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REVIEW

Key Plant Transcription Factors in Crop Tolerance to Abiotic Stresses

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ABSTRACT: Abiotic stresses, such as drought, heavy metals, salinity, and extreme temperatures, are among the most common adverse threats that restrict the use of land for agriculture and limit crop growth and productivity. As sessile organisms, plants defend themselves from abiotic stresses by developing various tolerance mechanisms. These mechanisms are governed by several biochemical traits. The biochemical mechanisms are the products of key genes that express under specific conditions. Interestingly, the expression of these genes is regulated by specialized proteins known as transcription factors (TFs). Several TFs, including those from the bZIP, bHLH, MYB, HSF, WRKY, DREB, and DOF families, play critical roles in regulating plant growth, development, and responses to environmental changes. By binding to specific DNA sequences, TFs can act as molecular switches to repress or activate the transcription of targeted genes. Moreover, some TF genes have been engineered to strengthencrop resilience to multiple abiotic stresses. Identifying and manipulating TFs is an interesting research area that could aid in improving crop abiotic stress tolerance. This review describs the harmful effects of salinity, drought, temperature and heavy metals on plant growth and development. We also provide an updated discussion on how TFs regulate and activate the plant tolerance under different abiotic constraints. Our aim is to extend understanding of how abiotic stresses affect the physiological characteristics of plants and how TFs alleviate these deleterious effects on plant growth and productivity.

KEYWORDS: Crop tolerance; drought; freezing; gene regulation; heat; heavy metals; salinity; transcription factors

1 Introduction

Plants are continuously exposed to several abiotic stresses that compromise their growth, development, and productivity [1]. Among these abiotic constraints, drought, heat, cold, freezing, salinity, and heavy metals are major factors limiting agricultural production worldwide [2–4]. Moreover, due to climate change, the effects of these stresses become more severe, restricting the use of land for agriculture and limiting crop growth and productivity [5]. Hence, as sessile organisms and to handle the different environmental constraints they face, plants developed multiple physiological, biochemical, cellular, and molecular tolerance mechanisms. In fact, the biochemical molecules that govern these responses are the products of crucial genes that are expressed only under certain conditions. Surprisingly, these divers' reactions are intriguingly influenced by specialized proteins known as transcription factors (TFs), which govern downstream stress-induced genes and pathways.

TFs are regulatory proteins that control the transcriptional activity through binding to specific DNA sequences in the promoter regions of target genes, thus allowing fine-tuned activation or repression of these genes in response to environmental signals [6,7]. By coordinating the expression of multiple genes, TFs orchestrate effective cellular responses to abiotic stresses, ranging from the synthesis of osmoprotectants to the modulation of hormonal signaling or the activation of antioxidant systems [8,9]. TFs normally contain highly conserved DNA-binding domains (DBDs) that regulate the spatiotemporal expression of target genes involved in stress resistance mechanisms in plants [10].

Several TF families have been reported to be involved in abiotic stress tolerance [11–14]. Interestingly, each family is characterized by distinct DNA-binding domains and plays a specific role in the perception and transduction of stress signals [14–16]. Moreover, some of these families are acid abscisic (ABA)-dependent, while others participate in abscisic acid-independent response pathways, highlighting the complexity and functional redundancy of transcriptional regulatory networks [17,18].

The objective of the present review is to provide an integrated overview of the major TF families, including bZIP, bHLH, MYB, HSF, WRKY, DREB, and DOF, and their cross-stress regulatory roles in enhancing crop resilience to major abiotic stresses, such as drought, salinity, heavy metals, heat, and cold stress. Unlike previous published reviews that focus either on individual TF families or on single stresses, the present work emphasizes their overlapping functions, shared signaling pathways, and potential applications in crop improvement strategies. Furthermore, beyond outlining specific TF families, this review emphasizes how the main TF families interact during abiotic stress responses. Recent advances to exploit the key TF families in developing crops more resilient to climate change were discussed.

2 Effect of Abiotic Stress on Crop Growth and Development

2.1 Effect of Drought Stress

In the context of climate change, water stress is one of the major challenges for agricultural production, particularly in arid and semi-arid regions characterized by little precipitation. Water deficit profoundly affects plants, disrupting physiological processes and altering growth and development [19]. It reduces cell turgor and relative water contents, which inhibit cell expansion, leading to stunted growth and reduced biomass [20]. Water deficit also triggers stomatal closure to minimize transpiration and water loss; however, this limits CO_2 assimilation, reducing photosynthesis and causing energy imbalances. Besides, prolonged water deficit induces oxidative stress by inducing an overaccumulation of reactive oxygen species (ROS), which damages cellular components, including lipids, proteins, and DNA [21]. Furthermore, water scarcity affects nutrient uptake and transport, exacerbating deficiencies that further compromise plant health and yield [22].

To alleviate the depressive effects of water deficit, plants activate a range of agro-morphological, physio-biochemical, and molecular responses. Morphologically, plants alter root architecture, extending root depth to access water reserves in deeper soil layers [23], and they reduce the leaf area and increase cuticle thickness to limit water loss. Optimal root system architecture plays an important role in enhancing plants' capacity to effectively uptake water and nutrients, which therefore strengthens their resilience against water stress [24].

At the physio-biochemical level, plants exhibited many changes to overcome water deficit stress. The osmotic adjustment, achieved through the accumulation of compatible solutes like proline and soluble sugars, led to maintaining cell turgor and enzyme function under low water availability [5]. Upregulating antioxidant defense systems to neutralize reactive oxygen species (ROS) constitutes an important mechanism associated with water deficit tolerance in many species. Enzymes, such as catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD), act synergistically with non-enzymatic antioxidants, like polyphenols, glutathione, and ascorbate to mitigate osmotic stress-induced oxidative damage [1]. Additionally, secondary metabolites, such as flavonoids and phenolics, not only scavenge ROS but also act as signaling molecules under drought stress [21]. The molecular responses focus on the signaling pathway, downregulation, and upregulation in gene expression. Hence, phytohormones such as ABA orchestrate water stress responses by inducing stomatal closure and regulating stress-related gene expression. Calcium (Ca) signaling acts as a secondary messenger in ABA-mediated pathways, amplifying stress signals and activating defense mechanisms. The regulation of aquaporin activity and gene expression is part of the adaptation mechanisms to water-deficient conditions, relying on complex processes and signaling pathways and complex transcriptional, translational, and post-transcriptional factors [25]. The aquaporin can play a key role in plant responses to water stress by maintaining water absorption and movement within the entire plant [26]. Molecular responses also include the activation of stress-responsive genes regulated by transcription factors, which modulate pathways involved in osmotic adjustment, antioxidant activity, and cell protection [27].

2.2 Effect of Salt Stress

Salt stress was considered among the severe abiotic stresses that seriously affect the agricultural yield and ecological security worldwide. In fact, more than 900 million hectares of land are considered salt-affected, which is predicted to increase in the near future because of climate change [28]. Saline soils accumulate excessive soluble salts, which are detrimental to plants as they limit plant growth and productivity. In fact, many studies indicated that salinity constraint significantly affected plant growth at different growth stages, from seed germination to plant yield. Indeed, at seed germination, the exposition of the seed to salt stress induced hormonal imbalance, oxidative and osmotic stress, and disturbed seed reserve mobilization, as a key process of this stage [1]. For example, during seed germination of salt-stressed *Medicago sativa* [29] and *Trigonella foenum-graecum* [30], the authors showed that the mobilization of protein and sugar reserves, antioxidant activity, and embryo viability were negatively affected after the accumulation of Na^+ in the embryo cells. Similarly, the other plant stages, including growth and yield productivity, were also destroyed after exposure to salinity stress [5]. Indeed, salt stress affects plant growth by two processes, namely, ionic toxicity and osmotic stress induction [31]. The high accumulation of salt ions, like Na^+, in plant cells disturbs plant physiology significantly by deactivating antioxidant enzymes, inducing overaccumulation of ROS, and perturbating membrane cell stability [32]. Excessive Na^+ ions in the soil could also mediate osmotic stress, as they reduce the water potential of the soil around the root surface, thereby limiting water availability for the plant and reducing plant water uptake [28]. In this way, salt stress leads to water deficit or osmotic stress in plants, which is one of the significant problems that plants grown in saline soils encounter. It also induces stomatal closure and disrupts photosynthetic pigments [32]. Salt-induced closure of stomata decreases the activity of CO_2-fixing enzymes, thereby reducing the amount of CO_2 available for fixation [3]. Additionally, due to the similarity between salt ions and essential nutrients for plant development, salt stress reduces the nutrient uptake, such as phosphorus (P), potassium (K), Ca, nitrogen (N), and iron (Fe) [5]. Altogether, salt stress reduces plant growth, reflected by the signification reduction in plant biomass in many plant species like *Lavandula angustifolia* [33], *Nigella sativa* [34], *Oryza sativa* [35], and *Triticum aestivum* [36]. In the same line, Lamsaadi et al. [37] correlated the significant reduction in plant growth and yield of *T. foenum-graecum* to the harmful effects of salt stress on water uptake, photosynthetic activity, antioxidant activity, and nutrient uptake.

2.3 Effect of Heavy Metals Stress

Environmental pollution by heavy metals has become a serious problem worldwide. In this context, extended human activities, in terms of urbanization and industrialization, have led to the wide distribution of pollutants and heavy metals in natural resources, like water, soil, and air. Various heavy metals are present in the environment in large amounts, like Nickel (Ni), Cobalt (Co), Cadmium (Cd), Mercury (Hg), and Arsenic (As), causing severe environmental problems [38]. Indeed, if they are present in the soil, they cause significant retardation in plant growth, decrease the nutritive value, reduce photosynthesis, and also pose harmful effects on human beings [2]. In addition, after their accumulation in plant cells, they cause numerous morphological, biochemical, and physiological alterations. In this context, many studies reported that plant exposure to heavy metals significantly inhibited seed germination, reduced root development, and limited the ability of the plant to uptake water and essential nutrients [21]. The negative effects of heavy metals on plant growth have been reported in several plant species, including *Vigna radiata* L. [39], *Hordeum marinum* Huds. [40], *O. sativa* L. [41] and *H. vulgare* L. [42]. Reduction in photosynthetic pigments, stomatal conductance, and gas exchange is also observed in plants exposed to heavy metal stress [43]. Moreover, another toxic effect of heavy metals on plant physiology is the high accumulation of ROS in plant cells, which induces oxidative stress leading to lipid and protein oxidation, and DNA damage, and eventually cell death [2]. Thus, heavy metals seriously affect many key physiological activities in plants, such as seed germination, photosynthesis, nutrient absorption, antioxidant activity, and cause significant reduction in plant growth and yield.

2.4 Effect of Extreme Temperatures Stress

One of the most harmful abiotic stresses for plants is the ongoing increase in surrounding temperature, which is exacerbated by climate change. Temperature rises severely disrupt the physiological functions of plants, reducing both growth and productivity [44]. Additionally, temperature drops, especially during freezing periods, pose significant challenges to plant survival by causing cellular damage and hindering development [45]. Both high and low temperatures can induce thermal stress, severely affecting plant growth and development, particularly germination, root development, and photosynthesis [4]. This stress often triggers excessive production of ROS, leading to cell membranes, DNA, and proteins damages, which disrupts fundamental physiological processes [46]. For example, when exposed to thermal stress at 30°C, *Spinacia oleracea* seeds show reduced germination rates and produce abnormal, less vigorous seedlings, a response associated with increased ROS production [47]. Hasanuzzaman et al. [48] demonstrated that high temperatures (around 33°C) in *T. aestivum* decreased cell viability and germination capacity. Moreover, under high temperatures (40°C), *Sesamum indicum* roots exhibit reduced growth due to oxidative damage and hormonal changes [46]. In *Solanum lycopersicum* L., the exposure of plants to a temperature of 42°C reduces root and shoot growth, disrupts sugar metabolism, and impairs photosynthesis, leading to decreased stomatal conductance and damage to photosynthetic enzymes [49]. At 40°C, *T. foenum-graecum* is adversely affected, with suppressed photosynthesis due to the downregulation of vital proteins, such as chlorophyll-binding proteins and ribulose-1,5-bisphosphate carboxylase. Reduced dry weight, along with shorter roots and shoots, are additional consequences of this stress. The plant's attempt to combat oxidative stress induced by high temperatures is observed as an adaptive response, marked by increased protein content and activation of antioxidant enzymes, including SOD, POD, and CAT [50].

Beyond the issues brought on by heat stress, crops are equally vulnerable to cold-induced thermal stress, which induces embryo dormancy, slows germination, and disrupts root growth, coleoptile length, and biomass production. For example, at 2°C, *T. aestivum* showed a significant reduction in germination and root growth [51]. However, prolonged exposure to −4°C can initially promote seed germination in *Brassica rapa*, though continued exposure reduces growth and biomass accumulation. Cold stress also disrupts membrane fluidity, affecting enzyme function and metabolic processes [52]. This response is not uniform across all plant species; some, such as *Gossypium hirsutum*, display variable responses. In fact, in *G. hirsutum*, cold-induced thermal stress leads to oxidative damage via ROS production, which activates antioxidant enzymes, disrupting membrane fluidity and hormonal regulation [52]. This stress is often mitigated by the production of protective proteins and soluble sugars, which help protect plants from oxidative damage [51]. Cold stress elicits diverse responses in plants, primarily through oxidative damage caused by overproduction of ROS, activation of antioxidant enzymes, and disruption of membrane integrity and hormonal balance [53]. Furthermore, exposure to low temperatures can cause tissue dehydration and water deficit by impairing water uptake, while leaf transpiration rates may remain unchanged, exacerbating the physiological stress [54].

3 Transcription Factors (TFs) and Plant Abiotic Stress Tolerance

3.1 Basic Helix-Loop-Helix (bHLH) TFs

Basic helix-loop-helix (bHLH) TFs are one of the most conversed TF families in plants, animals, and fungi [55]. It is among the key TFs that play many vital roles in plant development, and it includes 133 members [56]. Indeed, a defining feature of bHLH proteins is the conserved HER motif (His5-Glu9-Arg13), present in over 50% of plant bHLHs and essential for DNA binding [57]. In the same line, it was reported that bHLH TF is recognized for its significant involvement in plant responses to abiotic stresses, particularly under climate change constraints by regulating genes linked to stress tolerance mechanisms (Table 1). In fact, Li et al. [58] showed that the overexpression of *AhbHLH112* improves drought tolerance in *Arachis hypogaea* plants through promoting root and shoot growth and activating the antioxidant system mechanism to reduce ROS production in plants. Similarly, the overexpression of *MdbHLH130* enhances drought tolerance in *Nicotiana tabacum* by decreasing lipid peroxidation, as evidenced by lower electrolyte leakage level and malondialdehyde (MDA) content [59]. More than that, Liang et al. [60] evidenced that *Trifoliate orange* overexpressing *PtrbHLH66* exhibited significantly enhanced drought resistance via ROS detoxification and regulation of ABA biosynthesis genes. Similarly, Zhai et al. [61] demonstrated that the overexpression of *PlbHLH6*, *PlbHLH55*, and *PlbHLH64* could improve Pseudoroegneria seed germination under drought stress. In addition to water stress, bHLH also alleviates the harmful effect of salinity stress on plant growth and development (Table 1). In this context, Qiu et al. [62] indicated that the overexpression of *MfbHLH38* significantly enhanced salt stress tolerance in *Myrothamnus flabellifolia* through increasing the antioxidant activity and the accumulation of the osmoprotectant compound, resulting in a reduction of ROS and MDA production in plant cells. The same results were recorded in other plants species, like *Cyclocarya paliurus* and *Capsicum annuum*, were the obtained findings revealed that when overexpressing *CpbHLH36/68/146* and *CabHLH035*, respectively, an improved salt stress tolerance by enhancing photosynthetic performance, scavenging ROS and regulated the toxic level of salt ion like Na^+ in plant cell was observed in transgenic plants compared to the wild types [14,63]. The beneficial effects of *bHLH* overexpression were also observed under other abiotic stresses, including heavy metal and extreme temperature constraints. For instance, in manganese-stressed *Zea mays* plants, the overexpression of *ZmbHLH105* improved the stress tolerance by modulating antioxidant defenses and metal transporter expression [64]. Similarly, the overexpression of *SlbHLH* increases Cd stress tolerance in *S. lycopersicum* [65]. Likewise, in transgenic *Glycine max* that overexpresses *GmbHLH30*, increased root elongation and reduced ROS accumulation were observed under Al toxicity [6]. Moreover, the effect of *bHLH* TFs expression under extreme temperature stress is critically reported. In fact, Li et al. [66] showed that the overexpression of *bHLH116* in *M. sativa* inactivates CBF genes at low temperatures, whereas *A. thaliana* expressed *OrbHLH001* from Dongxiang Wild Rice showed high tolerance to freezing [67]. The same was shown for *PavbHLH28* and *IbbHLH79* TFs, where their overexpression significantly contributed to cold tolerance through CBF-independent ROS scavenging pathways and are promising candidates for molecular breeding in cold-sensitive crops such as sweet potato [68,69].

Table 1: Transgenic crop plants for abiotic stresses resilience: the role of transcription factors

TFs	Source	Transformed plants	Type of stress	Role	References
bHLH	*A. hypogaea*	*A. hypogaea*	Drought stress	Promoted root and shoot growth Enhanced antioxidant system Reduced oxidative stress	[58]
	M. domestica	*N. tabacum*		Reduced oxidative stress	[59]
	M. flabellifoliaby	*M. flabellifoliaby*	Salt stress	Enhanced osmoregulation Enhanced antioxydant system Reduced oxidative stress	[62]
	C. paliurus	*C. paliurus*		Improved photosynthesis Reduced Na^+ Reduced oxidative stress	[14]
	G. max	*G. max*	Aluminum stress	Enhanced root length Reduced oxidative stress	[6]
bZIP	*T. aestivum*	*T. aestivum*	Salt stress	Enhanced salt tolerance Reduced wilting Improved shoot and root growth Improved yield production Reduced oxidative stress	[70]
	B. juncea	*N. tabacum* *A. thaliana*	Cadmium stress	Improved Cd uptake and sequestration in shoots	[71]
	A. thaliana	*G. max*	Drought stress	Upregulated drought responsive genes (LEA18, dehydrin, and HSP70) Reduced oxidative stress	[72]
	D. longan	*D. longan*	Heat stress	Enhanced heat stress tolerance Activated heat stress responses	[13]
	O. sativa	*O. sativa*	Cold stress	Unregulated cold response genes Activated specific signaling pathways	[73]
	B. nivea	*A. thaliana.*	Salt stress	Improved seed germination and plant development	[74]
	P. alba	*P. alba*		Reduced oxidative stress	[75]
	Z. mays	*A. thaliana*		Mediated ABA accumulation Induced osmoregulation Improved K^{+}/Na^{+} ratio Reduced water loss Reduced oxidative stress	[7]

(Continued)

Table 1 (continued)

TFs	Source	Transformed plants	Type of stress	Role	References
	P. edulis	*O. sativa* *A. thaliana*	Drought stress	Improved water and chlorophyll contents Mediated osmoregulation Higher survival rates Reduced oxidative stress	[76]
DREB	*L. japonicus*	*A. thaliana*		Improved plant growth Mediated osmoregulation Upregulated proline metabolism related genes	[77]
	P. edulis	*A. thaliana*	Salt stress Cold stress	Improved plant tolerance Improved plant growth Modulated the expression of downstream cold-inducible genes	[78]
	E. songoricum	*N. tabacum*	Cold stress Heat stress	Enhanced plant growth and root architecture Mediated osmoregulation Increased chlorophyll content Reduced oxidative stress	[79]
	S. caninervis	*A. thaliana*	Salt stress	Enhanced plant growth and tolerance Mediated phenylpropanoid biosynthesis and starch metabolism Increased lignin, sucrose, and trehalose contents Enhanced sucrose phosphate synthase activities	[80]
	L. bicolor	*N. tabacum*	Copper stress	Increased soluble protein and proline contents Enhanced K^+/Na^+ ratio Upregulated antioxidant enzyme related genes	[81]
	S. caninervis	*A. thaliana*	Salt stress	Increased seed germination and improved seedling development Enhanced antioxidant system Reduced oxidative stress Upregulated stress marker genes (RD29B, COR47, LEA6, LEA7, ERD1, P5CS1, SOS1, SOS2, and SOS3)	[82]
	S. tuberosum	*S. tuberosum*	Cadmium stress	Increased plant growth Improved photosynthetic pigments Mediated osmoregulation Decreased oxidative stress	[83]

(Continued)

Table 1 (continued)

TFs	Source	Transformed plants	Type of stress	Role	References
DOF	*T. hispida*	*T. hispida*	Drought stress	Decreased oxidative stress Upregulated antioxidant enzyme related genes	[8]
		A. thaliana	Salt stress	Mediated osmoregulation Enhanced antioxidant enzyme activities	[84]
	V. yeshanensis	*N. benthamiana*	Drought stress	Improved photosynthetic pigments Mediated osmoregulation Decreased oxidative stress	[85]
	G. hirsutum	*G. hirsutum*	Cold stress Osmotic stress	Modulated proline metabolism	[86]
	K. bluegrass	*K. bluegrass*	Cadmium stress	Enhanced lipid and carbohydrate metabolism Improved cell wall and cell elongation Improved membrane stability	[87]
	J. regia	*A. thaliana*	Heat stress	Enhanced seed germination rate Enhanced antioxidant enzyme activities Reduced oxidative stress	[88]
HSFs	*S. alfredii*	*A. thaliana*	Cadmium stress	Enhanced antioxidant enzyme activities Reduced oxidative stress Upregulated heat shock proteins	[89]
	Z. mays	*A. thaliana*	Heat stress	Improved photosynthetic pigments Improved survival rates Upregulated heat shock proteins	[90]
	T. aestivum	*O. sativa*	Heat stress Drought stress Salt stress	Enhanced ABA accumulation Upregulated antioxidant enzyme related genes Upregulated oxidoreductase related genes	[9]
MYB	*G. max*	*G. max*	Drought stress	Increased root lengths Enhanced antioxidant enzyme activities Enhanced plant survival	[91]
	A. thaliana	*A. thaliana*	Salt stress	Upregulated Na^+ transporters activity Reduced Na^+ content	[15]
	S. brachiata	*N. tabacum*	Cadmium stress Nickel stress	Reduced metal concentrations Increased antioxidant enzyme activities	[92]
	M. crassipes	*M. crassipes*	Cold stress	Regulated flavonoid biosynthesis Enhanced antioxidant enzyme activities	[11]

(Continued)

Table 1 (continued)

TFs	Source	Transformed plants	Type of stress	Role	References
WRKY	*R. sativus*	*R. sativus*	Heat stress	Upregulated heat shock proteins Enhanced antioxidant enzyme activities Reduced oxidative stress	[93]
	E. japonica	*A. thaliana*	Drought stress	Modulated ABA synthesis Reduced oxidative stress	[94]

3.2 Basic Leucine Zipper (bZIP) TFs

Plants are continuously subjected to fluctuating environmental conditions and are often challenged by diverse abiotic stresses, such as drought, high salinity, extreme temperatures, and heavy metal toxicity (Table 1; Fig. 1). These adverse factors severely disrupt physiological and metabolic processes, ultimately imposing significant constraints on crop yield and quality [95]. To survive and thrive under such unfavorable conditions, plants have evolved intricate adaptation mechanisms encompassing physiological, biochemical, and molecular responses [96]. Central to these responses are TFs, which regulate gene expression pathways to mediate stress tolerance.

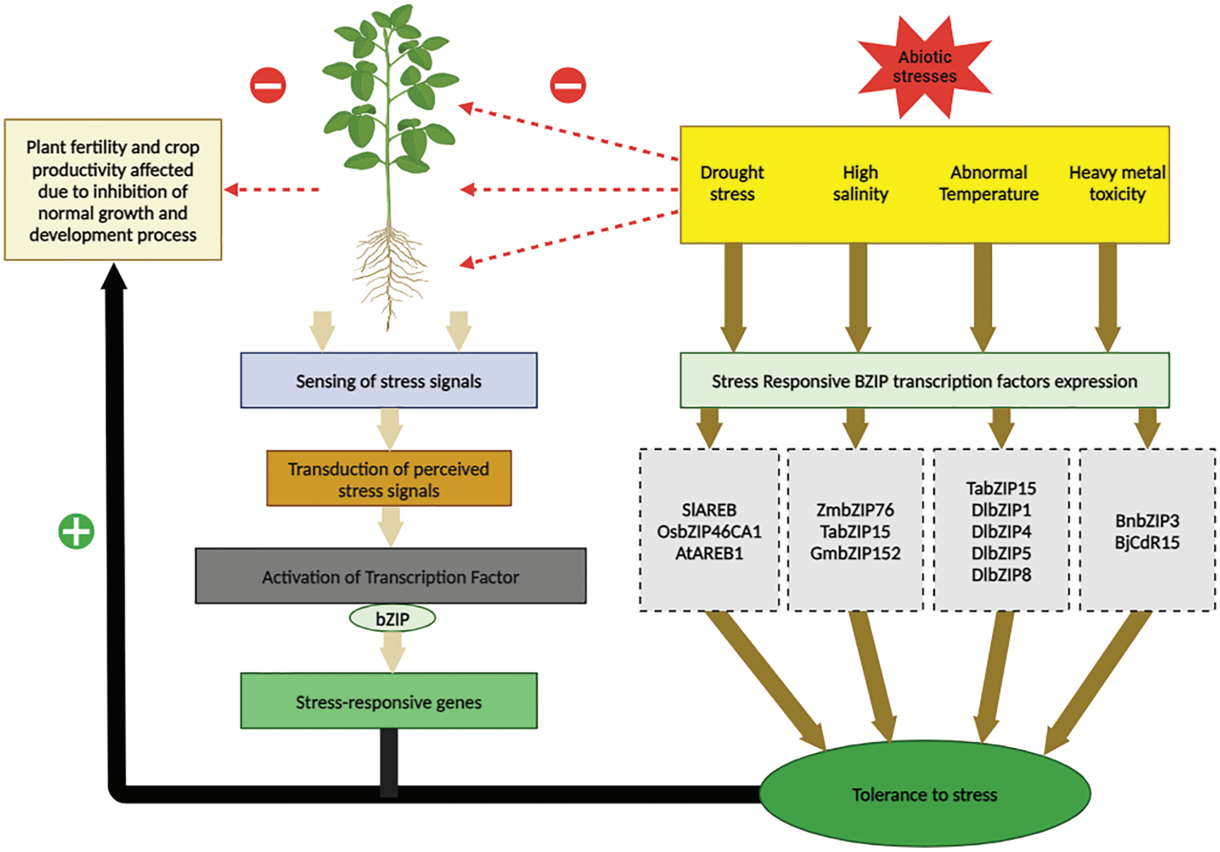

Figure 1: The role of bZIP TFs in crop tolerance to abiotic stresses

Among the key TFs, the basic leucine zipper (bZIP) family represents a highly conserved and extensively studied group of transcriptional regulators in eukaryotes. These proteins play main roles in orchestrating gene expression in response to various environmental stimuli [97]. Structurally, bZIP TFs are defined by two key features: a basic region responsible for highly conserved, sequence-specific DNA binding and a less conserved leucine zipper motif essential for dimerization [96]. In plants, bZIPs preferentially bind cis-regulatory DNA elements with an ACGT core sequence, such as A-box (TACGTA), C-box (GACGTC), and G-box (CACGTG), although examples of non-palindromic binding sites also exist [98]. Functionally, bZIP TFs are pivotal in regulating stress-responsive gene networks under abiotic stresses, such as drought, salinity, and extreme cold. They also play essential roles in plant defense mechanisms, seed development, and various physiological and developmental processes. Upon activation by environmental or physiological signals, bZIP proteins bind to specific cis-regulatory elements within the promoter regions of target genes, thereby modulating transcription to drive adaptive and stress-mitigating responses [99].

In plant genetic engineering, bZIP TFs have emerged as crucial regulators that can be manipulated to enhance plant resistance to various stresses (Fig. 1). For example, overexpression of the *T. aestivum TabZIP15*gene under salt stress activates metabolic pathways and induces salt tolerance by interacting with TaENO-b, resulting in improved growth, reduced damage, and higher grain yield under saline conditions [70]. Similarly, in *Z. mays*, the *ZmbZIP76* facilitates salt tolerance by interacting with TaENO-b in metabolic pathways [100]. Under salt and water deficit stress, Hsieh et al. [101] found that transgenic *S. lycopersicum* that overexpresses *SlAREB* was able to tolerate drought and salinity, as evidenced by better photosynthetic capacity and water content, upregulated stress-responsive genes, and enhanced overall stress resilience compared to wild-type plants. Under heavy metal stress, *N. tabacum* and *Arabidopsis thaliana* overexpressed *BnbZIP3* TFs from *B. juncea*showed enhanced tolerance to heavy metals, drought, and salinity through the activation of the glutathione-dependent pathway [71]. Additionally, the overexpression of the *B. napus BnbZIP3* in *A. thaliana* positively regulated tolerance to drought, salinity, and heavy metal stress, demonstrating its potential role in enhancing stress resilience [74]. Similarly, transferring and overexpressing *GmbZIP152* from *G. max* in the model plants *A. thaliana* strengthened the tolerance of the transgenic plants to heavy metals [102]. Besides, *Dimocarpus longan* overexpressing *DlbZIP1*, *DlbZIP4*, *DlbZIP5*, and *DlbZIP8* increased heat stress tolerance by initiating protective responses at 38°C [13]. Likewise, under drought stress, *G. max* overexpressing *AtAREB1* from *A. thaliana* revealed increased drought tolerance mediated by regulating key drought-responsive genes through ABA-mediated signaling [72]. Similarly, *O. sativa* plants overexpressing the *OsBZIP46CA1* were able to regulate the ABA signaling process and modulate physiological responses, such as stomatal closure and increased water uptake [103]. Moreover, in some aromatic and medicinal plants such as *Allium sativum*, the overexpression of *AsbZIP26* enhanced alliin biosynthesis, helping the plant to cope with mechanical stress [104]. Taking all together, the studies above underscore the significant role of bZIPs in regulating stress adaptation mechanisms across different plant species.

3.3 Dehydration Responsive Element Binding (DREB) TFs

Dehydration-responsive element binding (DREB) TFs comprise one of two subfamilies of the APETALA2/Ethylene Responsive Element Binding Factor (AP2/ERF) family of TFs with a single AP2 domain. Most DREB TFs bind to the dehydration-responsive element (DRE), which was initially identified in the promoter of the drought-responsive RD29A gene [105]. DREB TFs were discovered by demonstration of the fact that Arabidopsis nuclear protein extracts contain at least one protein able to cause a mobility shift of oligo-nucleotides containing the DRE sequence (TACCGAC) in gel retardation studies [105]. Afterward, DREB TFs have subsequently been identified and characterized for a large number of plant species, such as *Pennisetum glaucum* [106], *G. max* [107], *T. aestivum*, and *H. vulgare* [108]. The DREB proteins found in Arabidopsis were divided into six subgroups, designated A-1 to A-6 [109]. A-1 and A-2 subgroups contain abiotic stress-responsive TFs. The third subgroup of Arabidopsis TFs contains ABSCISIC ACID INSENSITIVE 4 (ABI4), the fourth subgroup includes TINY-like proteins, and the fifth and sixth subgroups comprise RELATED TO APETALA 2 (RAP2) TFs [109]. Expression of most DREB genes is regulated by different environmental factors, and this induction may be either ABA-dependent or ABA-independent [17]. For example, according to a large number of observations made in multiple studies, DREB1 TFs are activated by four or fewer major abiotic stresses, including low and high temperatures, drought, and salinity.

Recently, a large number of DREB TFs have been isolated from both dicot and monocot plants, and introduced to other plant species to investigate their responsiveness to different abiotic stresses (Table 1). The obtained results indicated that the plant tolerance to drought, high salinity, cold/freezing, and heat stresses was significantly improved in transgenic plants overexpressing DREB TFs [110]. In their work, Wang et al. [77] documented that the overexpression of DREB TF, extracted from *Lotus japonicas*, in *A. thaliana* significantly improved plant growth, antioxidant activity, and proline content by increasing the expression level of related genes, such as *AtP5CS1*, *AtP5CS2*, *AtRD29A*, and *AtRD29B* genes. Hu et al. [78] reported the same results under salinity and cold stresses, where a significant improvement in plant height and root length and activation of the expression of downstream cold-inducible genes were observed after overexpression of DREB TF in transgenic Arabidopsis. Similarly, the overexpression of *EsDREB*TF in transgenic *S. lycopersicum* plants significantly enhanced plant growth, chlorophyll content, and proline accumulation with a significant reduction in oxidative stress markers, like MDA content under cold and heat stress conditions [79]. Furthermore, Li et al. [82] showed that the overexpression of *ScDREB* TF in transgenic *A. thaliana* alleviated the harmful effects of salinity constraints during seed germination and seedlings development by decreasing oxidative stress indicators, improving POD, CAT, and SOD activities, and increasing the transcriptional levels of stress marker genes and *salt overly sensitive* (*SOS1*, *SOS2*, and *SOS3*) genes. Under heavy metal constraints, the authors reported the same beneficial effect in many transgenic plants overexpressing DREB TFs (Table 1). For instance, Charfeddine et al. [83] indicated that the overexpression of *StDREB* TF in transgenic *S. tuberosum* significantly improved plant growth, photosynthetic pigment content, antioxidant activity, and proline content under Cd stress. In the same line, Ban et al. [81] reported that transferring and overexpressing *LbDREB* TF in *N. tabacum* importantly increased the contents of soluble protein and proline, elevated the K^+/Na^+ ratio, and up-regulated some stress-related genes, including SOD (Cu/Zn SOD) and POD under copper stress.

However, other experiments showed opposite effects, where the overexpression of this TF induced undesirable effects on plant growth, together with abiotic stress tolerance improvement. For instance, Josine et al. [111] reported that the overexpression of *AtDREB2ACA* led to the activation of stress-responsive genes and, consequently, to improvement of salt tolerance of transgenic *Rosa chinensis* plants, but this was accompanied by several undesirable phenotypic changes, including a reduction in leaf starch and chlorophyll content and changes in cuticle development. Similarly, the overexpression of the *O. sativa OsDREB1A* in transgenic *A. thaliana* plants led to severe growth retardation of transgenic plants compared with control plants, despite a clear improvement of freezing and dehydration tolerance of the transgenic lines [112]. Conversely, other research reported that the constitutive overexpression of DREB genes produced few or no negative changes in phenotypes of transgenic plants. In this line, Oh et al. [113] documented that the constitutive overexpression of a gene (*AtDREB1A* from Arabidopsis) similar to the *O. sativa OsDREB1A*, enhanced *O. sativa* tolerance to drought and high salinity without producing any negative phenotypic changes. Overexpression of the DREB-like transcription factor gene *AhDREB1*, originating from the halophyte *Atriplex hortensis*, in *N. tabacum* improved plant tolerance to high salt levels [114]. Overexpression of the *O. sativa OsDREB2A* did not cause any phenotypic changes in the transgenic *A. thaliana* [112], although overexpression of *TaDREB1*, *TaDREB2*, *TaDREB3*, and *WDREB2* from *T. aestivum* and *ZmDREB2A* from *Z. mays* caused significant phenotypic changes and/or growth retardation of the transgenic *A. thaliana*, *N. tabacum*, and *H. vulgare* [108,114–116].

3.4 DNA Binding with One Finger (DOF) TFs

DOF is a plant-specific TF that belong to the member of the zinc finger family [10]. It consists mainly of 200–400 amino acid residues that are highly conserved. The DOF TFs hold two important domain structures. With 50–52 amino acid residues, the first domain is highly conserved and capable of forming a zinc finger [117]. It is known as the DNA-binding domain, which is located at the N-terminal region. The second domain is a less conserved transcriptional regulation domain located at the C-terminal region [10].

The DOF TFs family was discovered for the first time by Yanagisawa and Izui [118] in *Z. mays* plants. As an interesting TF family, other studies have been carried out earlier, which allow the characterization of 37 new DOF members in the model plant *A. thaliana* [119] and 30 DOF members in *O. sativa* [120]. Moreover, with the development of new tools, such as whole genome analysis, several DOF TFs have been identified with a species-dependent manner. For example, 35 DOF members were newly characterized in *Setaria italica* [121]. Another interesting study by Zhou et al. [122] evidenced the existence of 36 different DOF members in *Citrullus lanatus*. In 2021, other DOF members were identified, including 22 DOF in *Spinacia oleracea* [123], 24 DOF in *R. chinensis* [124], and 26 DOF in *Betula platyphylla* [125].

DOF TFs have been reported to play a central role in several biological processes, including the accumulation of seed reserve, dormancy and germination of seeds, photosynthesis, flowering, and other biological processes. For example, to elucidate the key role of *ZmDOF36* and *ZmDOF3* in starch accumulation during seed development, transgenic *Z. mays* were generated [126,127]. The authors demonstrated that the knockdown of the *ZmDOF3* gene resulted in a decrease in starch biosynthesis, while the line overexpressing the *ZmDOF36* gene was characterized by higher starch content. Additionally, in *H. vulgare*, the DOF proteins, such as *HvDOF17* and *HvDOF19*, were shown to contribute to seed germination by regulating the expression of genes encoding aleurone hydrolase [128]. DOF TFs could also control plant growth and development. In *A. thaliana*, Wei et al. [129] evidenced that plants overexpressing the DOF TF *COG1* exhibited larger rosettes and higher biomass, but the downregulation of the same TF dramatically reduced both rosette size and biomass.

Furthermore, DOF TFs have also been reported to play a key role in plant abiotic stress tolerance (Table 1). Thus, the overexpression of the *Tamarix hispida* DOF reduced the effect of drought-mediated ROS accumulation by modulating the expression of genes encoding antioxidant enzymes, including *ThSOD*, *ThPOD*, and *ThGPX* [8]. In the same way, transgenic *N. benthamiana* overexpressing *VyDOF8* TF from *Vitis yeshanensis* showed improved tolerance to water stress, evidenced by higher chlorophyll and proline contents and lower MDA and hydrogen peroxide (H_2O_2) contents [85]. Moreover, in *G. hirsutum*, Su et al. [86] showcased that the transgenic line overexpressing *GhDOF1* exhibited higher tolerance to cold and osmotic stresses. Authors related the higher tolerance of transgenic plants to the ability of *GhDOF1* to modulate the activity of proline metabolism enzymes, thereby increasing proline accumulation. More recently, Wang et al. [84] evidenced that *A. thaliana* overexpressing *ThDOF8* TF, from the salt-tolerant *Tamarix hispida*, exhibited higher proline levels and enhanced SOD and POD activities, and ultimately salt-stress tolerance. Likewise, Xian et al. [87] revealed that DOF TF strengthens *Kentucky bluegrass* tolerance to Cd stress by orchestrating the expression of several genes associated with lipid, carbohydrate, cell wall, cell elongation, and membrane stability.

3.5 Heat Shock Factors (HSFs) TFs

The Heat Shock Factors (HSFs) are one of the most identified TFs that play a vital role in regulating gene expression, which are involved in plant stress tolerance [9]. This TF is characterized by a modular structure that includes a DNA-binding domain (DBD) at the N-terminal responsible for recognizing heat shock elements (HSEs) and an oligomerization domain, required for the protein-protein interactions [130,131].

First, HSF TFs are recognized for their role in extreme temperature stress. Recently, they have also been identified as multifunctional regulators responding to various abiotic stresses, including salinity, drought, and toxic trace elements (Table 1; Fig. 2). *HSFA1* acts as a principal regulator of the heat stress response. It regulates signaling events and interacts with HSFs A2 and B1 [130,131]. Overexpression of this TF has improved thermotolerance in many plant species. For example, in *S. tuberosum*, overexpression of *StHSFA1* enhanced plant thermotolerance. This effect was linked to chromatin remodeling and activation of heat-responsive genes [132]. Similar findings were observed in *H. vulgare* [133], *A. thaliana* [134], and *T. aestivum* [135]. In these species, overexpression of *TaHSFA6b*, *HSFA1b*, and *TaHSFC2a*, respectively, improved ROS homeostasis, enhanced jasmonic acid-mediated heat responses, and increased *HSP* gene expression. This resulted in a significant increase in thermotolerance. Overexpression of *AmHSF01* in Arabidopsis led to improved chlorophyll content and greater tolerance against heat stress [90]. *TaHSFA6f* improved tolerance to heat, drought, and salinity and modulated ABA sensitivity [9]. Similarly, Wang et al. [136] and Ma et al. [137] observed that overexpression of *TaHSFA8a* and *TaHSFC3-4 in T. aestivum* significantly enhanced drought tolerance. These changes increased flavonoid accumulation, scavenged ROS, and regulated the ABA signaling pathway to mediate drought resistance. Under the same stress, Wang et al. [136] showed that overexpression of *MdHSFA8a* in *Malus domestica* led to increased flavonoid and anthocyanin accumulation, and upregulated ABA signaling and antioxidant enzymes under drought stress. Similar protective effects were documented under cold stress (Fig. 2). For instance, Gao et al. [138] showed that overexpression of *HSFB21* in *Z. mays* significantly promoted cold stress tolerance. It did so by modulating Bzip68 activity. Olate et al. [139] demonstrated that overexpression of *HSFA1* enhances cold resistance in Arabidopsis, which is closely linked with salicylic acid receptors. Similarly, *BnaHSFA2* overexpression improved ROS scavenging and reduced lipid peroxidation under freezing stress in transgenic *B. napus* [140].

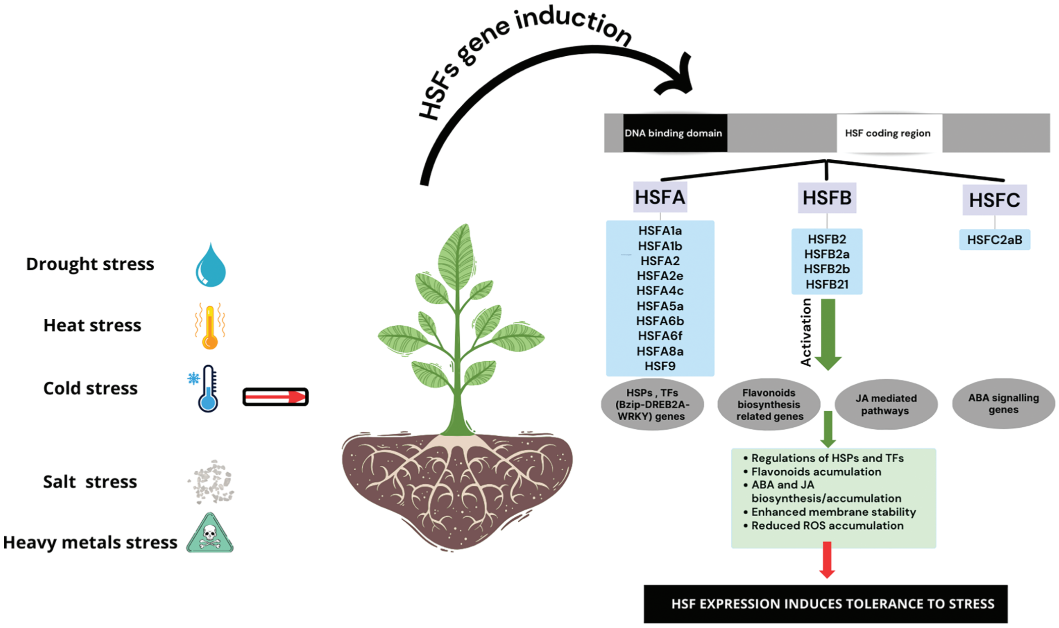

Figure 2: The roles of Heat Shock Factors TFs in crop tolerance to abiotic stresses

In *G. max* and *Populus alba*, Bian et al. [141] and Song et al. [142] demonstrated that the overexpression of *HSFB2b* and *HSFA5a* significantly alleviated the negative effect of salt stress by increasing the biosynthesis and the accumulation of antioxidant molecules like flavonoid, and remarkably improved root development under saline conditions. Under heavy metal stress, the overexpression of *HSF* also presented the same beneficial effects on plant tolerance. In this context, overexpressing *SaHSFA4c* from *Sedum alfredii* in transgenic Arabidopsis lines resulted in enhanced Cd tolerance by reducing ROS accumulation and maintaining chlorophyll content [89]. Furthermore, expression analyses have shown that multiple *HSF* genes respond to combinations of stresses, indicating the presence of cross-tolerance mechanisms. For example, *MsHSF* genes in *M. sativa* are differentially regulated under various abiotic stresses conditions [143]. Moreover, *H. vulgare* overexpressing *HvHSFA2e* and *S. tuberosum* overexpressing *SpHSFA4c* evidenced improved heat and drought tolerance through increasing enzymatic and non-enzymatic antioxidant defense and osmotic adjustment [144,145].

3.6 The Myeloblastosis (MYB) TFs

The myeloblastosis (MYB) TFs are one of the most functionally diverse families of TFs in plants that play a vital role in regulating plant response to abiotic stresses, like salt stress, water deficit, cold, heat, and heavy metal toxicity [146,147]. This TF is discovered as an oncogene in the avian myeloblastosis virus, and it is defined by a conserved N-terminal DNA-binding domain (DBD), and based on the number of MYB repeats, the MYB is categorized into four subgroups (1R, 2R, 3R, and 4R) [79]. In plants, the R2R3-MYB proteins, which are considered the largest MYB subfamily in plants, are particularly important in regulating the biosynthesis of secondary metabolism, the process of morphogenesis, and they are also important for plant tolerance to abiotic stress [148]. In fact, MYB TFs are frequently activated through ABA-dependent pathways, with specific members, such as MYB20, MYB15, and MYB41 [18]. In addition to ABA hormone, ethylene, jasmonic acid, auxin, gibberellin, cytokinin, and salicylic acid hormones could also modulate MYB-mediated stress responses [149].

Under stressed conditions, the MYB TFs have crucial roles in improving plant tolerance (Table 1). For example, MYBs TFs have numerous beneficial impacts in mediating the plant tolerance to heavy metal stress. For example, transgenic *N. tabacum* plants expressing *SbMYB15* from *Salicornia brachiata* displayed increased tolerance to Cd and Ni evidenced by lower concentrations of Cd and Ni, and higher antioxidant enzyme activities as compared to the wild type [92]. Moreover, *BnMYB2* from *Boehmeria nivea* has shown promise for phytoremediation regarding the elevated potential of the transgenic *A. thaliana* plants to accumulate Cd without any toxicity symptoms [150]. Likewise, Cd-stressed *Daucus carota* overexpressing *DcMYB62* displayed increased levels of Cd tolerance due to the increase in carotenoids, ABA, and hydrogen sulfide, which are important for stress tolerance [151]. MYB TFs have been reported to improve plant tolerance to other abiotic stress, such as heat, as shown in *A. thaliana* overexpressing the *TaMYB80* from *T. aestivum* [152]. Similar results were recorded under salt and drought-stressed conditions. In the study of Wang et al. [91], overexpressing *GmMYB84* strengthened the tolerance of *G. max* to drought, evidenced by longer roots, higher antioxidant activity, and better survival. Similarly, transferring *TaMYB30-B* from *T. aestivum* to *A. thaliana* improved drought tolerance in transgenic plants [153]. Besides, under salt stress, overexpressing *PfMYB44* in transgenic *A. thaliana* upregulates key genes, such as *AtNHX1* and *AtSOS1*, which are important for ion homeostasis and stress response [15]. Additionally, by upregulating *SOS2* and enabling Na^+ efflux, *MYB42* helps salt tolerance in *A. thaliana* [154].

3.7 WRKY TFs

The WRKY gene family is a crucial group of plant-specific TFs that significantly enhance plant resilience to abiotic stresses, such as drought, salinity, heavy metals, cold, and heat through diverse molecular pathways (Table 1; Fig. 3). Since the discovery of the first member, SWEET POTATO FACTOR 1 (SPF1) from *Ipomoea batatas* [155], extensive genome sequencing has revealed numerous *WRKY* genes across many species, including Arabidopsis, chickpea, sorghum, cucumber, and Miscanthus [156,157]. WRKY proteins, typically characterized by a conserved ~60 amino acid DNA-binding domain with the WRKYGQK motif and a C_2H_2 or C_2HC zinc finger motif, are categorized into three main groups (I, II, and III) and further subgroups based on structural features, allowing functional diversity and interaction with other proteins and transcription factors [158]. These TFs bind W-box elements in promoter regions to modulate stress-responsive gene expression, either activating or repressing pathways that control ROS detoxification, hormone signaling, and metabolic adjustments [159].

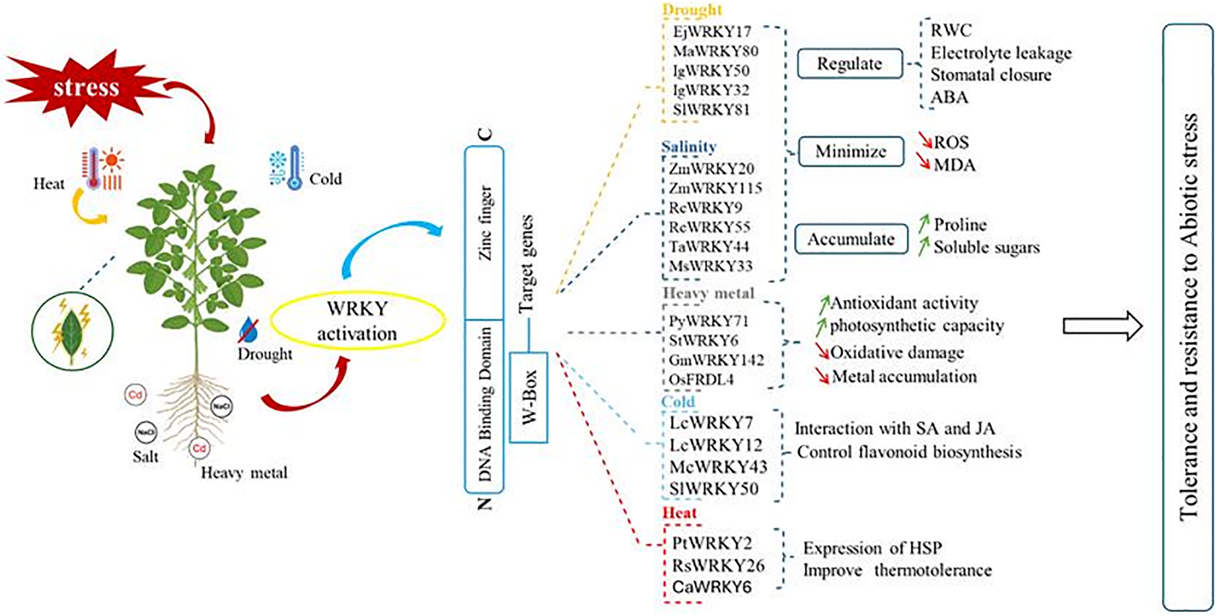

Figure 3: The roles of WRKY TFs in crop tolerance to abiotic stresses

In drought stress, *WRKY* genes, such as *EjWRKY17* and *MaWRKY80*, modulate ABA synthesis and ROS scavenging, which reduce water loss and improve tolerance, while *SlWRKY81* controls stomata behavior to mitigate dehydration [82,94,160]. WRKY TFs also regulate salt stress responses. For example, *ZmWRKY20* and *TaWRKY44* enhance ion homeostasis and antioxidant activity in *Z. mays* and *T. aestivum*, improving plant survival under saline conditions [161,162]. Heavy metal stress triggers WRKY activation via MAPK signaling, leading to enhanced expression of transporters, chelators, and antioxidant enzymes, with *GmWRKY142* and *StWRKY6* among those shown to increase Cd tolerance and accumulation capacity [163,164]. Furthermore, WRKYs contribute to Al tolerance by regulating citrate transporter expression, as seen in *O. sativa Oswrky22* mutants [165].

These TFs engage extensively with phytohormone signaling pathways, including salicylic acid and jasmonic acid, modulating gene expression in response to cold and heat stresses [166]. Overexpression of *WRKY* genes, such as *McWRKY43* and *SlWRKY50*, enhances flavonoid production and antioxidant defenses, conferring chilling tolerance [11,167]. WRKYs also regulate heat shock proteins and ROS detoxification pathways, exemplified by *PtWRKY2* and *RsWRKY26*, which improved heat tolerance in *A. thaliana* and *Raphanus sativus* respectively [93,168]. Notably, WRKY proteins can form regulatory networks by interacting with each other. For example, Cai et al. [169] evidenced that *CaWRKY6* activates *CaWRKY40* which strengthened *C. annuum* tolerance to combined heat and humidity stress. Collectively, the broad functional versatility and evolutionary conservation of WRKY transcription factors underscore their vital role in plant abiotic stress adaptation (Table 1; Fig. 3) and provide promising targets for crop improvement strategies.

4 Crosstalk among Key TFs Families in Abiotic Stress Responses

In higher plants, each TF family plays a key role not only in plant development but also in their adaptation to abiotic stresses [8,9]. However, these regulators do not function independently, but interact in integrated networks, modulating each other to orchestrate coordinated responses [170]. These interactions enable fine-tuned regulation of defense genes and contribute to strengthening plant tolerance to adverse environmental conditions. For instance, in *Chrysanthemum morifolium*, the overexpression of *CmDREB6* TF promoted the expression of *CmHsfA4* and *CmHSP90* TFs, which improve *C. morifolium* plant tolerance to heat stress, as reflected by a higher survival rate (85%) as compared to the wild-type (3.8%) [171]. Similarly, during heat stress conditions, *A. thaliana* plants lacking *bZIP28* TF showed enhanced activation of APXs and HSPs-dependent pathways together with a significant accumulation of *HsfA2* transcripts and H_2O_2 [172]. These findings suggest that HsfA2 TF may compensate for the deficiency in bZIP28 TF during heat stress. Moreover, in *G. max* submitted to osmotic stress, the *GmWRKY27* TF was found to interact with *GmMYB174 to bind to the W-boxes in the promoter of the* GmNAC29, a negative factor of stress tolerance, which enhances salt and drought tolerance [170]. In another interesting study by Zhang et al. [173] on *Poncirus polyandra*, authors used protein-protein interaction prediction to showcase that PpWRKY regulates stomatal movement through MYB TF mediated ABA signaling process.

In summary, plant tolerance to abiotic stress results from a synergistic network between different TFs. Thus, understanding these interactions opens the way to more effective biotechnological and varietal improvement approaches, capable of exploiting the complementarity of these regulators to sustainably strengthen crop resilience.

5 Conclusions

Abiotic stresses, such as drought, salinity, extreme temperatures, and soil contamination with heavy metals, pose major threats to the growth, development, and productivity of crop plants. These environmental constraints strongly disrupt the major plant physiological and biochemical processes, including photosynthesis, nutrient uptake, water balance, and cellular integrity. Moreover, the severity of their effects in the context of climate change justifies the intensified research efforts that aim to develop more tolerant plant varieties capable of maintaining their yields under hostile conditions.

In this context, transcription factors (TFs) play a fundamental role in orchestrating plant adaptive responses to stress. These proteins act upstream of signaling cascades by activating or repressing the expression of some genes involved in cellular defense, osmoregulation, detoxification of reactive oxygen species, biosynthesis of protective compounds (such as osmoprotectants and heat shock proteins), and adjustment of energy metabolism.

Our review highlights seven major families of TFs-bZIP, bHLH, MYB, HSF, WRKY, DREB, and DOF—that have been genetically introduced or overexpressed in various transgenic plants to enhance their tolerance to specific stresses. Each factor has distinct, sometimes complementary, roles in activating target genes linked to stress signaling pathways, cellular protection, secondary metabolism, or osmoregulation, which contribute to strengthening the resilience of transgenic plants. Research on these factors has identified effective strategies for inducing specific or combined tolerance mechanisms, depending on the type of stress.

Besides their key fundamental roles in plant response to stressful conditions, the TFs also represent a good target for biotechnological applications. Progress in transgenic techniques, synthetic biology, and genome editing provides chances to fine-tune TF networks, allowing for the creation of crop variants with increased resistance to a variety of abiotic challenges. Moreover, to further understand TF interactions and find new regulatory hubs, integrated omics and systems biology techniques will be crucial. Subsequent investigations ought to concentrate on converting these understandings into practical uses, connecting lab findings with sustainable farming methods.

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