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Harnessing the Potential of Plant Transcription Factors in developing Climate-Smart Crops: Future Prospects, Challenges, and Opportunities

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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 have 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. The above 50 species of plant TFs have been reported in nature. DREB, bZIP, MYB, NAC, Zinc-finger, HSF, Dof, WRKY, and NF-Y are important with respect to biotic and abiotic stresses whereas the role of many TFs is yet to explore. 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.

1. Introduction

Agricultural crops are important as they represent the in terms of 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 activation of multiple biotic and abiotic factors [1]. 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 [2]. Plants respond to

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different abiotic and biotic challenges through changes at the molecular, cellular, biochemical, and physiological levels. 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 [3]. 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 [2].

Transcriptional factors (TFs) are frontline defensive factors of plants against various biotic and abiotic stresses (Figure 1). These play a fundamental roles in plant tolerance/resistance to various abiotic and biotic stresses [2,4]. TFs usually respond to stress by binding their target sites within cis-acting elements in promoter regions of stress responsive genes (Figure 1E). TFs binding in promotor regions initiate a complex formation for biochemical, physiological, and molecular responses. The Stress response comprises signal perception, signal transduction, and expression of stress-responsive genes (Figure 1B–D). The stress signal is received by receptors in plant cell membranes, or the cell wall and transduced through intracellular elements, i.e., Ca^{2+}, Reactive Oxygen Species (ROS), phytochromes, phosphatases, and protein kinases to TFs. TFs then control gene expression and initiate expression of stress responsive genes [5].

Plant genomes contain a large complement of TF genes approximately 6 % of total ESTs (Table S1). However, a 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. TFs have become central due to the great variety of responses elicited and potent role in both biotic and abiotic stress tolerance, i.e., WRKY TFs simultaneously regulate drought, heat, cold stress, counter disease, as well as pest and nematode attacks [6].

In this review we summarize the current status of different plant TF classes, including DREB, bZIP, MYB, NAC, Zinc-finger, HSF, Dof, WRKY, and NF-Y, and their substantial roles in abiotic and biotic stress responses which may allow development of resistant and/or tolerant crop plants. Different crop improvement techniques, i.e. conventional breeding, mutation breeding, transgenic breeding, and gene editing and silencing are considered and current associated challenges and future opportunities are listed.

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 (Figure 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.

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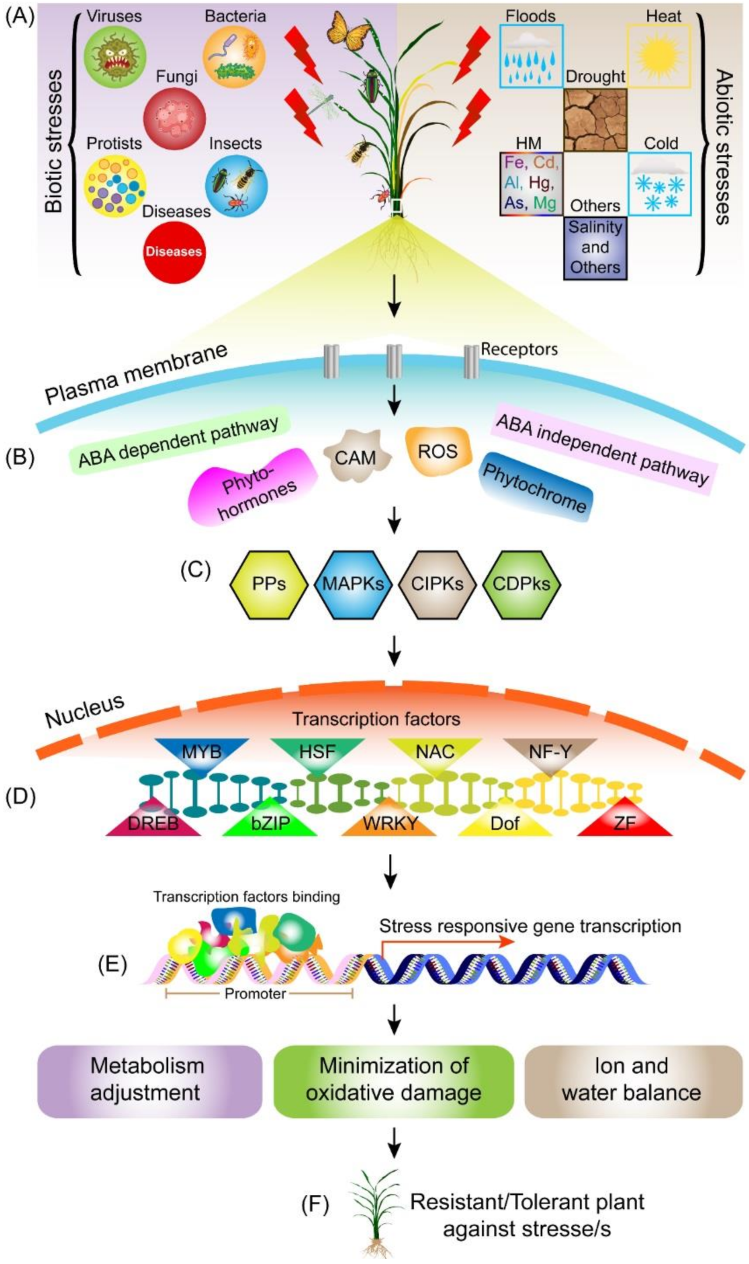

Figure 1. Mechanism of action of transcriptional factors (TFs) in development of resistance in plants against biotic and abiotic stresses. (**A**) Different biotic and abiotic stresses affect plant growth and development; however, plants have developed rapid response strategies to unfavorable conditions; 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

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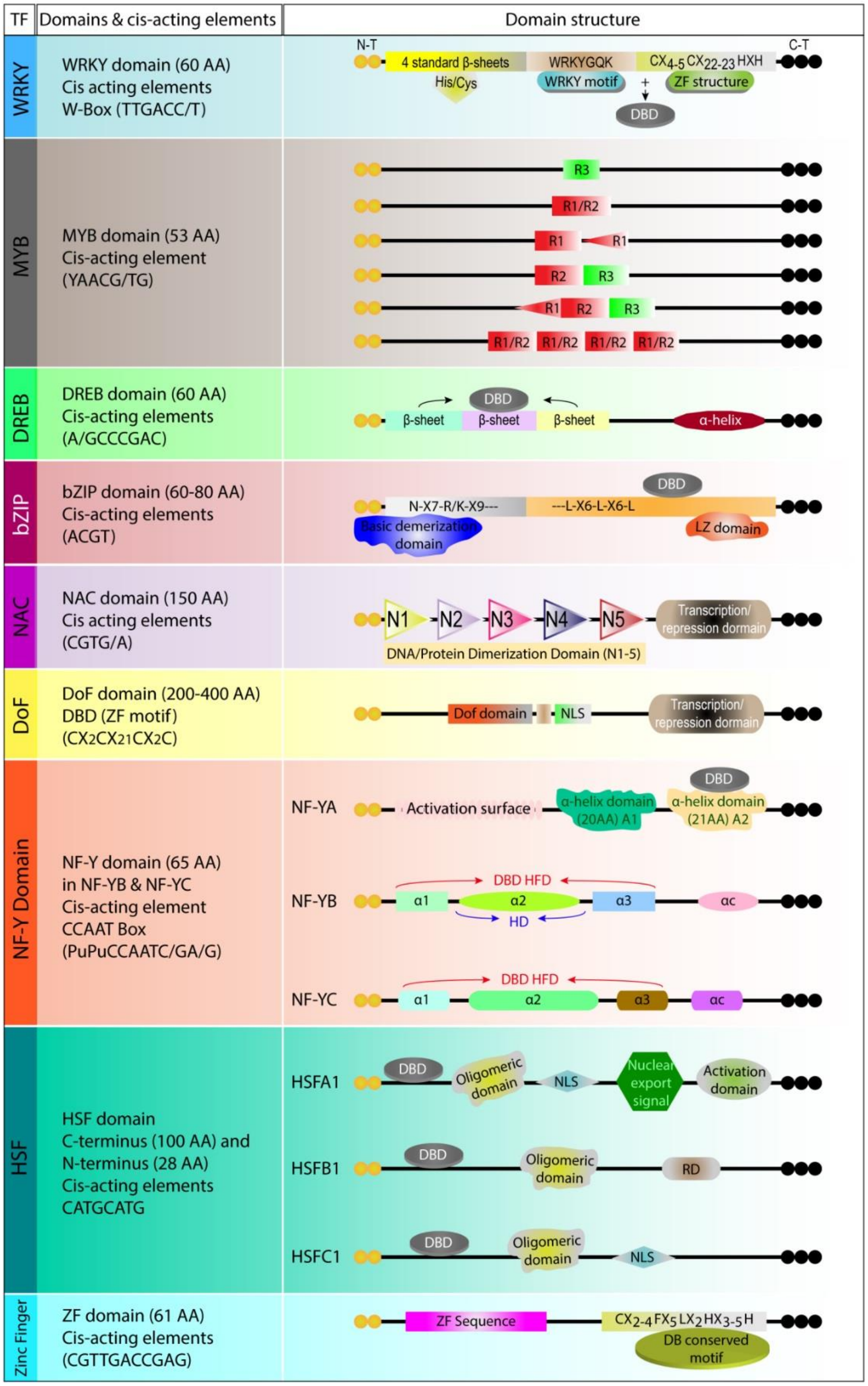
initial step of signal perception, plants activate two major signal cascades: the mitogen-activated protein kinase (MAPK) and calcium-dependent protein kinase (CDPK) pathways. Finally, specific TFs are upregulated or downregulated by protein kinases or phosphatases, and the TFs bind to cis-elements of stress-related genes to enhance or suppress their transcription. Finally, stress resistant/tolerant plants emerge.



TF	Domains & cis-acting elements
WRKY	WRKY domain (60 AA) Cis acting elements W-Box (TTGACC/T)
MYB	MYB domain (53 AA) Cis-acting element (YAACG/TG)
DREB	DREB domain (60 AA) Cis-acting elements (A/GCCCGAC)
bZIP	bZIP domain (60-80 AA) Cis-acting elements (ACGT)
NAC	NAC domain (150 AA) Cis acting elements (CGTG/A)
DoF	DoF domain (200-400 AA) DBD (ZF motif) ($CX_2CX_{21}CX_2C$)
NF-Y Domain	NF-Y domain (65 AA) in NF-YB & NF-YC Cis-acting element CCAAT Box (PuPuCCAATC/GA/G)
HSF	HSF domain C-terminus (100 AA) and N-terminus (28 AA) Cis-acting elements CATGCATG
Zinc Finger	ZF domain (61 AA) Cis-acting elements (CGTTGACCGAG)

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Figure 2. A detail description of Domain structure, domain composition, and cis-regulatory elements of nine TFs, i.e., 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 [7-11]. MYB: The MYB domain consists of 52 amino acids repeats forming 3α-helicase, in which the second and third helicase 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 grove. Two MYB repeats are bind in the major grove and recognize specific DNA target sequence during DNA contact [12,13]. DREB: The DBD of 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 latter within the DBD. DREB proteins attach with C-repeat sequence (A/GCCGAC) or dehydration responsive elements (DRE) for activation of stress responsive genes [14-16]. 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) [17,18]. 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 [19,20]. DOF: The Dof domain is 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. [21,22]. 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 [23-25]. 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 [26-29]. Zinc Finger: Most plants ZF genes have conserved the 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 [30-33].

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 metal stress. These environmental factors are menacing crop survival. Abiotic factors affect growth, productivity, and

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development of plants, and can reduce up to 50% yields of wheat, rice, maize, and cotton [19]. 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 (Figure 1B). The stress-related receptors receive environmental stimuli and activate the stress responsive genes [34]. 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 reduces seedling emergence, germination rate, vegetative growth, root & shoot dry matter, and hypocotyl length [35]. It decreases turgor pressure and limits cell elongation, cell growth, and leaf expansion. Acute shortage of water damages the thylakoid membranes and photosynthetic pigments and slowing the rate of photosynthesis. During drought stress, plants close stomata, thereby reducing intracellular CO2 concentration thus reducing photosynthesis and also inducing oxidative damage [36]. 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 [34].

WRKY TFs play an important role in improving stress tolerance, particularly drought and heat tolerance in various crop plants. *TaWRKY1* and *TaWRKY33* in Arabidopsis thaliana increases drought tolerance due to overexpression of downstream stress related 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 [28]; in transgenic *Arabidopsis ZmWRKY40*, activated stress related genes and generation of ROS. Overexpression of *TaWRKY2* in wheat increased drought tolerance and grain yield. Arabidopsis *AtWRKY30* overexpression in transgenic wheat increased biomass, plant growth, proline concentration, soluble sugar, protein, relative water content, chlorophyll content, and antioxidant enzymes activities to alleviate drought stress [19]. In *Arabidopsis thaliana*, the bZIP gene, *AtABP9* binds to an ABPR motif and increased photosynthetic activity. It increases production of abscisic acid (ABA) and changes composition of photosynthetic pigments. *ZmNF-YB16* overexpresses in young seedling under drought conditions, as a result, antioxidant enzymatic activity increases [34].

Similarly, *SlWRKY8* overexpressed under drought conditions activates malondialdehyde (MDA), hydrogen peroxide (H_2O_2) production, and antioxidant enzymatic activity. These changes trigger *SIRD29*, *SIAREB*, and *SIDREB2A* genes, which decreases 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 [37]. Similarly, soybean *GmNAC8* overexpressed under drought stress and binds to GmDi19-3 (drought-induced proteins), which activates proline and superoxide dismutase (SOD) activity. Overexpression of *ZmNAC111* increases water use efficiency of drought prone maize seedling by upregulating drought responsive genes [38].

3.2 Heat stress

Heat stress adversely affects plant growth and quality by changing their morphological, physiological, and biochemical features. It decreases chlorophyll content and simultaneously induces oxidative stress due to accumulation of hydroxyl (OH^-), hydroperoxyl (HO^{2-}), alkoxy (RO^-), and superoxide (O^{2-}) radicals. Oxidative stress hinders photosynthesis and respiratory activities, disrupts

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protein structure, and membrane integrity [39]. 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 [36]. 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 CO_2 and O_2, and slows down the photosynthetic rate [40].

Triticum aestivum, *Solanum lycopersicum*, *Cicer arietinum*, *Glycine max*, and *Sorghum bicolor* are heat-sensitive crops. Similarly, pollens formation, seed setting, and grain filling are highly heat-sensitive plant processes [41]. Plants have several adaptations against heat stress, i.e., degradation of oxyradicals, reduction in the lipid membrane transformation stage, and biological metabolism. Epigenetic modifications, i.e., acetylation, methylation, phosphorylation, and ribosylation also help plant survival during heat stress by modifying histone proteins after translation [42]. Another modification is evolution of heat shock factors (HSFs). 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 [43].

HSP70 makes a complex with heat stress RNA1 (*HSR1*) and translation elongation factor (*eEF1A*), which activates *HSF1*. HSF1 then activates the cell heat stress responsive machinery [44]. 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-chaperones [45]. Different WRKY i.e., *AtWRKY18*, *AtWRKY25*, *AtWRKY33*, *AtWRKY40*, and *AtWRKY46* also have roles to play during heat stress. *AtWRKY39* imparts heat stress tolerance in Arabidopsis thaliana by binding to a calmodulin binding TF [46]. The *AtDREB2A* binds to dehydration responsive elements (DRE) at the promoter site of *AtHSFA3*, and activates a stress response through an ABA-independent pathway [47].

3.3 Salinity stress

Around 30% of arable land is affected by salt stress and the proportions continue to increase at a rapid pace due to urbanization. Salt stress inhibits imbibition, and decreases root elongation and germination percentage [48]. Salinity and osmotic stress are related and plants have to undergo drought stress in media or soil causing salt stress [49]. Osmotic stress closes stomata, decreases photosynthetic rate, and disrupts action of the thylakoid membrane or Calvin cycle enzymes [50]. It alters leaf anatomy, i.e., thickness of epidermis, mesophyll, palisade length, and diameter. Plants start producing ROS (O^{2-} ion, H_2O_2 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 [51].

Plants maintain homeostasis within and outside the cytoplasm for normal growth [52]. Proteins, channel protein 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 [53]. These osmolytes help in protection of 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.

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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 [51]. All of these events are regulated by a large number of salt responsive genes controlled by different TFs, which percept signal and start defense mechanism [54].

Three types of genes play roles in responses to salt stress, which includes genes of sensing and signaling stress, transport regulators, and salt stress-response-related genes. 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, Ca^{2+}, and other hormones act as secondary messengers against salt stress and induce altered transcriptomic profile [55]. *AtNAC2*, a nuclear localized gene, is upregulated during salt stress; it promoted lateral root development [56]. Similarly, over-expression of *AtWRKY46* increases 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 [57]. Moreover *Reaumuria trigyna* derived *RtWRKY1* is overexpressed under salt stress and resulted in increased root growth, increased antioxidative enzymes, decreased Na^+ or Na^+/K^+ ratio [58]. Overexpression of *GmWRKY54* alleviates salt stress in soybean [59]. *AtbZIP24* increases salt tolerance by osmotic balance, ion homeostasis in cytoplasm, and increased growth and development, involving homo- and heterodimerization, or post-transcriptional modification [60]. 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 [61]. ROS causes oxidative damage in cells, reduced enzymatic activity, cause ionic imbalance, damaged cell membranes, reduced respiration rate, and degraded proteins. Plants also face low germination, delayed cell cycle, low leaf development rate, decreased seedling vigor, and yield [62]. 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 to pollen sterility, abortion of flower or ovules, distortion of pollen tubes, poor fruit setting, deformation of panicles, spikelet degeneration, and reduced productive tillers [63]. The photosynthetic rate decreases due to reduced CO_2 conductance in the mesophyll and stomata, restricted transport of metabolites and increased photo-inhibition [62].

Different TFs respond to cold stress by regulating expression of cold responsive genes, dehydrin, abscisic acid responsive genes, and late embryogenesis abundant genes. These TFs are present in the nucleus through as they possess nucleus-localization signals (NLSs). Under stress, membrane bound TFs are activated, enter the nucleus, and regulate gene expression. Nuclear-localized *SlNAC1* activate stress responsive genes and enhances cold tolerance. Similarly, *ZmSNAC1*, *OsNAC5*, and *TaNAC57* genes are overexpressed and enhance cold tolerance (Li et al., 2014). *Arabidopsis thaliana* and grapevine calli show overexpression of *VaWRKY12* and regulated expression of the genes encoding antioxidant enzymes, glutathione S-transferases, and peroxidase [64]. *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 [65]. *OsbZIP73* upregulates and plays an important role at flowering, seedling, and reproductive stages to counter cold stress. It co-expressed with *OsbZIP71* and enhanced seed set by affecting pollen fertility through an increase in concentration of soluble sugar in pollen and a decreased level of ABA in anthers [66].

OsbZIP87 and *OsbZIP38* also play an important role in enhancing cold tolerance [66]. *OsDREB1G* regulates expression of cold induced genes present in protoplasts. *Arabidopsis thaliana*

AtDREB1A/CBF1 and *AtCBF4* are overexpressed in response to cold stress (Moon et al., 2019). MYBs also play important roles in combating cold stress by affecting cell cycle, cellular morphogenesis, hormonal signaling, secondary metabolism, and gene expression. *AtMYB14* down regulates under cold stress and encodes 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 GmMYBJ1* is overexpressed and enhances cold tolerance. *GmMYBJ1* regulates expression of many stress responsive genes, such as *AtCOR15a*, *AtRD29B*, *AtP5CS*, and *AttCOR78*, as a result the plant tolerates cold stress. *OsMYB4* in *Arabidopsis thaliana* is also overexpressed and increases freezing tolerance [67].

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. Heavy metal enriched soil results in reduced growth, altered nutrients and water balance, inhibition of photosynthesis and chlorosis. Further, HMs affect chlorophyll content, photosystem II effectiveness, and Rubisco activity [68]. It leads to drop in reductant pool and less ATP production with less CO_2 fixation [69]. Heavy metal enhanced protease activity decreases ammonia glutamate dehydrogenase (GDH), glutamine oxoglutarate aminotransferase (GOGAT), glutamine synthetase (GS), nitrite reductase (NiR), and nitrate reductase (NR) activity [70]. ROS starts accumulating, cause oxidative stress by interacting with proteins, DNA, and lipids, and destabilizing cellular organization [71].

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, such as in *Arabidopsis thaliana* induction of MPK_3 and MPK_6, due to $CuSO_4$ and $CdCl_2$. *Oryza sativa* multiple stress responsive MK2 (*OsMSRMK2*), wound and JA-uninducible MK1 (*OsWJUMK1*), and *OsMSRMK3* are induced in presence of Cd^{2+} and Cu^{2+} in roots and leaves. 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 $CdCl_2$ and $CuCl_2$ [72]. Downstream TFs, i.e., activator protein 2 (AP2), WRKY, bZIP, MYB, DREB, ERF, and ZAT (C_2H_2 type ZF-) transcription factors are stimulated by activation of MAPKs as their targets. Due to Cd and Zn stress, MYB TFs, i.e., *AtMYB28*, *AtMYB72*, *AtMYB48*, *AtMYB124*, and *AtMYB4* are upregulated in *Arabidopsis thaliana*. A short duration stress of Cu to roots in *Arabidopsis* activates *AtWRKY22*, *AtWRKY25*, and *AtWRKY29*, whereas long duration stress of Cd activates *AtWRKY25* and *AtWRKY29*. Similarly, in *Glycine max*, up-regulation of *GmbZIP62* and down-regulation of *GmbZIP44* and *GmbZIP78* is associated with Cd stress. In *Arabidopsis thaliana*, Cd stress is responsible for expression of ethylene responsive factors, i.e., *AtERF1*, *AtERF5*, and *AtZAT6* to regulate plant metabolism [73].

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 [74]. Water logging results from prolonged rainfall, poor drainage of soil, and its intensity tends to increase every year [75]. Diffusion of gases in water is low when compared to air, which results in decreased oxygen availability and detrimental effects on plant health [76]. 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 [77]. 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 decrease; and the electron-transport chain and CO_2 assimilation are also affected [78]. Furthermore, toxic compounds and ROS

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accumulated. Certain redox enzymes, such as cupredoxins, are activated to maintain ROS balance [79].

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 [80]. The known transcription factors that play roles in regulation of water logging stress include bZIP, NAC, WRKY, MYB, and ERF families. But the highest number of transcription factors responding to waterlogging stress belong to the MYB and the AP2/EREBP families [81]. 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 [82]. In *Arabidopsis*, five ERF VII genes *AtHRE1*, *AtHRE2*, *AtRAP2.2*, *AtRAP2.3*, and *AtRAP2.12* are key regulators of flooding. 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 [80]. *ZmEREB180* increases waterlogging tolerance in maize seedlings. *ZmEREB180* has a conserved N terminal motif and its ectopic expression increases tolerance [83]. Overexpression of *AtSHYG* (*AtNAC047*) causes hyponastic growth in *Arabidopsis* [84]. Moreover, *SiWRKY51* and *SiWRKY65* also play important roles in roots of waterlogged plants [85]. 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% [19]. 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 [86]. The available data suggest that a decrease in annual crop productivity by arthropods is 18%–20% worldwide, amounting to US $470 billion. The area's most prone to biotic stresses are African and Asiatic countries [87]. Disease negatively affects morphological characteristics, i.e., plant height, chlorophyll content, and leaf architecture [88].

To deal with these challenges, the plant adopt coordination of different physiological, biochemical, and molecular processes through signal transduction mechanisms [89]. 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.

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

Stress	Crop	Transcriptional Factors/Genes	Reference
Drought	*Arabidopsis thaliana*	*AREB1*$^{\uparrow+}$, *AREB2/ABF4*$^{\uparrow+}$, *ATWRKY1*$^{\downarrow-}$, *AtWRKY57*$^{\uparrow+}$, *AtWRKY63/ABO3*$^{\downarrow+}$, *AtNAC019*$^{\uparrow+}$, *AtNAC055*$^{\uparrow+}$, *AtNAC072*$^{\uparrow+}$, *AtNF-YB7*$^{\uparrow+}$, *AtNF-YB3*$^{\uparrow+}$, *AtNF-YA5*$^{\uparrow+}$, *AtMYB12*$^{\uparrow+}$, *AtMYB15*$^{\uparrow+}$, *AtMYB33*$^{\uparrow+}$, *AtMYB35*$^{\downarrow+}$, *AtMYB60*$^{\downarrow-}$, *AtMYB44*$^{\uparrow+}$, *AtMYB88*$^{\uparrow+}$, *AtMYB99*$^{\downarrow+}$, *AtMYB96*$^{\uparrow+}$, *AtMYB102*$^{\uparrow+}$, *AtMYB110*$^{\downarrow+}$	[12,63,90-94]
	Triticum aestivum	*TaDREB2*$^{\uparrow+}$, *TaDREB3*$^{\uparrow+}$, *TaWRKY2*$^{\uparrow+}$, *TaWRK19*$^{\uparrow+}$, *TaWRKY10*$^{\uparrow+}$, *TaNAC69*$^{\uparrow+}$, *TaNAC2a*$^{\uparrow+}$, *TaPIMP1*$^{\uparrow+}$, *TaMYB1*$^{\uparrow+}$, *TaMYB2A*$^{\uparrow+}$, *TaMYB19*$^{\uparrow+}$, *TaMYB3R1*$^{\uparrow+}$, *TaMYB31*$^{\uparrow+}$, *TaMYBsdu1*$^{\uparrow+}$, *TaMYB30*$^{\uparrow+}$, *TaMYB33*$^{\uparrow+}$	[12,19,63,90-95]
	Oryza sativa	*OsDREB1F*$^{\uparrow+}$, *OsDREB2A*$^{\uparrow+}$, *OsEREBP1*$^{\uparrow+}$, *OsWRKY01*$^{\uparrow+}$, *OsWRKY2*$^{\uparrow+}$, *OsWRKY5*$^{\uparrow+}$, *OsWRKY7*$^{\uparrow+}$, *OsWRKY43*$^{\uparrow+}$, *OsWRKY11*$^{\uparrow+}$, *OsWRKY45*$^{\uparrow+}$, *OsWRKY47*$^{\uparrow+}$, *OsNAC10*$^{\uparrow+}$, *OsNAC2*$^{\uparrow+}$, *OsNF-YA7*$^{\uparrow+}$, *OsbZIP42*$^{\uparrow+}$, *OsbZIP46*$^{\uparrow+}$, *OsbZIP62*$^{+\uparrow}$, *OsMYB2*$^{\uparrow+}$, *OsMYB4*$^{\uparrow+}$, *OsMYB55*$^{\uparrow+}$, *MYB59*$^{\uparrow+}$, *OsMYB48-1*$^{\uparrow+}$	[12,19,63,90-95]
	Zea mays	*ZmDREB1A*$^{\uparrow+}$, *ZmDREB2A*$^{\uparrow+}$, *ZmDBF3*$^{\uparrow+}$, *ZmDREB2.7*$^{\uparrow+}$, *ZmWRKY106*$^{\uparrow+}$, *ZmNAC55*$^{\uparrow+}$, *ZmSNAC1*$^{\uparrow+}$, *ZmNAC111*$^{\uparrow+}$, *ZmNF-YB2*$^{\downarrow+}$, *ZmNF-YA3*$^{\downarrow+}$, *ZmHSF14*$^{\uparrow+}$, *ZmHSF20*$^{\uparrow+}$, *ZmbZIP72*$^{\uparrow+}$, *ZmbZIP4*$^{\uparrow+}$, *ZmbZIP60*$^{\uparrow+}$, *ZmMYB95*$^{\uparrow+}$, *ZmMYB36*$^{\uparrow+}$	[2,12,19,63,90-96]
	Glycine max	*GmDREB2A;2*$^{\uparrow+}$, *GmERF3*$^{\uparrow+}$, *GmWRKY54*$^{\uparrow+}$, *GsWRKY20*$^{\uparrow+}$, *GmNAC085*$^{\uparrow+}$, *GmNF-YA3*$^{\uparrow+}$, *GmMYB177*$^{\uparrow+}$, *GmbZIP2*$^{\uparrow+}$	[2,12,19,63,90-96]
	Vigna radiate	*VrDREB2A*$^{\uparrow+}$, *VrDREB2B*$^{\uparrow+}$	[92]
	Camellia sinensis	*CsDREB2A*$^{\uparrow+}$, *CsDREB2B*$^{\uparrow+}$	[92]
	Hordeum vulgare	*HvWRKY38*$^{\uparrow+}$	[90]
	Solanum lycopersicum	*SpWRKY1*$^{\uparrow+}$	[90]
	Solanum tuberosum	*StMYB1R-1*$^{\uparrow+}$	[97]
	Cicer arietinum	*CarNAC3*$^{\uparrow+}$	[63]
	Chrysanthemum	*CmMYB2*$^{\uparrow+}$	[97]
	Setaria italic	*SiNF-YA1*$^{\uparrow+}$, *SiNF-YB8*$^{\uparrow+}$	[91,94]
	Cynodon dactylon	*CdtNF-YC1*$^{\uparrow+}$	[91,94]
	Fagopyrum tataricum	*FtbZIP5*$^{\downarrow+}$	[2,98]
	Poncirus trifoliate	*PtrABF*$^{\uparrow+}$	[2,98]
	Vitis vinifera	*VvMYB60*$^{\uparrow+}$	[19,63]
	Gossypium hirsutum	*GhirNAC2*$^{\uparrow+}$	[99]
Heat	*Arabidopsis thaliana*	*WRKY39*$^{\uparrow+}$, *WRKY46*$^{\uparrow+}$, *AtWRKY25*$^{\downarrow+}$, *AtWRKY26*$^{\downarrow+}$, *AtWRKY33*$^{\downarrow+}$, *AtNAC42*$^{\uparrow+}$, *AtMYB3*$^{\uparrow+}$, *AtMYB6*$^{\uparrow+}$, *AtMYBL2*$^{\uparrow+}$, *AtMYB68*$^{\uparrow+}$,	[90,98,100]
	Oryza sativa	*OsDREB2B*$^{\uparrow+}$, *OsWRKY11*$^{\uparrow+}$, *OsNAC063*$^{\uparrow+}$, *OsTZF1*$^{\uparrow+}$, *OsMYB55*$^{\uparrow+}$	[46,47,90,92,100-102]
	Zea mays	*ZmDREB2A*$^{\uparrow+}$, *ZmWRKY106*$^{\uparrow+}$, *ZmNF-YA3*$^{\uparrow+}$, *ZmHSF14*$^{\uparrow+}$, *ZmHSF20*$^{\uparrow+}$, *ZmbZIP60*$^{\uparrow+}$, *ZmbZIP4*$^{\uparrow+}$, *ZmMYB-R1*$^{\uparrow+}$	[19,46,47,90,91,102]
	Glycine max	*GmHSP70*$^{\uparrow+}$, *GmDREB1*$^{\uparrow+}$	[102,103]

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	Capsicum	*CpDREB2*$^{\uparrow+}$	[102,104]
	Camellia sinensis	*CsNAM*$^{\uparrow+}$	[101]
	Gossypium hirsutum	*GhHSF37*$^{\uparrow+}$, *GhHSF24*$^{\uparrow+}$	[102]
	Capsicum annum	*CaHSFA2*$^{\uparrow+}$	[102]
	Malus domestica	*MdHSFA-9b*$^{\uparrow+}$	[102]
	Solanum lycopersicum	*SlHSF01*$^{\uparrow+}$, *SlHSFB1*$^{\uparrow+}$, *SlHSFA2*$^{\uparrow+}$, *SlHSF04*$^{\uparrow+}$, *SlHSF16*$^{\uparrow+}$, *SlHSF17*$^{\uparrow+}$, *SlHSF18*$^{\uparrow+}$	[102,105]
	Lycopersicum esculantum	*LeAN2*$^{\uparrow+}$	[100]
Cold	*Arabidopsis thaliana*	*DREB1A*$^{\uparrow+}$, *AtZFP1*$^{\uparrow+}$, *AtZFP2*$^{\uparrow+}$, *AtZF3*$^{\uparrow+}$, *AtNAC019*$^{\uparrow+}$, *AtMYB14*$^{\downarrow-}$, *AtMYB15*$^{\downarrow-}$, *AtMYB44*$^{\uparrow+}$, *AtMYBC1*$^{\uparrow+}$	[19,93]
	Triticum aestivum	*TaWRKY19*$^{\uparrow+}$, *TaNAC2a*$^{\uparrow+}$, *TaNAC4a*$^{\uparrow+}$, *TaNAC57*$^{\uparrow+}$, *TaMYB2A*$^{\uparrow+}$, *TaMYB3R1*$^{\uparrow+}$, *TaMYB56-B*$^{\uparrow+}$	[12,65]
	Oryza sativa	*OsDREB1A*$^{\downarrow+}$, *OsWRKY71*$^{\downarrow+}$, *OsNAC6*$^{\uparrow+}$, *OsNAC5*$^{\uparrow+}$, *OsNAC04*$^{\uparrow+}$, *OsbZIP73*$^{\uparrow+}$, *OsMYB2*$^{\uparrow+}$, *OsMYB4*$^{\uparrow+}$, *OsMYB3R-2*$^{\uparrow+}$, *OsMYBS3*$^{\uparrow+}$,	[92,106-108]
	Zea mays	*ZmDREB2A*$^{\uparrow+}$, *ZmDBP3*$^{\uparrow+}$, *ZmDREB1A*$^{\uparrow+}$, *ZmDBF3*$^{\uparrow+}$, *ZmSNAC1*$^{\uparrow+}$, *ZmNAC55*$^{\downarrow+}$, *ZmbZIP60*$^{\uparrow+}$, *ZmMYB53*$^{\uparrow+}$, *ZmMYB-R1*$^{\uparrow+}$	[92,106-108]
	Glycine max	*GmWRKY21*$^{\uparrow+}$, *GmNAC20*$^{\uparrow+}$, *GmMYB92*$^{\uparrow+}$, *GmbZIP44*$^{\uparrow+}$, *GmbZIP62*$^{\uparrow+}$	[19,65,92]
	Vitis acerifolia	*VaWRKY12*$^{\uparrow+}$	[106]
	Pyrus communis	*PcMYB10*$^{\uparrow+}$	[12]
Salinity	*Arabidopsis thaliana*	*AtDREB1A/CBF3*$^{\uparrow+}$, *AtWRKY25*$^{\downarrow+}$, *AtWRKY33*$^{\downarrow+}$, *AtNAC055*$^{\uparrow+}$, *AtNAC072*$^{\uparrow+}$, *AtNAC019*$^{\uparrow+}$, *AtNAC063*$^{\uparrow+}$,*ANAC069*$^{\downarrow-}$ *AtMYB20*$^{\uparrow+}$, *AtMYB41*$^{\uparrow+}$, *AtMYB44*$^{\uparrow+}$, *AtMYB73*$^{\downarrow-}$, *AtMYB88*$^{\uparrow+}$, *AtMYB124*$^{\uparrow+}$	[19,63,109,110]
	Triticum aestivum	*TaWRKY2*$^{\uparrow+}$, *TaWRKY19*$^{\uparrow+}$, *TaNAC2a*$^{\uparrow+}$, *TaNAC4a*$^{\uparrow+}$, *TaNAC6*$^{\uparrow+}$, *TaNAC7*$^{\uparrow+}$, *TaMYB1*$^{\uparrow+}$, *TaMYB2A*$^{\uparrow+}$, *TaMYB3R1*$^{\uparrow+}$, *TaMYBsdu1*$^{\uparrow+}$, *TaMYB33*$^{\uparrow+}$, *TaMYB73*$^{\uparrow+}$	[19,63]
	Oryza sativa	*OsDREB1F*$^{\uparrow+}$, *OsDREB2A*$^{\uparrow+}$, *OsWRKY43*$^{\uparrow+}$, *OsWRKY45*$^{\uparrow+}$, *OsWRKY5*$^{\uparrow+}$, *OsWRKY7*$^{\uparrow+}$, *OsWRKY30*$^{\uparrow-}$, *OsWRKY72*$^{\uparrow-}$, *OsNAC6*$^{\uparrow+}$, *OsNC5*$^{\uparrow+}$, *OsNAC1*$^{\uparrow+}$, *OsNAC063*$^{\uparrow+}$, *OsMYB2*$^{\uparrow+}$, *OsMYB3R-2*$^{\uparrow+}$, *OsMYB91*$^{\uparrow+}$, *OsMYB48-1*$^{\uparrow+}$, *OsZFP245*$^{\uparrow+}$, *OsZFP252*$^{\uparrow+}$, *Os ZFP182*$^{\uparrow+}$, *OsZFP179*$^{\uparrow+}$	[19,63,109,110]
	Zea mays	*ZmDREB2A*$^{\uparrow+}$, *ZmWRKY106*$^{\uparrow+}$, *ZmbZIP60*$^{\uparrow+}$, *ZmbZIP72*$^{\uparrow+}$, *ZmbZIP4*$^{\uparrow+}$, *ZmMYB36*$^{\uparrow+}$, *ZmMYB-R1*$^{\uparrow+}$, *ZmSNAC1*$^{\uparrow+}$	[63,92,93,109]
	Glycine max	*GmWRKY54*$^{\uparrow+}$, *GmWRKY20*$^{\uparrow+,}$ *GmWRKY13*$^{\uparrow-}$, *GmNAC20*$^{\uparrow+}$, *GmbZIP44*$^{\uparrow+}$, *GmbZIP110*$^{\uparrow+}$, *GmbZIP62*$^{\uparrow+}$, *GmMYB177*$^{\uparrow+}$, *GmMYB76*$^{\uparrow+}$, *GmMYB92*$^{\uparrow+}$	[63,90,92,93]
	Vigna radiate	*VrDREB2A*$^{\uparrow+}$	[109]
	Camellia sinensis	*CsDREB2A*$^{\uparrow+}$, *CsDREB2B*$^{\uparrow+}$, *CsNAM*$^{\uparrow+}$	[63,109]
	Agrostis stolonifera	*AsNAC60*$^{\uparrow+}$	[63,109]
	Setaria italic	*SiNAC*$^{\uparrow+}$, *SiNF-YA1*$^{\uparrow+}$	[91,111]
	Cynodon dactylon	*CdtNF-YC1*$^{\uparrow+}$	[91]
	Fagopyrum tataricum	*FtbZIP5*$^{\uparrow+}$	[92]
	Medicago truncatula	*MtMYB199*$^{\uparrow+}$, *MtMYB634*$^{\uparrow+}$, *MtMYB636*$^{\uparrow+}$, *MtMYB1070*$^{\uparrow+}$	[19]

	Gossypium hirsutum	*GhZFP1*$^{\uparrow+}$	[19]
Water logging	*Arabidopsis thaliana*	*AtNAC102*$^{\uparrow+}$, *AtNAC063*$^{\uparrow+}$, *AtAREB1*$^{\uparrow+}$, *AtAREB2/ABF4*$^{\uparrow+}$, *AtABF3*$^{\uparrow+}$, *AtABF2*$^{\uparrow+}$	[101]
	Zea mays	*ZmEREB180*$^{\uparrow+}$	[101]
	Camellia sinensis	*CsNAM* $^{\uparrow+}$	[101]
	Oryza sativa	*OsDREB2A*$^{\uparrow+}$	[101]
Heavy Metal Stress	*Arabidopsis thaliana*	*AtMYB48*$^{\uparrow+}$, *AtMYB28*$^{\uparrow+}$, *AtMYB72*$^{\uparrow+}$, *AtMYB124*$^{\uparrow+}$, *AtMYB4*$^{\uparrow+}$	[73]
	Zea mays	*ZmbZIP54*$^{\uparrow+}$	[19]
	Glycine max	*GmbZIP62*$^{\uparrow+}$, *GmbZIP44*$^{\downarrow+}$, *GmbZIP78*$^{\downarrow+}$	[19]
	Triticum aestivum	*TaHSFA4a*$^{\uparrow+}$	[29]

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

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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 effects rice, banana, tomato, and citrus fruits, and invades mostly xylem or parenchyma tissues [112]. *Xylella fastidiosa* is a xylem-limited phytopathogen, which causes diseases in grapes, almond, citrus, peach, coffee, and olive trees. *Pseudomonas syringea* causes infection in the tomato by forming a necrotic lesion surrounded by yellow chlorotic halo on the tomato (termed as bacterial speck) [113].

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. Rice *OsWRKY80* and *OsWRKY4* genes increase resistance against sheath blight. *OsWRKY80* attaches to a W-box in the promoter region of *OsWRKY4*, which activates defense response against *Rhizoctonia solani*. Moreover, *OsWRKY7*, *OsWRKY58*, *OsWRKY64*, and *OsWRKY76* genes are expressed in response to rice blast disease [19]. Overexpression of *VaERF20* increases resistance against *Pseudomonas syringae* and *Botrytis cinerea* in transgenic Arabidopsis [114]. *SlCabZIP* and *SlERF11* eliminates pathogenicity of *Pseudomonas syringae* Pv. tomato DC3000 and provide resistance [115]. *AtNAC032* represses activation of MYC on pest attack by blocking a coronatine mediated reopening of stomata to thus stopping the entry of *Pseudomonas syringae* Pv. tomato DC3000 [116]. *GhWRKY39-1* provides resistance to Root rot (*R. solani*) in *Gossypium hirsutum* [117]. *CaWRKY27*, *CaWRKY6* mediate bacterial wilt while *CaWRKY58* resists bacterial spot (*Xanthomonas axonopodis*) [5]. *SINAC35* counter bacterial wilt (*R. solanacearum*) and bacterial spot (*X. compestris*) infections in *Capsicum annuum* [19], 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 [118]. 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, WRKY, NAC, MYB, and MYC [119]. Overexpression of *AtWRKY72* enhances resistance against powdery mildew. Similarly, *AtWRKY8* and *AtWRKY28* enhance resistance against *Botrytis cinerea*. *TaWRKY49*, *TaWRKY62*, and *TaWRKY70* combat strip rust (*Puccinia striiformis*) by activating ROS, jasmonic acid, salicylic acid, and ethylene production [117].

In rice, overexpression of *OsWRKY45* and *OsWRKY22* enhance resistance to *Pyricularia oryzae*. *OsWRKY45* overexpresses and enhances resistance against fungal pathogen *Magnaporthe grisea*. *OsWRKY4* and *OsWRKY80* increase sheath blight resistance in rice. *OsWRKY80* binds to the W-box in the promotor region of *OsWRKY4* and works as a positive regulator for *Rhizoctonia solani* resistance. In *Brachpodium distachyon*, *BdWRKY8*, *BdWRKY50*, *BdWRKY34*, and *BdWRKY70* are upregulated and enhance resistance against *Fusarium graminearum*. In *Hordeum vulgare*, *HvWRKY1* cooperates with *HvMYB6* to counter powdery mildew [6]. Similarly, *TaNAC6* overexpresses and enhances powdery mildew resistance and decreases fungal haustoria. *OsNAC6* shows overexpression and enhances rice blast resistance. In barley, *HvNAC6* overexpresses under powdery mildew infection and increased resistance against *Blumeria gramini*. *VaERF20* increases resistance against *Botrytis cinerea* in transgenic *Arabidopsis*. In soybean, *GmbZIP1*, *GmbZIP62*, *GmbZIP105*, and *GmbZIP2* genes prevent infestation of Asian soybean rust [19].

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, less reduced set, wilting, and cell death [120]. 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* [121]. 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 Gezira 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 programsm [122]. 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 [123].

Different TFs play significant roles into resisting virus-induced damage. 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 [5]. 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: *SlNAC20*, *SlNAC24*, *SlNAC41*, and *SlNAC61* play a significant role in imparting resistance against Tomato Yellow Leaf Curl Virus (TYLCV) [124]. *Triticum aestivum* NAC TFs, i.e., *AtGRAB1* (Geminivirus Rep A-Binding) and *AtGRAB2*, interacts 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 inhibits virus infection [20]. Six WRKY genes, *SolyWRKY41*, *SolyWRKY42*, *SolyWRKY53*, *SolyWRKY54*, *SolyWRKY80*, and *SolyWRKY81* obtained from tomato reduce 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 [125].

4.4 Nematodes

Plant parasitic nematodes (PPNs) are economically important agricultural pests. Two classes exits 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* [126]. 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 [127]. These secondary metabolites reduce attraction of nematodes towards plant roots. Genes linked with synthesis of cytokinin, gibberellic acid, salicylic acid, jasmonates, and auxin signal responses are activated. *SlWRKY75* is activated in *Solanum lycopersicum* by infection with

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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 [128].

AtWRKY23 is overexpressed due to auxin stimulation at the feeding point of cyst nematode *Heterodera schachtii*. *OsWRKY11*, *OsWRKY70,* and *OsWRKY62* upregulate 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 *SlWRKY70* by salicylic acid, both *SlWRKY35* and *SlWRKY3* were activated [129]. *AtWRKY33* is stimulated by JA and works as a positive regulator against PPN attack. *AtWRKY33* overexpression along with different promoters confers resistance against *Heterodera schachtii*. *SlWRKY45* is implicated in signal transduction pathways during accumulation of nematodes in the root zone [130]. Five *Glycine max* WRKY genes of Glycine max; *GmWRKY5*, *GmWRKY28*, *GmWRKY36*, *GmWRKY62*, and *GmWRKY154* are highly responsive against SCN reducing by the 70% the population, while *GmWRKY136*, *GmWRKY86*, *GmWRKY53*, and *GmWRKY52* show moderate response by reducing 40%–60% the population and *GmWRKY71* and *GmWRKY8* caused a 10%–30% decline in SCN population [131].

4.5 Pest attack

Changing climate is promoting the growth of herbivores, as increased in temperature are shortening life cycles and increasing chances of appearance [132]. Insect possess different feeding mechanisms. Chewing insects such as beetles and caterpillars, consume plant tissues whereas piercing and sucking insects feed on the vascular system for example aphids which inserts 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 [133]. Moreover, spider mites, a phytophagous acarian belonging to Tetranychus genus, pierce parenchyma cells and suck the contents [134].

Some plants counter attack or activate emergency responses [135]. 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 activates 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 [133].

Few TFs have been shown to play a role I responding to herbivore induced plant damage. *OsERF3* is upregulated in response to feeding of striped stem borer (SSB) in *Oryza sativa*, which activates the transcript level of two MAPKs and two WRKY genes. As a result, the concentration of SA, JA, and trypsin protease inhibitor activity increases. *OsWRKY45* protects rice against infestation by Brown Plant hopper (*Nilaparvata lugens*) [136]. *TaMYB19*, *TaMYB44*, and *TaMYB29* act as co-regulators in phloem based defense response against English grain aphid in wheat. *AtMYB75* increases resistance against *Pieris brassicae* by modulating flavonoid metabolites. Overexpression of *GsMYB15* obtained from wild soybean increases *Arabidopsis* resistance against *Helicoverpa armigera* by a JA mediated insect response [137]. *CmMYB19* increases resistance of *Chrysanthemum* against aphids by promoting a lignin biosynthesis pathway [138]. *NbERF173* obtained from *Nicotiana benthamiana* provides resistance against *Phytophthora parasitica* [139]. *TaWRKY53* induces resistance mechanisms against Russian wheat aphid in *Triticum aestivum* [140]. Similarly, *OsWRKY53* provides resistance against *Chilo suppressalis* SSB [97].

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

Stress	**Crop**	**Disease**	**Gene**	**Reference**
Bacterial	*Arabidopsis thaliana*	Bacterial Leaf spot *(Pseudomonas syringae)*	*AtWRKY22*$^{+}$↓, *AtWRKY29*$^{+}$↓, *AtWRKY38*$^{-}$↑, *AtWRKY41*$^{+}$↑, *AtWRKY62*$^{-}$↑, *AtERF014*$^{+}$↑., *AtNAC19*$^{+}$↑, *AtNAC55*$^{+}$↑, *AtNAC72*$^{+}$↑, *AtMYB30*$^{+}$↑, *AtMTB44*$^{+}$↑, *AtMYB96*$^{+}$↑, *AtNAC042/JUB1*$^{-}$↑, *CBNAC/NTL9*$^{-}$↑,	[5,19,20,117]
	Vitis vinifera	Bacterial Leaf Spot (*Pseudomonas syringae*)	*VvERF20*$^{+}$↑	[5,117]
	Oryza sativa	Bacterial Blight (*Xanthomonas oryzae*)	*OsWRKY6*$^{+}$↑, *OsWRKY45*$^{+}$↑ *OsWRKY67*$^{+}$↑, *OsNAC58*$^{+}$↑, *OsNAC66*$^{+}$↑, *OsWRKY13*$^{+}$↑, *OsWRKY71*$^{+}$↑, *OsEREBP1*$^{+}$↑.	[5,19,20,117]
	Capsicum annuum	Bacterial Wilt (*Ralstonia solanacearum*)	*CaWRKY27*$^{+}$↑, *CaWRKY6*$^{+}$↑,	[5]
		Bacterial Spot (*Xanthomonas axonopodis*)	*CaWRKY58*$^{-}$↑	[5]
		Pepper Root Rot (*Bacillus thuringiensis*)	*CaPF1*$^{+}$↑	[117]
	Solanum lycopersicum	Bacterial Wilt (*Ralstonia solanacearum*)	*SlERF3*$^{+}$↑, *SlERF5*$^{+}$↑, *SlNAC35*$^{+}$↑	[5]
		Bacterial Spot (*Xanthomonas campestris*)	*SlERF1*$^{+}$↑, *SlNAC35*$^{+}$↑	[5]
	Glycine max	Bacterial Wilt (*Ralstonia solanacearum*)	*GmERF3*$^{+}$↑	[5]
	Nicotiana tabacum	Bacterial wilt *(Ralstonia solanacearum)*	*NtWRKY50*$^{+}$↑	[117]
	Manihot esculenta	Bacterial Blight (*Xanthomonas axonopodis*)	MebZIP3^{+}↑, MebZIP5^{+}↑	[5]
Fungal	*Arabidopsis thaliana*	Gray mold *(Botrytis cinerea)*	*AtERF1*$^{+,}$↑, *AtERF14*$^{+,}$↑	[19]
		Fusarium wilt *(Fusariuum oxysporum)*	*AtERF2*$^{+,}$↑, *AtERF4*$^{-}$ ↓	[19]
		Powdery Mildew (*Erysiphe cruciferarum*)	*AtbZIP10*$^{+}$↑	[5]
	Triticum aestivum	Yellow Rust *(Puccinia striiformis)*	*TaWRKY49*$^{+}$↓, *TaWRKY62*$^{+}$↑, *TaWRKY70*$^{+}$↑, *TaNAC1*$^{-}$↑, *TaNAC4*$^{+}$↑, *TaNAC8*$^{+}$↑, *TaNAC21/22*$^{-}$↑, *TabZIP74*$^{+}$ ↑, *TaNAC30*$^{-}$↑	[5,141]
		Leaf rust (*Puccinia triticina*)	*TaWRKY1B*$^{+}$	[142]
		Powdery mildew *(Erysiphe cruciferarum)*	*TaNAC6*$^{+}$ ↑, *TaNAC21/22*$^{-}$↑, *TaNAC30*$^{+}$ ↓	[143]
		Root Rot (Bipolaris sorokiniana)	*TaERF3*$^{-}$ ↓, *TaPIEP1*$^{+}$ ↑	[19]
		(Rhizoctonia cerealis)	*TaRIM1*$^{+}$ ↑	[19]
	Oryza sativa	Sheath blight (*Rhizoctonia solani*)	*OsWRKY4*$^{+}$↑, *OsWRKY80*$^{+}$↑	[5]
		Rice Blast (*Magnaporthe oryzae, Pyricularia oryzae*)	*OsWRKY7*$^{+}$↑, *OsWRKY45*$^{+}$↑, *OsWRKY58*$^{+}$↑,	[3,5]

			OsWRKY62$^{+\uparrow}$, *OsWRKY64*$^{+\uparrow}$, *OsWRKY76*$^{+\uparrow}$, *OsWRKY22*$^{+\uparrow}$, *OsNAC6*$^{+\uparrow}$, *OsNAC19*$^{+\uparrow}$, *OsNAC66*$^{+\uparrow}$, *OsNAC122*$^{+\uparrow}$, *OsNAC131*$^{+\uparrow}$	
	Gossypium hirsutum	Sheath blight (*Rhizoctonia solani)*	*GhWRKY39-1*$^{+\uparrow}$	[5]
	Brachpodium distachyon	Fusarium head blight (*Fusarium graminearum*)	*BdWRKY8*$^{+\uparrow}$, *BdWRKY34*$^{+\uparrow}$, *BdWRKY50*$^{+\uparrow}$, *BdWRKY70*$^{+\uparrow}$, *BdWRKY69*$^{+\uparrow}$	[5]
	Solanum lycopersicum	Gray Mold (*Botrytis cinerea*)	*SlSRN1*$^{-\downarrow}$	[143]
		Tomato Wilt (*Plectosphearella cucumerina)*	*SlERF1*$^{+\uparrow}$	[19]
		Rhizopus Soft Rot (*Rhizopus nigricans*)	*SlERF1*$^{+\uparrow}$	[19]
	Saccharum officinarum	Red Rot (*Colletotrichum falcatum*)	*SobZIP4*$^{+\uparrow}$, *SobZIP15*$^{+\downarrow}$, *SoNACH*$^{+\downarrow}$	[144]
	Solanum tubersum	Late Blight (*Phytophthora infestans*)	*StNAC4*$^{+\uparrow}$, *StNAC5*$^{+\uparrow}$, *StNAC18*$^{+\uparrow}$, *StNAC48*$^{+\uparrow}$, *StNAC81*$^{+\uparrow}$, *StERF3*$^{-\uparrow}$	[3,19]
	Hordium vulgare	Powdery mildew (*Blumeria gramini*)	*HvWRKY10*$^{+\uparrow}$, *HvWRKY19*$^{+\uparrow}$, *HvWRKY28*$^{+\uparrow}$, *HvNAC6*$^{-\downarrow}$	[5]
		Spot Blotch (*Bipolaris sorokiniana*)	*HvMYB6*$^{+\uparrow}$	[19]
	Glycine max	Root Rot (Phytophthora sojae)	*GmERF5*$^{+\uparrow}$, *GmERF113*$^{+\uparrow}$	[19]
		Soybean Rust (*Phakospora pachyrhizi*)	*GmbZIP1*$^{+\uparrow}$, *GmbZIP2*$^{+\uparrow}$, *GmbZIP62*$^{+\uparrow}$, *GmbZIP105*$^{+\uparrow}$	[19]
	Nicotiana benthamiana	Anthracnose (*Colletotrichum orbicular*)	*NbWRKY8*$^{+\downarrow}$	[5]
	Vitis vinifera	Grey Mold *(Botrytis cinerea*)	*VvERF20*$^{+\uparrow}$	[19]
	Populus trichocarpa	Popular leaf Rust *(Melampsora medusae)*	*PtrWRKY18*$^{+\uparrow}$, *PtrWRKY35*$^{+\uparrow}$, *PtrWRKY89*$^{+\uparrow}$	[5]
Viral	*Arabidopsis thaliana*	Tobacco mosaic virus (TMV)	*AtWRKY8*$^{+,\uparrow}$, *AtWRKY61*$^{+,\uparrow}$, *ATAF2*$^{+,\uparrow}$	[5,117]
	Nicotiana tobacam	Tobacco mosaic virus (TMV)	*WRKY8*$^{+,\uparrow}$, *NtERF5*$^{+,\uparrow}$	[5,117]
	Oryza sativa	Rice Dwarf Virus (RDV)	*OsNAC*$^{+,\uparrow}$	[143]
		Rice Stripe Mosaic Virus (RSMV)	*OsMYB4*$^{+,\uparrow}$	[5]
	Solanum lycopersicum	Tomato Yellow Leaf Curl Virus (TYLCV)	*SlNAC20*$^{+,\uparrow}$, *SlNAC24*$^{+,\uparrow}$, *SlNAC47*$^{+,\uparrow}$, *SlNAC61*$^{+,\uparrow}$	[143]
Nematodes	*Arabidopsis thaliana*	Cyst nematode (*Heterodera schachtii*)	*AtWRKY23*$^{+,\downarrow}$, *AtMYB12*$^{+,\uparrow}$, *AtWRKY6*$^{+,\downarrow}$, *At WRKY11*$^{+,\downarrow}$, *AtWRKY17*$^{+,\downarrow}$ *and AtWRKY33*$^{+,\downarrow}$. *(Downregulation)*	[145]
		Root-Knot Nematodes (*Meloidogyne incognita*)	*AtMYB12*$^{+,\downarrow}$	[145]
	Solanum lycopersicum	Root Knot Nematode (*Meloidogyne javanica)*	*SlWRKY45*$^{-,\uparrow}$, *SlWRKY3*$^{+,\uparrow}$, *SIWRKY70*$^{+,\downarrow}$	[129,130]

	Glycine Max	Soybean Cyst Nemadtode (*Heterodera glycines*)	*GmWRKY136*$^{+,\uparrow}$, *GmWRKY53*$^{+,\uparrow}$, *GmWRKY86*$^{+,\uparrow}$	[146]
Insects	*Arabidopsis thaliana*	*Cabbage moth (Pieris brassicae)*	*AtMYB75*$^{+,\uparrow}$	[137]
	Triticum aestivum	English grain aphid (*Sitobion avenae)*	*TaMYB19*$^{+,\downarrow}$, *TaMYB2*$^{+,\downarrow}$, *TaMYB44*$^{+,\downarrow}$	[137]
		Russian wheat aphid *(Diuraphis noxia)*	*TaWRKY53*$^{+,\downarrow}$	[140]
	Oryza sativa	Brown plant hopper (*Nilaparvata lugens)*	*OsWRKY45*$^{+,\downarrow}$	[147]
		Striped stem borer *(Chilo suppressalis)*	*OsWRKY53*$^{+,\downarrow}$	[97]
			OsERF3$^{+,\uparrow}$	[136]
	Chrysanthemum	Aphid *(Aphidodea)*	*CmMYB15*$^{+,\uparrow}$, *CmMYB19*$^{+,\uparrow}$	[138]

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.

5 Crop Improvement Techniques and TFs

The implication of TFs from signal perception to signal transduction and expression of stress responsive genes, as summarized in this review. A single TF gene may respond to numerous stresses for example *SbNAC58* which is effective against drought, cold, and salinity stress [19]. In view of the crucial role of TFs, they have potential to be exploited using different genome modifying molecular techniques for developing climate resilient crops (Table 3) as explained in Figure 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 [148]. 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. Knockdown these TFs in separate experiments slowed disease development [20].

Different genome editing tools, such as ZF-nucleases (ZFNs), homing endonucleases or mega nucleases, or 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 [149]. 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 [150].

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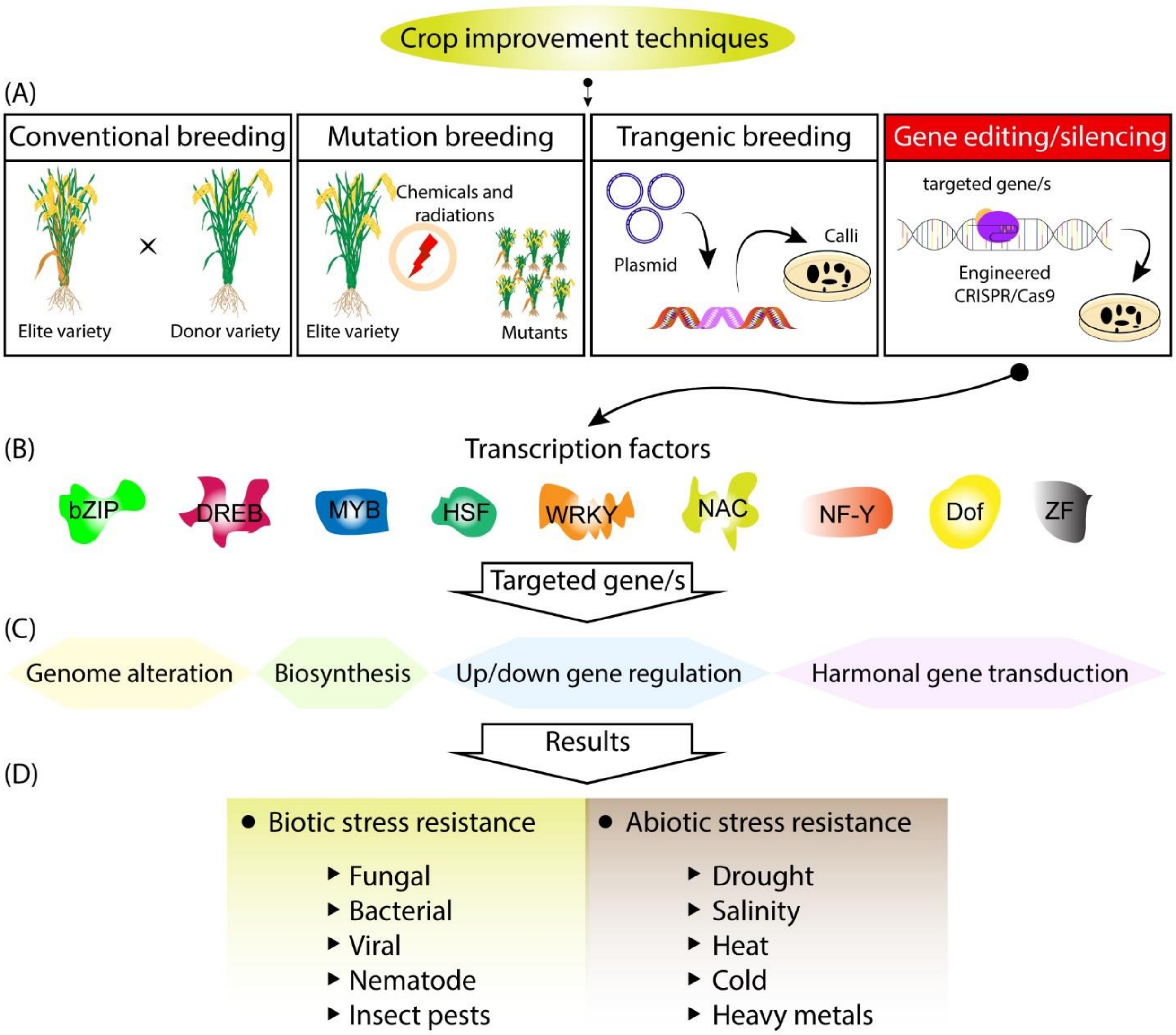

Figure 3. Schematic illustration of different crop improvement techniques particularly targeted modifications in TFs via gene editing/silencing for crop improvement. (**A**) Overview of different crop improvement techniques. (**B**) Different transcriptional factors that can be used for incorporation 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.

Table 3. Crop improvement by targeting of TFs through gene silencing and transgenic and gene editing approaches.

Technique	Crop	Gene	Objective	Reference
RNAi silencing	*Arabidopsis thaliana*	*AtNAC042/JUB1, CBNAC/NTL9*	Bacterial Leaf spot	[143]
	Triticum aestivum	*TaNAC1, TaNAC21/22, TaNAC30*	Yellow rust and powdery mildew resistance	[143]
Genome editing	*Arabidopsis thaliana*	*AtWRKY11, AtWRKY70*	Pathogen resistance	[151]
	Triticum aestivum	*TaDREB2, TaERF3*	Drought tolerance	[106]
	Oryza sativa	*OsNAC2, OsNAC14, OsbZIP62*	Drought tolerance	[152]
		OsERF922	Rice blast tolerance	[151]

	Brassica napus	*BnWRKY11, BnWRKY70*	Pathogen resistance	[151]
Transgenic approach	*Arabidopsis thaliana*	*AtDREB1A, AtWRKY57*	Drought tolerance	[149,153]
		GmbZIP1, GmDREB2,	Drought, cold, salinity tolerance	
		ZmMYB3R, OsWRKY45	Drought, salinity tolerance	
	Triticum aestivum	*AtDREB1A*	Drought tolerance	
		GmbZIP1, GhDREB	Drought, salinity, cold tolerance	
	Oryza sativa	*OsWRKY30, JERF1, OsbZIP23, OsbZIP46*	Drought tolerance	
		SNAC1, SNAC2	Drought, salinity tolerance	
	Nicotiana tabacum	*AtDREB1A, GmERF3*	Drought tolerance	

Marker assisted breeding (MAB) has a wide variety of applications in stacking of multiple genes in crop plants for various purposes and had been widely used in studying wheat rust [154]. 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 [155]. Another very successful example of MAB is the introduction of the *SUB1* region into rice, which increases submergence tolerance without effecting yield, grain quality or development [156]. Similar marker systems could be developed for WRKY and other TFs responding to under various biotic and abiotic stresses for foreground selection prior to plantation of plants in the field. 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 [157], or the use of wheat *TaNAC29* to enhance salt and drought tolerance in Arabidopsis [158], 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 promotor, 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 [36].

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. The evidence suggests that increasing TFs are an important factor for increasing organismic complexity [159]. 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 [160].

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7 Future Prospects, Challenges, and Opportunities

TFs have a great potential for boosting the yield potential and stress tolerance in field crops. Significant achievements have been made in unraveling the potential role of TFs under various biotic and abiotic stresses. However detailed studies of pathways explaining the role of TFs under stress is yet to be explored. Approximately 50 TFs families have been reported with less than ten, i.e., WRKY, DREB, NAC, HSF, MYB, ZF-s, Dof, bZIP, and NAC being functionally characterized under various biotic and abiotic stresses. The Role of the remaining TF families is currently unexplored, which provides a great platform for young researchers to build their future carriers in this field.

There is a need to establish crosstalk between different TF gene families and how they respond under stress conditions [161]. Focus should shift towards development of climate resilient crops with biotic as well as abiotic stress tolerance. In this context, WRKY TFs have a very positive role to play due to their involvement in biotic and abiotic stress tolerance [162]. Not only WRKY, but other TFs also resist 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 cultivars 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. For this reason, development of transgenic plants using TF candidate genes in crops is not yet fully exploited. Overexpressing some TFs improving stress tolerance can lead to impaired growth responses, i.e., low yield, late flowering, and dwarfing, which is still a challenge to be addressed [163]. Use of tissue specific promotors (*SynR1* and *SynR2* are root specific) as explained by Ali et al. [164] would help in overcoming the off target affects. Although the majority of TFs play a positive role during different biotic and abiotic stresses. However some genes of NAC TFs promote disease development, i.e., *TaNAC1* promotes yellow rust and downy mildew in wheat.

At present most functional studies exploring the role of TFs are conducted in model plants, i.e., tobacco [157] and Arabidopsis [158], 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 transformation of TFs in field crops, however stacking of multiple stresses responsive TFs is just a beginning. Similarly, the role of TFs against heavy metal stress and nematode and insect attacks needs more attention. Another area of improvement is development of functional marker systems, i.e., SSR markers, SNPs, or dCAPS for MAB of different TFs. Only a few examples exist in literature for development of functional marker systems for characterization of TFs [154-156]. Functional markers will help identification of TFs in successive generations for marker-assisted crop improvement.

8 Conclusions

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 with the changing climate. There is an urgent need for development of crops tolerant to biotic and abiotic stresses by targeting different genes and gene families. TFs have emerged as a key potential contributor towards biotic and abiotic stress tolerance in plants, which play a role through signal transduction and activation of stress responsive genes. Different crop improvement approaches, i.e. RNAi silencing, and genome editing promise to deliver safer food to human beings, and ensure food security. Although numerous reports have been available about the use of TFs for crop improvement, the majority of studies are focused on model plants, i.e., Arabidopsis and tobacco. Further, the transgenic plants are frequently evaluated in laboratories under artificial conditions without exposing them to natural environmental conditions for their whole life span. Little is known about engineering of multiple TFs for response against multiple biotic and abiotic stresses. In particular, WRKY TFs have diversified roles in biotic and abiotic stress events that need to be elucidated using different omics approaches to explore the mechanisms underlying these complex responses.

9 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

10 Author Contributions

R.S., S.J., and S.A. conceived the idea. X.W. provided the literature and technical assistance. R.S., S.J., A.N., Z.A., S.S., have drafted the manuscript. S.A., R.S., A.N., and Z.A. have prepared illustrations. R.S., S.A., S.J., M.Z.I., R.T. and R.M.A. have reviewed and improved the draft. All authors listed have made substantial, direct, and intellectual contributions to the work, and approved it for publication.

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