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Transcriptional Network Involved in Drought Response and Adaptation in Cereals

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Abstract

Drought is the major abiotic stress in many wheat environments, decreasing grain yields and farmer's income. Finding ways to improve drought tolerance in wheat is therefore a global effort. Transcription factors (TFs) play important roles in drought tolerance by stimulating plant's protective genome activities in response to heat and water limitation. TFs are specialized proteins which can bind to specific DNA elements in gene promoters and modulate gene expression in response to various external and internal stimuli. Thus TFs is a crucial part of plant signal transduction pathway mediated by signal receptors, phytohormones and other regulatory compounds. The activities of TFs are closely related to their structure, and their binding specificity is determined by the homo-/hetero-dimerization of TFs. The expression of downstream genes may produce a subset of TFs or regulate other functional proteins involved in physiological drought adaptation. Thus, the hierarchic regulations of TF activities, downstream gene expression and protein-protein interaction comprise a complex regulatory network, which participates in drought response and adaptation in cereal crops. Basic mechanisms of this regulatory network have been described, but more insight is needed to find new tools for enhancing cereals' adaptation to drought stress.

Keywords: Abiotic stress, cereals, drought, regulatory networks, transcription factors

1. Introduction

Drought is the major environmental factor that limits crop growth and yield globally. Improving crop performance under water limiting conditions is, therefore, an important research focus of plant scientists around the world. Limited water availability evokes adaptive physiological responses regulated by changes in expression of numerous stress-responsible genes.

Transcription factors (TFs) are groups of proteins that bind to specific regulatory DNA elements located in gene promoters upstream of transcription initiation sites, repressing or activating target gene expression. Intensive research in recent years has shown that temporal and spatial modulation of stress-related TFs provides an efficient way for plants to deal with unfavourable growth conditions. TFs involved in drought response were identified and characterized in various cereal species, including all major food crops such as in rice [1–4], wheat [5–8], barley [9, 10], and maize [11, 12]. Overexpression of several target genes encoding stress-responsive TFs led to improved survival rate under water limitation in transgenic plants [4, 10, 12–14].

The activities of TFs are closely related to their structure. TFs usually contain a DNA-binding domain (DBD) and a transcriptional activation domain (TAD) [15]. The DBD enables TFs to bind with specific promoter elements of target genes, and TAD mediates regulation of the downstream gene either directly or in cooperation with other proteins. TAD usually represents a low-complexity sequence that prevents protein self-folding and facilitates protein–protein interactions (PPI). The transcriptional response to drought in cereals is controlled by a large number of TFs, which have been grouped into several different families based on their structure and binding specificity. The main TFs discussed in this article belong to the following families: the DRE-binding protein/C-repeat binding factors (DREB/CBF) [1, 13, 16, 17], the NAM/ATAF1/CUC2 (NAC) factors [18, 19], the MYB family [20, 21], the WRKY family [9, 22], the basic leucine zipper family (bZIP) [14, 23–25], and the homeodomain-leucine-zipper (HD-Zip) family [26–28].

When plants suffer water deficiency, receptors from the cell membrane/cell wall sense the extracellular stress signals and convert them into intracellular secondary messengers such as Ca^{2+} and inositol phosphate [29]. How exactly the signal is transmitted toward gene activation is still poorly understood and is a subject of intensive multidisciplinary investigations. However, it is well agreed that plant hormones, especially abscisic acid (ABA), play significant role in drought stress-related transcription, in many cases through modulating phosphorylation status of transcription factors and other regulatory proteins.

The objective of this article is to review the involvement of TFs in drought response and adaptation in cereals and to illuminate the complexity of the factors and processes involved. The article is subdivided into four sections, which will (1) give examples of drought-related hierarchy in TF interactions regulated by plant hormones, (2) provide an overview of major families of cereal TFs involved in drought response, (3) overview existing data on TF target gene networks activated in response to drought, and (4) describe the homo- and heterodimerization in relation to TF's activities.

2. Plant hormone crosstalk in drought relevant regulatory pathways

Phytohormones play critical roles in linking the stress-responsive signaling cascades. ABA is a key plant hormone that functions as a link between environmental stress reception and adaptive transcriptional programs such as the regulation of cellular mechanisms, carbohydrate

and lipid metabolism. Similar to ABA, gibberellic acid (GA) and jasmonic acid (JA) play important functions in cellular stress network signaling. Different receptors have been reported to recognize and bind with these plant growth regulators in order to activate or modulate downstream responses [30].

Drought and ABA-mediated signals are perceived through three main pathways by different receptors (see Figure 1). The first receptor PYR/PYL/RCARs (PYRABACTIN RESISTANCE / PYRABACTIN RESISTANCE-LIKE / REGULATORY COMPONENT OF ABA RECEPTOR-SPYR) binds ABA and inactivates the type 2C protein phosphatases (PP2Cs), which leads to the accumulation of SNF1-RELATED PROTEIN KINASES (SnRK2s) [30]. SnRK2s activate ABA-responsive TFs such as *Arabidopsis* AREB1, AREB2, and AREB3. These TFs regulate ABA-dependent gene expression involved in several physiological processes such as the movement of stomatal guard cells, thereby increasing the tolerance to drought [30]. AtMYB44 is one of the TFs that negatively regulate the target genes coding PP2Cs, which leads to stomatal closure and reduced transpiration losses [31]. Protein-coupled receptor-type G proteins (GTGs) such as GTG1/GTG2 are involved in the second ABA reception pathway, which was first reported in *Arabidopsis* [30]. GTG1/GTG2 proteins are membrane-localized receptors with functions in seedling and pollen tube growth and development, acting through voltage-dependent anion channels. The third ABA receptor is the H subunit of Mg-chelatase (CHLH/ABAR), which regulates the lipid metabolism linked to drought tolerance in plants [30].

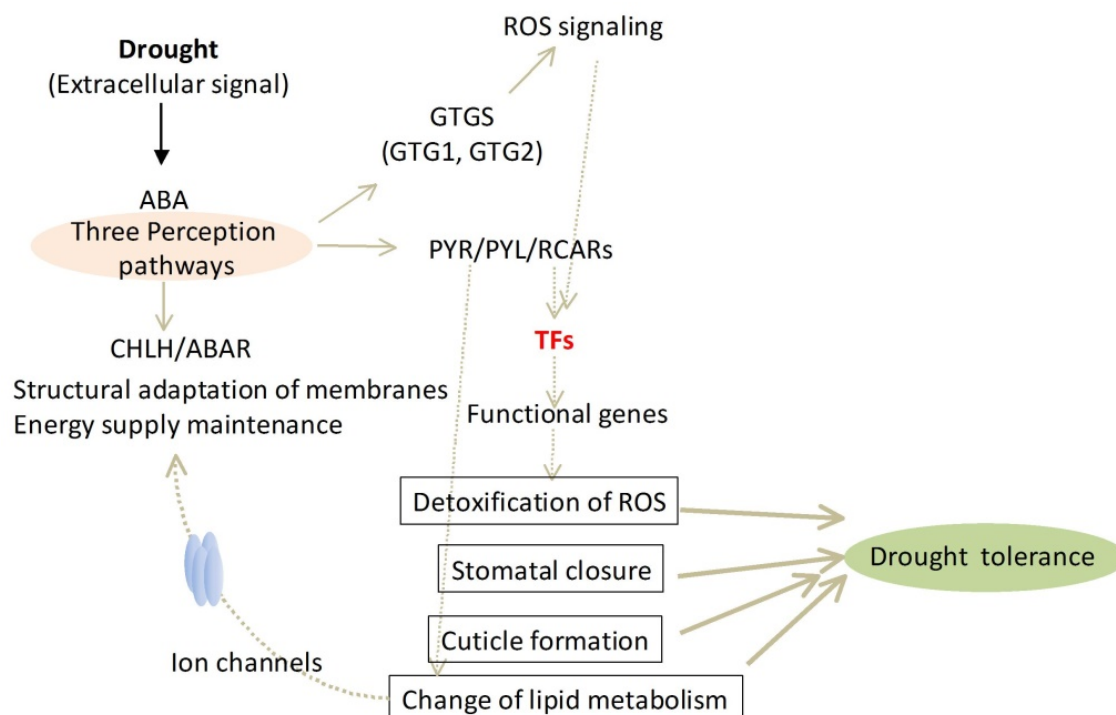


Figure 1. A schematic model of the signal chain from drought stress perception to physiological responses and drought tolerance.

It was also demonstrated that ABA can increase the transcription level of reactive oxygen species (ROS) network genes [30]. ROS are reactive oxygen-based molecules such as superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH^\cdot), which not only toxically damage cells through membrane peroxidation and de-esterification under environmental stresses but also trigger stress endurance in plants [30]. For example, ABA has been shown to trigger the activity of cytosolic aldehyde oxidase and xanthine dehydrogenase, which separately produce H_2O_2 and O_2^- in drought [32].

The GA receptor GA INSENSITIVE DWARF1 (GID1) was reported from rice and is a homolog of the *Arabidopsis* GID1a/b/c [30]. GA-responsive TFs GRAS (GA insensitive [GAI], REPRESSOR of *ga1-3* [RGA], and SCARECROW [SCR]) are GA signaling repressors involved in GA-controlled plant development [30]. Subgroup of GRAS, called DELLA proteins, can interact with GID1 and lead to DELLA protein degradation. The downstream gene of DELLA TFs encoding a RING-H2 zinc finger factor XERICO is involved in ABA and GA transduction pathways under abiotic stresses [30]. Further, the DELLA protein RGL3 can be responsive to JA and interact with the JA regulator OsJAZ (jasmonic acid ZIM-domain protein) under drought [30]. Thus, DELLA proteins can be considered as the interface of ABA, GA, and JA signaling pathways in response to water deficiency [30].

The regulation network of TFs plays an important role in stress-relevant hierarchic regulatory pathways. OsNAC10, a NAC TF, can up-regulate the downstream genes encoding AP2 and WRKY TFs involved in ROS detoxification and scavenging for drought response through the ABA synthesis pathway. The mechanisms of plant response to drought include cell wall development and cuticle formation [30]. The promoter region of the gene *OsNAC6* contains various recognition sites such as ABREs, MYBRS, MYCRS, W-boxes, and GCC boxes, which can be separately recognized by TFs AREB/ABF, MYB, MYC, WRKY, and ERF [33]. These TFs are likely to bind to the corresponding *cis*-elements and co-regulate the expression of *OsNAC6* that participate in the ABA induction pathway and abiotic stress response in plants. In the bZIP family, the gene encoding OsbZIP12 was also found to have MYBRS, MYCRS, and W-box motifs in its promoter region, which can be recognized by TFs MYB, MYC, and WRKY, respectively [34]. Besides, OsNAC5 and OsbZip23 might co-regulate the expression of the downstream gene *OsLEA3* since both of them enhance the transcription level of *OsLEA3* [35]. OsDREB1F might interact directly/indirectly with some bZIP family members in the ABA-dependent pathway that activate transcription of the ABA responsive genes *rd29B* and *RAB18* [3]. However, more in-depth studies are needed to identify these events and to explain the underlying mechanism.

3. Major families of cereal TFs involved in drought response

Transcription factors are classified into several family groups mainly based on characteristic amino acid sequences of its conserved DBDs [36, 37]. Of these, the families DREB/CBF, NAC, MYB, WRKY, bZIP, and HD-Zip are the main TFs involved in drought. Their structural features, classification, and representative family members in cereals are summarized in Table 1 and Figure 2.

TF	Species	TFs name	Cis-element recognition	Downstream genes	Accession/or locus number	Reference	ABA (D/I)	Transgenic plants	Stress inducible/tolerance
DREB	Rice	OsDREB1A	DRE/CRT (G/ACCGAC)	e.g., <i>cor15A</i> , <i>rd29A</i> , <i>rd17</i>	AF001168	[1, 129]	D	Rice, <i>Arabidopsis</i>	Drought, salt, cold
		OsDREB1E	DRE/CRT (G/ACCGAC)	U	AY785896	[44]	I	Rice	Drought
		OsDREB1F	DRE/CRT (G/ACCGAC)	<i>rd29A</i> , <i>COR15a</i> , <i>rd29B</i> , <i>RAB18</i>	AY345234	[3]	D/I	Rice, <i>Arabidopsis</i>	Drought, salt, cold
		OsDREB1G	DRE/CRT (G/ACCGAC)	U	XM_483622	[44]	I	Rice	Drought
		OsDREB2A	DRE/CRT (G/ACCGAC)	U	AF300971	[45]	I	Rice	Drought
		OsDREB2B	DRE/CRT (G/ACCGAC)	U	AK099221	[44]	I	Rice	Drought
	Wheat	TaDREB1	DRE/CRT (TACCGACAT)	<i>rd29A</i>	AF303376	[41]	I	Rice, <i>Arabidopsis</i>	Drought, salt, cold
		TaDREB2	DRE/CRT (G/ACCGAC)	e.g., <i>TaRAB16.5</i> , <i>TaWZY2</i> , <i>TaWlt10</i>	GU785008	[13]	I	Barley, wheat	Frost, drought
		TaDREB3	DRE/CRT (G/ACCGAC)	e.g., <i>TaRAB16.5</i> , <i>TaWZY2</i> , <i>TaWlt10</i>	GU785009	[13]	I	Barley, wheat	Frost, drought
	Barley	HvDREB1	DRE/CRT (G/ACCGAC)	<i>rd29A</i>	DQ012941	[47]	D/I	<i>Arabidopsis</i>	Drought, salt, cold
		HvCBF4	DRE/CRT (G/ATCGAC)	e.g., <i>Atase</i> , <i>LRR</i> , <i>CytP450</i>	AF298230	[48]	I	Rice	Drought, salt, cold
	Maize	ZmDREB1A	DRE/CRT (G/ACCGAC)	e.g., <i>COR15A</i> , <i>KIN1</i> , <i>KIN2</i>	AF450481	[11]	I	<i>Arabidopsis</i>	Drought, cold, salt
		ZmDREB2A	DRE/CRT (G/ACCGAC)	<i>rd29A</i> , <i>rd29B</i>	AY108198	[110]	I	<i>Arabidopsis</i>	Drought, heat
		ZmDREB2.7	DRE/CRT (G/ACCGAC)	U	GRMZM2G028386	[46]	I	<i>Arabidopsis</i>	Drought
NAC	Rice	OsNAC5	NACRS (CACG)	<i>OsLEA3</i> , <i>Os06g0681200</i>	AK102475	[35, 57, 130]	D	Rice	Drought, salt, cold,
		OsNAC6	NACRS (CACG)	<i>AK104277</i> , <i>AK110725</i>	B028185.1	[33, 35, 58]	D	Rice	Drought, cold, salt
		OsNAC9	NACRS	e.g., <i>NCED</i> , <i>Ca²⁺ATPase</i> , <i>CCR</i>	GSE31855	[59]	U	Rice	Drought
		OsNAC10	U	U	U	[60]	D	Rice	Drought, salinity
		OsNAC52	NACRS	e.g., <i>rd29A</i> , <i>rd29B</i> , <i>RD22</i>	AAT44250	[61]	D	<i>Arabidopsis</i>	Drought
		ONAC045	NACRS	<i>OsLEA3-1</i> , <i>OsPM1</i>	CT829509	[19]	D	Rice	Drought, salt
		SNAC1	U	U	AK067690	[18]	D	Rice	Drought, salt
	Wheat	TaNAC-2	NACRS	e.g., <i>rd29A</i> , <i>rd29B</i> , <i>RD22</i>	U	[52]	D/I	<i>Arabidopsis</i>	Drought
		TaNAC67	NACRS	<i>DREB2A</i> , <i>COR15</i> , <i>ABI1</i> , <i>ABI2</i>	KF646593	[54]	D	<i>Arabidopsis</i>	Drought, salt, cold
		TaNAC69	NACRS	<i>Chitinase</i> , <i>ZIM</i> , <i>glyoxalase I</i>	U	[53]	U	Wheat	Drought
		TaNAC69-1	U	U	AY625682	[131]	U	N	Drought, salinity, heat
	Maize	ZmSNAC1	U	U	U	[132]	D	Sorghum	Drought, cold, salt
		ZmSNAC052	U	U	KM987612	[55]	U	N	Drought, cold
		Zma000584	U	U	KP283536	[55]	U	N	Drought, cold
		Zma006493	U	U	KM670443	[55]	U	N	Drought
		Zma001259	U	U	KM670444	[55]	U	N	Drought, cold, salt
MYBs	Rice	OsMYB3R-2	MYBRS	<i>Dehydration-responsive element-binding protein 2A</i> , <i>COR15A</i> , <i>RCI2A</i>	BAD81765	[20]	U	<i>Arabidopsis</i>	Drought
		OsMYB4	U	U	Y11414	[71]	U	Apple	Drought, cold
		OsMYB48-1	MYBRS	e.g., <i>OsPP2C68</i> , <i>RAB21</i> , <i>OsNCED4</i>	Os01g74410.2	[72]	D	Rice	Drought, salinity
	Wheat	TaMYB3R1	U	U	HQ236494	[73]	D	N	Drought, salt, cold
		TaMYB30-B	MYBRS	<i>rd29A</i> , <i>ERD1</i>	U	[7]	I	<i>Arabidopsis</i>	Drought
	Maize	ZmMYB-R1	U	U	JQ337942	[70]	D	N	Drought, salt, heat, cold
WRKY	Rice	OsWRKY3	U	U	Os03g55080	[81]	D	N	Drought
		OsWRKY4	U	U	Os06g44010	[81]	U	N	Drought, cold, flood
		OsWRKY8	U	U	Os11g02480	[81]	U	N	Drought, cold
		OsWRKY11	U	U	AK108745	[22]	U	Rice	Drought, heat
		OsWRKY18	U	U	Os02g08440	[81]	U	N	Drought, cold, flood
		OsWRKY22	U	U	Os01g61080	[81]	U	N	Drought, cold, flood
		OsWRKY24	U	U	Os01g43650	[81, 82]	D	N	Drought, cold

Table 1. Overview on the main cereal transcription factor family members involved in drought.

TF	Species	TFs name	Cis-element recognition	Downstream genes	Accession/or locus number	Reference	ABA (D/I)	Transgenic plants	Stress inducible/tolerance
WRKY	Rice	OsWRKY42	U	U	Os04g21950	[81]	U	N	Drought, cold
		OsWRKY45	U	U	Os05g14370	[78]	D	<i>Arabidopsis</i>	Drought, disease
		OsWRKY50	U	U	Os02g26430	[81]	U	N	Drought, cold, flood
		OsWRKY53	U	U	Os08g29660	[81]	U	N	Drought, cold, flood
		OsWRKY78	U	U	Os11g29870	[81]	U	N	Drought, cold, flood
		OsWRKY84	U	U	Os01g54600	[81]	U	N	Drought, cold, flood
		OsWRKY96	U	U	Os01g14440	[81]	U	N	Drought, cold, flood
		OsWRKY100	U	U	Os09g16510	[81]	U	N	Drought, cold, flood
	Wheat	TaWRKY2	U	STZ	EU665425	[82]	D	<i>Arabidopsis</i>	Drought, salt
		TaWRKY10	U	U	HQ700327	[83]	U	Tobacco	Drought, salinity
		TaWRKY19	U	<i>Cor6.6, rd28A, rd29B</i>	EU665430	[82]	D	<i>Arabidopsis</i>	Drought, salt, freezing stress
		TaWRKY44	(TTGACC/ TTAACC)	<i>e.g., NtSOD, NtAPX, NtCAT</i>	KR827395	[111]	U	Tobacco	Drought, salt, osmotic stresses
	Barley	Hv-WRKY38	U	U	CAD60651	[133]	U	N	Drought
	Rice	OsZip23	ABRE	<i>OsLEA3-1</i> , et al.	AK072062	[23, 92]	D	Rice	Drought, salt
		OsZip12	ABRE	<i>LEA3, Rab16</i>	U	[34]	D	Rice	Drought
		OsZip16	ABRE	<i>LEA3-1, RAB16C</i>	Os02g09830	[91]	D	Rice	Drought
		OsZip45	ABRE	U	Os05g0569300	[92]	D	Rice	Drought
		OsZip46	ABRE	<i>e.g., RAB21</i>	AK103188	[98]	D	Rice	Drought, heat, hydrogen peroxide
		OsZip52/ RISBZ5	G-box	<i>OsLEA3, OsTPP1, RAB25</i>	Os06g45140	[24]	I	Rice	Drought, cold
		OsZip71	ABRE or DRE	<i>OsCAT, OsNHX1, OsMY</i>	Os09g13570	[25]	D	Rice	Drought, salt
		OsZip72	ABRE	<i>LEA3, Rab16</i>	Os09g28310	[25, 93]	D	Rice	Drought
	Wheat	TabZip60	ABRE	<i>e.g., Atrd29A, Atrd20, Atrd29B</i>	KJ562868, KJ806555-KJ806560	[84]	D	<i>Arabidopsis</i>	Drought, salt, freezing stress
		TaABP1	U	U	HQ166718	[134]	D	Tobacco	Drought, salt, cold
bZIP	Barley	HvbZip13	U	U	U	[86]	D	N	Drought
		HvbZip15	U	U	AK365526.1	[86]	D	N	Drought
		HvbZip18	U	U	AK251589.1	[86]	D	N	Drought
		HvbZip20	U	U	AK359622.1	[86]	D	N	Drought
		HvbZip23	U	U	AK374525.1	[86]	D	N	Drought
		HvbZip29	U	U	AK359391.1	[86]	D	N	Drought, cold
		HvbZip34	U	U	AK365082.1	[86]	D	N	Drought
		HvbZip40	U	U	AK249686.1	[86]	D	N	Drought
		HvbZip42	U	U	AK368116.1	[86]	D	N	Drought
		HvbZip49	U	U	AK369418.1	[86]	D	N	Drought
		HvbZip52	U	U	AK372616.1	[86]	D	N	Drought
		HvbZip53	U	U	AK359129.1	[86]	D	N	Drought
		HvbZip77	U	U	U	[86]	D	N	Drought
	Maize	ZmbZip17	U	U	NM_001158672	[89]	D	N	Drought, heat, salt
		ZmbZip37	U	U	GRMZM5G858197	[88]	U	N	Drought
		ZmbZip72	ABRE	<i>e.g., rd29B, RAB18, HIS1-3</i>	HQ328839	[90]	D	<i>Arabidopsis</i>	Drought, salt, osmotic stress
		ZmbZip74	U	U	GRMZM2G448607	[88]	U	N	Drought
		ZmbZip112	U	U	GRMZM2G103647	[88]	U	N	Drought
HD-Zip	Rice	Oshox22	CAAT (G/C) ATTG	U	AY224440	[27]	D	Rice	Drought, salt
		OsHox4	U	U	AF145728	[104]	U	Rice	Drought
	Maize	Zmhdz10	CAATAATTG	U	JX514832	[108]	D	Rice, <i>Arabidopsis</i>	Drought, salt

U, Unknown; D, ABA-dependent; I, ABA-independent; N, No transgenic.

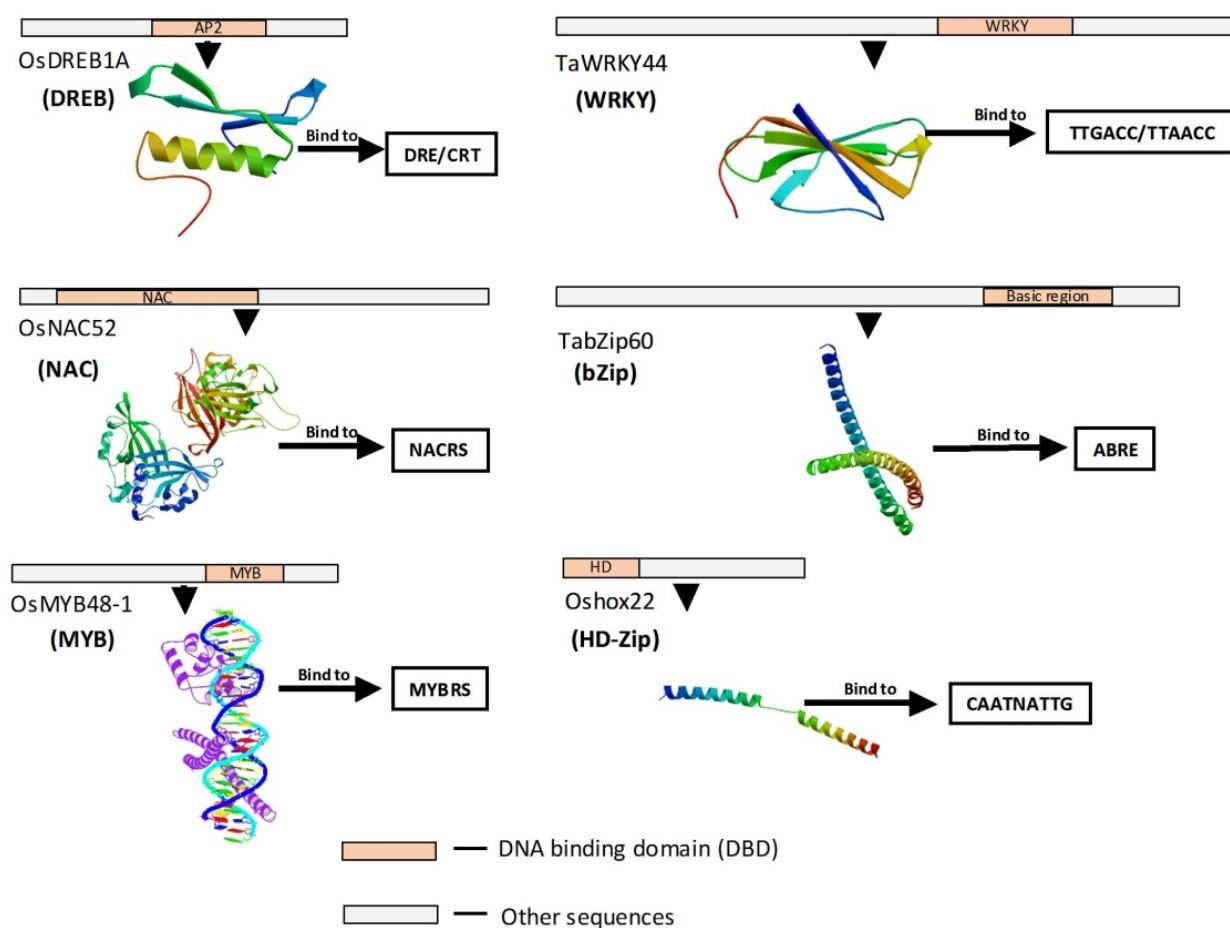


Figure 2. Schematic representation of domain compositions, secondary structures, and recognition sites of major drought-related TF families. The secondary structures were predicted using SWISS-MODEL (<http://swissmodel.expasy.org/>).

3.1. DREB/CBF family

The DREB/CBF family is a member of the AP2/EREBF superfamily of TFs, responsive to several stresses including drought [3, 8]. A cDNA encoding the first identified DREB/CBF family member CBF1 was isolated from *Arabidopsis thaliana* and characterized by Stockinger et al. [38]. DREB/CBF TFs possess about 60 amino acid long AP2 DBD which specifically recognizes a dehydration-responsive C-repeat (DRE/CRT) *cis*-element. The AP2 is a highly conserved domain of DREB family members. It contains two conserved motifs: the YRG and RAYD motifs. The YRG motif is considered to determine DNA binding and the RAYD motif, which forms an α -helix on the C-terminus, is supposed to play a role in PPI [39]. Drought responsive DREB TFs were also found in other plant species such as *Brassica napus* [40], *Triticum aestivum* [41], *Atriplex hortensis* [17], and *Oryza sativa* [42].

Many reported drought-inducible cereal DREBs were shown to be regulators improving stress endurance. In wheat, the gene *TaDREB1* [41] was induced by drought, salt, and cold. The transgenic barely containing *TaDREB2* and *TaDREB3* [13] showed improved tolerance in drought and low temperature conditions. In rice, 13 transcriptional factors including seven

DREB1 types (OsDREB1A, 1B, 1C, 1D, 1E, 1F, and 1G) and six DREB2 types (OsDREB2A, 2B, 2C, 2D, 2E, and OsAB14) [43] were isolated and analyzed. The overexpression of OsDREB1A [1] and OsDREB1F [3] resulted in transgenic *Arabidopsis* and rice plants with higher tolerance to salt, drought, and low temperature. OsDREB1G, 2A, and 2B were identified to be strong candidates in drought responsive pathways, while OsDREB1E could slightly improve the drought survival rate in transgenic rice [44, 45]. In different wheat cultivars, TaDREB1 was demonstrated to be inducible by drought, salt, low temperature, and ABA [41]. TaDREB2 and TaDREB3 significantly improved frost and drought tolerance in transgenic barley and wheat [13]. In maize, ZmDREB1A [11], -2A [94], and ZmDREB2.7 [46] contributed to drought tolerance. In barley, the gene *HvDREB1* [47] was induced by drought, salt, and low temperature, while the constitutive expression of *HvCBF4* [48] increased the survival rate of transgenic rice under drought.

3.2. NAC family

The NAM/ATAF/CUC (NAC) TFs contain a unique feature, a conserved N-terminus DBD and a dissimilar C-terminus regulatory domain, and they are spread across the plant kingdom [37]. The name NAC is an abbreviation of three genes designated as no apical meristem (*NAM*), *Arabidopsis* transcription activation factor (*ATAF*), and cup-shaped cotyledon (*CUC*), which encode proteins containing homologous sequences as the NAC domain [49, 50]. *NAM* isolated from petunia by Souer et al. [49] was the first gene demonstrated to encode a NAC protein, followed by the gene *CUC2* from *Arabidopsis* [50]. Mutation of both genes resulted in the absence of apical shoot meristems [51] and led to floral abnormalities such as the alteration of petal primordia positions during the development stage. These evidences show that the TFs *NAM* and *CUC* play important roles in shoot apical meristem formation and determine the organ primordia positions in the floral meristem [49, 50]. But in relation to abiotic stress, the wheat genes *TaNAC2* [52] and *TaNAC69* [53] were strongly expressed under water deficiency and salinity. *TaNAC67* was found to decrease the cell membrane instability, preventing water loss and enhancing other physiological processes that were considered to be responsive to drought, low temperature, and salt stress [54]. In maize, *ZmNAC052*, *Zma000584*, *Zma006493*, *Zma001259z* [55], and *ZmSNAC1* showed increased transcription levels under water deficiency, indicating their potential role in drought tolerance regulation. In rice, *SNAC1* [56], *OsNAC5* [57], -6 [58], -9 [59], and -10 [60] altered the root structure for plant adaptation during drought. Further, the overexpression of *OsNAC045* [19] and *OsNAC52* [61] induced ABA sensitivity and conferred drought resistance in transgenic rice and transgenic *Arabidopsis*, respectively.

3.3. MYBs family

MYB is a group of ancient TFs found in viruses [62] and eukaryotes such as plants, animals, and fungi [63]. The first gene (c1) identified to encode MYB in plants was from *Zea Mays* [64]. MYB TFs contain a conserved DBD called MYB domain characterized by one to three imperfect repeated amino acid sequences (R1, R2, and R3). Each repeat sequence has around 50–53 amino acids which form three α -helices [65]. These three α -helices form a helix-turn-helix structure

when interacting with DNA. The MYB TFs are mostly classified into three classes according to the number of the MYB domain repeats: R1-MYB, R2R3-MYB [66], and R1R2R3-MYB [67]. These TFs participate in responses to dehydration, salt, cold, and drought [20, 68, 69]. In maize, the ZmMYB-R1 was induced by ABA, drought, low temperature, high salt, and heat [70]. The overexpression of rice genes *OsMYB3R-2* [20], *OsMYB4* [71], and *OsMYB48-1* [72] improved the adaptive response to drought and other stresses in transgenic plants. In wheat, TaMYB3R1 [73] and TaMYB30-B [7] were found to be potentially involved in drought adaptation.

3.4. WRKY family

WRKY proteins belong to the superfamily WRKY-GCM1 of zinc finger TFs [74]. They exist in numerous plant species [75] and were reported to be involved in several biotic and abiotic stress responses and developmental processes such as embryogenesis and leaf senescence [75]. WRKY family members contain a highly conserved WRKY domain with 60 amino acids comprised of two motifs. One is the conserved WRKYGQK motif on the N-terminus and the other one is a zinc-finger-like motif on the C-terminus [76]. There are three main groups in the WRKY family according to the different number of WRKY domains and the variable structure of the zinc-finger-like motif [76]. Group I has two WRKY domains, whereas groups II and III have one WRKY domain. The zinc finger motifs of the WRKY domain in groups I and II are the same, but different in group III [75]. The group II has been divided into five subgroups by Eulgem et al. [76], designated as IIa, IIb, IIc, IId, and IIe, according to the conserved motifs outside the WRKY domain. Within these five subgroups, Zhang et al. [77] distinguished another three new groups (2_a+2_b, 2_c, 2_d+2_e). Several drought-related WRKY TFs were found in rice, wheat, and barley [78–80]. In rice, *OsWRKY3*, -4, -8, -18, -22, -24, -42, -50, -53, -78, -84, -96, and -100 were found to be co-expressed in drought and cold stress, and some of them were even expressed in different organs of flooded plants [81]. *OsWRKY11* was identified to be involved in drought and heat response [22]. *OsWRKY45* was found to be sensitive to ABA and considered to play a role in stomatal closure to improve drought and salt tolerance [78]. In barley, *HvWRKY38* was shown to have a function in drought and cold response [9]. In wheat, the overexpression of TaWRKY2, -19 [82], and -10 [83] led to improved drought and salt adaptation in transgenic plants.

3.5. bZIP family

The basic leucine zipper (bZIP) family is another big group of TFs involved in diverse functions such as hormone and sugar signaling and organ development [84]. bZIP proteins commonly have a basic region for DNA binding and a conserved leucine zipper motif [85]. These TFs specifically bind to a DNA sequence with a core *cis*-element ACGT-like TACGTA (A-box), GACGTC (C-box), CACGTG (G-box), and an ABA-responsive element (ABRE) [84]. Some bZIP members were identified to participate in transducing ABA-dependent stress signals and were named as ABRE binding proteins (AREBs) or ABRE binding factors (ABFs) [86]. Numerous bZIP proteins were demonstrated or predicted to be involved in abiotic stress response in cereal plants, e.g., 89 in rice [87], 171 in maize [88], and 141 in barley [86]. They were classified into 11 groups A, B, C, D, E, F, G, H, I, S, and U according to the phylogenetic trees and DNA

binding motif [86] in maize, rice, and barely. The overexpression of several cereal bZIP TFs was identified to be in response to drought stress. In barley, 11 HvbZIP members were identified to be down- or up-regulated by drought [86]. In maize, ZmbZIP37, -17, and -112 showed high expression levels in drought stress conditions [88, 89] and the overexpression of ZmbZIP72 enhanced the drought tolerance in transgenic *Arabidopsis* [90]. In rice, OsbZIP12 [34], -16 [91], -23, -45 [92], -71 [25], and -72 [93] play a positive role in drought tolerance through ABA signal, while OsbZIP52 [24] and -46 [94] were suggested to be a negative regulator in water deficiency. In wheat, the gene encoding *TabZIP60* was highly induced by salt, cold, and ABA, and the overexpression of *TabZIP60* enhanced the drought and frost tolerance in transgenic *Arabidopsis* [84].

3.6. HD-Zip family

The homeodomain leucine zipper (HD-Zip) family is a group of proteins that are unique to the plant kingdom. All members of the HD-Zip family contain the combination of homeodomain (HD) [6] with a following leucine zipper (Zip or LZ). HD is a conserved protein domain containing a 60 amino acids sequence, which is present in all eukaryotic species [95]. HD is a folded structure with three helices, which are responsible for the specific protein-DNA interactions [95]. HD-Zip family proteins have been classified into HD-Zip I, HD-Zip II, HD-Zip III, and HD-Zip IV [96–100] according to different domain structure and functions. According to Chan et al. [101], HD-Zip I TFs have less conserved motifs than HD-Zip II, and the sequences of HD-Zip I outside the HD-Zip domain are quite different, whereas HD-Zip II TFs have several common sequences outside the HD-Zip domain. The HD-Zip III TFs have four additional amino acids on the conjunction of HD and LZ compared with other three subfamilies [102]. HD-Zip I TFs contain no lipid/sterol-binding domain, designated StAR-related lipid transfer (START) domain, which was found in HD-Zip III and HD-Zip IV TFs [102]. Hence, the special structural feature of HD-Zip I TFs is the presence of HD and leucine zipper and the absence of common sequences outside the HD-Zip domain [103].

In rice, the *HD-Zip I* subfamily has 14 members: *Oshox4-6*, *Oshox8*, *Oshox12-14*, *Oshox16*, and *Oshox20-25* [104]. Three of them, *OsHOX6*, *OsHOX22* and *OsHOX24*, are homologs of the ABA and abiotic stress-inducible genes *AtHB7* and *AtHB12* in *Arabidopsis* [105]. *OsHOX22* and *OsHOX24* have been identified to be involved in drought, cold, and ABA response. *OsHOX22* is strongly activated by high salinity and ABA, but it is weakly induced by frost [27]. Zhang et al. [27] found that the insertion of T-DNA into the *OsHOX22* promoter region led to a decreased gene expression level of *OsHOX22* and reduced ABA content, but improved drought and salt endurance of rice seedlings. The authors believe that *OsHOX22* is a negative regulator for stress response by regulating an ABA-mediated signal transduction pathway and ABA biosynthesis [27]. The *OsHOX24* promoter has shown strong activation by water deficiency and high salinity [106]. According to the results of Agalou et al. [104], *OsHOX22* and *OsHOX24* can be induced by drought in drought-sensitive and drought-resistant cultivars, whereas *OsHOX6* can only be induced in drought sensitive cultivars. Although the role of *OsHOX6* and *OsHOX24* TFs is still not clear, the homologs of these TFs, *AtHB7* and *AtHB12*, have been found to be involved in ABA modulation by regulating the protein phosphatase 2C

activation and an ABA receptor gene activity [107]. In short, TFs Oshox6, -22, and -24 are responsive to dry conditions, similarly as the *ATHB7* and *ATHB12*, and their involvement in drought response might have relevance for ABA synthesis regulation [104].

In maize, the HD-Zip TF Zmhdz10 was found to play an important role in drought response [108], and in wheat, only two HD-Zip TFs, TaHDZipI-1 and TaHDZipI-2, were reported so far [109]. However, there is no information about the function of wheat HD-Zip proteins in drought response.

4. TFs target gene network activated in response to drought

TFs are involved in target gene network regulation through their DBD interaction with different gene promoter *cis*-elements mediated by ABA-dependent or ABA-independent signal transduction pathway (see Figure 3).

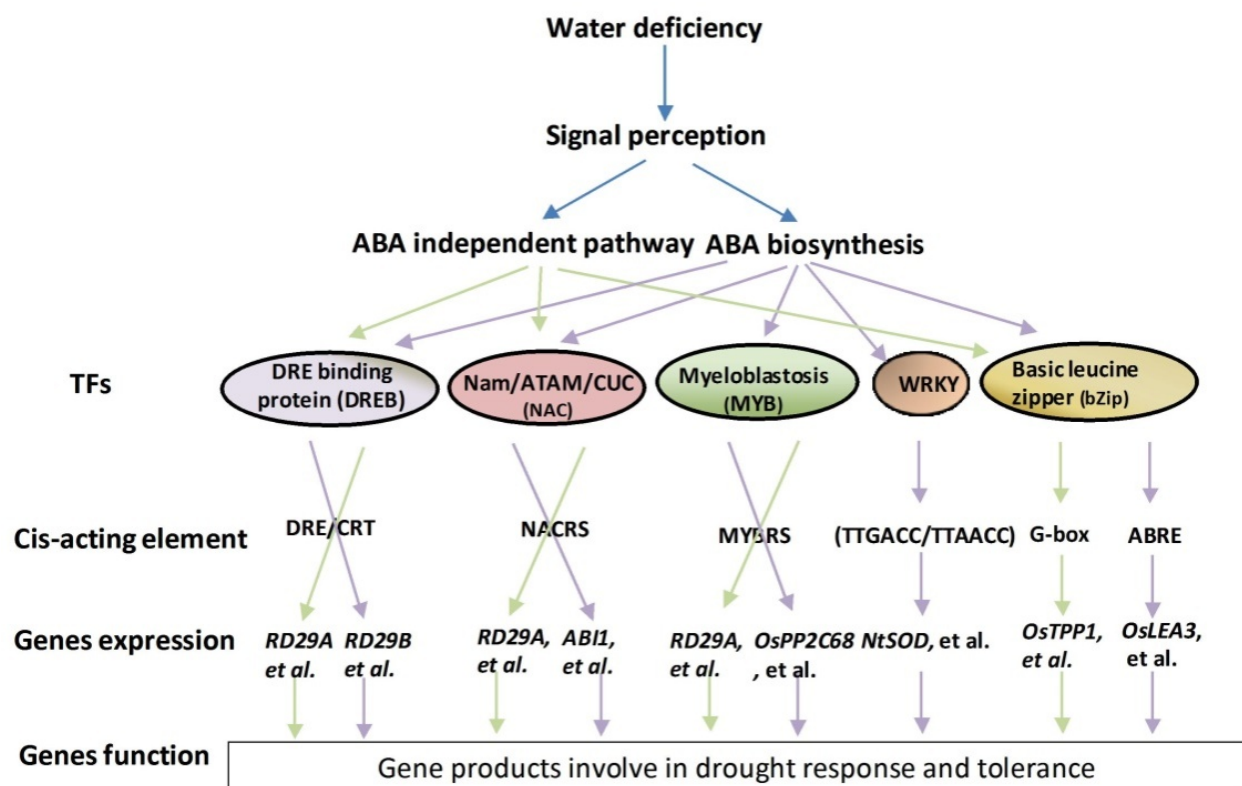


Figure 3. Cereal TFs target gene networks in response to drought through ABA-dependent and -independent pathways. The green arrows show the ABA-independent pathway and the purple arrows show the ABA-dependent pathway.

Most DREB family members such as OsDREB1A [1] and TaDREB1 [41] were found to be activated in ABA-independent pathways. They can enhance the stress tolerance by activating the expression of downstream genes such as late embryogenesis abundant (*LEA*) genes driven

by DRE/CRT *cis*-element. *LEA* genes, such as *COR15A* and *rd29A* (*Cor78*), are also designated as dehydrins (DHNs) or cold-responsive (COR) genes. Their expression products participate in cells protection from stresses by enhancing the membrane stability and correction of protein folding [13]. However, recent studies showed that some members of DREB also participate in ABA-dependent pathways. Wang et al. [3] found that the overexpression of *OsDREB1F* in transgenic rice results in the expression of ABA-induced genes *rd29B* and *RAB18*, whose promoters only contain an AREB element that cannot be recognized by DREB TFs. So far, there is no explanation on illuminating the way for *OsDREB1F* activating the expression of these two genes. The hypothesis is that *OsDREB1F* might interact with bZIP family members that can bind with an AREB element and modulate the transcription of *rd29B* and *RAB18* [3]. The same is true for *ZmDREB2A* [110] and the mechanism is still not clear. Besides, *ZmDREB2A* was identified to activate some downstream genes encoding detoxification enzymes that can protect cells from ROS. However, these genes do not contain a DRE/CRT element. Hence, it is possible that *ZmDREB2A* indirectly affects these genes' expression [110]. Besides, DREBs in different species might have different preference in regulating the expression of downstream genes with different core elements in their promoters. The rice *OsDREB1A*, e.g., prefers to interact with the CRT/DRE core element GCCGAC of genes such as *cor15A*, *rd29A*, and *rd17* instead of core element ACCGAC, while the *Arabidopsis* DREB1A and maize *ZmDREB1A* have equal competition for recognizing core element GCCGAC and core element ACCGAC in the downstream genes [1, 11].

In the WRKY family, more than 10 TFs isolated from rice were found to co-express under drought and cold stresses, but the downstream genes were still not determined [81]. TaWRKY44 from wheat was identified to recognize the core element (TTGACC/TTAACC) in the promoter region of downstream genes and up-regulate genes encoding antioxidant enzymes such as NtSOD, stress-defensive proteins such as NtERD10C, and lipid-transfer proteins such as NtLTP1 to increase plants survival rate in drought. Thus, TF TaWRKY44 participates in regulating antioxidant enzyme activity and decreasing the ROS levels in order to prevent oxidative damage in plant cells [111].

Members of the MYB family regulate the expression level of different target genes involved in the ABA-dependent and independent pathways. The overexpression of *OsMYB48-1* was found to regulate genes such as *OsPP2C68*, *RAB21*, and *OsNCED4*, respectively, involving in ABA early signaling, late response, and the ABA synthesis pathway, contributing to increased drought tolerance under water deficiency [72]. In transgenic *Arabidopsis*, the overexpression of *OsMYB3R-2* increased the expression level of the downstream genes *DREB2A*, *COR15A*, and *RCI2A* and enhanced the plants adaptation to abiotic stresses [20]. Besides, TaMYB30-B was found to induce the expression of stress inducible genes *rd29A* and *ERD1*, involved in the ABA-independent pathway [7].

Members of the bZIP family were also found to regulate downstream gene transcription through the ABA-dependent and independent pathway. OsbZIP52 was suggested to bind to G-box *cis*-elements and down-regulate genes such as *OsLEA3* and *OsTPP* that can improve drought or cold tolerance in rice via the ABA-independent pathway [24]. The expression of

downstream genes *LEA3* and *Rab16* was activated by the transcription factor OsbZIP12 under water deficiency mediated by the ABA synthesis pathway [34].

Most TFs in the NAC family participate in the ABA synthesis pathway. OsNAC5 and OsNAC6 can recognize a core sequence (CACG) of the downstream gene *OsLEA3* and regulate the gene expression that changed root structure and resulted in higher drought tolerance through the ABA signaling pathway [35]. OsNAC6 also participates in up-regulating the transcription of genes encoding peroxidase, which can catalyze a series of oxidative reactions [33]. Some TFs even participate in both ABA-dependent and independent pathways. For example, TaNAC67 was found to up-regulate 10 abiotic stress responsive genes such as *rd29A* and *rd29B*, which were separately related to ABA-independent and -dependent pathways and four ABA synthesis/responsive genes such as *ABI1* [54], thereby improving stress tolerance in plants.

5. Homo- and hetero-dimerization of TFs

Homo- and hetero-dimerization of TFs plays an important role in certain cases and is considered as a pre-requisite for binding of DNA *cis*-elements. Formation of homo- and hetero-dimers plays a further function in modulating the DNA-binding specificity of TFs. Inability to form a dimeric complex may absolutely abolish the DNA binding ability of certain classes of TFs. The high complexity in the selection of hetero-dimerization partners and inability of some TFs to homo-dimerize but hetero-dimerize suggests that homo- and hetero-dimerization of TFs are not random processes, but that specific interactions between monomeric TFs forms are preferred. Hence, dimerization is likely to fulfill specific functions in gene regulation.

The dimerization ability of NAC proteins has been localized to the NAC domain [112, 113]. The residues in the highly conserved NAC domain are involved in the dimer contact and consist of hydrophobic interactions, a twisted anti parallel β -sheet sandwiched between two helices and two prominent salt bridges formed by the conserved arginine and glutamate [114, 115]. Experimental data suggest that NAC TFs are capable of forming both homo- and hetero-dimers. The NAC domain of NAC1 [116] and ANACO19 [113, 114] were shown to form homo-dimers. The NAC domains of OsNAC5 were shown to interact with the NAC domains of OsNAC5, OsNAC6, and SNAC1, generating both homo- and hetero-dimeric complexes. BnNAC14, a *Brassica napus* NAC protein, was shown to form hetero-dimers with BnNAC5-8, BnNAC485, and BnNAC3, but not homo-dimers. Mutational and deletion studies suggested that conserved NAC domains, in particular, the amino acids in close proximity to both the amino and carboxy-terminals, are necessary for mediating the formation of homo- or hetero-dimers [106, 112, 117].

Dimerization of the bZIP class of TFs is mediated by leucine zipper motifs, i.e., non-canonical repeats of leucine or other hydrophobic amino acid residues creating an amphipathic α -helix. The electrostatic attraction and repulsion of the polar residues situated next to the hydrophobic residues enables the formation and stabilization of dimers [118, 119]. Homo-dimeric rice OsbZIP71 is capable of exchanging its subunit to form hetero-dimers with members of the Group-C, in particular, with OsbZIP15, OsbZIP20, OsbZIP33, and OsbZIP88, suggesting a

possible role of hetero-dimerization in efficient binding to *cis*-elements on promoters of target genes [25]. A member of Group-A, the G-box-binding factor AtGBF4, interacts with the Group-G AtGBF1 and the Group-H AtGBF2. Similarly, the members of *Arabidopsis* Group-E, bZIP34 and bZIP61, form hetero-dimers with bZIP51 of Group-I and bZIP43 of Group-S, but none of these TFs belonging to Groups E and I can form homo-dimers due to electrostatic violations in the leucine zipper regions [15, 120, 121]. These data suggest that dimerization between members of within and between groups of bZIP TFs is highly specific and acts as a crucial mechanism to modulate the affinity for *cis*-elements and function of TFs.

In HD-Zips, the leucine zipper that is immediately downstream of the helical domain enables dimerization of HD-Zip TFs, which is a pre-requisite for DNA binding. The HD-Zip leucine zipper is a canonical repeat of leucine amino acid at every seventh residue creating an amphipathic α -helix, which forms a coiled coil structure during dimerization. Formation of hydrophobic interface and complementary charge interactions by the residues present in the coiled coil structure permit or inhibit the formation of dimers from monomeric HD-Zip TFs [105]. *In-vitro* studies have shown that dimerization of HD-Zip is a pre-requisite for DNA binding, and it is assumed that members of HD-Zip Class I and Class II families form hetero-dimers exclusively with other members of their own family [105, 122–124].

Though there is clear evidence for homo- and hetero-dimerization of WRKY proteins, the extent to which they form a functional dimer is unknown and yet to be determined. Of the seven WRKY subclasses, interaction between members of four WRKY class TFs have been experimentally demonstrated. In Group IIa WRKY TFs, dimerization is mediated by a canonical leucine zipper sequence, whereas in members belonging to other Group II and Group III subclasses, presence of leucine/isoleucine/valine residues at approximate seven-residue intervals at their N-termini form an amphipathic alpha helices similar to the secondary structure of a basic leucine zipper and mediate dimerization [125]. It is suggested that these potential leucine zipper sequences might mediate the formation of homo- and hetero-dimers within and between members of different subclasses of WRKY TFs. For example, *Arabidopsis* WRKY TFs belonging to the Group IIa, AtWRKY 18, AtWRKY40, and AtWRKY60, form homo- and hetero-dimers [126]. Similarly AtWRKY30 interacted with AtWRKY53, AtWRKY54, and AtWRKY70 and formed hetero-dimers through leucine zipper motifs present at the N-termini of the subclass of WRKY TFs [127]. Interaction between different subclasses was observed in rice. OsWRKY71, a Group IIa WRKY TF, interacted not only with itself, but also with a Group IId WRKY protein, OsWRKY51 [128]. Formation of homo- and hetero-dimer complexes between different WRKY TFs can have positive or negative effects on their DNA binding activities.

Formation of homo- and hetero-dimers offers an additional large combinatorial flexibility in the regulation of transcription. Performing an accurate analysis and developing a deeper understanding of roles of TFs in various biological processes will require the knowledge of other interacting partners, downstream genes, and location of expression in plant organs along with mechanism of homo- and hetero-dimerization of particular TFs. Thus, it may prove difficult to attempt to make informative conclusions about the roles of specific TFs on the basis of their singular overexpression without this level of knowledge.

6. Conclusions

TFs play a vital role in regulating gene transcription through different signal pathways to enable plants to adapt to harsh environments and abiotic stresses such as drought. Those TFs can recognize and interact with specific *cis*-elements of target genes via DBDs. Some TFs can up-/down-regulate downstream gene transcription, which encodes a subset of TFs integrated in plant hormone signaling pathways, forming a complex hierarchic regulatory network. ABA, JA, and GA, the main plant hormones, act as key regulators in balancing plant growth and abiotic stress response. TFs, as the node of the cellular stress network and growth process, function as the interface of different phytohormone signal transduction pathways. A further layer of complexity is the formation of homo- and hetero-dimers, playing an important role in regulating DNA-binding specificity of TFs. These networks of signal pathways are regulating the activity of stress response TFs and other stress-relative genes, which in turn modulate physiological functions, such as stomatal movement, cuticle formation, and carbohydrate and lipid metabolism, to limit water loss and adapt to drought conditions. However, the hierarchy of TF interactions, the downstream genes' network, the interaction mechanism of the signal transduction pathways, and the protein-protein dimerization are not fully explored and still need more effort to be understood. More knowledge about plant protection system in hostile environments will help to find new tools for enhancing the plants to adapt to abiotic stresses.

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