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Review

Harnessing the potential of plant transcription factors in developing climate resilient crops to improve global food security: Current and future perspectives



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ABSTRACT

Crop plants should be resilient to climatic factors in order to feed ever-increasing populations. Plants have developed stress-responsive mechanisms by changing their metabolic pathways and switching the stress-responsive genes. The discovery of plant transcriptional factors (TFs), as key regulators of different biotic and abiotic stresses, has opened up new horizons for plant scientists. TFs perceive the signal and switch certain stress-responsive genes on and off by binding to different *cis*-regulatory elements. More than 50 families of plant TFs have been reported in nature. Among them, DREB, bZIP, MYB, NAC, Zinc-finger, HSF, Dof, WRKY, and NF-Y are important with respect to biotic and abiotic stresses, but the potential of many TFs in the improvement of crops is untapped. In this review, we summarize the role of different stress-responsive TFs with respect to biotic and abiotic stresses. Further, challenges and future opportunities linked with TFs for developing climate-resilient crops are also elaborated.

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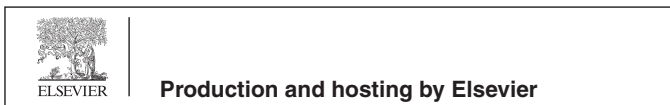
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1. Introduction

Agricultural crops are important as they represent the largest source of calories (70–80%) and protein (60–70%) intake for mankind. However, the changing climate is adversely affecting plant health and causing food insecurity due to outbreak of multiple biotic and abiotic stresses (Mall et al., 2017). Plants have adopted different resistance mechanisms for survival under changing environmental conditions. For example, in response to drought stress, plants start developing a strong root system and promote lateral roots to increase the water catchment area. Similarly, in response to terminal heat stress, plants shift their growth patterns from vegetative to reproductive growth to limit the effect of terminal heat stress on reproduction; many other similar examples exist (Lan Thi Hoang et al., 2017). Plants respond to different biotic and abiotic challenges by modulation of molecular, cellular, biochemical, and physiological responses. In many cases, the driving forces behind these changes are genes encoding transcription activators and repressors that regulate expression of downstream stress responsive genes and modulate different developmental and metabolic pathways (Tolosa and Zhang, 2020). During the past couple of decades, extensive research has focused on the identification of the key factors associated with regulating the molecular response to stress signal perception (Lan Thi Hoang et al., 2017).

Transcriptional factors (TFs) are frontline defensive factors of plants against various biotic and abiotic stresses (Fig. 1). These play fundamental roles in plant tolerance/resistance to various biotic and abiotic stresses (Lan Thi Hoang et al., 2017; Javed et al., 2020). TFs usually respond to stress by binding their target sites within *cis*-acting elements in promoter regions of stress responsive genes (Fig. 1E). TFs binding in promoter regions initiate a complex formation for biochemical, physiological, and molecular responses. The stress response comprises of signal perception, signal transduction, and expression of stress-responsive genes (Fig. 1B–D). The stress signal is received by receptors in plant cell membranes, or the cell wall and transduced through intracellular elements, i.e., Ca²⁺, Reactive Oxygen Species (ROS), phytochromes, phosphatases, and protein kinases to TFs. TFs then control gene expression and initiate expression of stress responsive genes (Erpen et al., 2018).

Plant genomes contain a large complement of TF genes; approximately 6% of total expressed sequence tags (ESTs) (Table S1). However, the major roles under biotic and abiotic stresses are played by dehydration responsive element binding (DREB), basic leucine zipper (bZIP) domain, MYB, no apical meristem (NAM), ATAF1/2, and cup-shaped cotyledon (CUC2) (NAC), heat shock factors (HSF), DNA-binding with one ZF-proteins (Dof), WRKY, Nuclear factor Y (NF-Y), and Zinc-fingers. Meanwhile, TFs have become core part of plants' research due to huge variation in responses elicited and potent role in both biotic and abiotic stress

tolerance such as, WRKY TFs simultaneously regulate drought, heat, cold stress, counter disease, as well as pest and nematode attacks (Jiang et al., 2017).

Keeping in view of the above mentioned facts, we have summarized the current status of different plant TF classes, including DREB, bZIP, MYB, NAC, Zinc-finger, HSF, Dof, WRKY, and NF-Y, and their substantial role in biotic and abiotic stress responses which may facilitate development of resistant and/or tolerant crop plants. Moreover, different crop improvement techniques, particularly gene editing technique is proposed as one of the potential tools for crop improvement by editing TFs. Further, current associated challenges and future opportunities are listed as well.

2. Structure, function, and mechanism of action of various groups of TFs

TFs are classified according to the presence of characteristic sequence motifs which correspond in general to their DNA-binding domains (Fig. 2). Although, there is no strict correlation between sequence type and function, different TF classes tend to have different roles in the hierarchy of responses, although many interact as part of their response, as will be evident from a comparison of the principal classes.

3. Role of transcription factors under abiotic stresses

Global warming is becoming an increasing threat to crop productivity as it exposes crops to a plethora of stresses i.e., drought, heat, flooding, salinity, and heavy metals. These environmental factors are menacing crop survival. Abiotic factors affect growth, productivity, and development of plants, and can reduce up to 50% yields of wheat, rice, maize, and cotton (Baillo et al., 2019). Plants respond to stress by certain physiological adjustments i.e., increasing ion fluxes, production of ROS, accumulation of amino acids and soluble sugars, maintaining homeostasis and osmotic potential, and change in phytohormone concentrations (Fig. 1B). The stress-related receptors receive environmental stimuli and activate the stress responsive genes (Leng and Zhao, 2019). The role of different genes/TFs in response to different stresses is discussed below (Table 1).

3.1. Drought stress

Drought is a devastating abiotic stress, which occurs due to shortage of ground water, high temperature, and/or low rainfall. Drought stress reduces seedling emergence, germination rate, vegetative growth, root & shoot dry matter, and hypocotyl length (Zeid and Shedeed, 2006). It decreases turgor pressure and limits cell

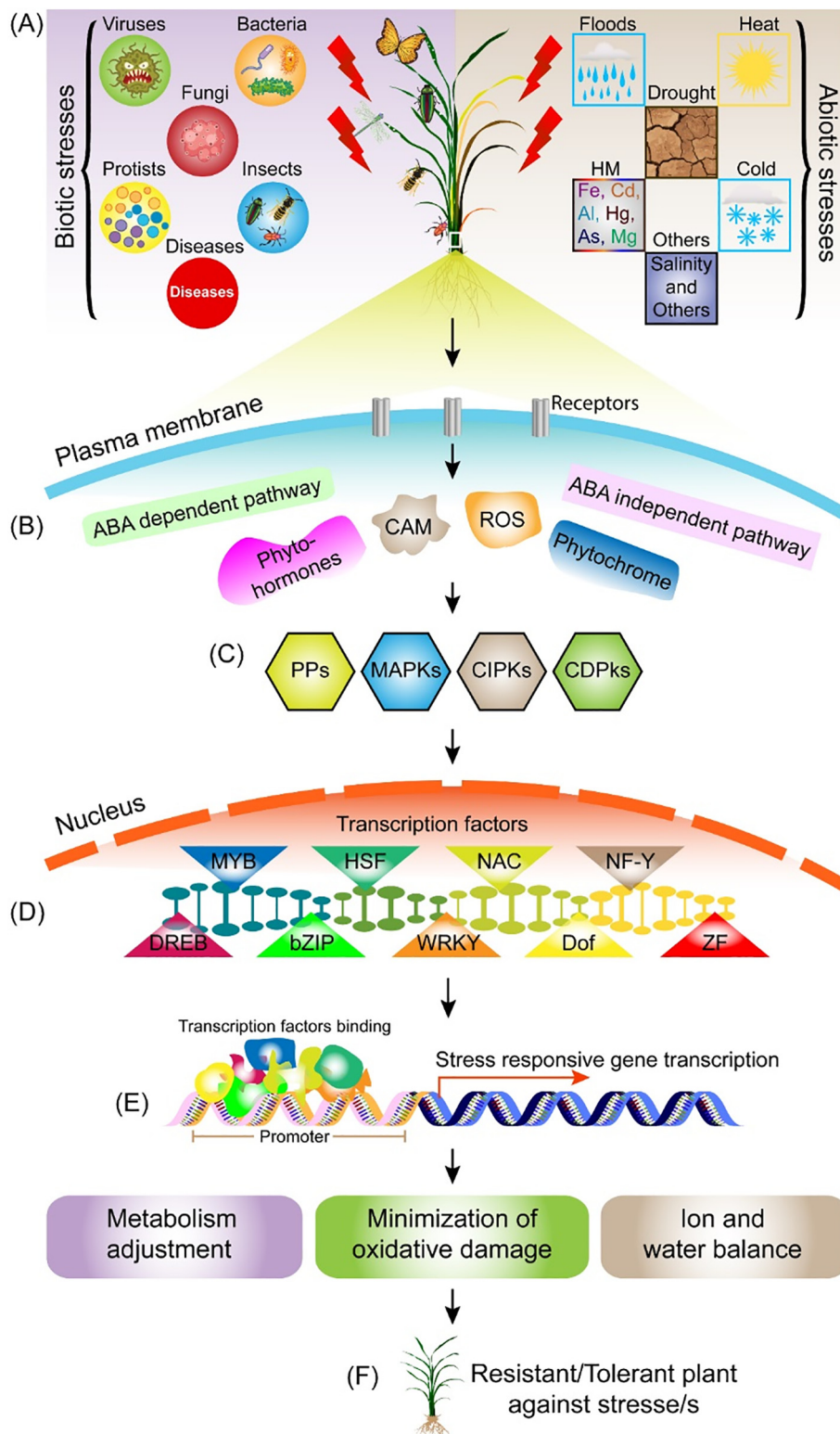
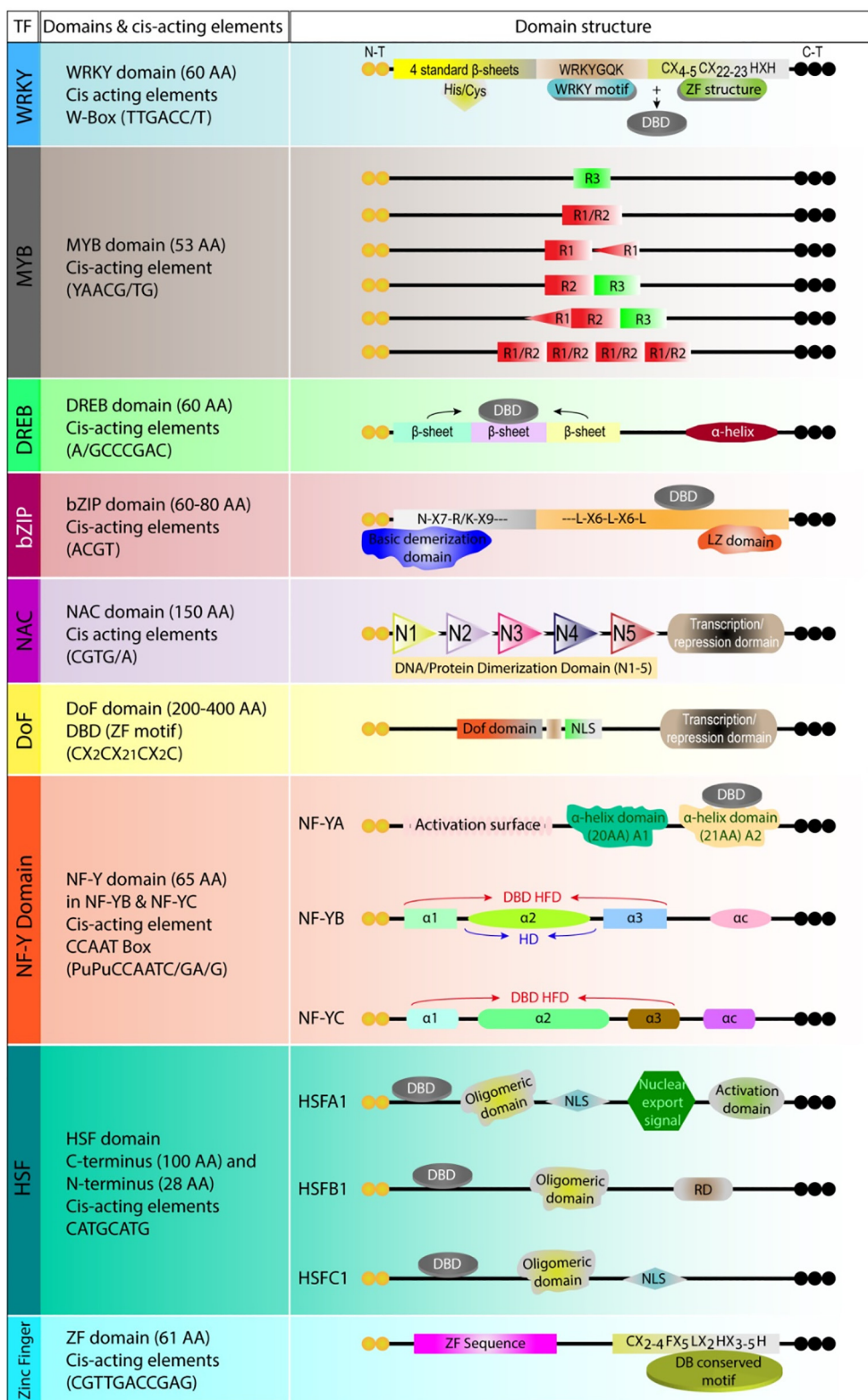


Fig. 1. Mechanism of action of transcriptional factors (TFs) for development of resistance in plants against biotic and abiotic stresses. (A) Different biotic and abiotic stresses affect plant growth and development; however, plants have developed rapid response strategies to unfavorable conditions; these involve interconnected networks at the molecular level controlled by signal cascades. The different components of stress responses are (B) signal perception, and (C) signal transduction, (D) transcriptional regulation, (E) gene expression, (F) gene adoption. When plant cells perceive a stress signal, receptors or sensors in the cell wall or membrane detect the stress stimulus, followed by a rapid response that transduces the external signal to intracellular signals. Signal cascades involving intracellular molecules or ions are activated along with kinase cascades, which are generally cytoplasmic. Major cascades are associated with reactive oxygen species (ROS) and calcium ions (Ca^{2+}). Phytohormones, including abscisic acid, jasmonic acid, salicylic acid, and ethylene, are powerful second messengers that coordinate signal transduction pathways during stress responses. These signals activate several parallel transduction pathways, which often involve phosphatases and protein kinases. Following the initial step of signal perception, plants activate two major signal cascades: the mitogen-activated protein kinase (MAPK) and calcium-dependent protein kinase (CDPK) pathways. Finally, specific TFs are upregulated or downregulated by protein kinases or phosphatases, and the TFs bind to *cis*-elements of stress-responsive genes to enhance or suppress their transcription. Finally, stress resistant/tolerant plants emerge.

elongation, cell growth, and leaf expansion. Acute shortage of water damages the thylakoid membranes and photosynthetic pigments and reduces the photosynthetic rate. During drought stress, plants close stomata, thereby reducing intracellular CO₂ concentration thus reducing photosynthesis and also inducing oxidative damage (Fahad et al., 2017). Plants respond to stress by certain physiological adjustments, i.e., increasing ion fluxes, production

of ROS, accumulation of amino acids, and soluble sugars and changes in phytohormone levels. TFs play an important role in orchestrating these processes by activating genes that execute stress responses (Leng and Zhao, 2019).

WRKY TFs play an important role in improving stress tolerance, particularly drought and heat in various crop plants. *TaWRKY1* and *TaWRKY33* in *Arabidopsis thaliana* increases drought tolerance due



to overexpression of downstream stress responsive genes. *AtWRKY1* locates in the nucleus and binds to the W-box domains of *AtDREB1A*, *AtMYB2*, and *AtAB15* to control their transcription and regulate stomatal conductance (Qiao et al., 2015); in transgenic *Arabidopsis ZmWRKY40*, activated stress related genes and generation of ROS. Overexpression of *TaWRKY2* in wheat increased drought tolerance and grain yield. *Arabidopsis* based *AtWRKY30* was overexpressed in transgenic wheat, resultantly biomass, plant growth, proline concentration, soluble sugar, protein, relative water content, chlorophyll content, and antioxidant enzymes activities were increased to alleviate drought stress (Baillio et al., 2019; Wang et al., 2021). In *Arabidopsis thaliana*, the bZIP gene, *AtABP9* binds to an ABPR motif and increase photosynthetic activity. It increases production of abscisic acid (ABA) and changes composition of photosynthetic pigments. *ZmNF-YB16* overexpressed in young seedling of maize under drought conditions, as a result, antioxidant enzymatic activity was increased to normalize the stress effects (Leng and Zhao, 2019).

Similarly, *SlWRKY8* overexpressed under drought conditions and activated malondialdehyde (MDA), hydrogen peroxide (H₂O₂) production, and antioxidant enzymatic activity. These changes triggered stress responsive genes i.e. *SIRD29*, *SIAREB*, and *SIDREB2A* genes, which resulted in decrease stomatal aperture, oxidative pressure, and increases relative water and proline contents to alleviate drought stress. *DREB1A* overexpressed in *Arabidopsis thaliana*, resulted in high accumulation of solutes and initiation of late embryogenesis abundant protein (Kudo et al., 2017). Similarly, soybean *GmNAC8* overexpressed under drought stress and regulated expression of *GmDi19-3* (drought-induced genes), which increased proline and superoxide dismutase (SOD) accumulation. Overexpression of *ZmNAC111* increased water use efficiency of drought prone maize seedling by upregulating drought responsive genes (Yang et al., 2020).

3.2. Heat stress

Heat stress adversely affects plant growth by reduced chlorophyll contents and induction of oxidative stress due to accumulation of hydroxyl (OH⁻), hydroperoxyl (HO²⁻), alkoxy (RO⁻), and superoxide (O²⁻) radicals. Oxidative stress hinders photosynthesis and respiratory activities, disrupts protein structure, and mem-

brane integrity (Wassie et al., 2020). Heat stress causes burning of leaves and branches, patch formation on leaves, reduction in germination and growth, reduced tillering, and reduction of grain size and grain yield (Fahad et al., 2017). Elevated temperature uplifts the rate of transpiration, which adversely affects root growth. Sucrose phosphate synthase, adenosine diphosphate-glucose pyro-phosphorylase, and invertase are highly sensitive enzymes that disturb sucrose and starch synthesis pathways during heat stress. On the other hand, high temperature increases catalytic activity of Rubisco, but decreases its ability to bind with CO₂ and O₂, and slows down the photosynthetic rate (Crafts-Brandner and Salvucci, 2002).

Triticum aestivum, *Solanum lycopersicum*, *Cicer arietinum*, *Glycine max*, and *Sorghum bicolor* are heat-sensitive crops. Similarly, pollen formation, seed setting, and grain filling are highly heat-sensitive plant stages (Hinojosa et al., 2019). Plants have several adaptations against heat stress, i.e., degradation of oxradicals, reduction in the lipid membrane transformation stage, and biological metabolism. Epigenetic modifications, i.e., acetylation, methylation, phosphorylation, and ribosylation also play role in plant survival during heat stress by modifying histone proteins after translation (Hou et al., 2019). Evolution of heat shock factors (HSFs) is another modification of plants in response to heat stress. *HsfA1s* are prime activators in response to heat stress, while in non-stress conditions; these are suppressed by heat shock proteins, i.e., HSP70 and HSP90. These regulate expression of some TFs, i.e., dehydration responsive element binding 2A (*DREB2A*), heat shock factors A2 (*HsfA2*), heat shock factor B (*HsfBs*), *DREB2C*, multiprotein binding factor 1C (*MBF1C*), and NAC. HSPs are involved in homeostasis at the cellular level and plant defence. At the onset of heat stress, inactive HSFs are activated through oligomerization and shuttle signalling between the cytoplasm and nucleus (Lohani et al., 2019).

HSP70 makes a complex with heat stress *RNA1* (*HSR1*) and translation elongation factor (*eEF1A*), which activates *HSF1* which in turn activates the cell heat stress responsive machinery (Rangan et al., 2020). A complex of TFs network consisting of MYB, bZIP, NAC, and a homeobox linked with Leucine zipper is recognized as effective elements in long-term heat stress conditions. General heat stress responsive elements and stabilizers for protein metabolism are *HSP10s*, *HSP20s*, *HSP60s*, *HSP90s*, and co-

Fig. 2. Illustration of domains' structure, composition, and *cis*-regulatory elements of nine TFs including WRKY, MYB, DREB, bZIP, NAC, Dof, NF-Y, HSF, and Zinc finger. **WRKY:** The WRKY TFs contains the N-terminal WRKYGQK domain, while at the C-terminal, Zinc Finger (ZF) motifs are present. The ZF-motif may be either CX₄₋₅CX₂₂₋₂₃HxH or CX₇CX₂₃HxC. The WRKY domain spans around 60 amino acids and is a DNA binding protein, which binds to W-BOX (TTGACT/C) and many other binding sites (Eulgem et al., 2000; Ülker and Somssich, 2004; van Verk et al., 2008; Rushton et al., 2010; Rushton et al., 2012). **MYB:** The MYB domain consists of 52 amino acids repeats forming 3 α -helix, in which the second and third helix form helix structure with three equally spaced tryptophan, forming hydrophobic core in a three-dimensional (3D) helix structure. The third helix is the "recognition helix" that directly binds to DNA and inserts it into a major groove. Two MYB repeats are bind in the major groove and recognize specific DNA target sequence during DNA contact (Dubos et al., 2010; Zhong and Ye, 2015). **DREB:** The DBD of DREB family members is the AP₂/ERF type with a conserved region of 60 amino acids; AP₂ family members have α -helix and β -sheet stretches at a highly conserved region, the later within the DBD. DREB proteins attach with C-repeat sequence (A/GCCGAC) or dehydration responsive elements (DRE) for activation of stress responsive genes (Fujita et al., 2005; Sharoni et al., 2011; Chen et al., 2016). **bZIP:** The bZIP domain is made up of a basic region at the N-terminal linked to C-terminal leucine zipper. About 16 amino acids are present in the basic region, which form an invariant motif (N-x₇-R/K) that is responsible for binding to DNA. The bZIP domain consists of two structures: N-x₇-R/K-x₉ (DNA binding site) and leucine zipper (hydrophobic amino acids, i.e., Val, Met with heptad repeats of Leu) (Liao et al., 2008; Banerjee and Roychoudhury, 2017). **NAC:** The NAC domain spans approximately 150 amino acids, and has five conserved sub-domains (N₁-N₅) that form motifs for protein-protein interaction, DNA binding, or TF dimerization. Structural studies have shown that DBD is located at N-terminal while regulatory domain is located at the C-terminal (Baillio et al., 2019; Yuan et al., 2019b). **Dof:** The Dof TFs consists of a bi-functional domain, having dual activity for DNA-binding as well as protein-protein interaction. A single ZF-is present in the C₂/C₂ domain needed for binding the target 5'-(T) AAAG-3' sequence or its reversibly orientated sequence, CTTT, with a conserved region of target DNA sequence. The C-terminal region helps in regulation of the transcription process by interacting with different regulatory proteins. (Yanagisawa, 2002; Noguero et al., 2013). **NF-Y:** NF-YA has two domains with α helix structure. The N-terminal conserved region has 20 amino acids α helix A1 domain, responsible for interaction with NF-YB and NF-YC, while the C-terminal which binds with the CCAAT element has a 21 amino acid α -helix A₂ domain. NF-YB and NF-YC, is formed through the Histone Fold Domain. These domains bind with each other through head to tail. Subgroups of NF-Y are NF-YA, NF-YB, and NF-YC, binds to the CCAAT box (Petroni et al., 2012; Nardini et al., 2013; Zhao et al., 2017). **HSFs:** Conserved regions of HSFs include three helical structures an N-terminal DBD with four inverted β -sheets arranged in parallel fashion. The binding sites sequence termed heat responsive elements (5'-AGAAnnTTCT-3') is recognized by the DBD hydrophobic region, which has a helix-turn-helix conformation. At the N-terminal, the oligomeric domain contains two regions of hydrophobic heptapeptide repeats HR-A and HR-B, having five and six heptapeptide repeats, respectively (Yura and Nakahigashi, 1999; Nover et al., 2001; Åkerfelt et al., 2010; Qiao et al., 2015). **Zinc Finger:** Most plants ZF genes have conserved QALGGH amino acid motif within the ZF domain that forms a Q-type C₂H₂ plant specific ZF subfamily. This motif is present at the N terminal on an alpha helix. The ZF-motif has zinc, along with two cysteine and two histidine molecules at base, and one alpha helix or two beta-pleated sheets arranged in anti-parallel fashion in a finger like projection. ZFs play role in sub cellular localization and stress responses (Rajavashisth et al., 1989; Iuchi, 2001; Figueiredo et al., 2012; Kaur and Subramanian, 2016).

Table 1
Role of different transcriptional factor gene families in abiotic stress tolerance in plants.

Stress	Crop	Transcriptional Factors/Genes	Reference	
Drought	<i>Arabidopsis thaliana</i>	AREB1 ⁺ , AREB2/ABF4 ⁺ , ATWRKY1 ⁻ , AtWRKY57 ⁺ , AtWRKY63/ABO3 ⁺ , AtNAC019 ⁺ , AtNAC055 ⁺ , AtNAC072 ⁺ , AtNF-YB7 ⁺ , AtNF-YB3 ⁺ , AtNF-YA5 ⁺ , AtMYB12 ⁺ , AtMYB15 ⁺ , AtMYB33 ⁺ , AtMYB35 ⁺ , AtMYB60 ⁻ , AtMYB44 ⁺ , AtMYB88 ⁺ , AtMYB99 ⁺ , AtMYB96 ⁺ , AtMYB102 ⁺ , AtMYB110 ⁺	(Dubos et al., 2010; Tripathi et al., 2014; Feng et al., 2015; Li et al., 2015a; Joshi et al., 2016; Kimotho et al., 2019; Wei et al., 2020)	
	<i>Triticum aestivum</i>	TaDREB2 ⁺ , TaDREB3 ⁺ , TaWRKY2 ⁺ , TaWRK19 ⁺ , TaWRKY10 ⁺ , TaNAC69 ⁺ , TaNAC2a ⁺ , TaPIMP1 ⁺ , TaMYB1 ⁺ , TaMYB2A ⁺ , TaMYB19 ⁺ , TaMYB3R1 ⁺ , TaMYB31 ⁺ , TaMYBsd1 ⁺ , TaMYB30 ⁺ , TaMYB33 ⁺	(Dubos et al., 2010; Tripathi et al., 2014; Feng et al., 2015; Li et al., 2015a; Joshi et al., 2016; Li et al., 2016; Baillo et al., 2019; Kimotho et al., 2019; Wei et al., 2020)	
	<i>Oryza sativa</i>	OsDREB1F ⁺ , OsDREB2A ⁺ , OsEREBP1 ⁺ , OsWRKY01 ⁺ , OsWRKY2 ⁺ , OsWRKY5 ⁺ , OsWRKY7 ⁺ , OsWRKY43 ⁺ , OsWRKY11 ⁺ , OsWRKY45 ⁺ , OsWRKY47 ⁺ , OsNAC10 ⁺ , OsNAC2 ⁺ , OsNF-YA7 ⁺ , OsbZIP42 ⁺ , OsbZIP46 ⁺ , OsbZIP62 ⁺ , OsMYB2 ⁺ , OsMYB4 ⁺ , OsMYB55 ⁺ , MYB59 ⁺ , OsMYB48-1 ⁺	(Dubos et al., 2010; Tripathi et al., 2014; Feng et al., 2015; Li et al., 2015a; Joshi et al., 2016; Li et al., 2016; Baillo et al., 2019; Kimotho et al., 2019; Wei et al., 2020)	
	<i>Zea mays</i>	ZmDREB1A ⁺ , ZmDREB2A ⁺ , ZmDBF3 ⁺ , ZmDREB2.7 ⁺ , ZmWRKY106 ⁺ , ZmNAC55 ⁺ , ZmSNAC1 ⁺ , ZmNAC111 ⁺ , ZmNF-YB2 ⁺ , ZmNF-YA3 ⁺ , ZmHSF14 ⁺ , ZmHSF20 ⁺ , ZmbZIP72 ⁺ , ZmbZIP4 ⁺ , ZmbZIP60 ⁺ , ZmMYB95 ⁺ , ZmMYB36 ⁺	(Dubos et al., 2010; Tripathi et al., 2014; Feng et al., 2015; Li et al., 2015a; Joshi et al., 2016; Li et al., 2016; Lan Thi Hoang et al., 2017; Baillo et al., 2019; Kimotho et al., 2019; Li et al., 2020b; Wei et al., 2020)	
	<i>Glycine max</i>	GmDREB2A;2 ⁺ , GmERF3 ⁺ , GmWRKY54 ⁺ , GsWRKY20 ⁺ , GmNAC085 ⁺ , GmNF-YA3 ⁺ , GmMYB177 ⁺ , GmbZIP2 ⁺	(Dubos et al., 2010; Tripathi et al., 2014; Feng et al., 2015; Li et al., 2015a; Joshi et al., 2016; Li et al., 2016; Lan Thi Hoang et al., 2017; Baillo et al., 2019; Kimotho et al., 2019; Li et al., 2020b; Wei et al., 2020)	
	<i>Vigna radiate</i>	VrDREB2A ⁺ , VrDREB2B ⁺	(Joshi et al., 2016)	
	<i>Camellia sinensis</i>	CsDREB2A ⁺ , CsDREB2B ⁺	(Joshi et al., 2016)	
	<i>Hordeum vulgare</i>	HvWRKY38 ⁺	(Tripathi et al., 2014)	
	<i>Solanum lycopersicum</i>	SpWRKY1 ⁺	(Tripathi et al., 2014)	
	<i>Solanum tuberosum</i>	StMYB1R-1 ⁺	(Hu et al., 2016)	
	<i>Cicer arietinum</i>	CarNAC3 ⁺	(Li et al., 2015a)	
	<i>Chrysanthemum</i>	CmMYB2 ⁺	(Hu et al., 2016)	
	<i>Setaria italica</i>	SiNF-YA1 ⁺ , SiNF-YB8 ⁺	(Feng et al., 2015; Wei et al., 2020)	
	<i>Cynodon dactylon</i>	CdtNF-YC1 ⁺	(Feng et al., 2015; Wei et al., 2020)	
	<i>Fagopyrum tataricum</i>	FtbZIP5 ⁺	(Lan Thi Hoang et al., 2017; Li et al., 2020a)	
	<i>Poncirus trifoliata</i>	PtrABF ⁺	(Lan Thi Hoang et al., 2017; Li et al., 2020a)	
	<i>Vitis vinifera</i>	VvMYB60 ⁺	(Li et al., 2015a; Baillo et al., 2019)	
	<i>Gossypium hirsutum</i>	GhirNAC2 ⁺	(Shang et al., 2020)	
	Heat	<i>Arabidopsis thaliana</i>	WRKY39 ⁺ , WRKY46 ⁺ , AtWRKY25 ⁺ , AtWRKY26 ⁺ , AtWRKY33 ⁺ , AtNAC42 ⁺ , AtMYB3 ⁺ , AtMYB6 ⁺ , AtMYBL2 ⁺ , AtMYB68 ⁺	(Tripathi et al., 2014; Casaretto et al., 2016; Li et al., 2020a)
<i>Oryza sativa</i>		OsDREB2B ⁺ , OsWRKY11 ⁺ , OsNAC063 ⁺ , OsTZF1 ⁺ , OsMYB55 ⁺	(Yoshida et al., 2008; Li et al., 2010; Nuruzzaman et al., 2013; Tripathi et al., 2014; Casaretto et al., 2016; Guo et al., 2016; Joshi et al., 2016)	
<i>Zea mays</i>		ZmDREB2A ⁺ , ZmWRKY106 ⁺ , ZmNF-YA3 ⁺ , ZmHSF14 ⁺ , ZmHSF20 ⁺ , ZmbZIP60 ⁺ , ZmbZIP4 ⁺ , ZmMYB-R1 ⁺	(Yoshida et al., 2008; Li et al., 2010; Tripathi et al., 2014; Feng et al., 2015; Guo et al., 2016; Baillo et al., 2019)	
<i>Glycine max</i>		GmHSP70 ⁺ , GmDREB1 ⁺	(Kidokoro et al., 2015; Guo et al., 2016)	
<i>Capsicum</i>		CpDREB2 ⁺	(Yoshida et al., 2010; Guo et al., 2016)	
<i>Camellia sinensis</i>		CsNAM ⁺	(Nuruzzaman et al., 2013)	
<i>Gossypium hirsutum</i>		GhHSF37 ⁺ , GhHSF24 ⁺	(Guo et al., 2016)	
<i>Capsicum annuum</i>		CaHSFA2 ⁺	(Guo et al., 2016)	
<i>Malus domestica</i>		MdHSFA-9b ⁺	(Guo et al., 2016)	
<i>Solanum lycopersicum</i>		SIHSF01 ⁺ , SIHSFB1 ⁺ , SIHSFA2 ⁺ , SIHSF04 ⁺ , SIHSF16 ⁺ , SIHSF17 ⁺ , SIHSF18 ⁺	(Guo et al., 2016; Yang et al., 2016)	
<i>Lycopersicon esculantum</i>		LeAN2 ⁺	(Casaretto et al., 2016)	
Cold		<i>Arabidopsis thaliana</i>	DREB1A ⁺ , AtZFP1 ⁺ , AtZFP2 ⁺ , AtZF3 ⁺ , AtNAC019 ⁺ , AtMYB14 ⁻ , AtMYB15 ⁻ , AtMYB44 ⁺ , AtMYBC1 ⁺	(Baillo et al., 2019; Kimotho et al., 2019)
		<i>Triticum aestivum</i>	TaWRKY19 ⁺ , TaNAC2a ⁺ , TaNAC4a ⁺ , TaNAC57 ⁺ , TaMYB2A ⁺ , TaMYB3R1 ⁺ , TaMYB56-B ⁺	(Dubos et al., 2010; Kim et al., 2016)
		<i>Oryza sativa</i>	OsDREB1A ⁺ , OsWRKY71 ⁺ , OsNAC6 ⁺ , OsNAC5 ⁺ , OsNAC04 ⁺ , OsbZIP73 ⁺ , OsMYB2 ⁺ , OsMYB4 ⁺ , OsMYB3R-2 ⁺ , OsMYB53 ⁺ , ZmDREB2A ⁺ , ZmDBP3 ⁺ , ZmDREB1A ⁺ , ZmDBF3 ⁺ , ZmSNAC1 ⁺ , ZmNAC55 ⁺ , ZmbZIP60 ⁺ , ZmMYB53 ⁺ , ZmMYB-R1 ⁺	(Joshi et al., 2016; Kim et al., 2018; Moon et al., 2019; Yubing et al., 2019)
		<i>Zea mays</i>	ZmDREB2A ⁺ , ZmDBP3 ⁺ , ZmDREB1A ⁺ , ZmDBF3 ⁺ , ZmSNAC1 ⁺ , ZmNAC55 ⁺ , ZmbZIP60 ⁺ , ZmMYB53 ⁺ , ZmMYB-R1 ⁺	(Joshi et al., 2016; Kim et al., 2018; Moon et al., 2019; Yubing et al., 2019)
		<i>Glycine max</i>	GmWRKY21 ⁺ , GmNAC20 ⁺ , GmMYB92 ⁺ , GmbZIP44 ⁺ , GmbZIP62 ⁺	(Joshi et al., 2016; Kim et al., 2016; Baillo et al., 2019)
		<i>Vitis acerifolia</i>	VaWRKY12 ⁺	(Kim et al., 2018)

Table 1 (continued)

Stress	Crop	Transcriptional Factors/Genes	Reference
Salinity	<i>Pyrus communis</i>	PcMYB10 [†]	(Dubos et al., 2010)
	<i>Arabidopsis thaliana</i>	AtDREB1A/CBF3 [†] , AtWRKY25 [†] , AtWRKY33 [†] , AtNAC055 [†] , AtNAC072 [†] , AtNAC019 [†] , AtNAC063 [†] , ANAC069 [–] , AtMYB20 [†] , AtMYB41 [†] , AtMYB44 [†] , AtMYB73 [–] , AtMYB88 [†] , AtMYB124 [†] , TaWRKY2 [†] , TaWRKY19 [†] , TaNAC2a [†] , TaNAC4a [†] , TaNAC6 [†] , TaNAC7 [†] , TaMYB1 [†] , TaMYB2A [†] , TaMYB3R1 [†] , TaMYBsdu1 [†] , TaMYB33 [†] , TaMYB73 [†]	(Golldack et al., 2011; Li et al., 2014; Li et al., 2015a; Baillo et al., 2019)
	<i>Triticum aestivum</i>		(Li et al., 2015a; Baillo et al., 2019)
	<i>Oryza sativa</i>	OsDREB1F [†] , OsDREB2A [†] , OsWRKY43 [†] , OsWRKY45 [†] , OsWRKY5 [†] , OsWRKY7 [†] , OsWRKY30 [–] , OsWRKY72 [–] , OsNAC6 [†] , OsNC5 [†] , OsNAC1 [†] , OsNAC063 [†] , OsMYB2 [†] , OsMYB3R–2 [†] , OsMYB91 [†] , OsMYB48–1 [†] , OsZFP245 [†] , OsZFP252 [†] , Os ZFP182 [†] , OsZFP179 [†]	(Golldack et al., 2011; Li et al., 2014; Li et al., 2015a; Baillo et al., 2019)
	<i>Zea mays</i>	ZmDREB2A [†] , ZmWRKY106 [†] , ZmbZIP60 [†] , ZmbZIP72 [†] , ZmbZIP4 [†] , ZmMYB36 [†] , ZmMYB–R1 [†] , ZmSNAC1 [†]	(Golldack et al., 2011; Li et al., 2015a; Joshi et al., 2016; Kimotho et al., 2019)
	<i>Glycine max</i>	GmWRKY54 [†] , GmWRKY20 [†] , GmWRKY13 [–] , GmNAC20 [†] , GmbZIP44 [†] , GmbZIP110 [†] , GmbZIP62 [†] , GmMYB177 [†] , GmMYB76 [†] , GmMYB92 [†]	(Tripathi et al., 2014; Li et al., 2015a; Joshi et al., 2016; Kimotho et al., 2019)
	<i>Vigna radiate</i>	VrDREB2A [†]	(Golldack et al., 2011)
	<i>Camellia sinensis</i>	CsDREB2A [†] , CsDREB2B [†] , CsNAM1 [†]	(Golldack et al., 2011; Li et al., 2015a)
	<i>Agrostis stolonifera</i>	AsNAC60 [†]	(Golldack et al., 2011; Li et al., 2015a)
	<i>Setaria italica</i>	SiNAC [†] , SiNF–YA1 [†]	(Feng et al., 2015; Li et al., 2015b)
	<i>Cynodon dactylon</i>	CdtNF–YC1 [†]	(Feng et al., 2015)
	<i>Fagopyrum tataricum</i>	FtbZIP5 [†]	(Joshi et al., 2016)
	<i>Medicago truncatula</i>	MtMYB199 [†] , MtMYB634 [†] , MtMYB636 [†] , MtMYB1070 [†]	(Baillo et al., 2019)
<i>Gossypium hirsutum</i>	GhZFP1 [†]	(Baillo et al., 2019)	
Water logging	<i>Arabidopsis thaliana</i>		AtNAC102 [†] , AtNAC063 [†] , AtAREB1 [†] , AtAREB2/ABF4 [†] , AtABF3 [†] , AtABF2 [†]
	(Nuruzzaman et al., 2013)		
	<i>Zea mays</i>	ZmERE180 [†]	(Nuruzzaman et al., 2013)
	<i>Camellia sinensis</i>	CsNAM 1 [†]	(Nuruzzaman et al., 2013)
	<i>Oryza sativa</i>	OsDREB2A [†]	(Nuruzzaman et al., 2013)
Heavy Metal Stress (Jalmi et al., 2018)	<i>Arabidopsis thaliana</i>		AtMYB48 [†] , AtMYB28 [†] , AtMYB72 [†] , AtMYB124 [†] , AtMYB4 [†]
	<i>Zea mays</i>	ZmbZIP54 [†]	(Baillo et al., 2019)
	<i>Glycine max</i>	GmbZIP62 [†] , GmbZIP44 [†] , GmbZIP78 [†]	(Baillo et al., 2019)
	<i>Triticum aestivum</i>	TaH5FA4a [†]	(Åkerfelt et al., 2010)

Upward arrow (↑) indicates gene upregulation; Downward arrow (↓) indicates gene downregulation; “+” sign indicates positive role of TFs; “–” sign indicates negative role of TFs, under stress conditions.

chaperones (Jung et al., 2012). Different WRKY i.e., AtWRKY18, AtWRKY25, AtWRKY33, AtWRKY40, and AtWRKY46 also play vital role during heat stress. AtWRKY39 imparts heat stress tolerance in *Arabidopsis thaliana* by binding to a calmodulin binding TF (Li et al., 2010). The AtDREB2A bind to dehydration responsive elements (DRE) at the promoter site of AtH5FA3, and activates a stress response through an ABA-independent pathway (Yoshida et al., 2008).

3.3. Salinity stress

Globally, around 30% of arable land is affected by salt stress and the proportions continue to increase at a rapid pace due to driving force of urbanization. Salt stress inhibits imbibition, decreases root elongation and germination percentage (Kaymakanova, 2009). Salinity and drought are sister stresses, plants face drought stress in media or soil affected by salt stress (Shahbaz and Ashraf, 2008). Osmotic stress closes stomata, decreases photosynthetic rate, and disrupts action of the thylakoid membrane or Calvin cycle enzymes (Hussain and Reigosa, 2015). It alters leaf anatomy, i.e., thickness of epidermis, mesophyll, palisade length, and diameter. Plants start producing ROS

(O^{2–} ion, H₂O₂ and OH[–]) in chloroplast, cytosol, apoplastic space, and mitochondria. Activation of ROS results in oxidation of carbohydrates, lipids, proteins, nucleic acid, and impacts membrane integrity. OH[–] ion causes damage to DNA by disrupting purine and pyrimidine (Shahzad et al., 2019).

Plants maintain homeostasis within and outside the cytoplasm for normal growth (Hasegawa, 2013). Channel proteins, anti porters and symporters, maintain ion transport during homeostasis. Moreover, compatible osmolytes, i.e., free amino acid sugars, quaternary ammonium compounds, and proline are produced (Ashrafjoui et al., 2010). These osmolytes protects cell structure and maintain osmotic balance by continuous water flux. Glycine betaine, an organic compound, plays a significant role in lowering salt stress by osmotic adjustment, protecting photosynthetic machinery, and protein stabilization. Various antioxidant enzymes, such as superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), glutathione peroxidase (GPX), and non-enzymatic antioxidants, such as carotenoids and tocopherols, act as scavengers against ROS (Shahzad et al., 2019). All these events are regulated by large number of salt responsive genes which are governed by TFs, which percept signal and start defense mechanism (Ciarmiello et al., 2014).

Three types of genes involved in sensing and signaling stress, transport regulators, and salt stress-response-related genes, play key role under salt stress. When stress occurs, Na⁺ ion enters the cell via non-selective cation channels and other membrane transporters. These Na⁺ ions are recognized by unknown sensory elements. In the second step, ROS, Ca²⁺, and other hormones act as secondary messengers against salt stress and induce altered transcriptomic profile (Amirbakhtiar et al., 2019). Some common examples of role of transcriptional factors in response to salt stress are illustrated below. *AtNAC2*, a nuclear localized gene, is upregulated during salt stress and promoted lateral root development (He et al., 2005). Over-expression of *AtWRKY46* increase lateral root development through an ABA signaling pathway. Overexpression of *Gossypium hirsutum* derived *GhWRKY34* in *Arabidopsis* increased salt tolerance by inducing selective uptake of Na⁺ or K⁺ ions in roots and leaves (Finatto et al., 2018). *Reaumuria trigyna* derived *RtWRKY1* overexpressed under salt stress and resulted in increased root growth, anti-oxidative enzymes and decreased Na⁺ or Na⁺/K⁺ ratio (Du et al., 2017). Overexpression of *GmWRKY54* alleviated salt stress in soybean (Zhou et al., 2008). *AtbZIP24* increased salt tolerance by osmotic balance, ion homeostasis and increased growth and development, involving homo- and heterodimerization, or post-transcriptional modification (Yang et al., 2009). Overexpression of *GmERF3* in tobacco increased free proline and soluble carbohydrates and relieved salt stress.

3.4. Cold stress

Cold stress affects cellular metabolism by decreasing the rate of biochemical reaction, concentration of nucleic acid, and protein. Plants respond to cold stress by increasing proline contents, membrane fluidity, and ROS activation (Zheng et al., 2019). ROS causes oxidative damage in cells, reduced enzymatic activity, cause ionic imbalance, damaged cell membranes, reduced respiration rate, and degrade proteins. Plants also face low germination, delayed cell cycle, low leaf development rate, decreased seedling vigor, and yield (Hussain et al., 2018). Root development is also affected, resulting in lowered biomass and root length, and reduced root volume. Onset of cold stress at the reproductive stage leads towards pollen sterility, abortion of flower or ovules, distortion of pollen tubes, poor fruit setting, deformation of panicles, spikelet degeneration, and reduced productive tillers (Li et al., 2015a). The photosynthetic rate decreases due to reduced CO₂ conductance in the mesophyll and stomata, restricted transport of metabolites and increased photo-inhibition (Hussain et al., 2018).

Different TFs respond to cold stress by regulating expression of cold responsive genes i.e. dehydrin genes, abscisic acid responsive genes, and late embryogenesis abundant genes. These TFs are present in the nucleus throughout as they possess nucleus-localization signals (NLSs). Under stress, membrane bounded TFs are activated, enter the nucleus, and regulate gene expression. Some of the highlighted examples are illustrated here. Nuclear-localized *SINAC1* activate stress responsive genes and enhances cold tolerance. *ZmSNAC1*, *OsNAC5*, and *TaNAC57* genes are overexpressed and enhance cold tolerance (Li et al., 2014). *Arabidopsis thaliana* and grapevine calli showed overexpression of *VaWRKY12* and affected downstream located genes encoding antioxidant enzymes, glutathione S-transferases, and peroxidase in response to cold stress (Zhang et al., 2019). *OsWRKY71* was upregulated in rice under cold stress. Overexpression of *CsWRKY* enhanced cold tolerance by affecting root development, germination rate, seed development, flowering, and dormancy in cucumber (Kim et al., 2016). *OsZIP73* upregulated and played an important role at flowering, seedling, and reproductive stages to counter cold stress. It co-expressed with *OsZIP71* and enhanced seed set by affecting pollen fertility through an increased production of soluble sugar

in pollen and decreased accumulation of ABA in anthers (Liu et al., 2019).

OsZIP87 and *OsZIP38* also played an important role in enhancing cold tolerance in rice (Liu et al., 2019). *OsDREB1G* regulates expression of cold induced genes present in protoplasts. *Arabidopsis thaliana* based TFs, *AtDREB1A/CBF1* and *AtCBF4* are overexpressed in response to cold stress (Moon et al., 2019). MYBs also play vital role in combating cold stress by affecting cell cycle, cellular morphogenesis, hormonal signaling, secondary metabolism, and gene expression. *AtMYB14* was down regulated under cold stress and encoded the proteins that act as the R2R3-MYB activator. As a result, CBF proteins (*CBF1*, *CBF2*, and *CBF3*) are activated, which initiate cold responsive genes. In transgenic *Arabidopsis thaliana* *GmMYB1* was overexpressed and enhanced cold tolerance. *GmMYB1* regulated expression of many stress responsive genes i.e. *AtCOR15a*, *AtRD29B*, *AtP5CS*, and *AtCOR78* increased cold tolerance. *OsMYB4* in *Arabidopsis thaliana* was also overexpressed and increased freezing tolerance (Su et al., 2014).

3.5. Heavy metal stress (HMS)

Heavy metals (HMs) are generally defined as metals with relatively high densities, atomic weights, or atomic numbers, i.e., Mo, Ni, Cd, Cr, and Zn. HMs enriched soil results in reduced growth, altered nutrients and water balance, inhibition of photosynthesis and chlorosis of crop plants. Further, HMs affect chlorophyll content, photosystem II effectiveness, and Rubisco activity (Maleva et al., 2012). These decreases reductant pool as a result less ATPs are produced and less CO₂ is fixed (Singh et al., 2016). Heavy metals enhances protease activity decreases ammonia glutamate dehydrogenase (GDH), glutamine oxoglutarate aminotransferase (GOGAT), glutamine synthetase (GS), nitrite reductase (NiR), and nitrate reductase (NR) activity (Chaffei, 2003). ROS accumulation, cause oxidative stress by interacting with proteins, DNA, and lipids, and destabilizing cellular organization (Sharma et al., 2012).

Cd stimulates the myelin basic protein (MBP) kinase gene and *OsMAPK2* in *Oryza sativa*. Due to heavy metal stress, different mitogen activated protein kinases (MAPKs) are activated. *Oryza sativa* multiple stress responsive *MK2* (*OsMSRMK2*), *wound* and *JA-uninducible MK1* (*OsWJUMK1*), and *OsMSRMK3* are induced in response to Cd²⁺ and Cu²⁺ in roots and leaves (Ali et al., 2019). Similarly, *Stress Activated MAPK* (*SAMK*), *Medicago MAP kinase3* (*MMK3*), *Medicago MAP kinase2* (*MMK2*), and *salt stress induced MAPK* (*SIMK*) are activated in *Medicago sativa* in response to CdCl₂ and CuCl₂ stress (Opdenakker et al., 2012b). Downstream TFs i.e., activator protein 2 (AP₂), WRKY, bZIP, MYB, DREB, ERF, and ZAT (C₂H₂ type ZF-) are stimulated by activation of MAPKs as their targets. Likewise, *Arabidopsis thaliana*, in response to CuSO₄ and CdCl₂ stress, starts accumulation of MPK₃ and MPK₆. Moreover, different TFs i.e. *AtMYB28*, *AtMYB72*, *AtMYB48*, *AtMYB124*, and *AtMYB4* are upregulated in *Arabidopsis* plants subjected to Cd and Zn stress. A short duration exposure of *Arabidopsis* roots to Cu stress activated *AtWRKY22*, *AtWRKY25*, and *AtWRKY29*, whereas long term exposure activated *AtWRKY25* and *AtWRKY29* (Opdenakker et al., 2012a). In *Arabidopsis thaliana*, Cd stress upregulated ethylene responsive factors i.e., *AtERF1*, *AtERF5*, and *AtZAT6* to manipulate plant metabolism for stress tolerance (Jalmi et al., 2018). Similarly, in *Glycine max*, up-regulation of *GmbZIP62* and down-regulation of *GmbZIP44* and *GmbZIP78* was observed under Cd stress (Hong et al., 2017).

3.6. Waterlogging stress

Water logging is a combination of two important stresses: submergence (when the whole plant is under water) and water logging (when only roots are submerged) (Zhao et al., 2018). It

results from prolonged rainfall, poor drainage of soil, and its intensity tends to increase every year (Sundgren et al., 2018). Diffusion of gases in water is low in comparison to air, which give rise to oxidative stress (Colmer and Greenway, 2011). Different physiological and biochemical processes are activated, which shift aerobic respiration to anaerobic fermentation. Moreover, certain toxic compounds, such as alcohol and aldehydes are accumulated in the cytoplasm (Zhou et al., 2020). There are two stages of water logging, hypoxia (partial depletion of oxygen) and anoxia (complete depletion of oxygen). Different plant processes, i.e., cytoplasmic pH, cellular energy, stem elongation, and adventitious root formation decreases. In addition, fresh and dry mass decreases; and the electron-transport chain and CO₂ assimilation are also affected (Barickman et al., 2019). Furthermore, toxic compounds and ROS accumulated. Certain redox enzymes, such as cupredoxins, are activated to maintain ROS balance (Jin et al., 2017).

Roots also play an important role in response to water logging stress, as aerenchyma and adventitious roots are established. The function of aerenchyma is to increase internal diffusion of oxygen from aerial parts to waterlogged roots to facilitate an aerobic environment (Fukao et al., 2019). The known transcription factors that play roles in regulation of water logging stress include bZIP, NAC, WRKY, MYB, and ERFs. But the highest number of transcription factors responding to waterlogging stress belong to the MYB and the AP2/EREBP gene families (Borrego-Benjumea et al., 2020). Low oxygen-induced genes are characterized by an anaerobic response element (ARE) present in the promoter. ARE has GC and the GT motifs, which are important for gene activity and signal transduction (Dennis et al., 2000). In *Arabidopsis*, five ERF VII genes *AtHRE1*, *AtHRE2*, *AtRAP2.2*, *AtRAP2.3*, and *AtRAP2.12* played significant role under waterlogging conditions. Rice *SUB1A* is considered a master regulator against water logging stress. These ERF VII tandem repeats are responsible for increasing inter-nodal elongation and enable the plants to overcome waterlogged conditions (Fukao et al., 2019). *ZmEREB180* increased waterlogging tolerance in maize seedlings due to conserved N terminal motif and its ectopic expression (Yu et al., 2019). Overexpression of *AtSHYG* (*AtNAC047*) caused hyponastic growth in *Arabidopsis* (Hofmann, 2013). Moreover, *SiWRKY51* and *SiWRKY65* also play important roles in roots of waterlogged plants (Li et al., 2017). However, exploring the role of TFs under waterlogging stress needs further attention.

4. Role of transcriptional factors under biotic stresses

Biotic stresses such as diseases, insects, and nematodes adversely affect plant growth, development, survival, and crop productivity. Reported losses due to biotic stresses are up to 35% (Baillo et al., 2019). Yield losses in USA due to *Fusarium* head blight and wheat rust amounted to US \$3 billion and US \$5 billion, respectively. In the middle of the 19th century, during the Irish potato famine, the crop were completely destroyed due to late blight (*Phytophthora infestans*), leaving millions of farmers empty handed (Rashad and Moussa, 2020). The available data suggests that a decrease in annual crop productivity by arthropods is 18–20% worldwide, amounting to US \$470 billion. The most prone area's to biotic stresses are African and Asiatic countries (Sharma et al., 2017). Diseases negatively affects morphological characteristics, i.e., plant height, chlorophyll content, and leaf architecture (Cerdeira et al., 2017).

To deal with these challenges, plant adopt coordination of different physiological, biochemical, and molecular processes through signal transduction mechanisms (Amorim et al., 2017). Pathogen attack signals are recognized through pathogen-associated molecular patterns (PAMPs) present on the host surfaces that trigger a basic immune response PAMP-triggered immunity (PTI). Plants

have resistance proteins (R) that directly or indirectly identify effectors and activate effector-triggered immunity (ETI), such as hypersensitive response (HR). The detailed infection process of bacterial, fungal, and viral pathogens, insects, and nematodes, is described below, along with a variety of defense responses for each infection.

4.1. Bacterial infections

More than 200 pathogenic bacterial species have been identified in plants. The most important bacterial infections belongs to genera *Pseudomonas*, *Ralstonia*, *Agrobacterium*, *Xanthomonas*, *Erwinia*, *Xylella*, *Pectobacterium*, and *Dickeya*. Pathogenic bacteria produce cell wall degrading enzymes, which provide passage for infiltration and maceration in plant tissue for feeding. *Erwinia amylovora* causes fire blight of the Rosaceae family, apple, and pear (Mansfield et al., 2012). *Ralstonia solanacearum* causes bacterial wilt of tomato, tobacco, banana, and the brown rot of potato. *Xanthomonas* mainly effect rice, banana, tomato, and citrus fruits, and invades mostly xylem or parenchyma tissues (Ryan et al., 2011). *Xylella fastidiosa* is a xylem-limited phytopathogen, which causes diseases in grapes, almond, citrus, peach, coffee, and olive trees. *Pseudomonas syringae* causes infection in the tomato by forming a necrotic lesion surrounded by yellow chlorotic halo on the tomato (termed as bacterial speck) (Buttimer et al., 2017).

After a pathogen attack, TFs activate pathogen related (PR) genes and promote HR. HR is responsible for tissue necrosis by systemic acquired resistance (SAR). Defense-related TFs include bZIP, AP₂/ERF, NAC, MYB, DOF, and WRKY, which play an important role in defense response against pathogen attacks. Some examples pertaining to role of TFs in response to bacterial disease are explained below however detailed information is summarized in the Table 2. *OsWRKY80* and *OsWRKY4* genes incorporate resistance against rice sheath blight. *OsWRKY80* attached to a W-box in the promoter region of *OsWRKY4* and activated defense response against *Rhizoctonia solani*. Moreover, *OsWRKY7*, *OsWRKY58*, *OsWRKY64*, and *OsWRKY76* are also upregulated in the rice plants subjected to rice blast (Baillo et al., 2019). Overexpression of *VaERF20* increased resistance against *Pseudomonas syringae* and *Botrytis cinerea* in transgenic *Arabidopsis* (Wang et al., 2018a). *SICabZIP* and *SIERF11* eliminated pathogenicity of *Pseudomonas syringae* Pv. tomato DC3000 and provide resistance (Lee et al., 2003). *AtNAC032* repressed activation of MYC on pest attack by blocking a coronatine mediated reopening of stomata and thus stopped the entry of *Pseudomonas syringae* Pv. tomato DC3000 (Allu et al., 2016). *GhWRKY39-1* provides resistance to Root rot (*R. solani*) in *Gossypium hirsutum* (Chen et al., 2017). *CaWRKY27*, *CaWRKY6* mediate bacterial wilt while *CaWRKY58* resisted bacterial spot (*Xanthomonas axonopodis*) (Erpen et al., 2018). *SINAC35* counter bacterial wilt (*R. solanacearum*) and bacterial spot (*X. campestris*) infections in *Capsicum annum* (Baillo et al., 2019), as explained in Table 2.

4.2. Fungal diseases

Economically important fungal diseases are yellow rust, leaf rust, stem rust, spot rust, red rot, sheath blight, rice blast, powdery mildew, downy mildew, and stem canker. Fungal infestation prevents closing of the stomata, damages the xylem cells, disrupt the cuticle layer, causes extensive water loss, decreases leaf and shoot water potential, decrease fresh weight, root number, and length, produces large numbers of brown roots, and reduces uptake and availability of nutrients (Pandey et al., 2017; Jamil et al., 2020a). When plants are subject to fungal attacks, they produce plant hormones, i.e., ethylene, salicylic acid, and jasmonic acid. Plant hormones activates expression of TFs, i.e., AP₂/ERF,

Table 2
Role of different transcriptional factor gene families in biotic stress tolerance in plants.

Stress	Crop	Disease	Gene	Reference
Bacterial	<i>Arabidopsis thaliana</i>	Bacterial Leaf spot (<i>Pseudomonas syringae</i>)	<i>AtWRKY22</i> ⁺ , <i>AtWRKY29</i> ⁺ , <i>AtWRKY38</i> ⁻ , <i>AtWRKY41</i> ⁺ , <i>AtWRKY62</i> ⁻ , <i>AtERF014</i> ⁺ , <i>AtNAC19</i> ⁺ , <i>AtNAC55</i> ⁺ , <i>AtNAC72</i> ⁺ , <i>AtMYB30</i> ⁺ , <i>AtMTB44</i> ⁺ , <i>AtMYB96</i> ⁺ , <i>AtNAC042/JUB1</i> ⁻ , <i>CBNAC/NTL9</i> ⁻	(Chen et al., 2017; Erpen et al., 2018; Baillo et al., 2019; Yuan et al., 2019b)
	<i>Vitis vinifera</i>	Bacterial Leaf Spot (<i>Pseudomonas syringae</i>)	<i>VvERF20</i> ⁺	(Chen et al., 2017; Erpen et al., 2018)
	<i>Oryza sativa</i>	Bacterial Blight (<i>Xanthomonas oryzae</i>)	<i>OsWRKY6</i> ⁺ , <i>OsWRKY45</i> ⁺ , <i>OsWRKY67</i> ⁺ , <i>OsNAC58</i> ⁺ , <i>OsNAC66</i> ⁺ , <i>OsWRKY13</i> ⁺ , <i>OsWRKY71</i> ⁺ , <i>OsEREBP1</i> ⁺	(Chen et al., 2017; Erpen et al., 2018; Baillo et al., 2019; Yuan et al., 2019b)
	<i>Capsicum annuum</i>	Bacterial Wilt (<i>Ralstonia solanacearum</i>)	<i>CaWRKY27</i> ⁺ , <i>CaWRKY6</i> ⁺ ,	(Erpen et al., 2018)
		Bacterial Spot (<i>Xanthomonas axonopodis</i>)	<i>CaWRKY58</i> ⁻	(Erpen et al., 2018)
		Pepper Root Rot (<i>Bacillus thuringiensis</i>)	<i>CaPF1</i> ⁺	(Chen et al., 2017)
	<i>Solanum lycopersicum</i>	Bacterial Wilt (<i>Ralstonia solanacearum</i>)	<i>SIERF3</i> ⁺ , <i>SIERF5</i> ⁺ , <i>SINAC35</i> ⁺	(Erpen et al., 2018)
		Bacterial Spot (<i>Xanthomonas campestris</i>)	<i>SIERF1</i> ⁺ , <i>SINAC35</i> ⁺	(Erpen et al., 2018)
	<i>Glycine max</i>	Bacterial Wilt (<i>Ralstonia solanacearum</i>)	<i>GmERF3</i> ⁺	(Erpen et al., 2018)
	<i>Nicotiana tabacum</i>	Bacterial wilt (<i>Ralstonia solanacearum</i>)	<i>NtWRKY50</i> ⁺	(Chen et al., 2017)
<i>Manihot esculenta</i>	Bacterial Blight (<i>Xanthomonas axonopodis</i>)	<i>MebZIP3</i> ⁺ , <i>MebZIP5</i> ⁺	(Erpen et al., 2018)	
Fungal	<i>Arabidopsis thaliana</i>	Gray mold (<i>Botrytis cinerea</i>)	<i>AtERF1</i> ⁺ , <i>AtERF14</i> ⁻	(Baillo et al., 2019)
		Fusarium wilt (<i>Fusarium oxysporum</i>)	<i>AtERF2</i> ⁺ , <i>AtERF4</i> ⁻	(Baillo et al., 2019)
		Powdery Mildew (<i>Erysiphe cruciferarum</i>)	<i>AtbZIP10</i> ⁺	(Erpen et al., 2018)
	<i>Triticum aestivum</i>	Yellow Rust (<i>Puccinia striiformis</i>)	<i>TaWRKY49</i> ⁺ , <i>TaWRKY62</i> ⁺ , <i>TaWRKY70</i> ⁺ , <i>TaNAC1</i> ⁻ , <i>TaNAC4</i> ⁺ , <i>TaNAC8</i> ⁺ , <i>TaNAC21/22</i> ⁻ , <i>TabZIP74</i> ⁺ , <i>TaNAC30</i> ⁻	(Erpen et al., 2018; Wang et al., 2018b)
		Leaf rust (<i>Puccinia triticina</i>)	<i>TaWRKY1B</i> ⁺	(Kumar et al., 2018)
		Powdery mildew (<i>Erysiphe cruciferarum</i>)	<i>TaNAC6</i> ⁺ , <i>TaNAC21/22</i> ⁻ , <i>TaNAC30</i> ⁺	(Yuan et al., 2019a)
		Root Rot (<i>Bipolaris sorokiniana</i>)	<i>TaERF3</i> ⁻ , <i>TaPIEP1</i> ⁺	(Baillo et al., 2019)
	<i>Oryza sativa</i>	(<i>Rhizoctonia cerealis</i>)	<i>TaRIM1</i> ⁺	(Baillo et al., 2019)
		Sheath blight (<i>Rhizoctonia solani</i>)	<i>OsWRKY4</i> ⁺ , <i>OsWRKY80</i> ⁺	(Erpen et al., 2018)
	<i>Oryza sativa</i>	Rice Blast (<i>Magnaporthe oryzae</i> , <i>Pyricularia oryzae</i>)	<i>OsWRKY7</i> ⁺ , <i>OsWRKY45</i> ⁺ , <i>OsWRKY58</i> ⁺ , <i>OsWRKY62</i> ⁺ , <i>OsWRKY64</i> ⁺ , <i>OsWRKY76</i> ⁺ , <i>OsWRKY22</i> ⁺ , <i>OsNAC6</i> ⁺ , <i>OsNAC19</i> ⁺ , <i>OsNAC66</i> ⁺ , <i>OsNAC122</i> ⁺ , <i>OsNAC131</i> ⁺	(Erpen et al., 2018; Tolosa and Zhang, 2020)
		Sheath blight (<i>Rhizoctonia solani</i>)	<i>GhWRKY39-1</i> ⁺	(Erpen et al., 2018)
	<i>Gossypium hirsutum</i>	Fusarium head blight (<i>Fusarium graminearum</i>)	<i>BdWRKY8</i> ⁺ , <i>BdWRKY34</i> ⁺ , <i>BdWRKY50</i> ⁺ , <i>BdWRKY70</i> ⁺ , <i>BdWRKY69</i> ⁺	(Erpen et al., 2018)
	<i>Solanum lycopersicum</i>	Gray Mold (<i>Botrytis cinerea</i>)	<i>SISRN1</i> ⁻	(Yuan et al., 2019a)
		Tomato Wilt (<i>Plectosphaerella cucumerina</i>)	<i>SIERF1</i> ⁺	(Baillo et al., 2019)
	<i>Solanum lycopersicum</i>	Rhizopus Soft Rot (<i>Rhizopus nigricans</i>)	<i>SIERF1</i> ⁺	(Baillo et al., 2019)
Red Rot (<i>Colletotrichum falcatum</i>)		<i>SobZIP4</i> ⁺ , <i>SobZIP15</i> ⁺ , <i>SoNACH</i> ⁻	(Muthiah et al., 2013)	
<i>Solanum tuberosum</i>	Late Blight (<i>Phytophthora infestans</i>)	<i>StNAC4</i> ⁺ , <i>StNAC5</i> ⁺ , <i>StNAC18</i> ⁺ , <i>StNAC48</i> ⁺ , <i>StNAC81</i> ⁺ , <i>StERF3</i> ⁻	(Baillo et al., 2019; Tolosa and Zhang, 2020)	

Table 2 (continued)

Stress	Crop	Disease	Gene	Reference
	<i>Hordium vulgare</i>	Powdery mildew (<i>Blumeria graminii</i>)	<i>HvWRKY10</i> [†] , <i>HvWRKY19</i> [†] , <i>HvWRKY28</i> [†] , <i>HvNAC6</i> ^{-↓}	(Erpen et al., 2018)
		Spot Blotch (<i>Bipolaris sorokiniana</i>)	<i>HvMYB6</i> [†]	(Baillo et al., 2019)
	<i>Glycine max</i>	Root Rot (Phytophthora sojae)	<i>GmERF5</i> [†] , <i>GmERF113</i> [†]	(Baillo et al., 2019)
		Soybean Rust (<i>Phakospora pachyrhizi</i>)	<i>GmbZIP1</i> [†] , <i>GmbZIP2</i> [†] , <i>GmbZIP62</i> [†] , <i>GmbZIP105</i> [†]	(Baillo et al., 2019)
	<i>Nicotiana benthamiana</i>	Anthraco-nose (<i>Colletotrichum orbicular</i>)	<i>NbWRKY8</i> [†]	(Erpen et al., 2018)
	<i>Vitis vinifera</i>	Grey Mold (<i>Botrytis cinerea</i>)	<i>VvERF20</i> [†]	(Baillo et al., 2019)
	<i>Populus trichocarpa</i>	Poplar leaf Rust (<i>Melampsora medusae</i>)	<i>PtrWRKY18</i> [†] , <i>PtrWRKY35</i> [†] , <i>PtrWRKY89</i> [†]	(Erpen et al., 2018)
Viral	<i>Arabidopsis thaliana</i>	Tobacco mosaic virus (TMV)	<i>AtWRKY8</i> [†] , <i>AtWRKY61</i> [†] , <i>ATAF2</i> ^{-†}	(Chen et al., 2017; Erpen et al., 2018)
	<i>Nicotiana tobacum</i>	Tobacco mosaic virus (TMV)	<i>WRKY8</i> [†] , <i>NtERF5</i> ^{-†}	(Chen et al., 2017; Erpen et al., 2018)
	<i>Oryza sativa</i>	Rice Dwarf Virus (RDV)	<i>OsNAC</i> ^{-†}	(Yuan et al., 2019a)
		Rice Stripe Mosaic Virus (RSMV)	<i>OsMYB4</i> ^{-†}	(Erpen et al., 2018)
Nematodes	<i>Solanum lycopersicum</i>	Tomato Yellow Leaf Curl Virus (TYLCV)	<i>SINAC20</i> ^{-†} , <i>SINAC24</i> ^{-†} , <i>SINAC47</i> ^{-†} , <i>SINAC61</i> ^{-†}	(Yuan et al., 2019a)
	<i>Arabidopsis thaliana</i>	Cyst nematode (<i>Heterodera schachtii</i>)	<i>AtWRKY23</i> ^{+↓} , <i>AtMYB12</i> ^{+↓} , <i>AtWRKY6</i> ^{+↓} , <i>AtWRKY11</i> ^{+↓} , <i>AtWRKY17</i> ^{+↓} and <i>AtWRKY33</i> ^{+↓} . (Downregulation)	(Hamamouch et al., 2020)
		Root-Knot Nematodes (<i>Meloidogyne incognita</i>)	<i>AtMYB12</i> ^{+↓}	(Hamamouch et al., 2020)
	<i>Solanum lycopersicum</i>	Root Knot Nematode (<i>Meloidogyne javanica</i>)	<i>SlWRKY45</i> ^{-↓} , <i>SlWRKY3</i> ^{+↓} , <i>SlWRKY70</i> ^{+↓}	(Chinnapandi et al., 2017; Chinnapandi et al., 2019)
	<i>Glycine Max</i>	Soybean Cyst Nematode (<i>Heterodera glycines</i>)	<i>GmWRKY136</i> ^{+↓} , <i>GmWRKY53</i> ^{+↓} , <i>GmWRKY86</i> ^{+↓}	(Yang et al., 2017b)
Insects	<i>Arabidopsis thaliana</i>	Cabbage moth (<i>Pieris brassicae</i>)	<i>AtMYB75</i> ^{+†}	(Shen et al., 2018)
	<i>Triticum aestivum</i>	English grain aphid (<i>Sitobion avenae</i>)	<i>TaMYB19</i> ^{+↓} , <i>TaMYB2</i> ^{+↓} , <i>TaMYB44</i> ^{+↓}	(Shen et al., 2018)
		Russian wheat aphid (<i>Diuraphis noxia</i>)	<i>TaWRKY53</i> ^{+↓}	(Van Eck et al., 2014)
	<i>Oryza sativa</i>	Brown plant hopper (<i>Nilaparvata lugens</i>)	<i>OsWRKY45</i> ^{+↓}	(Huang et al., 2016)
		Striped stem borer (<i>Chilo suppressalis</i>)	<i>OsWRKY53</i> ^{+↓}	(Hu et al., 2016)
		<i>Chrysanthemum</i>	Aphid (Aphidodea)	<i>OsERF3</i> ^{-†} <i>CmMYB15</i> ^{+†} , <i>CmMYB19</i> ^{+†}

Upward arrow (†) indicates gene upregulation; Downward arrow (↓) indicates gene downregulation; "+" sign indicates positive role of TFs; "-" sign indicates negative role of TFs, under stress conditions.

WRKY, NAC, MYB, and MYC (Luo et al., 2019). The following section covers some of the key examples of role of TFs in resisting fungal pathogens in plants. Overexpression of *AtWRKY72* enhanced resistance against powdery mildew in *Arabidopsis*. Similarly, *AtWRKY8* and *AtWRKY28* enhanced resistance against *Botrytis cinerea*. *TaWRKY49*, *TaWRKY62*, and *TaWRKY70* combat strip rust (*Puccinia striiformis*) by activating ROS, jasmonic acid, salicylic acid, and ethylene production (Chen et al., 2017).

In rice, overexpression of *OsWRKY45* and *OsWRKY22* enhanced resistance to *Pyricularia oryzae*. *OsWRKY45* overexpressed and enhanced resistance against fungal pathogen *Magnaporthe grisea*. *OsWRKY4* and *OsWRKY80* increase sheath blight resistance in rice. *OsWRKY80* binds to the W-box in the promoter region of *OsWRKY4* and works as a positive regulator for *Rhizoctonia solani* resistance. In *Brachypodium distachyon*, *BdWRKY8*, *BdWRKY50*, *BdWRKY34*, and *BdWRKY70* were upregulated and enhanced resistance against *Fusarium graminearum*. In *Hordeum vulgare*, *HvWRKY1* cooperated

with *HvMYB6* to counter powdery mildew (Jiang et al., 2017). Similarly, *TaNAC6* overexpressed and enhanced powdery mildew resistance and decreased fungal haustoria. *OsNAC6* shows overexpression and enhanced rice blast resistance. In barley, *HvNAC6* overexpressed under powdery mildew infection and increased resistance against *Blumeria graminii*. *VaERF20* increased resistance against *Botrytis cinerea* in transgenic *Arabidopsis*. In soybean, *GmbZIP1*, *GmbZIP62*, *GmbZIP105*, and *GmbZIP2* genes prevented infestation of Asian soybean rust (Baillo et al., 2019).

4.3. Viral diseases

Viruses cause a variety of plant diseases. The main symptoms of all diseases are decreased internodal distance, deficiency of chlorophyll, and reduction in growth. Other related symptoms are reduced germination rate, rolled leaf blade, less nodulation, swelling of stem, tumors on stem, roots and leaves, reduced pollen

fertility, reduced seed set, wilting, and cell death (Matthews, 2012). Economically important viruses are sorghum mosaic virus (SrMV), sugarcane mosaic virus (SCMV), and sugarcane streak mosaic virus (SCSMV). SrMV and SCMV are effective pathogens for *Sorghum bicolor*, gramineous plants and *Zea mays* (Ling et al., 2018). Other less virulent viruses are yellow vein mosaic virus in okra, urd bean leaf crinkle virus, strawberry mild yellow edge virus, rice stripe mosaic virus, cotton leaf curl virus, sugarcane yellow leaf virus, barley yellow dwarf virus, and maize chlorotic mottle virus. Rapid mutations of viral strains is a major factor behind failure of breeding programs (Jamir et al., 2020). Plant activate hormonal responses, gene silencing, metabolic regulation, cellular protein degradation by the ubiquitin proteasome pathway (UPS), signaling of immune receptors and PAMP-triggered immunity to stop replication of viruses. Accumulation of ROS and plant hormones, i.e., salicylic acid, jasmonic acid, abscisic acid, brassinosteroids, cytokinin, auxin, ethylene, and gibberellin play role in plant defense against viruses (Calil and Fontes, 2017).

Different TFs play significant roles in resisting virus-induced damage as illustrated in the following examples and Table 2. Overexpression of *OsMYB4* is responsible for resistance against viral diseases. The *MtWRKY* gene of *Medicago truncatula* provides resistance against tobacco mosaic virus in *Nicotiana tabacum*. The *Gossypium hirsutum* based *GhWRKY15* gene, when introduced in *Nicotiana tabacum*, showed activity against the tobacco mosaic virus (Erpen et al., 2018). NAC TFs play vital roles in plant immunity by specific signals and virulence action of pathogenic effectors. Viral infection proteins sometime hijack NAC TFs to enable viral replication and decrease host immunity. However, some examples of NAC TFs imparting resistance are as follows: *SINAC20*, *SINAC24*, *SINAC41*, and *SINAC61* played a significant role in imparting resistance against Tomato Yellow Leaf Curl Virus (TYLCV) (Huang et al., 2017). *Triticum aestivum* NAC TFs, i.e., *AtGRAB1* (Geminivirus Rep A-Binding) and *AtGRAB2*, interacted with Wheat Dwarf Geminivirus (WDV) Rep A protein and hinder DNA replication of WDV. *Arabidopsis thaliana AtAF2* interact with the Tobacco Mosaic Virus (TMV) helicase domain and its overexpression inhibited virus infection (Yuan et al., 2019b). Six WRKY genes, *SolyWRKY41*, *SolyWRKY42*, *SolyWRKY53*, *SolyWRKY54*, *SolyWRKY80*, and *SolyWRKY81* obtained from tomato reduced TYLCV infection. Interaction analysis provided evidence of interaction between WRKY group III, isochorismate synthase (ICS), and Mitogen-Activated Protein Kinase5 (MAPK) in response to viruses (Huangfu et al., 2016).

4.4. Nematodes

Plant parasitic nematodes (PPNs) are economically important agricultural pests. Two classes exist i.e., cyst nematodes (CNs) and root knot nematodes (RKNs), causing together an estimated annual loss of US \$80 billion. PPNS affect a wide range of hosts among economically important crops, i.e., *Solanum lycopersicum*, *Solanum tuberosum*, *Gossypium hirsutum*, *Glycine max*, *Oryza sativa*, *Zea mays*, and *Triticum aestivum* (Warmerdam et al., 2018). PPNS rich in ascaroside (Ascr# 18) induce the plant immune systems trigger production of jasmonic acid and salicylic acid, as well as trigger PTI and MAPKs. PPN's induce secondary metabolite production in plants, i.e., chlorogenic acid, ethylene, and flavonoids in roots (Sato et al., 2019). These secondary metabolites reduced attraction of nematodes towards plant roots. Genes linked with synthesis of cytokinin, gibberellic acid, salicylic acid, jasmonates, and auxin signal responses are activated (Macharia et al., 2019). The role of TFs to reduce the negative impact of PPNS on plant growth is briefly summarized in the Table 2 and some examples are discussed below.

SIWRKY75 is activated in *Solanum lycopersicum* by infection with *Meloidogyne javanica* and stimulate the JA pathway for regulation

of the JA signaling mechanism. *CsWRKY23* is overexpressed in cucumber plants during infection of *Meloidogyne incognita* for contributing to early resistance (Macharia et al., 2019). *AtWRKY23* is overexpressed due to auxin stimulation at the feeding point of cyst nematode *Heterodera schachtii*. *OsWRKY11*, *OsWRKY70*, and *OsWRKY62* are upregulated in response to *Hirschmanniella oryza* attack. Similarly, *OsWRKY13*, *OsWRKY59*, and *OsWRKY62* are upregulated against RKN infection. Nineteen WRKY genes in *Solanum lycopersicum* responded to nematode infection, i.e., upregulation of *SIWRKY70* by salicylic acid, both *SIWRKY35* and *SIWRKY3* were activated (Chinnapandi et al., 2019). *AtWRKY33* was stimulated by JA and worked as a positive regulator against PPN attack. *AtWRKY33* overexpression along with different promoters conferred resistance against *Heterodera schachtii*. *SIWRKY45* is implicated in signal transduction pathways during accumulation of nematodes in the root zone (Chinnapandi et al., 2017). Five *Glycine max* WRKY genes i.e. *GmWRKY5*, *GmWRKY28*, *GmWRKY36*, *GmWRKY62*, and *GmWRKY154* were found more responsive against SCN and reduced 70% of its population, while *GmWRKY136*, *GmWRKY86*, *GmWRKY53*, and *GmWRKY52* showed moderate response by reducing 40–60% population and *GmWRKY71* and *GmWRKY8* showed a 10–30% control against SCN population (Yang et al., 2017a).

4.5. Pest attack

Changing climate is promoting the growth of herbivores and shortening their life cycles. However, rise in temperature is increasing chances of their appearance (Ximénez-Embún et al., 2017; Jamil et al., 2021; Ahmad et al., 2019). On the basis of feeding mode, insects are classified into different classes i.e. chewing insects such as beetles and caterpillars; consume plant tissues, whereas piercing and sucking insects feed on the vascular system for example aphids which insert their stylets into the phloem. Meanwhile, thrips combine sucking and rasping methods to feed on its host. Some mining type feeders such as larvae of certain beetles, moths, and flies form serpentine cavities when feeding between epidermal cells in leaf tissues and cause twisting or curling of leaves (Santamaria et al., 2018). Moreover, spider mites, a phytophagous acarion belonging to Tetranychus genus, pierce parenchyma cells and suck the contents (Bensoussan et al., 2016).

Some plants counter attack or activate emergency responses (Santamaria et al., 2013). The plant defense systems are activated when specific pattern recognition receptors (PRRs) detect phytophagous pests through herbivore-associated molecular patterns (HAMPs), microbe-associated molecular patterns (MAMPs), and damage associated molecular patterns (DAMPs). With recognition of molecular patterns, plants activates short-term downstream responses at the membrane levels, i.e., Ca^{2+} influx, potential depolarization, and generation of ROS or reactive nitrogen species (RNS) as a result, secretion of JA, SA, and ethylene starts, which activate TFs. TFs regulate expression of downstream-located genes through a cascade of CDPKs. These events, of recognition to response, take place within minutes to hours after herbivore attack (Santamaria et al., 2018).

Few TFs are upregulated in response to herbivore induced plant damage indicating their role in plant defense. *OsERF3* was upregulated in response to feeding of striped stem borer (SSB) in *Oryza sativa* and enhanced the transcript level of two MAPKs and two WRKY genes. As a result, the concentration of SA, JA, and trypsin protease inhibitor activity increased. *OsWRKY45* protected rice against infestation of Brown Plant hopper (*Nilaparvata lugens*) (Lu et al., 2011). *TaMYB19*, *TaMYB44*, and *TaMYB29* acted as co-regulators in phloem based defense response against English grain aphid in wheat. *AtMYB75* increased resistance against *Pieris*

brassicae by modulating flavonoid metabolites. Overexpression of *GsMYB15* obtained from wild soybean increased *Arabidopsis* resistance against *Helicoverpa armigera* by a JA mediated insect response (Shen et al., 2018). *CmMYB19* increased resistance of *Chrysanthemum* against aphids by promoting a lignin biosynthesis pathway (An et al., 2019). *NbERF173* obtained from *Nicotiana benthamiana* provided resistance against *Phytophthora parasitica* (Yu et al., 2020). *TaWRKY53* induced resistance mechanisms against Russian wheat aphid in *Triticum aestivum* (Van Eck et al., 2014). Similarly, *OsWRKY53* provided resistance against *Chilo suppressalis* SSB (Hu et al., 2016).

5. Crop improvement techniques and TFs

The implication of TFs from signal perception to signal transduction and expression of stress responsive genes was summarized in this review. A single TF gene may respond to numerous stresses for example *SbNAC58* incorporate tolerance against multiple abiotic stresses i.e. drought, cold, and salinity stress (Baillo et al., 2019). TFs have potential to be exploited using different genome modifying molecular techniques for developing climate resilient crops (Table 3) as explained in Fig. 3.

Gene silencing through RNAi provides a platform for exploring the role of different TFs in plant development and in response to various stresses. RNAi uses double-stranded RNA to activate ribonucleases to target homologous mRNA and degrade it. The resulting phenotypes are either null or partially affected. Thus RNAi can help to elucidate role of different TFs under biotic and abiotic stresses (Agrawal et al., 2003). This knowledge can be exploited by incorporating favorable alleles in suitable genetic backgrounds, and using different biotechnological tools, for stress tolerance. RNAi silencing could be used to knockdown TFs, which promote disease development. It can also be useful for knocking out undesirable TFs, which promote the development of stresses. *AtNAC042/JUB1*, *CBNAC/NTL9* promotes bacterial leaf spot of *Arabidopsis*. Similarly, *TaNAC1*, *TaNAC21/22*, *TaNAC30* promotes yellow rust and downy mildew attack on wheat. Knocking down these TFs in various experiments showed progress and have slowed down the disease establishment processes (Yuan et al., 2019b).

Different genome editing tools, such as ZF-nucleases (ZFNs), homing endonucleases or mega nucleases, and transcription activator-like effector nucleases (TALENs) create targeted double-strand breaks that promote recombination at a specific locus and

have potential in exploring the role of different TFs (Rabara et al., 2014). Similarly, Clustered Regulatory Interspaced Short Palindromic Repeats (CRISPR) are used to establish knockout lines of TF genes for functional genetics. In the CRISPR/Cas9 system, the genomic target site is cleaved by Cas9, located at the site by the guide RNA (gRNA) with which it complexes. As a result, a double stranded break occurs at the target site, the repair of which causes mutations in the form of insertions or deletions or in some cases frameshifts. These mutants can clarify the role of the TF under consideration (Ahmad et al., 2020; Monsur et al., 2020).

Marker assisted breeding (MAB) has a wide variety of applications (Jamil et al., 2020b; Jamil et al., 2020c) in stacking of multiple genes in crop plants for various purposes and had been widely used in studying wheat rust (Liu et al., 2020). All we need to find out for marker-assisted breeding is the tight linkage of a molecular marker (with TF as our interest). MAB was used previously for *MdMYB1*, associated with apple fruit skin color. *MdMYB1* imparts red color to the fruit whereas its absence results in green color. A dCAPS marker was developed for selection of fruit color in apples at early plant developmental stages using MAB (Zhu et al., 2011). Another very successful example of MAB is the introduction of the *SUB1* region into rice genetic backgrounds, which increases submergence tolerance without effecting yield, grain quality or development (Oladosu et al., 2020). Similar marker systems could be developed for WRKY and other TFs responding to various biotic and abiotic stresses for foreground selection prior to plantation. This will save time and labor, and will facilitate stacking of TF genes for multiple responsiveness in crop plants.

Development of transgenic plants using TFs has a wide variety of potential applications in development of stress tolerant crops. An example is the production of drought tolerant tobacco plants through the use of *MdDREB76* from apple (Sharma et al., 2019), or the use of wheat *TaNAC29* to enhance salt and drought tolerance in *Arabidopsis* (Huang et al., 2015), and many more examples exist in the literature (Table 3). During development of transgenic plants, TFs is most frequently put under the control of a constitutive promoter, i.e., *CAMV35S* that is expressed in each cell at all growth stages of the plants. Thus, great potential exists for development of transgenic plants using multiple stresses responsive TFs and evaluating their expression in various crops through development of transgenic crops. However, in successive generations of transgenic, rigorous selection criteria should be used to select stress tolerant plants with no negative effects (Fahad et al., 2017).

Table 3

Crop improvement by targeting of TFs through gene silencing and transgenic and gene editing approaches.

Technique	Crop	Gene	Objective	Reference
RNAi silencing	<i>Arabidopsis thaliana</i>	<i>AtNAC042/JUB1</i> , <i>CBNAC/NTL9</i>	Bacterial Leaf spot	(Yuan et al., 2019a)
	<i>Triticum aestivum</i>	<i>TaNAC1</i> , <i>TaNAC21/22</i> , <i>TaNAC30</i>	Yellow rust and powdery mildew resistance	(Yuan et al., 2019a)
Genome editing	<i>Arabidopsis thaliana</i>	<i>AtWRKY11</i> , <i>AtWRKY70</i>	Pathogen resistance	(Ahmad et al., 2020)
	<i>Triticum aestivum</i>	<i>TaDREB2</i> , <i>TaERF3</i>	Drought tolerance	(Kim et al., 2018)
	<i>Oryza sativa</i>	<i>OsNAC2</i> , <i>OsNAC14</i> , <i>OsbZIP62</i> <i>OsERF922</i>	Drought tolerance Rice blast tolerance	(Yang et al., 2019) (Ahmad et al., 2020)
Transgenic approach	<i>Brassica napus</i>	<i>BnWRKY11</i> , <i>BnWRKY70</i>	Pathogen resistance	(Ahmad et al., 2020)
	<i>Arabidopsis thaliana</i>	<i>AtDREB1A</i> , <i>AtWRKY57</i>	Drought tolerance	(Rabara et al., 2014; Wu et al., 2019)
		<i>GmbZIP1</i> , <i>GmDREB2</i> , <i>ZmMYB3R</i> , <i>OsWRKY45</i>	Drought, cold, salinity tolerance Drought, salinity tolerance	
	<i>Triticum aestivum</i>	<i>AtDREB1A</i>	Drought tolerance	
	<i>Oryza sativa</i>	<i>GmbZIP1</i> , <i>GhDREB</i> <i>OsWRKY30</i> , <i>JERF1</i> , <i>OsbZIP23</i> , <i>OsbZIP46</i>	Drought, salinity, cold tolerance Drought tolerance	
	<i>Nicotiana tabacum</i>	<i>SNAC1</i> , <i>SNAC2</i> <i>AtDREB1A</i> , <i>GmERF3</i>	Drought, salinity tolerance Drought tolerance	

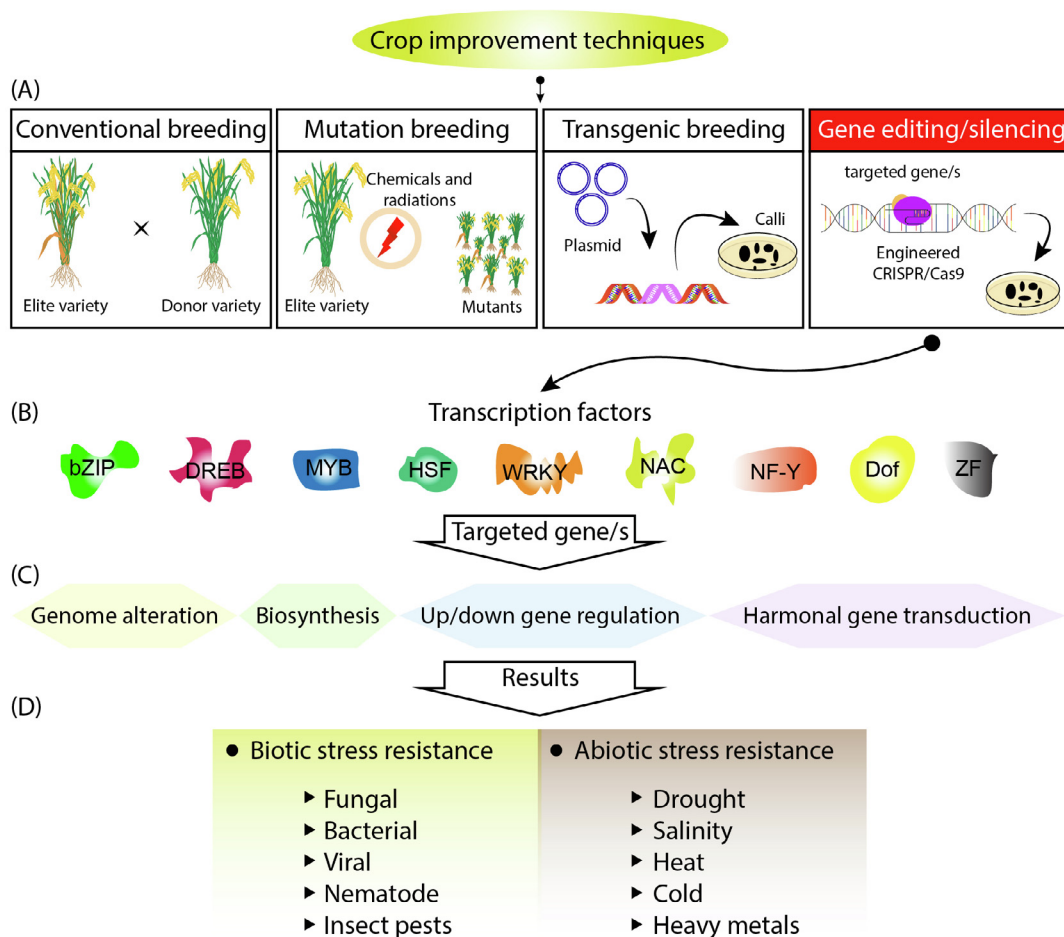


Fig. 3. Schematic illustration of different crop improvement techniques particularly targeted modifications in TFs via gene editing/silencing for crop improvement. (A) Overview of different crop improvement techniques. (B) Different transcriptional factors that can be used for incorporation of biotic and abiotic stress tolerance in crops. (C) Different signal transduction pathways that are activated or modified by TFs. (D) Biotic and abiotic stresses that are alleviated by action of TFs.

6. Ductility and flexibility in TFs to carry out their function

TFs are the most flexible proteins in nature, and this characteristic is very important to conduct regulatory function. It is predicted that 83–94% of TFs possess extended regions of ductile/disordered residues in eukaryotic organisms. It is observed that organismic complexity is positively and strongly correlated with total number of TFs, the number of their spliced variants, and their total disordered residue content. Transcriptional factor families that take part in cell cycle, cell size, cell proliferation, and cell differentiation have more disordered residues and are more flexible. These evidence suggested that increasing TFs are an important factor for increasing organismic complexity (Yruela et al., 2017). This ductility of TFs helps plants combat multiple abiotic stress responses by acting as protein chaperones or protecting other cellular components and structures. TFs have complex and versatile networks to efficiently respond to environmental changes. TF disorder plays an important role in plants, providing them with a fast mechanism to obtain complex, interconnected, and versatile molecular networks (Yruela, 2015).

7. Future perspectives

TFs have great potential for boosting the yield and stress tolerance in field crops. Though, significant achievements have been made in unraveling the potential role of TFs under various biotic

and abiotic stresses (Li et al., 2020c). But, pathways explaining the role of TFs under stresses are yet to be explored. Approximately 50 TFs families have been reported and among those, less than ten including WRKY, DREB, NAC, HSF, MYB, ZF-s, Dof, bZIP, and NAC have been functionally characterized under various biotic and abiotic stresses in different crops. Meanwhile, there is an immense potential to explore the role of remaining TF families in plants' health and yield improvement, and utilize them in crop improvement programs according to their role. Moreover, the information may open new horizons for young researchers to contribute in crop improvement by utilizing different TFs. Similarly, there is an opportunity to establish crosstalk between different TF gene families and then find how they respond under stress conditions Focus should shift towards development of climate resilient crops with biotic as well as abiotic stress tolerance. For instance, majority of WRKY TF genes have their positive role against biotic and abiotic stresses in plants (Li et al., 2020c). Nevertheless, other TFs also resist both biotic as well as abiotic stresses simultaneously. There is a need to identify TF genes that interplay during different stresses. TF genes expressing under multiple stresses should be privileged for breeding climate-smart varieties through conventional as well as modern plant breeding tools.

Transgenic crops promises to be a good source of resistance against biotic and abiotic stresses. However, delivery of TFs to various genetic backgrounds using transgenic technologies still pose a great challenge to researchers due to unexplored metabolic pathways. Nevertheless, the role of many TFs has been fully

characterized (Table 1 and 2) and those can be utilized in breeding climate-smart crops. Currently, there are many new and smart breeding techniques such as genome editing, speed breeding etc., that can be used for developing climate resilient crops by using certain appropriate TFs. For example, *AtMYB14* and *AtMYB15* TFs play their negative role against abiotic stress tolerance in *Arabidopsis* (Table 1). This means that these TFs are involved in the activation of such gene that promotes sensitivity against stresses in plants. Thus, if we manipulate these TFs or their binding sites in the promoter of their respective gene/s then they will be unable to bind and regulate their respective sensitivity gene/s. Ultimately, plants will be more tolerant to the corresponding stress because the TFs and/or gene that was facilitating the proliferation of biotic and/or abiotic stress has been knocked out. Likewise, similar proteins in other species can also be found through certain bioinformatics analysis and can be targeted through genome editing tools for manipulating their negative role in plants.

Concomitantly, many negative regulators can also be found against biotic stress tolerance. For instance, some genes of NAC TFs i.e., *TaNAC1* promotes yellow rust and downy mildew in wheat thus effect wheat growth and yield. On the other hand, it can be seen from tables (Tables 1 and 2) that maximum of the TFs has their positive role in tolerance against biotic and abiotic stresses in plants, hence over-expression of these TFs can improve tolerance against biotic and abiotic stresses in different plant species. Although, these techniques are robust, efficient and have been widely used in plants since last decade, but due to certain limitations and issues such as “off-target effects”, these techniques need to be improved and might not be enough to achieve global food security with current pace of development (Deniaud et al., 2009). Recently, many efforts have been made to resolve the issue of “Off-target effects” and make the genome editing tool as a model and robust tool for genome modifications. For example, use of tissue specific promoters (*SynR1* and *SynR2* are root specific), as explained by Ali et al. (Ali and Kim, 2019), would help in overcoming the off-target effects.

Moreover, most of the functional studies, involved in exploring the role of TFs, are conducted in model plants i.e., tobacco (Sharma et al., 2019) and *Arabidopsis* (Huang et al., 2015), which are relatively easy to handle. The focus should be shifted to cultivated crops (i.e., wheat, rice, maize, and other field crops) for biotic and abiotic stress tolerance. Although, reports are available on the transformation of TFs in field crops, but stacking of multiple stress responsive TFs is just a beginning. Similarly, the role of TFs against heavy metal stress, nematodes and insect attacks needs more attention as these are neglected fields and limited studies were conducted in these directions. Another area of improvement is development of functional marker systems, i.e., SSR markers, SNPs, or dCAPS for MAB of different TFs. To the best of our knowledge, only few examples exist in literature related to the development of functional marker systems for characterization of TFs (Zhu et al., 2011; Liu et al., 2020; Oladosu et al., 2020). Functional markers will help identification of TFs in successive generations for marker-assisted crop improvement. Taken together, TFs have immense potential and opportunities for crop improvement and to achieve global food security.

8. Conclusions

Genome wide studies of different plant TFs gene families have played crucial role in unravelling the role of TFs in various metabolic pathways and identify the key genes which respond to biotic and abiotic stresses. These studies have provided insights about the potent role of TFs in combating different environmental stresses and their utilization to obtain relatively high yield under stress

conditions. Different biotic stresses (i.e., bacterial, fungal and viral diseases, insects and nematodes) and abiotic stresses (i.e., drought, waterlogging, heat, cold, salinity, and heavy metals) are becoming an alarming threat to crop productivity due to changing climate. There is an urgent need for the development of biotic and abiotic stress tolerant crops by targeting different genes and/or their regulators. In this regard, different crop improvement approaches including RNAi silencing, genome editing, speed breeding etc., promise to deliver safer food to human beings and ensure food security. TFs should be exploited by new breeding tools for developing climate-resilient varieties. These varieties will not only combat different biotic and abiotic factors but also improve yield and overcome food insecurity.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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