examined (Table 1; Table S1), so that TF genes for drought tolerance may be used in future for developing drought tolerant cultivars in some important crops including wheat (Fig. 1).

A number of wheat genes for TFs (*TabZIP1*, *TabZIP60*, *TaABRE3*, *TaDREB1*, *TaPIMP1*, *TaNAC29* and *TAW-RKY44*) have been shown to exhibit induced expression during exposure to drought stress, suggesting that these genes may be used for improving stress tolerance in wheat (Egawa et al. 2006; Cao et al. 2012; Zhang L et al. 2012; Zhang Z et al. 2012; Zhang L et al. 2015; Huang et al.

Table 1 Five different drought-related TF families that are known in plants, along with specific details of wheat TFs belonging to these five groups and their characteristics

TF family	TFs reported in wheat	Abiotic stress	References
I. AP2/EREBP	TaDREB1, WCBF2, WDREB2, TaERF3	Drought, cold, salt	Shen et al. (2003); Kume et al. (2005); Egawa et al. (2006); Rong et al. (2014)
II. bZIP	WLIP19, TabZIP1, TaABP1, TabZIP60, TaABL1, TaABRE3	Drought, salt, cold, ABA	Kobayashi et al. (2008); Zhang et al. (2009); Cao et al. (2012); Xu et al. (2014); Zhang et al. (2015); Wang J et al. (2016)
III. MYB/MYC	TaMYB2A, TaMYB3R1, TaPIMP1, TaMYB19, TaMYB30-B, TaMYB33	Drought	Mao et al. (2011); Qin et al. (2012); Zhang L et al. (2012); Zhang Z et al. (2012); Cai et al. (2015); Zhang et al. (2014)
IV. NAC	TaSNAC1, TaNAC2, TaNAC4, TaNAC8, TaNAC29, TaNAC47, TaNAC67, TaNAC69, TaNAC69-1	Drought, salt, cold, ABA	Xia et al. (2010a, b); Baloglu et al. (2012); Xue et al. (2011); Mao et al. (2012); Tang et al. (2012); Mao et al. (2014); Huang et al. (2015); Zhang et al. 2016
V. WRKY	TaWRKY1, TaWRKY02, TaWRKY07, TaWRKY10, TaWRKY12, TaWRKY16, TaWRKY19, TaWRKY20, TaWRKY24, TaWRKY32, TaWRKY33, TaWRKY34, TaWRKY44, TaWRKY59, TaWRKY60, TaWRKY61, TaWRKY82	Drought, salt, cold	Niu et al. (2012); Zhu et al. (2013); Wang et al. (2013); Okay et al. (2014); Wang et al. (2015); He et al. (2016)

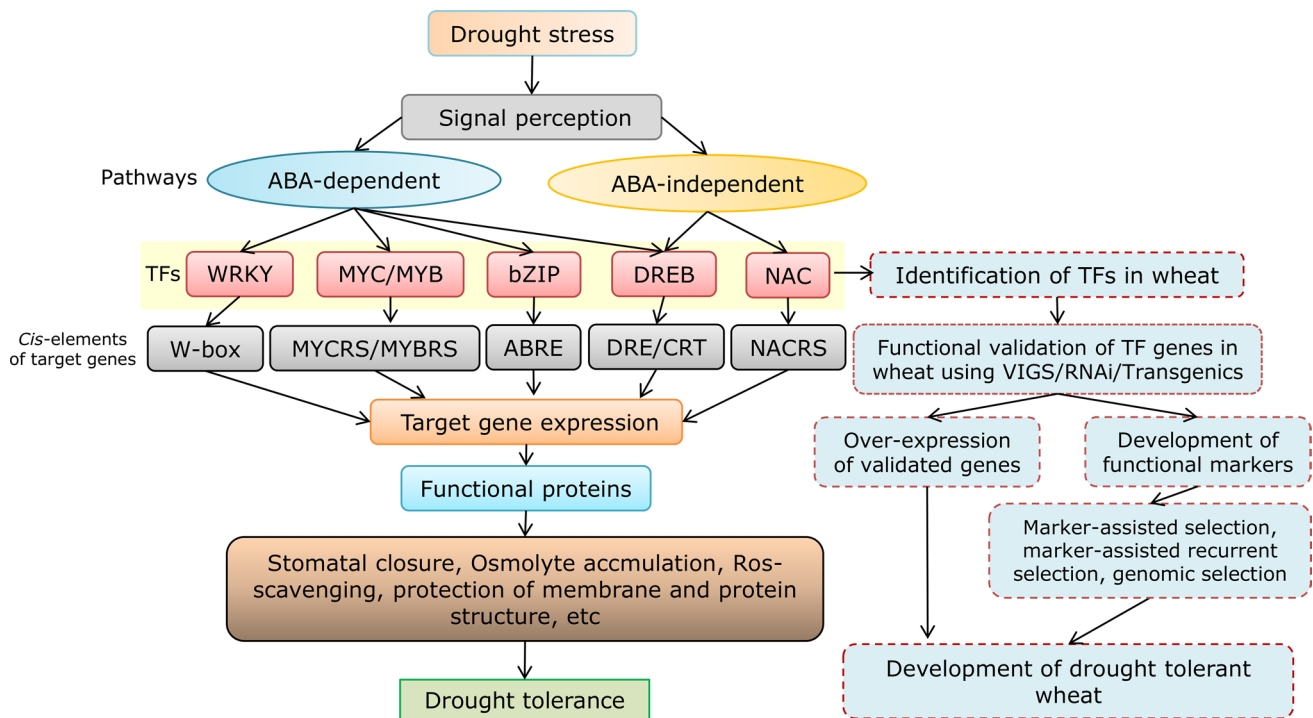


Fig. 1 A schematic representation of drought stress signal perception and gene expression via ABA-dependent and ABA-independent pathways in plants; their utilization in the development of drought tolerant

wheat cultivars using marker-assisted selection is also shown (Modified from Shinozaki and Yamaguchi-Shinozaki 2000)

2015; Wang et al. 2015; Wang J et al. 2016). The wheat gene *TaGT2L1* encoding a TF belonging to GT family has also been recently shown to play a role in regulation of stomatal density and drought tolerance (Zheng et al. 2016). Genes for TFs involved in stress tolerance have also been studied in two model plant systems, *Arabidopsis* and rice, the latter often having orthologues in wheat (Hu et al. 2006; Lu et al. 2009; Fang et al. 2015).

In this brief review, we first describe regulons involving TFs of the above five major families and their interaction with *cis*-regulatory elements (CREs) that are available in the promoters of drought responsive genes; at the whole genome level, these *cis*-elements in a species constitute, what are described as cistrome and epicistrome for that species (O'Malley et al. 2016). We are aware that some details about TF regulons are also available in earlier recent reviews (Nakashima et al. 2009, 2014; Singh and Laxmi 2015; Joshi et al. 2016), but this review has a focus on TFs involved in drought tolerance and that too in wheat. Other novel features of this review include a brief account of reversible phosphorylation involved in the function of TFs and the co-regulatory networks, which involve either only TFs, or TFs with miRNAs. A brief account of databases of plant TFs and cistrome/epicistrome is also included.

Regulons involved in drought tolerance: TFs and their target genes

A TF generally has two domains, the DNA binding (DB) domain and an activation domain (AD). With the help of DB domain, a TF binds to a *cis*-acting element (also described as TF binding site or TFBS) available in the promoter of a stress responsive gene; this brings AD in close proximity of the concerned gene thus facilitating activation or repression of the target gene. A number of genes that carry the same *cis*-acting element (s) and thus induced by the same TF (s) constitute a regulon. A number of such drought responsive regulons along with associated TFs are now known (Table 2). Five classes of such extensively studied regulons that are involved in drought response, along with their TFs will be described in brief (more details are available in some recent reviews, Nakashima et al. 2009, 2014; Singh and Laxmi 2015).

bZIP TFs: the *AREB/ABF* regulons

Basic leucine zipper (bZIP) TFs represent one of the most diverse and largest TF family (Pérez-Rodríguez et al. 2010). TFs belonging to this family have been classified in ten groups/subfamilies on the basis of sequence

Table 2 *Cis*-acting elements and the corresponding drought responsive genes that are involved in imparting tolerance to drought

TF families/sub-families	Relevant domain in TF	<i>Cis</i> -acting element (core sequence)	Gene containing <i>cis</i> -acting element (ABA dependent/independent)	References
I. AP2/EREBP				
(a) DREB	AP2/ERF domain (60 amino acids)	DRE (TACCGACAT)	<i>RD29A</i> (independent)	Stockinger et al. (1997); Liu et al. (1998)
(b) ERF	AP2/ERF domain (60 amino acids)	GCC box (AGCCGCC)	Several genes of abiotic stress (N/A)	Zhu et al. (2010)
II. bZIP (AREB/ABF)	bZIP domain	ABRE (ACGTGGC)	<i>Em</i> gene (dependent)	Marcotte et al. (1989)
III. MYB/MYC	MYB domain in MYB/basic-helix-loop-helix (bHLH) domain in MYC	MYBR (TAACNA/G) and MYC (CNNTG)	<i>RD22</i> (dependent)	Abe et al. (2003); Lippold et al. (2009); Seo JS et al. (2011); Seo PJ et al. (2011); Shin et al. (2011)
IV. NAC	NAC domain	NACRS (TCN ₇ -ACAGCATGT)	<i>ERD1</i> gene (independent)	Hu et al. (2006, 2008); Mao et al. (2012)
V. WRKY	WRKYGQK	W-box TTGAC (C/T)	<i>RD29A</i> , <i>RD29B</i> , <i>COR6.6</i> , <i>DERB2A</i> (dependent)	Niu et al. (2012); Van Aken et al. (2013)

similarity of basic region and the presence of additional conserved motifs (Jakoby et al. 2002). An important sub-family of these bZIP TFs, which regulate expression of stress responsive gene via abscisic acid (ABA) belong to group A. An analysis of ABA-inducible genes revealed that each of these genes carry a conserved *cis*-acting element (ACGTGGC) in their promoters, designated as ABA-responsive element (ABRE), which is a subset of the G-box sequence (CACGTG); therefore, sometimes these response elements are also described as G-ABRE, the corresponding; bZIP TFs are described as ABRE binding protein/factor (AREB/ABF) (Table S1). AREB/ABF TFs harbor a highly conserved bZIP domain composed of two structural features [a basic region and a leucine (Leu) zipper]; the basic region comprises ~16 amino acid residues with the invariant motif N-x7-R/K-x9 and is responsible for nuclear localization and DNA binding, whereas the Leu zipper is composed of heptad repeats of Leu or other bulky hydrophobic amino acids and mediates homo- and/or heterodimerization of bZIP proteins (Jakoby et al. 2002; Fig. 2a). In rice, bZIP TFs have also been shown to be involved in feedback regulation of ABA level during drought stress by targeting the ABA biosynthesis gene *OsNCED4* (Zong et al. 2016).

TFs of bZIP family that are involved in AREB/ABF regulons provide a good example of interaction between TFs and the stress responsive genes (which carry *cis*-acting element, ABRE), particularly in the context of drought tolerance (Choi et al. 2000; Fujita et al. 2005; Nakashima et al. 2009; Wang J et al. 2016). In wheat, the first example of such an AREB/ABF and the corresponding ABRE became available, when ABA-induced transient expression assay in rice protoplasts was used to identify an ABA-responsive promoter in some wheat genes (Marcotte et al. 1988); an ABRE sequence was also identified soon in the wheat gene *Em* (early maturity; Marcotte et al. 1989). Subsequently, ABREs were detected in a number of ABA-responsive genes (i.e., *RD29*, *COR15*, *COR47* etc.) in several plant species (for a review, see Kim 2006).

Recently, an AREB wheat gene (*TaAREB3*) encoding a bZIP TF was also identified and characterized (Wang J et al. 2016). When this gene was overexpressed in *Arabidopsis*, the transgenic lines were found to be relatively more sensitive to ABA and also more tolerant to drought and freezing. Functional analysis showed that the TF encoded by *TaAREB3* can bind promoters of four drought responsive genes (*RD29A*, *RD29B*, *COR15A* and *COR47*) and activate their expression under stress conditions like drought and freezing (Wang J et al. 2016). These four genes are key ABA signaling regulators and are involved in freezing tolerance. Another wheat bZIP TF gene *TabZIP60*, when overexpressed in *Arabidopsis* transgenic plants, imparted improved drought tolerance. These transgenic plants also exhibited

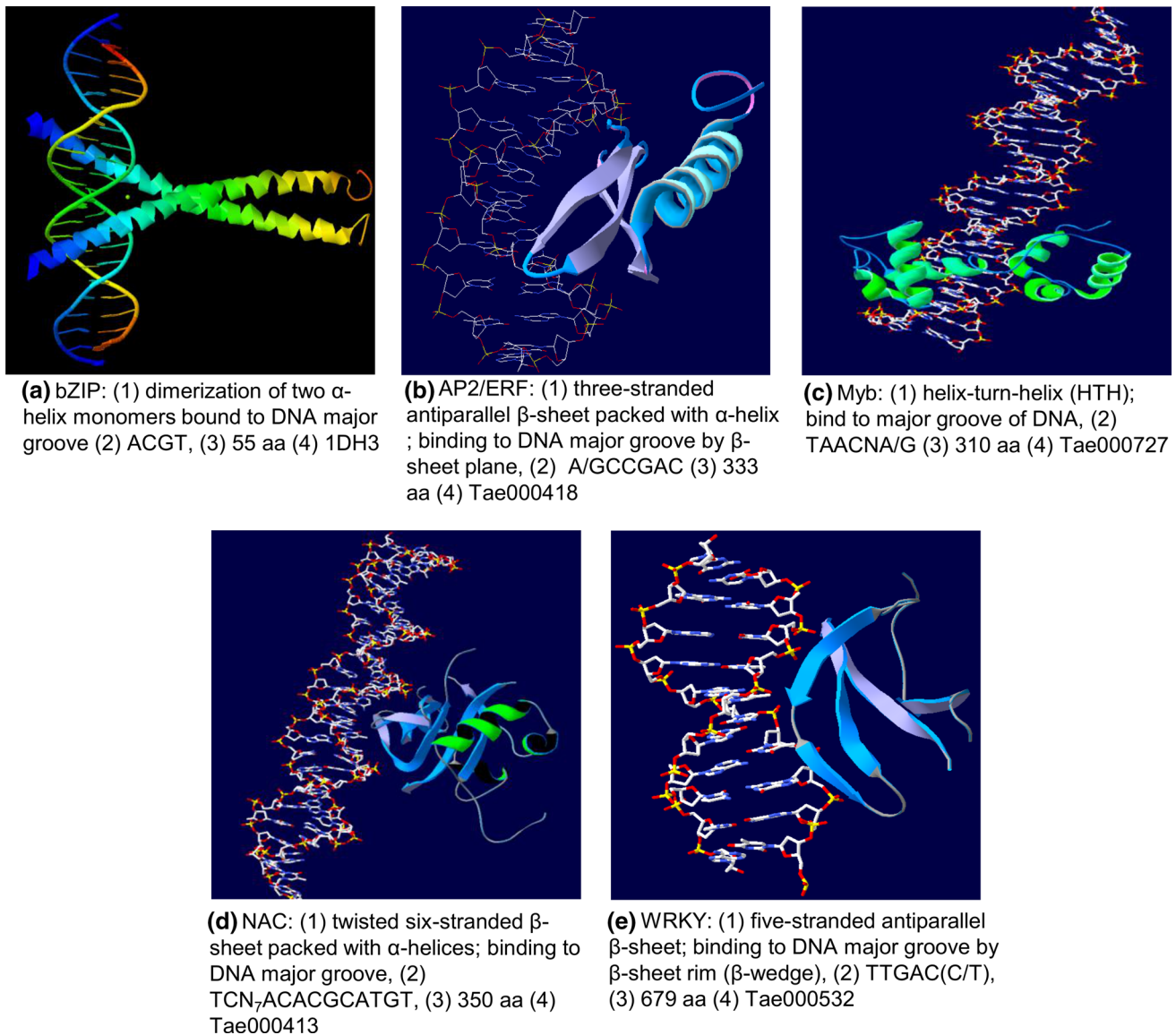


Fig. 2 Ribbon structures of TF-DNA complexes involving five families of wheat TFs. **a** AP2/ERF **b** bZIP **c** Myb **d** NAC **e** WRKY. In each case, information on the following features is written in the corresponding legend: (1) structural features, (2) recognition sequences, (3) number of amino-acids (aa) (4) Plant TFDB v3 (<http://planttfdb.cbi.pku.edu.cn/index.php>) entry codes of wheat TF (except bZIP; structure taken from RCBS protein data bank; <http://www.rcsb.org/pdb/home/home.do>). The figures for molecules were drawn using TFmodeller (<http://maya.ccg.unam.mx/~tfmodell/>) and PDB file view on SWISS PDB viewer v4 (Guex et al. 2009)

higher expression of four key ABA signaling regulators and cold-responsive genes (*AtRD29A*, *AtRD20*, *AtRD29B* and *AtCOR47*) under drought. These results suggested that *TabZIP60* is involved in regulating the expression of some key ABA signaling regulators and cold-responsive genes under drought condition (Zhang et al. 2015).

The promoters of drought responsive genes may also each carry one or more distal or proximal coupling elements (CE), such as CE1 and CE3 to induce expression of drought responsive genes. For instance, CEs in barley have been shown to form an abscisic acid response

complex (ABRC), which might be necessary and sufficient to confer ABA response or to trigger ABA-mediated gene expression (Shen et al. 1996). Binding sites have also been identified in CEs, where ABFs bind (Choi et al. 2000; Niu et al. 2002). TFs belonging to AP2/ERF proteins could also interact with CE1 (Lee et al. 2010a).

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DREB (AP2/ERF) TFs and DREB/CBF regulons

The dehydration-responsive element-binding (DREB) proteins (TFs) play an important role in response to drought

stress. They represent a large subfamily of TFs belonging to the family AP2/EREBP or AP2/ERF (APETALA2/ethylene-responsive element-binding protein/factor). Several members of this subfamily have been identified in different plant species (details are given in Table S1). Each DREB TF contains one AP2/ERF DNA-binding domain (highly conserved region of about 60 to 70 amino acids) that binds to the *cis*-acting element DRE consisting of 9-bp core sequence (TACCGACAT) that is available in promoters of drought responsive genes (Fig. 2b). The presence of this DRE has been reported in several drought responsive genes (e.g., *RD29A* and *RD29B* in *Arabidopsis*; Yamaguchi-Shinozaki and Shinozaki 1994). Similar *cis*-acting elements named C-repeat (CRT), each containing A/GCCGAC motif (found in DRE) have also been reported in the promoters of cold inducible genes in *Arabidopsis*, where CRT is used for binding of the TF CBF (CRT binding factor) under cold stress (Saleh et al. 2005).

A DREB TF and the corresponding one or more *cis*-acting elements (e.g., DRE) constitute a regulon, thus providing another important example of well characterized interaction between a TF and a *cis*-element. In wheat, *DREB1/CBF* and *DREB2* genes were identified and named *TaDREB1A* and *WDREB2* (Vagujfalvi et al. 2005; Egawa et al. 2006; Nakashima et al. 2009; Hassan et al. 2015). Overexpression of these two wheat genes in transgenic *Arabidopsis* or tobacco plants resulted in overexpression of downstream stress-inducible genes (*RD29A*, *Wdhm13*, *Wrab17*, *Wrab18* and *Wrab19*) having DRE in their promoter region; these transgenic lines also exhibited tolerance to abiotic stresses such as drought and freezing (Pellegrineschi et al. 2004; Egawa et al. 2006). Similar, results were also obtained using *Arabidopsis* genes for DREB TFs. For instance, transgenic *Arabidopsis* plants exhibiting overexpression of its own gene *AtDREB1/CBF* were found to exhibit tolerance to drought, high salinity and cold stress (Jaglo-Ottosen et al. 1998; Liu et al. 1998; Kasuga et al. 1999) suggesting that DREBs/CBFs target multiple genes. The target genes for DREB/CBF include genes encoding LEA (late embryogenesis abundant) proteins, KIN (cold-inducible) proteins, osmoprotectant biosynthesis proteins, and protease inhibitors, which are known to function in response to abiotic stresses. More than 40 such target genes containing either DRE/CRT or other core motifs in their promoters have so far been identified (Seki et al. 2001; Fowler and Thomashow 2002; Maruyama et al. 2004).

MYB/MYC TFs and MYB/MYC regulons

The TFs belonging to the MYB (myeloblastosis)/MYC (myelocytomatosis) family of proteins are found in both plants and animals and have varied functions (Abe et al. 2003). Each TF of MYB family contains a MYB domain with 1–3 imperfect repeats, each with about 52 amino acid

residues, which acquire a helix-turn-helix (HTH) conformation and intercalates in the major groove of DNA (Yanhui et al. 2006; Fig. 2c). Similarly, each MYC TF harbors a highly conserved basic helix-loop-helix (bHLH) domain (Kazan and Manners 2013). MYB and MYC TFs are often together involved in constituting, common regulons described as MYB/MYC regulons.

MYB/MYC regulons participate in some important transcriptional pathways that are involved in drought stress responses via ABA-dependent signaling systems (Abe et al. 1997; Baldoni et al. 2015). In wheat, MYB TF gene *TaMYB30-B* was found to be involved in drought stress responses. *Arabidopsis* transgenic plants, overexpressing *TaMYB30-B* gene also exhibited altered expression levels of some drought stress-responsive genes (*RD29A*, *ERD1*); they also carried improved drought stress tolerance during germination and seedling stages (Zhang L et al. 2012). Another wheat MYB TF gene *TaPIMP1* is also involved in regulation of genes involved in drought response; its own expression level is also positively correlated with drought tolerance (as shown in transgenic plants). Electrophoretic mobility shift assay and yeast-one-hybrid assays suggested that the TF *TaPIMP1* can bind to MYB-binding site, and activate the expression of the genes with the Myb *cis*-element. The TF *TaPIMP1* was also shown to upregulate the expression of a subset of defense- and stress-related genes (e.g., *RD22*, *TLP4* and *PR1a*) as revealed through microarray analysis. (Zhang Z et al. 2012). Another wheat MYB TF gene *TaMYB3R1* was also found to be involved in drought stress response. In transgenic *Arabidopsis* lines overexpressing *TaMYB3R1*, enhanced mRNA levels were observed for several dehydration inducible genes including both, ABA-dependent genes (*RD29A*, *RD29B*, and *ABF3*) and ABA-independent genes (*COR15A*, *ADH1* and *CBF4*). These results suggested that *TaMYB3R1* also affects expression of dehydration-responsive genes in both ABA-dependent and ABA-independent pathways (Cai et al. 2015).

In the model plant *Arabidopsis* also, induced expression of *RD22* gene has been shown to be mediated by abscisic acid (ABA), although it lacks ABRE *cis*-element in its promoter region; its expression is regulated by two closely located putative recognition sites, namely MYCR, CNNTG for the MYC TF (*AtMYC2*) and MYBR, TAACNA/G for MYB TF (*AtMYB2*) (Abe et al. 1997, 2003). This represents an example of a regulon, where same gene may carry two binding sites for two TFs. Overexpression of two *Arabidopsis* TF genes (*AtMYC2* and *AtMYB2*), which overexpressed in transgenic *Arabidopsis* plants (studied through microarray analysis) suggested that their target genes include many ABA- or jasmonic-acid (JA)-inducible genes (e.g., *RD22*, *AtADH1*). These transgenic plants were also found to be ABA responsive and carried improved osmotic tolerance (Abe et al. 2003).

NAC TFs and NAC regulons

The TFs of NAC family (NAM, ATAF and CUC) have also been shown to be involved in activation of drought responsive genes. These TFs are unique to plants and have not been reported in animal systems. NAC TFs share a conserved N-terminal with ~150–160 amino-acids long DNA binding region (NAC domain) carrying five sub-domains (A–E) and a variable C-terminal (Ooka et al. 2003) that is responsible for the observed differences in the regulatory function of NAC proteins (Jensen et al. 2010). Some NAC proteins, described as NTL or transmembrane motif (TMs) 1-like, also contain α -helical transmembrane motifs at their C-terminals (Kim et al. 2010) (Fig. 2d), which allow activation or repression of a variety of downstream genes thus regulating multiple cellular or molecular processes (Nakashima et al. 2012; Puranik et al. 2012).

NAC TF genes and their corresponding *cis*-acting elements (NACRS) constitute NAC regulons, and provide another important example of well characterized interaction between a TF and one or more *cis*-elements that work during drought stress. Recently it was shown that *Arabidopsis* transgenic plants overexpressing three wheat NAC TF genes (*TaNAC47*, *TaNAC67* and *TaNAC29*) exhibited an improved tolerance to drought stress. In transgenic plants carrying *TaNAC47*, the expression levels of six stress-responsive genes (*RD29A*, *RD29B*, *COR47*, *RD20*, *GSTF6* and *P5CS1*) increased. Similarly, in transgenic plants carrying *TaNAC67*, the expression of five stress-responsive genes (*DERB1A*, *RD29B*, *RD29A*, *RAB18* and *ABI5*) increased. The promoters of these genes carried NAC-binding *cis*-elements, suggesting that these genes might be transcriptionally activated by *TaNAC47/TaNAC67* and constitute a NAC regulon (Mao et al. 2014; Zhang et al. 2016). In contrast, in the transgenic plants carrying *TaNAC29*, the expression level of some key ABA signaling regulators and senescence-associated genes (*RD29B*, *SAG13*, *SAG113*, *AIB1*, *ERD11* and *ABI5*) was significantly reduced (Huang et al. 2015), thus suggesting that wheat NAC TFs may be either involved in activation or repression of downstream genes.

NAC TFs have also been studied in two model plant systems including *Arabidopsis* and rice. For instance JUB1 (*JUNGBRUNNEN1*) regulates the Gibberellins (GAs)/brassinosteroids (BRs)-DELLA signaling in *Arabidopsis*; in doing so, JUB1 causes accumulation of DELLA proteins in two different ways: (1) suppression of the activity of genes *GA3ox1* and *DWF4*, thus negatively regulating the synthesis of GA and BR biosynthesis; (2) direct activation of genes, *GAI* (*GA INSENSITIVE*) and *RGL1* (*RGA-LIKE*). DELLAs, in turn, cause inhibition of cell elongation, reduction of intracellular H₂O₂ levels, and promotion of stress tolerance (Shahnejat-Bushehri et al. 2016). Another *Arabidopsis* gene *ERD1* (*early dehydration stress 1*) is

also induced by several NAC TFs including ANAC019, ANAC055, ANAC072 (Tran et al. 2004, 2007). Recently in rice, OsNAM (a NAC TF) was shown to regulate the expression of five genes (*OsCESA*, *OsGDP*, *OsMtn3*, *OsAH* and *OsGdpD*) under drought stress (Dixit et al. 2015). Examples of such NAC TFs, which use NACRS motif for binding include ANAC019, ANAC055, and ANAC072 in *Arabidopsis* (Tran et al. 2004) and SNAC1, ENAC1 and SNAC2 in rice (Hu et al. 2008; Sun et al. 2012).

WRKY TFs and WRKY regulons

WRKY is the largest superfamily of TFs that are unique to plants. These TFs not only impart tolerance against abiotic stresses, but also regulate plant growth and development (Wu et al. 2008; Tripathi et al. 2012, 2014; Zhu et al. 2013). Several members of this family have been identified in various plant species (details were given in Table S1; Rushton et al. 2010; Banerjee and Roychoudhury 2015; Xu et al. 2016). TFs of this family are characterized by the presence of WRKY domain (~60 aa), which is composed of highly conserved WRKYGQK sequence followed by a zinc-finger motif. This WRKY domain exhibits high binding affinity for the *cis*-acting element called W-box (TTGACC/T), which occurs in several drought responsive genes (Ulker and Somssich 2004; Rushton et al. 2010; Fig. 2e).

The genes encoding TFs of WRKY family and the *cis*-acting element W-box constitute another class of regulons, which are involved in drought stress response and signaling. In wheat also, WRKY regulons have been reported to be involved in drought stress. Transgenic *Arabidopsis* plants overexpressing wheat genes *TaWRKY2* and *TaWRKY19* exhibited increased tolerance to drought stress. *TaWRKY2* and *TaWRKY19* are two nuclear proteins (TFs), which displayed specific binding to W box; *TaWRKY2* binding the promoter of downstream gene *RD29B*, and *TaWRKY19* binding the promoters of three genes (*RD29A*, *RD29B* and *COR6.6*). In both cases, TF binding leads to increase in expressions of downstream genes during drought stress (Niu et al. 2012).

In another study, Wang et al. (2013) identified ten (10) *TaWRKY* genes, designated *TaWRKY1–TaWRKY10*. Among these genes, *TaWRKY10* was examined in more detail, and was shown to confer drought tolerance by regulating osmosis and reducing ROS accumulation. Overexpression of *TaWRKY10* in tobacco transgenic plants significantly activated the expression of following three stress-related genes, which can be classified into the following two groups: (1) *NtERD10C* (encoding early response to drought 10C) and *NtSPSA* (encoding sucrose-phosphate synthase activity) both dealing with osmotic stress, and (2) *NtGPX* (encoding glutathioneperoxidase) involved in scavenging ROS.

Another wheat WRKY TF gene (*TaWRKY44*) that was overexpressed in tobacco transgenic plants, imparted an improved tolerance to drought stress with increased relative water content (RWC), proline and soluble sugar accumulation, improved antioxidant system (Wang et al. 2015). The 14 ROS-related and stress-responsive genes that, were upregulated in these transgenic plants, could be classified in the following four groups: (1) genes encoding enzymes for ROS detoxification (*NtSOD*, *NtAPX*, *NtCAT*, *NtPOX*, and *NtGST*); (2) genes encoding enzymes involved in the biosynthesis of polyamine (*NtADC1* and *NtSAMDC*), sucrose (*NtSPSA*) or ABA (*NtNCED1*); (3) stress-defensive protein gene (*NtERD10C*); and (4) lipid-transfer protein genes (*NtLTP1* and *TobLTP1*). These results suggested that TaWRKYs are involved in regulating the expression of some key ROS-related and stress responsive genes under drought.

WRKY regulons were also reported in the model plant *Arabidopsis*. Transgenic *Arabidopsis* lines exhibiting overexpression of its own genes *WRKY18*, *WRKY40* and *WRKY60* had altered plant sensitivity to ABA, salt and osmotic stress. During drought stress, TFs *WRKY18* and *WRKY60* were found to be positive regulators of ABA signaling, and the TF *WRKY40* was found to be a negative regulator. They bind to the promoters of multiple genes including some stress-inducible downstream genes (*RD29A* and *COR47*) and some TF genes (e.g., *ABI5*, *DREB1A/CBF3*, *DREB2A* and *MYB2*), and influence their expression (Chen et al. 2010; Shang et al. 2010). Further, a transgenic *Arabidopsis* line exhibiting overexpression of *ABO3* gene that encodes a WRKY TF (*AtWRKY63*) was also found to exhibit hypersensitive response for ABA in the seedling stage, associated with reduced drought tolerance. It was also found that a mutant *ABO3* downregulates the expression of two downstream genes (*RD29A* and *COR47*) on ABA treatment. A study involving gel-shift assay revealed that *ABO3* protein binds to the W-box localized in the *ABF2* promoter (Ren et al. 2010).

Kinases and phosphorylation of TFs for drought tolerance

The products of TF genes in the form of transcripts and proteins (TFs) have been shown to undergo post-transcriptional and post-translational modifications respectively. The major modifications at the post-transcriptional level include alternate splicing, while modifications at the post-translational level include phosphorylation and protein–protein interactions. Of these modifications, however, phosphorylation seems to be the most common and widespread modification that has been witnessed in almost all TFs. Phosphorylation in TFs has also been shown to be induced as a response to abiotic stresses (Luan 2003; You et al.

2014). During phosphorylation, a protein kinase transfers the terminal phosphate group of an ATP molecule to the hydroxyl group on a Ser, Thr, or Tyr side chain of the protein. Reversible phosphorylation allows TFs to switch rapidly from dephosphorylated state to phosphorylated state and vice versa, thus permitting plants to respond to stress stimuli rapidly and accurately.

Variations have been observed in the kinases that cause phosphorylation and also in the specific amino acid residues of TFs that are involved in phosphorylation (i.e., Ser, Thr and Tyr). Serine-threonine kinases (e.g., SnRKs) are generally used in phosphorylation of bZIP, NAC and DREB TFs, mitogen-activated protein kinases (MAPKs) are used for phosphorylation of MYB/MYC and WRKY TFs, and calcium-dependent protein kinases (CDPKs) are involved in phosphorylation of some bZIP TFs (e.g., ABF1 and ABF4). In the following section, some details about kinases and phosphatases involved in reversible phosphorylation of TFs, involved in response to drought stress are presented. Modifications of transcripts and TFs other than phosphorylation will not be described, since either they don't appear to be so widespread, or else these have not been worked out as extensively as the kinases and phosphatases and their involvement in reversible phosphorylation.

The members of SnRK2 family are plant-specific serine/threonine kinases involved in phosphorylation that is involved in plant response to abiotic stresses (Kulik et al. 2011). It has been shown that the AREB/ABF TFs activate expression of genes only after phosphorylation of their conserved regions (Ser/Thr residues of R-XX-S/T sites) (Furihata et al. 2006; Fujita et al. 2011). This phosphorylation is catalyzed by phosphorylated form of a SnRK2 kinase itself that is negatively regulated by a phosphatase PP2C (protein phosphatase 2C), which in turn is negatively regulated by a complex between ABA and its receptors including PYR/PYL/RCARs (pyrabactin resistance/pyrabactin resistance 1-like/regulatory component of ABA receptors). This complex inhibits phosphatase activity of PP2C, so that SnRK2 remains phosphorylated and active, and brings about phosphorylation of AREB/ABF. It is only in its phosphorylated form that AREB/ABF induces expression of downstream genes (Umezawa et al. 2010). Later, the phosphatase activity of PP2C is restored due to dissociation of PYR/PYL/RCAR, so that now it dephosphorylates and thereby inactivates SnRK2. This inactivated and released dephosphorylated SnRK2 gets accumulated in the cell, where it gets phosphorylated again to initiate another cycle of AREB/ABF phosphorylation (Fig. 3a). The SnRK2 kinases are also involved in phosphorylation of NAC TFs, which get phosphorylated at Thr-142 due to the kinase SnRK2.8 under drought conditions in *Arabidopsis* (Kim et al. 2012).

In wheat, both kinases (e.g., SnRK2) and phosphatases (*TaPP2Ac-1*) and the corresponding genes for reversible

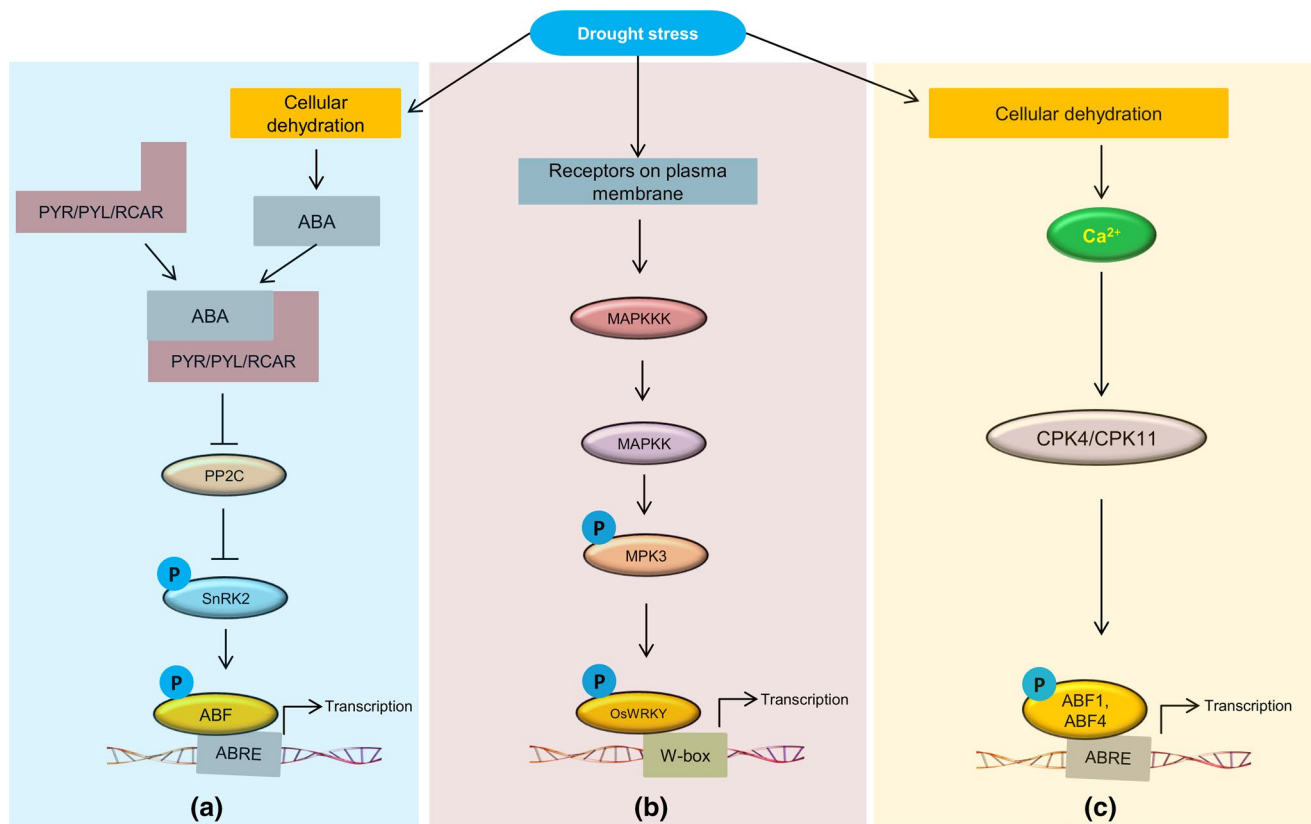


Fig. 3 Models showing phosphorylation: **a** ABF TFs using SnRK2 pathway **b** WRKY TFs using MAPK pathway and **c** ABF TFs using CDPK pathway in plant response to drought stress. (Modified from Zhu S-Y et al. 2007; Kulik et al. 2011; Banerjee and Roychoudhury 2015). ABA abscisic acid, ABF ABRE binding protein/factors, CPK

calcium-dependent protein kinase, *PYR/PYL/RCARs* pyrabactin resistance/pyrabactin resistance 1-like/regulatory component of ABA receptors, *MAPK* mitogen-activated protein kinase, *MAPKK* MAP kinase kinase, *MAPKKK* MAP kinase kinase kinase

phosphorylation have been reported and their involvement in response to abiotic stress tolerance has been demonstrated (Mao et al. 2010). In some cases, it has also been shown that the TFs have sites for phosphorylation, suggesting that the TaSnRK2 genes may be involved in phosphorylation of TFs. For instance, an SnRK2 ortholog named PKABA1 was initially reported, which phosphorylates wheat AREB1 ortholog, TaABF (Johnson et al. 2002, 2008; Fig. S1). Another TF, TaAREB3 was shown to contain a conserved N-terminal of 145 amino acids (aa) with Ser/Thr-like protein kinase phosphorylation sites, a variable M region (146–257 aa) and a conserved C-terminal region with a bZIP domain (258–311 aa). Alignment and phylogenetic analysis also revealed that TaAREB3 is similar to AtAREB3 (a member of AREB subgroup) that belongs to A group of bZIP family (Wang J et al. 2016).

More recently, 10 different genes encoding wheat SnRK2s have been isolated and characterized (Zhang et al. 2016). Based on their kinase domains and the C-terminus, the 10 SnRK2s were classified into three subclasses (I, II and III) (Fig. S2). Expression pattern analysis revealed that

all *TaSnRK2s* were involved in responses to PEG, NaCl, and cold stress. *TaSnRK2s* in subclass III were strongly induced by ABA, those in subclass II responded weakly to ABA, whereas those in subclass I were not activated by ABA treatment. Physical and functional interaction between TaSnRK2s and a typical group A PP2C (TaABI1) was also examined, suggesting that PP2C interacted physically with subclass III TaSnRK2s, while having no interaction with TaSnRK2s from subclasses I and II. It was concluded that subclass III TaSnRK2s were involved in ABA regulated stress responses, whereas subclasses I and II TaSnRK2s responded to other abiotic stressors in an ABA-independent manner. Rice SnRK2 orthologs, SAPK8, SAPK9 and SAPK10 have also been shown to phosphorylate the AREB1 ortholog TRAB1, as demonstrated through experiments conducted in vitro (Johnson et al. 2002; Kagaya et al. 2002; Kobayashi et al. 2005).

MAPKs represent another class of important kinases that are generally involved in phosphorylation of WRKY and MYB/MYC TFs, thus playing a crucial role in signal transduction as a response to external stresses (Sheikh

et al. 2016). It has been shown that the WRKY TFs activate expression of their target genes (containing W-box *cis*-element) only after phosphorylation of their conserved regions by MAPKs; these cascades are also involved in transduction of downstream signals in ABA-dependent manner during stress response (Banerjee and Roychoudhury 2015; Fig. 3b). For instance, a MAPK in *Arabidopsis* (AtMPK3) phosphorylates AtWRKY46 TF (Sheikh et al. 2016), and in rice, OsMPK3 phosphorylates OsWRKY30, which is known to enhance drought tolerance (Shen et al. 2012). An example of MAPK mediated phosphorylation of MYB TFs is also available in pine (*Pinus taeda*). In this study, a MAPK protein (PtMAPK6) phosphorylates a Ser-236 residue, located in the C-terminal activation domain of MYB TF (PtMYB4) during early stages of xylem development (Morse et al. 2009).

In wheat also, 19 MAPK genes (including six MAP kinase kinase kinase genes, two MAP kinase kinase genes, and 11 MAP kinase genes) were recently characterized (Wen et al. 2015). Apparently these kinases are involved in phosphorylation in response to deprivation of N/P, salinity and drought. Temporal expression profiles of these MAPKs indicated that these genes were each regulated by stress and exhibited typical recovery responses, when these genes were exposed again to normal growth conditions.

Other kinases namely Calcium-dependent protein kinases (CDPKs), OPEN STOMATA 1 (OST1) and Calcium/calmodulin-dependent protein kinase (CCaMK) are also involved in phosphorylation of TFs. CDPKs, (also written as CPKs; e.g., *Arabidopsis AtCPK1–AtCPK34*), are exclusive to plants (and certain protists) and have been reported to be involved in Ca^{2+} -responsive kinase activity in plants during abiotic stress response and abscisic acid (ABA) signaling (Cheng et al. 2002; Wei et al. 2014). For instance, *Arabidopsis* CDPKs (CPK4 and CPK11) are involved in ABA signaling by phosphorylating bZIP TFs (ABF1 and ABF4) (Zhu S-Y et al. 2007) (Fig. 3c). Also, in *in vitro* kinase assays of CPK3 protein with a suite of substrates demonstrated that CPK3 phosphorylates some TFs (including ERF1, HsfB2a and CZF1/ZFAR1) in the presence of Ca^{2+} (Kanchiswamy et al. 2010). OST1 was initially identified for its role in stomatal closure in response to drought in *Arabidopsis* (Mustilli et al. 2002). In maize, ZmOST1 was shown to cause phosphorylation of the ZmSNAC1 (Vilela et al. 2013) and ZmCCaMK was shown to phosphorylate ZmNAC84 (Zhu et al. 2016) leading to enhanced drought tolerance in both the cases.

The above examples suggest that the system of regulation of TFs due to reversible phosphorylation by different protein kinases/phosphatases should be conserved among plant species, which needs further investigation for a better understanding of the mechanism involved in activation of stress responsive genes under drought.

Database for TFs in plants

Efforts to develop databases for eukaryotic TFs started more than 20 years ago (Wingender 1988) and resulted in a number of publicly available plant TF databases (Table 3). PlnTFDB was the first comprehensive database for plant TFs and initially contained TFs for the following five species: *A. thaliana*, *P. trichocarpa*, *O. sativa*, *Chlamydomonas reinhardtii* and *Ostreococcus tauri* (Riano-Pachon et al. 2007). Current version of PlnTFDB (v3.0) contains a total of 26,184 distinct proteins representing 84 families of different TFs and transcriptional regulators from 19 plant species (Pérez-Rodríguez et al. 2010). Another important comprehensive database for plant TFs is PlantTFDB 1.0 (Guo et al. 2008) with 26,402 TFs from 22 species; its latest updated version (PlantTFDB 3.0) contains information for 129,288 TFs representing 58 families of TFs from 83 species (Jin et al. 2014); genome sequences are also available for 67 of these 83 species.

Two wheat specific TF databases (wDBTF; Romeu et al. 2010 and wheatTFDB; Chen et al. 2015) are also publicly available. The wDBTF contains 3,820 wheat TF genes belonging to 40 families and 84 subfamilies (Romeu et al. 2010). This includes 295 AP2/EREBP, 167 bZIP, 116 MYB, 269 NAC and 187 WRKY TFs, which are actively involved in drought tolerance. Similarly, wheatTFDB contains 2,407 putative TFs belonging to 63 families. This database also includes 226 AP2/EREBP, 110 bZIP, 127 MYB, 193 NAC and 135 WRKY TFs, which are actively involved in drought tolerance (Chen et al. 2015). This database also includes 1,257 developmental stage-specific TFs and 1104 tissue-specific TFs, which were identified based on publicly available gene expression databases. The above two wheat databases will be useful in identifying target TFs involved in response to drought stress at a specific stage of development.

Databases for TFs and corresponding *cis*-elements in the promoters of drought responsive genes belonging to individual plant species other than wheat are also available. For instance, TRANSFAC is an important database of *cis*-acting elements and trans-acting TFs (Matys et al. 2006), which mainly includes TFs from *A. thaliana*. Other TF databases focusing on individual plant species include the following: (1) AtTFDB (Davuluri et al. 2003), DATF (Guo A et al. 2005), RARTF (Iida et al. 2005) and STIFDB (Shameer et al. 2009) for *A. thaliana*; (2) DRTF (Gao et al. 2006) and RiceSRTFDB (Priya and Jain 2013) for rice (*O. sativa*), (3) DPTF (Zhu QH et al. 2007) for *P. trichocarpa*, (4) TOBFAC (Rushton et al. 2008) for *N. tabacum*, (5) SoyTFKB (http://www.igece.org/Soybean_TF) and SoyDB (Wang et al. 2010) for soybean (*G. max*), and (6) DMTR (Mochida et al. 2010) for *M. truncatula*.

Table 3 A list of databases for plant transcription factors (TFs)

S.no.	Database	Species	URL	References
1.	AtTFDB	<i>A. thaliana</i>	http://arabidopsis.med.ohio-state.edu/AtTFDB	Davuluri et al. (2003)
2.	RARTF	<i>A. thaliana</i>	http://rarge.psc.riken.jp/rartf/	Iida et al. (2005)
3.	DATF	<i>A. thaliana</i>	http://datf.cbi.pku.edu.cn/	Guo A et al. (2005)
4.	DRTF	<i>O.sativa</i>	http://drtf.cbi.pku.edu.cn/	Gao et al. (2006)
5.	TRANSFAC	Eukaryotes	http://www.gene-regulation.com/pub/databases.html	Matys et al. (2006)
6.	DPTF	<i>P.trichocarpa</i>	http://dptf.cbi.pku.edu.cn/	Zhu QH et al. (2007)
7.	PlanTAPDB	Algae	http://cosmoss.org/bm/plantapdb	Richardt et al. (2007)
8.	TOBFAC	<i>N. tabacum</i>	http://compsysbio.achs.virginia.edu/tobfac	Rushton et al. (2008)
9.	DATFAP	13 plant species including Wheat	http://cgi-www.daimi.au.dk/cgi-chili/dat-fap/frontdoor.py	Fredslund (2008)
10.	GrassTFDB	5 plant species	http://grassius.org/grasstfdb.html	Yilmaz et al. (2009)
11.	STIFDB	<i>A.thaliana</i>	http://caps.ncbs.res.in/stifdb/	Shameer et al. (2009)
12.	LegumeTFDB	<i>Glycine max, Lotus japonicus and Medicago truncatula.</i>	http://legumetfdb.psc.riken.jp/	Mochida et al. (2010)
13.	SoyDB	<i>G. max</i>	http://www.webcitation.org/query.php?url=http://casp.rnet.missouri.edu/soydb/&ref=doi=10.1186/1471-2229-10-14	Wang et al. (2010)
14.	SoyTFKB 2.0	<i>G. max</i>	http://www.igece.org/Soybean_TF	–
15.	wDBTF	<i>T.astevium</i>	http://wwwappli.nantes.inra.fr:8180/wDBFT/	Romeuf et al. (2010)
16.	DMTR	<i>M. truncatula</i>	http://bioinfo3.noble.org/dmtr/	Mochida et al. (2010)
17.	PlnTFDB	19 plant Species	http://plntfdb.bio.uni-potsdam.de/v3.0/index.php?sp_id=ATH	Pérez-Rodríguez et al. (2010)
18.	PlantTFDB 2.0	49 plant Species	http://plantfdb.cbi.edu.cn/	Zhang et al. (2011)
19.	RiceSRTFDB	<i>O. sativa</i>	http://www.nipgr.res.in/RiceSRTFDB.html	Priya and Jain (2013)
20.	PlantTFDB 3.0	83 plant Species	http://plantfdb.cbi.pku.edu.cn/	Jin et al. (2014)
21.	WheatTFDB	<i>T. aestivum</i>	http://xms.sicau.edu.cn/wheatTFDB/	Chen et al. (2015)

A ‘plant cistrome database (PlantCistromeDB)’ giving details of genome-wide transcription factor binding sites, the TFBSs (*cis*-elements) including cistrome and epicistrome has also been recently developed (O’Malley et al. 2016). In this database, TFBS for 529 *Arabidopsis* TFs (of 1,812 TFs comprising 80 families, surveyed) and details of methylated sites, which inhibit or promote TF binding are available (<http://neomorph.salk.edu/> PlantCistromeDB). In future, data on cistromes and epicistromes of other plant species will certainly be added to this PlantCistromeDB.

Cross-talks and networking involving TFs

There is evidence that individual TFs generally do not function in isolation and that often there are cross-talks between the signaling pathways involving two or more TFs. At least two examples of such cross-talks of TFs from the family ABF (a subfamily) of bZIP are available, one involving crosstalk with DREB, and the other involving cross-talk

with NAC. However, such interactions are yet to be discovered in wheat.

Interaction between ABF and DREB

The TFs belonging to ABF and DREB families are often involved in a network as shown in case of *Arabidopsis* drought-responsive gene *RD29A*, which carries with it two *cis*-elements, ABRE and DRE/CRT-core motifs that are used for binding of two different TFs. A detailed study of the involvement of ABRE and DRE in ABA-dependent gene expression suggested that ABRE and DRE are interdependent and are synergistic in action for induction of the stress-responsive expression of *RD29A* gene. DRE motif sometimes also functions as a coupling element (CE) for ABRE (Narusaka et al. 2003).

Using yeast two hybrid system, ABF TFs (ABF2, ABF3 and ABF4) have also been shown to interact physically with DREB/CBF TFs (DREB1A/CBF3, DREB2A

and DREB2C) (Lee et al. 2010b). In another study, it was found that DREB2A promoter contains ABRE and coupling element 3 (CE3)-like sequences that are necessary for promoter activity under osmotic stress conditions, such as dehydration. Using yeast one-hybrid and chromatin immunoprecipitation (ChIP) assays, it was also found that the AREB/ABF bZIP TFs can bind DREB2A promoter and activate the expression of *DREB2A* gene in an ABRE-dependent manner (Kim et al. 2011).

Interaction between ABF and NAC

Interactions between the AREB/ABF and NAC TFs have also been demonstrated in some studies. For instance, ATAF1 (an *Arabidopsis* NAC TF) has been shown to regulate the ABA biosynthetic gene *9-cis-epoxycarotenoid dioxygenases 3 (NCED3)* in *Arabidopsis*, suggesting that SNACs may regulate the expression of genes from AREB/ABF regulons (Jensen et al. 2013). Cooperation between NAC TF and TFs AREB/ABF of the bZIP family during dehydration stress was also reported in two other studies. In one of these studies, ANAC096 was shown to interact synergistically with ABF2 and ABF4 for inducing activation of *RD29A* (Xu et al. 2013), while in the other study, a NAC TF (ANAC016) and the protein encoded by its target gene NAP, were both shown to bind to a site in the promoter of AREB1, leading to repression of AREB1 transcription. This was described as a trifurcate feed-forward pathway involving functions of NAC016, NAP, and AREB1 in the drought stress response (Sakuraba et al. 2015).

MicroRNA and TF co-regulatory networks for drought tolerance

Generally, TFs regulate expression of protein-coding genes at the transcription level (Fire et al. 1998; Stefani and Slack 2008). However, during last more than a decade, non-coding RNA mediated riboregulation of gene expression at the post-transcriptional level has attracted attention of the scientific community. A major component of this riboregulation is a class of small non-coding RNA represented by microRNAs (miRNAs), which are ~19–24 bp long and repress expression of a large number of genes in all known eukaryotic systems (Chen 2004; Cobb et al. 2005). Interestingly, about 50 % of the miRNA targets that have been identified are genes encoding TFs, which are involved in regulation of abiotic stress responses in plants (Bartel 2004; Kidner and Martienssen 2005; Zhang et al. 2006; Zhang, 2015; Zhang and Wang 2015).

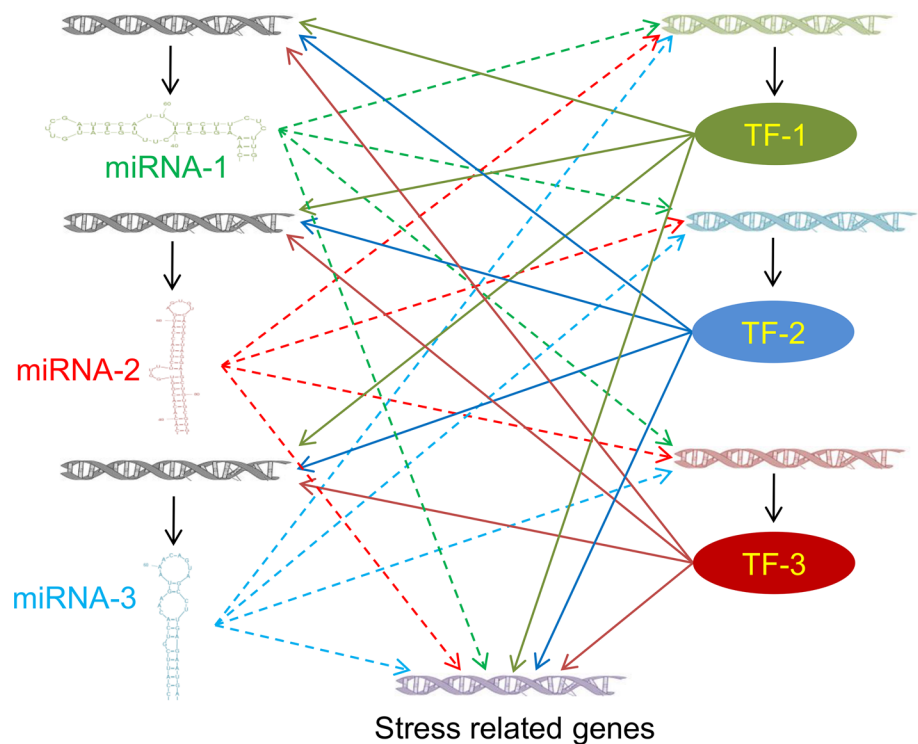
In bread wheat and emmer wheat also, expression of miRNAs under drought stress was examined. For instance,

a number of miRNAs (miR1867, miR474, miR398, miR1450, miR1881, miR894, miR156 and miR1432) are induced by drought in wild emmer wheat (*Triticum dicoccoides*) (Kantar et al. 2011). Similarly, in bread wheat genotype C306, following five miRNAs were found to be differentially expressed under dehydration stress (Gupta et al. 2014): miR159, miR164, miR393, miR529 and miR1029. In another study, 367 miRNAs were found to be differentially expressed, when a drought tolerant genotype (Hanxuan10) and a drought sensitive genotype (Zhengyin1) were grown under dehydration stress, and expression analysis was conducted using a deep-sequencing method (Ma et al. 2015). The gene targets of the differentially expressed miRNAs encoded proteins that were involved in metabolic processes, response to stress, and regulation of transcription (including TFs). For instance, gene target of miR159a encodes the MYB3 TF, which plays a role in drought-stress. The target of miR164b is the NAC TF family, which is also having functions related to various abiotic stresses including drought (Ma et al. 2015). Majority of miRNAs regulate plant growth and development involving plant architecture, and are therefore also involved in imparting tolerance to biotic and abiotic stresses. Sometimes, they do so by controlling the level of TFs (Zhang et al. 2006; Rubio-Somoza and Weigel 2011; Ma et al. 2015). In such cases, there is a complex networking between TFs and miRNAs, which ultimately regulate gene expression (Fig. 4). The function of one TF may be affected by one or more miRNAs, and one miRNA may affect more than one TF (Zhang et al. 2006). It is also known that the synthesis of a specific miRNA itself may also be affected by one or more TFs and that one TF may affect synthesis of more than one miRNAs (Gutierrez et al. 2009; Meng et al. 2011). Because the expression of miRNAs often depends on the regulation of TF synthesis and vice versa, it is not surprising that both families of regulators are tightly related to each other in gene regulatory networks. The coordinated transcriptional regulation of miRNAs and their target genes by TFs also involves a network, which will be illustrated using some specific examples of coregulation by miRNAs and TFs in wheat and in two model plants (*Arabidopsis* and rice). A summary of miRNAs and their target TFs is given in Table 4.

miR164 and miR169 and NAC/NFY TFs co-regulate drought tolerance

The miRNAs form miRNA164 family are crucial players in regulation of response to drought stress; they target and regulate the activity of a number of TFs of the NAC family, which in turn regulate signal transduction pathways involved in a variety of developmental processes (lateral

Fig. 4 A hypothetical diagram of complex network of co-regulatory system of TFs and miRNAs



root emergence, formation of vegetative and floral organs and age-dependent cell death) thus imparting tolerance against abiotic stresses (Guo HS et al. 2005; Kim et al. 2009). In wheat, it has been shown that miR164 accumulates in the seedlings of the cultivar C-306 during drought stress (Gupta et al. 2014), suggesting that, miR164 might target NAC TFs and influence response to drought stress (including root development) as earlier reported in rice and *Arabidopsis* (Kim et al. 2009; Fang et al. 2014). In rice, six miR164-targeted NAC genes (*OMTN1–OMTN6*) were characterized for drought response. Over-expression of four of these six genes (*OMTN2*, *OMTN3*, *OMTN4* and *OMTN6*) significantly reduced drought tolerance at the reproductive stage, suggesting that the OMTNs function as negative regulators of drought tolerance in rice, in addition to their role in some developmental processes (Fang et al. 2014).

Another important miRNA family that is involved in response to drought stress is miR169, which targets CAAT-box NFY TFs (Li et al. 2008), which are responsive to drought stress in wheat (Stephenson et al. 2007). In another study in wheat, it was shown that, miR169d was repressed in the drought-tolerant cultivar after dehydration stress, which might target the CAAT-box TFs, and also influence ABA-responsive transcription resulting in enhanced drought tolerance (Ma et al. 2015). Studies have also been conducted in model plant *Arabidopsis*, where miRNA169 targets NFY TFs and regulates drought tolerance (Zhao et al. 2009).

miR160, miR167 and ARF TFs co-regulate adventitious rooting

In *Arabidopsis*, miR160 and miR167 are known to regulate ARF TFs at post-transcription level (*ARF10*, *ARF16* and *ARF17* in case of miR160; *ARF6* and *ARF8* in case of miR167) and are involved in development of adventitious roots (Rhoades et al. 2002; Mallory et al. 2005; Gutierrez et al. 2009). ARF17 is a negative regulator, whereas ARF6 and ARF8 are positive regulator of adventitious rooting, suggesting their involvement in a response to drought through root development. The above three ARFs also regulate each other's expression at both transcriptional and posttranscriptional levels by modulating the availability of miR160 and miR167. This feedback regulation of micro-RNA homeostasis by their target TFs causes adventitious rooting in *Arabidopsis* (Gutierrez et al. 2009).

miR156, miR172 and SPL/AP2-like TFs co-regulate developmental timing

In *Arabidopsis*, the regulatory network for developmental timing involves two miRNAs (miR156 and miR172) and some TFs from SPL/AP2 family (Wu et al. 2009). The miR156 targets 10 members of the SPL TF family (*SPL2*, *SPL3*, *SPL4*, *SPL5*, *SPL6*, *SPL9*, *SPL10*, *SPL11*, *SPL13* and *SPL15*), while miR172 targets six AP2-like TFs (*AP2*, *TOE1*, *TOE2*, *TOE3*, *SMZ* and *SNZ*). However, since, five of the above 10 SPL TFs (*SPL3*, *SPL4*, *SPL5*,

Table 4 Micro-RNA (miRNA) involved in drought response, and their target TF genes in different plant species

S. no.	MiRNA	Plant species	Target genes	Target protein class (function of target gene)	References
1.	miR156/157	<i>A. thaliana</i>	<i>SPL2, SPL3, SPL10</i>	SQUAMOSA-promoter binding proteins (TF)	Kasschau et al. (2003); Chen (2004); Vázquez et al. (2004); Schwab et al. (2005)
2.	miR159	<i>A. thaliana</i>	<i>TCP2, CP3, TCP4, CPI10, TCP24, GAMYB</i>	TCP, a bHLH TF, MYB (leaf development and cell division, hormone response)	Palatnik et al. (2003), Sunkar and Zhu (2004); Achard et al. (2004); Schwab et al. (2005)
3.	miR159a,b	<i>T. aestivum</i>	<i>MYB, WRKY</i>	MYB, WRKY TF (abiotic stress, auxin signaling)	Liu et al. (2013); Gupta et al. (2014); Ma et al. (2015)
4.	miR160a	<i>T. aestivum</i>	<i>ARF</i>	Auxin responsive factor TF (stress adaptation)	Liu et al. (2013)
5.	miR164	<i>A. thaliana, O. sativa, T. aestivum</i>	<i>CUC1, CUC2, NAM, NAC1</i>	NAC domain TF (plant morphogenesis, auxin signaling and root, oxidative stress response)	Mallory et al. (2004); Guo HS et al. (2005); Kim et al. (2009); Gupta et al. (2014); Fang et al. (2014)
6.	miR165/166/166 h	<i>A. thaliana, T. aestivum</i>	<i>PHB, PHV, REV, RLD1, ATHB15, Class-III HD-ZIP protein 4</i>	HD-ZIP TFs (meristem formation, vascular development, stress response)	Floyd and Bowman (2004); Juarez et al. (2004); Kim et al. (2005); Gupta et al. (2014)
7.	miR169d	<i>T. aestivum</i>	<i>CCAAT-box TF</i>	<i>CCAAT-box TF</i> (ABA-responsive transcription, drought tolerance)	Ma et al. (2015)
8.	miR172	<i>A. thaliana, O. sativa, T. aestivum</i>	<i>AP2, TOE1, TOE2, TOE3, GLL15</i>	APETALA2-like TF (floral development, phage change, stress response)	Aukerman and Sakai (2003); Chen (2004); Lauter et al. (2005); Schwab et al. (2005); Gupta et al. (2014)
9.	miR319	<i>T. aestivum</i>	<i>MYB3</i>	MYB TF (abiotic stress tolerance)	Zhou et al. (2010)
10.	miR393	<i>A. thaliana, O. sativa, T. aestivum</i>	<i>TIR1, bHLH</i>	F-box protein-bHLH TFs (hormone response, signaling pathway, basal defence)	Jones-Rhoades and Bartel (2004); Gupta et al. (2014)
11.	miR1029	<i>T. aestivum</i>	<i>AP2, DREB</i>	Apetala2-like, DREB TF (abiotic stress signaling)	Gupta et al. (2014)

Table 5 A list of important yield QTLs identified under drought environments along with their chromosomal locations, associated markers and R^2 values; TF genes located on the same wheat chromosomes are also shown

QTL	Chromosome location	Associated marker	R^2 (%)	References	Co-localized TF genes on same chromosome ^a (present study)
<i>Qyld.aaw.2B.1</i>	2B	<i>Ppd-B1</i>	N/A	Maphosa et al. (2014)	<i>TaNAC29, TaWRKY19, TaWRKY20</i>
<i>qGYWD.3B.2</i>	3BS	<i>gpw7774</i>	19.6	Shukla et al. (2014)	<i>TaABP1, TaWRKY10</i>
<i>qGYWD.3B.3</i>	3BS	<i>gwm389</i>	21.8	Shukla et al. (2014)	
<i>Q.Yld.aaw-3B-2</i>	3BL	<i>wPt8845</i>	22.0	Bennett et al. (2012)	
<i>QTL-4A-a</i>	4A	<i>gwm397</i>	23.9	Pinto et al. (2010)	<i>TaWRKY12, TaWRKY16</i>
<i>Qdt.ksu-4A</i>	4A	<i>wmc89</i>	N/A	Kirigwi et al. (2007); Alexander et al. (2012)	
<i>QTgw.ipk-4A-FS4</i>	4A	<i>Xgwm0160</i>	21.0	Nezhad et al. (2012)	
<i>qDSI.4B.1</i>	4B	<i>barc20</i>	14.0	Kadam et al. (2012)	<i>TaWRKY44</i>
<i>Qyld.csdh.7AL</i>	7AL	<i>wmc273.3</i>	N/A	Quarrie et al. (2006)	<i>TaWRKY82</i>

^a TF genes were assigned to corresponding wheat chromosomes/arms by BLAST against the mapped wheat sequences available at EnsemblPlants database (Table S2)

SPL9 and *SPL10*) are involved in regulation of developmental timing, it is evident that miR156 also regulates developmental timing by repressing the expression of these five SPL TFs. Two of the above five SPLs (*SPL9* and *SPL10*) also promote the transcription of miR172 indicating the involvement of miR156 in the regulation of expression of miR172 via SPLs 9 and 10. The same two SPLs are in turn involved in regulation of miR156 and miR172 thus forming a negative feedback loop. These interlinking connections ultimately form a regulatory cascade miR156-SPL-miR172-AP2 which is involved in developmental timing in *Arabidopsis* (Wu et al. 2009), thus suggesting their indirect involvement in drought tolerance.

The above results suggest that the TF-miRNA regulation is one of the most important aspects of the study of both miRNAs and TFs for their role in drought stress. Recent interest in TF-miRNA regulation led to the creation of a manually curated database called ‘TransmiR’ (Wang et al. 2009), which is a valuable resource for the study of TF-miRNA regulation. This database would be helpful for understanding not only the mechanisms by which TFs regulate miRNAs, but also about their contribution to plant development and tolerance to biotic/abiotic stress.

TF genes versus major QTL for yield under drought stress

A number of QTLs for drought tolerance have also been reported in wheat and several other crops. Since genes encoding TFs involved in drought tolerance are also known, it was considered fruitful to examine if at least some of the QTLs may actually represent the genes encoding TFs involved in drought tolerance. For this purpose, BLAST

search was conducted against the mapped wheat sequences available at EnsemblPlants database (Yates et al. 2016). Interestingly, out of 42 wheat TF genes, nine TF genes (*TaNAC29, TaABP1, TaWRKY10, TaWRKY12, TaWRKY16, TaWRKY19, TaWRKY20, TaWRKY44* and *TaWRKY82*) were mapped on five wheat chromosomes/arms that were already known to harbor major QTLs for drought tolerance (Table 5; Table S2; Fig. S3; Quarrie et al. 2006; Kirigwi et al. 2007; Pinto et al. 2010; Alexander et al. 2012; Kadam et al. 2012; Nezhad et al. 2012; Maphosa et al. 2014; Shukla et al. 2014). Phenotypic variance explained (PVE; R^2) for these QTLs ranged from 14.0 to 23.9 %.

Presence of both drought TFs and major yield QTL under drought stress on the same chromosome indicated that the above-mentioned five wheat chromosomes are important in imparting drought tolerance. However, it was not possible to identify specific regions of these chromosomes, because at least in some cases, the positions of TF genes and QTLs did not seem to overlap. Further studies to find out if some of the QTLs represent genes encoding TFs may be rewarding.

Meta-QTLs (MQTLs) with precise and narrow confidence intervals prove useful in deducing the candidate genes for the concerned trait. MQTL analyses for grain yield and its related traits under drought stress have been conducted in rice (Swamy et al. 2011), barley (Li et al. 2013) and wheat (Acuna-Galindo et al. 2015). In these studies several candidate genes located in the regions of MQTLs were reported, and were found to be stress-inducible, and were known to be involved in growth, development, signal transduction (including TFs) and sugar transport. The important TF genes includes NAC, MADS box, Zinc finger and CCAAT box. The candidacy of above genes including TF genes for their role in drought stress

has already been proved in rice and other crops (Swamy et al. 2011).

Transgenic plants for drought tolerance

A number of reports are now available on development of transgenic plants for drought tolerance using TF genes (Yang et al. 2010); these reports are listed in a recent review (Wang H et al. 2016). However, no drought-tolerant cultivar has been released using these TFs, although a transgenic wheat developed for *DREB1A* gene at Japan International Research Center for Agricultural Sciences is under field testing (Blum 2014; Waltz 2014). One of the limitations in such studies is lack of precision in phenotyping for drought tolerance.

For developing drought-tolerant transgenics, phenotyping is generally done under controlled environments and the results generally are not reproducible under field conditions. This led to the failure in utilizing the results of these studies in plant breeding programs. In wheat, 14 transgenic wheat lines (*DREB1A*-wheat) that were selected under greenhouse conditions for survival to severe drought (SURV) and for high water use efficiency (WUE) failed to outperform the controls in terms of grain yield under water deficit; however, the events selected for WUE were identified as lines that combine an acceptable yield under well irrigated conditions (Pierre et al. 2012). Most of the studies for drought tolerance in transgenic plants suggested improved performance under laboratory and greenhouse conditions only (Dubouzet et al. 2003; Yang et al. 2010; Wang H et al. 2016), except few studies that confirmed improved drought resistance in transgenics under field conditions [SNAC1 (Hu et al. 2006), NFYB1 (Nelson et al. 2007), and *DREB1A/CBF3* (Xiao et al. 2009)].

From the above account, it is obvious that phenotyping for drought tolerance is very crucial and should be conducted under suboptimal field conditions (Yang et al. 2010). This will enable us to draw correct conclusions about the real function of the discovered genes towards drought tolerance and their utilizations in plant breeding. Since drought tolerance is a complex trait, and several phenotypic parameters are available to measure it, a combination of the following phenotypic parameters may prove useful for improving yield under water-limited conditions- (1) water use efficiency, (2) root architecture, (3) carbon isotope discrimination, (4) stomatal conductance, (5) osmotic adjustment, (6) remobilization of water-soluble carbohydrates, (7) chlorophyll concentration, (8) stay-green, and (9) delayed leaf senescence (Gupta et al. 2012; Tuberosa 2012).

Molecular markers for TF genes and their possible use in MAS

Marker-assisted selection (MAS) involving markers associated with TF genes can also be used for the development of drought tolerant genotypes (Lata et al. 2011; Budak et al. 2013, 2015). As many as 16 gene specific markers have been listed by Budak et al. (2015), of which 10 markers are associated with genes for DREB and WRKY TFs (Wei et al. 2009; Huseynova and Rustamova 2010; Mondini et al. 2012, 2015; Edae et al. 2013). In one of these studies (Wei et al. 2009), five primer pairs based on the available sequences of *DREB1* genes in common wheat and related species were designed. Two of these primer pairs (P21F/P21R and P25F/P25R) were A genome specific (located on 3A), one primer pair (P18F/P18R) was B genome specific (located on 3B), and two primer pairs (P20F/P20R and P22F/P22R) were D genome specific (located on 3D). The *DREB1* gene that was amplified using primer pair specific to B genome carried two SNPs (S646 and S770), which showed polymorphism between the two parents of a mapping population (Opata 85 and W7984). However, no polymorphism was observed between the orthologues from A and D genomes. One of these SNPs (S770) also helped in mapping the *DREB1* gene between the markers *Xmwig818* and *Xfbb117* on chromosome arm 3BL (Wei et al. 2009). In another study, four SNPs were identified within *DREB1A*, which were found to be associated with four traits, including final biomass, normalized vegetation index (NDVI), days to heading, and spikelet number. The percentage of phenotypic variation explained by those SNPs ranged from 6.4 % for heading date to 9.7 % for NDVI (Edae et al. 2013). Also, HRM (high resolution melting) technology was used to identify and characterize SNPs in EREBP/AP2 domain of genes *DREB2*, *DREB3* and *DREB4* in some durum wheat (*T. turgidum* L. var durum) cultivars, which differed in the level of drought tolerance (Mondini et al. 2015).

In addition to the above studies, microsatellite markers derived from genome-wide TF genes were also identified in two legume species. These included a large number of microsatellite markers associated with TF genes that are involved in drought tolerance in chickpea (Kujur et al. 2013) and in *Medicago truncatula* (Liu et al. 2015). Some of these TFs included the following: AP2/ERF, bZIP, WRKY, NAC, NAM, bHLH and MYB. However, to our knowledge, no such SSRs associated with drought-related TFs have been reported in wheat. Therefore, one may like to search such markers in wheat, so that the same along with those discussed above may be used for the development of drought tolerant wheat cultivars using MAS (Fig. 1).

Conclusions and perspectives

The research area of TF-mediated gene regulation in plants has shown rapid progress in recent years. This resulted in a better understanding of the role of TFs in imparting tolerance against different abiotic stresses including drought (Bartels and Sunkar 2005; Yoshida et al. 2014). Progress has also been made in understanding the complex mechanisms underlying various aspects of plant responses to drought and other abiotic stresses. Nevertheless, keeping in view the fact that as much as 5 % of the genome in a crop plant encodes TFs, further studies on the function of TFs and their use in imparting drought tolerance in crop plants should prove useful.

To achieve a better understanding of the role of TFs in providing tolerance against drought stress, it is critical to identify not only the interaction of TFs with *cis*-regulatory elements (CREs), but also to identify the target-downstream genes for TFs. Post-transcriptional/post-translational modifications (including phosphorylation) of TFs and miRNA-TF co-regulatory networks under drought stress are other areas of research, which will receive increased attention in future. While conducting these future studies, we also need to keep in mind that the regulation of gene expression by TFs is also highly context-dependent. Human ENCODE project (The ENCODE Project Consortium 2012) provides strong evidence to support the assumption that the binding of a TF to its TF specific binding site (TFBS) is also dependent on its chromatin state, DNA methylation and numerous additional factors (Wang H et al. 2012; Wang J et al. 2012; Yanez-Cuna et al. 2012). This has led to the concept of Epicistrome; the genome wide information on epicistrome has been collected recently in *Arabidopsis* (O'Malley et al. 2016), and in future, similar information should become available in crop plants (including wheat) also. These features of the function of TFs are difficult to measure and predict, and constitute the so-called “cellular context” that influences the expression level of genes. In future, an understanding of the complex mechanisms of signaling and transcriptional regulation operated by TFs under drought stress will certainly improve. This will help in developing improved drought tolerant cultivars in wheat and in other important crops for increasing yield and quality under drought stress, thus contributing to sustainable agriculture.

Author contribution statement PKG conceived, outlined, edited and wrote a part of the review. VG prepared outline and wrote the first draft of the manuscript and assisted PKG in finalising the manuscript. VJ wrote MicroRNA and TF co-regulatory networks section and AK wrote the TF database section.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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