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TRANSCRIPTION FACTOR GENES INVOLVED IN PLANT RESPONSE TO ABIOTIC STRESS FACTORS

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❀ Hypothermia, drought, salinity and heavy metals are the most widespread stress factors negatively affecting plant growth and development. Plants respond to these stress factors on molecular, cellular, and physiological levels through the complicated mechanisms of signal perception and transduction, subsequently inducing various defense mechanisms. Transcription factors controlling the expression of numerous defense proteins are the most significant abiotic stress reaction regulators. Mainly, the negative environmental influence activates the AP2/ERF, WRKY, MYB, NAC, bZIP transcription factors. The numerous transcription factors genes can be used in genetic engineering of agricultural crops resistant to abiotic stress. These genes are also of great interest in marker assisted selection of cultivated plants. This review is dedicated to description of transcription factors and their genes, involved in plant response to hypothermia, drought, salinity and heavy metals.

❀ **Keywords:** transcription factors; abiotic stresses; hypothermia; drought; salinity; heavy metals; AP2/ERF; WRKY; MYB; NAC; bZIP.

ГЕНЫ ТРАНСКРИПЦИОННЫХ ФАКТОРОВ, ЗАДЕЙСТВОВАННЫХ В ОТВЕТЕ РАСТЕНИЙ НА АБИОТИЧЕСКИЕ СТРЕССОВЫЕ ФАКТОРЫ

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❀ Гипотермия, засуха, засоление и тяжелые металлы — наиболее распространенные стрессовые факторы, негативно влияющие на рост и развитие растений. Растения на эти стрессовые факторы реагируют на молекулярном, клеточном и физиологическом уровнях через сложную сеть восприятия и передачи сигналов стресса, которая впоследствии инициирует множество защитных механизмов. Важнейшими регуляторами абиотических стрессовых реакций, как и других сигнальных путей, являются транскрипционные факторы, контролирующие экспрессию многочисленных защитных генов. В ответ на действие абиотических стрессовых факторов в растениях активируются транскрипционные факторы, относящиеся прежде всего к семействам AP2/ERF, WRKY, MYB, NAC и bZIP. Многочисленные гены транскрипционных факторов могут быть использованы при создании стрессоустойчивых трансгенных и генетически редактированных сельскохозяйственных растений. Гены этих транскрипционных факторов также представляют большой интерес в качестве мишеней при маркер-ориентированной селекции культурных растений. Данный обзор посвящен рассмотрению основных групп транскрипционных факторов и их генов, участвующих в ответе растений на гипотермию, засуху, засоление и воздействие тяжелых металлов.

❀ **Ключевые слова:** транскрипционные факторы; абиотический стресс; гипотермия; засуха; засоление; тяжелые металлы; AP2/ERF; WRKY; MYB; NAC; bZIP.

BACKGROUND

Hypothermia, drought, salinity, and heavy metals (HMs) are the most widespread stress factors negatively affecting agricultural plants. Due to their fixed way of life, plants are required to adapt to unfavorable abiotic environmental conditions. Plants respond to stress factors by activating numerous regulatory systems. One of the first plant responses to stress is the increase of the level of active oxygen forms, which can lead to cell death as a result of their negative effect on proteins, lipids, and nucleic acids [1]. When the level of oxygen active forms is increased in plants, the complicated antioxidant system is activated, which is normally balanced with the prooxidant system. In general, plant resistance to any stress factor is determined by the expression of numerous genes coding protective proteins. However, the most important regulators of all abiotic stress responses are transcription factors (TFs), which control gene transcription coding protective proteins. One can suppose that all major TF groups are involved in response to stress factors; however, some of their families are involved to a greater extent. In general, plant TFs depending on the homology of the primary and secondary structures of the DNA-binding domain can be split in four large groups: (1) group with domains enriched with the main amino acids such as leucine zipper, (2) group with DNA-binding domains such as zinc finger, (3) group with domains such as helix-turn-helix, and (4) group with domains such as β-scaffold [2]. However, it is more convenient to use TF splitting into families, which are classified by the principle of difference in the cis-regulatory elements of promoters. Thus, TFs attributed to APETALA2/ethylene-responsive factor (AP2/ERF), WRKY, myeloblastosis (MYB), NAM/ATAF/CUC (NAC), and basic leucine zipper (bZIP) families are the first to be activated in case of abiotic stress [3, 4].

TFs are the key regulators of protective gene expression, and these factor genes are more and more often considered as the targets for developing stress-resistant Transgenic plants as well as the targets for marker-assisted selection. The selection of the target gene is an important stage when planning for works of genetic engineering and selection of plants; TF genes are the most suitable for this purpose, as their quantity should be much less than the quantity of genes of protective proteins. This article examines TFs and their genes, which serve as the key regulators of responses to such abiotic stress factors crucial for plants as hypothermia, drought, salinity, and HMs.

TF INVOLVED IN COLD RESISTANCE REGULATION

Temperature is one of the determining factors of plant spreading, which is especially important for the vast territory of Russia with cold continental climate. According to different information, more than 70% of the territory of Russia is attributed to the risk farming area; the main limiting factor is cold. Plants develop different ways of adaptation to the cold stress in the process of evolution; major plants obtain cold resistance as a result of hardening [5, 6]. Acclimatization to cold is often connected to the reduction of daylight duration. This results in the termination of growth; plants put all their efforts to resist hypothermia [7]. The cold resistance of plants depends on the time as well as on the speed of acclimatization and the plant development stage. The mechanisms of cold and frost resistance are very similar; however, the development of the latter one is closely connected to sugar accumulation. Respiration intensity goes down at the temperature close to zero, and photosynthesis intensity goes up [8, 9]; therefore, available sugars are used to support cellular functions. Thus, winter cereals can accumulate sugars and therefore can acclimatize to cold; this ability was not detected in spring crops [10]. It was demonstrated that circadian rhythm is important for acclimatization. For example, plants cannot pass acclimatization at a low temperature in the dark even if protective genes are activated [11, 12]. The membrane is the first to respond to temperature reduction. The structure of its rigidity is changed [13], which results in the violation of the processes of membrane penetration by water and ions; consequently, protective genes connected to cold are induced [14]. Two types of stress resistance gene expression regulation exist: ABA dependent and ABA independent. ABA-independent genes in the promoter area demonstrate cis-element C-repeat/dehydration-responsive element (DRE) (A/GCCGAC) [15], in which TF C-repeat binding factors (CBFs) can interact. Talanova et al. [16] demonstrated that TFs of WRKY, which increase resistance to low temperatures of *Triticum aestivum* (common wheat), can be also attributed to ABA-independent regulation. Genes induced by ABA in the promoter area exhibit a sequence of nucleotide ABA-responsive element (ABRE) (ACGTGG/T). ABA-dependent TFs include MYB and bZIP. However, regardless of the connection to ABA, the so-called cold-regulated (*COR*) genes coding COR proteins are activated to enhance cold resistance. The regulation of *COR* genes by all above-mentioned TFs is closely connected and includes cross-action, joint regulation, and interlock of the individual pathways.

Proteins of the WRKY family are TFs characterized by the availability of conservative DNA-binding domain WRKY consisting of 60 amino acid residues at the N-end and atypical structure with zinc fingers at the C-end. The expression of *WRKY16* and *WRKY34* genes is increased under the cold effect in common wheat, reaching the maximum value after one day of stress effect [17]. Increased expression of *TaWRKY19* of common wheat in transgenic plants *Arabidopsis thaliana* resulted in an increase of resistance to low temperatures by means of indirect activation of *COR* genes [18].

CBF/DRE-binding proteins (DREB) are attributed to TFs of the AP2/ERF family. CBF1, CBF2, and CBF3 (also known as DREB1b, DREB1c, and DREB1a, respectively) [19] regulate the expression of *COR* genes. About 2,000 *COR* genes were detected, 1,200 of which were connected to low temperature stress and about 170 of which were regulated by TF CBF [20]. *CBF* genes were identified in several *Poaceae* species such as rye (*Secale cereale*) [21], rice (*Oryza sativa*) [22, 23], barley (*Hordeum vulgare*) [23–25], and common wheat (*T. aestivum*) [21, 23, 26, 27]. The increase in the level of expression of gene *CBF* starts at the early stage of response to low temperature. As the temperature reduces, the transcription of gene *CBF* becomes more and more intense [28]. According to other data, the expression of *CBF* is increased immediately after cold treatment, reaching its maximum in 3 h and then it is reduced. *COR* genes are activated later; their expression reaches its maximum 24 h after the beginning of stress effect [29]. In *A. thaliana*, six *CBF* genes were identified, among which *CBF1* to *CBF3* are involved in the regulation of gene expression connected to low temperature [6, 30]. The deactivation of the expression of *CBF1* or *CBF3* gene resulted in the sensitivity of *A. thaliana* plants to cold after hardening [31]. However, mutant plant *cbf2* is resistant to freezing in standard conditions as well as after cold treatment.

The analysis of gene expression demonstrated that *CBF2* negatively affects the transcription of *CBF1* and *CBF3* [32]. The overexpression of *A. thaliana CBF* gene in the other plant species or the overexpression of gene *CBF* of the other species in *A. thaliana* provides elevated frost resistance. Researchers determined that the level of expression of *CBF* and *COR* genes in *A. thaliana*, which grows in warm climates, after treatment with low temperatures, is lower than in plants growing northward [33–35]. The elevated expression of *CBF* gene often results in the enhancement of frost resistance of different plant species. Thus, overexpression in barley of *TaDREB3*, *TaCBF14*, and *TaCBF15* wheat genes and *H. vulgare HvCBF2A* gene caused an increase in resistance to freezing by means of increasing the level of transcripts of the lower-level target genes such as *COR14b* and *DHN5* [36–38]. Liu et al. [30] transferred *DREB1A* gene regulated by 35S CaMV and rd29A promoters to *A. thaliana* and thereby improved resistance of transgenic plants to low temperature, salt, and alkali. This gene from the cold-resistant plant *Adonis amurensis* (*AaDREB1*) was cloned and transferred to rice plants and *A. thaliana* under the control of the constitutive 35S CaMV promoter. The analysis demonstrated that transgenic plants became more resistant to low temperature as well as to drought and salinity [39].

TFs of the bZIP family are involved in the response to biotic and abiotic stress factors. bZIP proteins contain bZIP domains consisting of two structural components: main DNA-binding domain and domain of dimerization of leucine zipper [40]. This group of TFs exhibits a regulatory effect on drought, extreme temperatures, and salinity, first of all. Liu et al. [41] determined that *bZIP73* gene increases resistance to low temperature stress in rice, and its expression is increased after acclimatization to cold. It is supposed that *bZIP73* is the only gene connected to cold resistance at the seed germination stage of rice plants [42].

TFs of MYB family include the conservative DNA-binding domain MYB and are divided into four subfamilies: 1R, R2R3, R1R2R3, and 4R-MYB. MYB TFs exhibit both positive and negative effects on cold tolerance [43]. It is known that at low temperatures the level of expression of *MYB15* gene is increased. MYB15 is connected to promoters of *CBF1* to *CBF3* genes. However, reduced levels of transcripts *CBF1* to *CBF3* were detected in transgenic plants with the overexpression of *MYB15* gene after cold treatment; increased levels of expression of *CBF1* to *CBF3* were detected in plants with deleted *MYB15* gene. Consequently, increased expression of *MYB15* gene results in the reduction of tolerance to hyperthermia, whereas the removal of this gene promotes the increase of tolerance to freezing. Therefore, the *MYB15* gene negatively regulates the expression of *CBF* gene [44]. *MdMYB23* gene from an apple tree (*Malus domestica*) affects the resistance to cold by means of direct binding with promoters of *MdCBF* genes. Overexpression of *MdMYB23* increases resistance to cold [45]. *AtMYB14* and *AtMYB15* genes play an important role in the regulation of response to cold stress in *A. thaliana* [46]. Rice gene *OsMYB2* is also involved in the response to cold stress [47]. Xie et al. [48] demonstrated that *MYB88* and *MYB124* are cold-induced genes, which are required for ensuring resistance to hypothermia in apple tree and *A. thaliana* (Table 1).

Table 1

Some genes of TFs involved in response to the effect of abiotic stress factors

Family	Gene	Plant species	Effect on plant	Accession number in GenBank	Reference to the source
WRKY	*WRKY16*	*T. aestivum*	Increase of cold resistance	EU665428	[17]
	WRKY34	*T. aestivum*	Increase of cold resistance	EU669664.1	[17]
	TaWRKY44	*T. aestivum*	Increase of resistance to drought and salinity	KR827395.1	[95]
	TaWRKY2	*T. aestivum*	Increase of resistance to drought	EU665425.1	[18]
	TaWRKY19	*T. aestivum*	Increase resistance to cold and drought	EU665430.1	[18]
	OsWRKY45	*O. sativa*	Increase of resistance to drought, cold, and salt	DQ298181	[70]
CBF	*TaCBF14*	*T. aestivum*	Increase of cold resistance	AY785901.1	[37]
	TaCBF15	*T. aestivum*	Increase of cold resistance	MH264449	[37]
	HvCBF2A	*H. vulgare*	Increase of cold resistance	AY785843.1	[38]

Table 1 (continued)

Family	Gene	Plant species	Effect on plant	Accession number in GenBank	Reference to the source
DREB	*TaDREB3*	*T. aestivum*	Increase of cold resistance	DQ353853.1	[36]
	TaDREB1A	*T. aestivum*	Increase of resistance to drought, cold, and salt	AF303376.1	[87]
	TaDREB2B	*T. aestivum*	Increase of resistance to drought, cold, and salt	AB193608.1	[89]
	AaDREB1	*Adonis amurensis*	Increase of resistance to drought, cold, and salt	HQ889135.1	[39]
bZIP	*ABP9*	*Z. mays*	Increase resistance to drought and heat	GU237073	[73]
	ThbZIP1	*Tamarix hispida*	Increase resistance to salinity and heavy metals	FJ752700.1	[104]
MYB	*MdMYB23*	*M. domestica*	Increase of cold resistance	DQ074471.1	[45]
	AtMYB14	*A. thaliana*	Increase of cold resistance	Z95741.1	[46]
	AtMYB15	*A. thaliana*	Increase of resistance to drought and salinity	Y14207.1	[78]
	OsMYB2	*O. sativa*	Increase of cold resistance	D88618.1	[47]
	MYB88	*M. domestica*	Increase of cold resistance	KY569647.1	[48]
	MYB124	*M. domestica*	Increase of cold resistance	KY569648.1	[48]
	OsMYB3R-2	*O. sativa*	Increase of resistance to drought, cold, and salt	BAD81765.1	[93]
NAC	*SNAC1*	*O. sativa*	Increase of drought resistance	DQ394702.1	[61]
	OsNAC6/ SNAC2	*O. sativa*	Increase of resistance to drought, salt, and cold during seed emergence	AB028185.1/ EU846994	[62]/[60]
	TaNAC2a	*T. aestivum*	Increase of drought resistance	HM027577.1	[65]
	TaNAC69	*T. aestivum*	Increase of resistance to drought, cold, and salinity	AY625682.1	[63]
Homeodomain Leu zipper (HD-ZIP)	*HDG11*	*A. thaliana*	Increase of drought resistance	NP_177479.1	[75]

TF INVOLVED IN DROUGHT RESISTANCE REGULATION

Drought is one of the abiotic factors limiting plant growth and development. This stress factor is very important for Russia, especially for the main agricultural regions in the southern part of the country. Although all plants have the ability to fight drought, they are different in this parameter. To obtain agricultural plants with enhanced resistance to stress caused by drought, the basic understanding of the physiological, biochemical, and genetic regulatory networks is required. As the molecular biology is developed, the genetic engineering approach to use genes of stress resistance is more frequently used to enhance plant resistance to drought. In general, the methods of molecular biotechnology used for increasing crop productivity become the predominant tools of plant growing; therefore, reviewing individual genes ensuring drought resistance is important [49, 50]. Plant genes expressed in drought conditions can be divided into two groups: (1) genes whose products are functional proteins and enzymes, such as proteins of late embryogenesis, aquaporins, and proline synthetases, and genes whose products are TFs regulating the expression of genes coding such proteins as bZIP, MYB, DREB, etc. [51]. Initially, genes of the first group were studied; they helped obtain transgenic plants resistant to drought [49, 52]. However, TFs play the most significant role in the network of signal transfer from stress signal perception to expression of genes sensitive to stress; therefore, this group of regulators shall be the priority field of research in the area of biotechnology and genetics of plant drought resistance.

TF DREB can activate up to 12 functional genes of drought resistance depending on the so-called DRE-bound cis-regulation in stress conditions. The elevated expression of these genes contributes to the increase of proline content, which results in the enhancement of resistance to such stress factors as drought, cold, and salinity [30, 51]. Keeping resistance to drought at the initial stages of growth (as material basis of the future harvest is made) as well as at the later stages is important for many plants. Thus, the study of the genetics of drought resistance at the seed germination stage is a required approach for initial screening for drought resistance. TFs DREBlA and DREB2A in *A. thaliana* mostly regulate the transcription of *RD17*, *KIN1*, *Cor6.6*, *Cor15a*, *ERD10*, *RD29A* genes, etc., which are associated with tolerance to drought and other abiotic stress factors. These genes are expressed in the best conditions, but during drought and low temperature their expression is significantly increased [53]. Oh Se-Jun et al. [54] transferred TF genes CBF3/DREB1A of *A. thaliana* to rice and therefore increased plant resistance to drought, low temperature, salt, and alkaline, whereas transgenes did not exhibit any negative effect on any agricultural parameters of rice plants. Researchers also demonstrated that the above-mentioned *CBF1* to *CBF3* genes play an important role during hypothermia as well as during drought and high concentrations of salts [30, 55] (see Table 1). Jun-Wei et al. [56] used TF DREB gene of *A. thaliana* as the target and obtained transgenic plants of common wheat, which are characterized by the increase of proline content and consequently with enhanced drought resistance.

Besides DREB, other TFs are known, which are involved in the regulation of plant resistance to drought. The TF NAC family is one of the largest families of plant TFs [57]. More than 100 genes of this family were identified in *A. thaliana* and rice [58, 59]. However, only few of them were functionally characterized. The three *NAC* genes of *A. thaliana* (*ANAC019*, *ANAC055*, and *ANAC072*) were found with the promoter area *ERD1*, which is characterized as a gene sensitive to stress, and the excessive expression of these three *NAC* genes in *A. thaliana* results in the enhancement of drought resistance [60]. The role of two genes *NAC* of rice in the development of drought resistance is described [61, 62]. The overexpression of TF coded by rice gene *SNAC1* enhanced seed germination by 22% to 34% in comparison to control plants in drought conditions in the field conditions as transgenic plants of rice lost water slower, closing the major part of stomata [61]. In the same way, the excessive expression of *OsNAC6/SNAC2* gene in rice resulted in the enhancement of resistance to drought, salt, and cold during seed emergence [61, 62]. The overexpression of different *TaNAC* genes of common wheat is responsible for the enhanced resistance to biotic and abiotic stress factors [63, 64]. Tang et al. [65] demonstrated that transgenic tobacco plants with *TaNAC2a* gene of *T. aestivum* enhanced resistance to drought. A specific role in response to water deficit is connected to dehydrin proteins, which help plant cells to manage osmotic changes; their expression can be regulated with *NAC* gene too [65].

TFs of the WRKY family are of great value for the development of abiotic stress responses specified by drought [66, 67]. The overexpression of *TaWRKY146* increased resistance to dehydration stress in *A. thaliana* by means of the induction of closed stomata, which resulted in the reduction of transpiration speed [68]. Researchers also detected that plants with the overexpression of *TaWRKY2* demonstrate an increased expression of *STZ* and *RD29B* genes. As for transgenic plants with gene *TaWRKY19*, they exhibited higher levels of expression of *DREB2A*, *RD29B*, *Cor6.6*, and *RD29A* genes [69]. Qiu et al. [70] determined that the expression of *OsWRKY45* gene in rice was caused by drought as well as by cold, heat, and salt, which in turn indicated the key role of TF of OsWRKY45 in a wide range of abiotic processes. They also demonstrated that the overexpression of *OsWRKY45* of *A. thaliana* causes an elevated resistance to water deficit. The authors explained such elevated resistance of *A. thaliana* with the closing of stomata and the induction of *OsWRKY45* gene connected to stress. This can also be connected to the fact that *OsWRKY45* is involved in the regulation of the biosynthesis of ABA, which ultimately activates the signal cascade, resulting in transpiration reduction and enhancement of drought resistance [70].

TFs of the bZIP family are involved in many regulatory processes of plants, such as ABA-dependent pathways of regulation, transfer of stress signals, seed maturation, and flower development [71, 72]. One of the TF bZIP genes was cloned from corn and designated as ABRE-binding protein 9 (*ABP9*), which is specifically bound to the motif ABRE2. This gene was used to study its role during drought and heat separately or in combination with the effectiveness of the use of carbon and light together with the other factors such as ABA content in leaves and their pigment content [73]. It was determined that *A. thaliana* expressed *ABP9* gene was characterized by improved photosynthetic ability in effect of both stress factors (drought and heat) by means of the regulation of photosynthetic pigment composition, dissemination of excessive light energy, and enhancement of the effectiveness of carbon use and increase of ABA content.

It is known that *HDG11* gene coding homeodomain-containing TF leucine zipper (HD-ZIP) class IV [74] plays a significant role in drought resistance, improving the water homeostasis of plants. The overexpression of *HDG11* gene in tobacco plants improves some features of plants such as the reduction of stomata density and the improvement of the root system branching, which together promotes plant resistance to drought [75]. In the same manner, *AtMYB60* and *AtMYB44* are involved in stomata movements; these genes function as transcription repressors of *A. thaliana*, and their expression is negatively regulated in protective cells during drought [76, 77]. These data confirm that many TF genes evolved as regulators of drought resistance and often as stress resistance in general, being involved in ensuring the expression of many unrelated protective proteins.

A. thaliana with the overexpression of *MYB15* demonstrates resistance to drought, salinity, and hypersensitivity to exogenous ABA at different stages of development [78]. Information exists that the overexpression of *MYB15* improves drought and salt resistance by means of gene expression enhancement protecting against stress and the effective closing of stomata during water deficit. Lee et al. [79] mentioned that *A. thaliana MYB96* gene under the control of 35S CaMV promoter was overexpressed in the transgenic plant *Camelina sativa*. *C. sativa* demonstrated normal growth and demonstrated elevated sensitivity to drought, thanks to the increase of the production of cuticular wax on the surface of transgenic leaves. Thus, TFs involved in responses on stomata and leaves not exhibiting harmful pleiotropic effects are attractive targets for work planning aimed to reduce water losses in plants [80].

TF INVOLVED IN SALT RESISTANCE REGULATION

Large areas of salted lands are a crucial issue for Russia. Such lands are frequent in the southeast of the European part of Russia, especially in the middle and south Volga areas, northeast pre-Caucasian region, at the south of West and East Siberia, i. e. at the areas with well-developed agriculture. Salinity is one of the most destructive abiotic stress factors significantly reducing crop productivity of agricultural plants. It exhibits a negative effect on plant growth by means of reduction of carbon assimilation, cell division, and expansion [81, 82] as well as negatively affects nitrogen metabolism [83, 84]. Numerous TF genes were detected, which were induced by salinity and probably involved in the resistance to this stress factor. Genes of the AP2/ERF family, DREB subfamily, are well studied, which regulate the expression of many genes induced in case of osmotic stress [85, 86]. TFs TaDREB1A and TaDREB2B are induced in *T. aestivum* at low temperatures, under ABA effect, in case of salinity and drought [87–89]. TFs DREB affect the regulation of the expression of genes of glutamine synthetase (GS) and nitrate reductase, the main enzymes of nitrogen assimilation and connected to carbon metabolism. Thus, *TaDREB* gene affects nitrogen metabolism by means of induction of gene expression connected to GS activity. TaDREB1A and TaDREB2B exhibit positive effects on TaGS1 and TaGS2 during salinity and water deficit [84]. Understanding of the molecular mechanisms of plant responses to salinity and drought and their connections to the physiological indicators of photosynthesis and nitrogen exchange can provide important information for wheat genotype screening, which are the most resistant to these abiotic stress factors [84].

The other TFs involved in response to salinity are NAC factors. Thirty-three *NAC* genes [90] were expressed at high levels in *A. thaliana* during salinity, and 40 *NAC* genes responded to drought or salinity in rice plants [91]. Xue et al. [63] studied *T. aestivum TaNAC69* gene expressed at increased levels in drought, cold, and salinity. Accurate regulation of *NAC* genes in plant responses to abiotic stress promotes the occurrence of complicated signal networks; the important role of *NAC* genes in plant responses to abiotic stress makes them significant candidates for establishing transgenic plants resistant to stress [63] (see Table 1).

Representatives of the large family of TF MYB are involved in responses to salt resistance. Yu et al. [92] functionally characterized TF induced by wheat salinity of MYB, subfamily R2R3-TaSIM. Researchers demonstrated that *TaSIM* gene was induced by drought, salinity, low temperature, and ABA treatment. Resistance to salinity was increased in transgenic plants with *TaSIM* gene overexpression. Besides, the content of transcripts of *RD22* (ABA-dependent) and *RD29A* (ABA-independent) genes involved in stress signal transfer was higher in transgenic plants with *TaSIM* gene overexpression compared to wild-type. These results certified that *TaSIM* exhibits a positive effect on resistance of salt stress and can be a gene candidate for marker-assisted selection for obtaining agricultural crops resistant to salinity. It is known that *OsMYB3R-2* gene overexpression increases the tolerance of *A. thaliana* to cold, drought, and salinity [93]. *OsMYB48-1* gene overexpression in rice improved resistance to drought and salinity [94]. Wang et al. [95] also demonstrated that the constitutive expression of *TaWRKY44* in tobacco plants enhances resistance to drought and salinity.

TF INVOLVED IN HM RESISTANCE REGULATION

Soil contamination with HMs is one of the most critical issues in agriculture of Russia. HMs are one of the most hazardous chemicals, which disturb the function of plant systems in case of exceedance of the maximum allowable concentration. HMs exhibit high resistance, are able to be accumulated in almost all organs, and exhibit toxic effect on plant vital activity as well as on consumers of agricultural products. The HM group includes about 40 chemicals; even a small concentration in the environment results in unfavorable consequences for plants. The effect of HMs activates a large number of gene and protein binding signal pathways that ensure HM resistance [96–100]. The expression of numerous protective genes is activated by TF in the same way as for the other stress factors.

TFs of the AP2/ERF family demonstrate an important role in providing plant resistance to HM. Repkina et al. [101] studied the effect of cadmium on gene expression coding TF of CBF1 and DREB1 in the leaves of winter wheat sprout (*T. aestivum*), variety Moskovskaya 39. The effect of 100 μm cadmium increased the content of transcripts 15 min after the beginning of treatment and was kept at a high level for 7 days. Such increased expression of *CBF1* and *DREB1* genes can be considered as proof of their involvement in the unspecific protective and adaptive responses of wheat to the effect of cadmium ions. *OsDREB1A* and *OsDREB1B* genes in rice roots were activated 3 h after the beginning of the effect of 10 μm cadmium [102]. Besides, researchers determined that cadmium, as well as zinc, increases the gene expression coding TF of the MYB family (*MYB4*, *MYB10*, and *MYB72*) in *A. thaliana* [103]. An increase of the content of transcripts of *MYB72* gene affected with cadmium and zinc was observed in leaves rather than in roots of *A. thaliana*. The effect of cadmium significantly increased the expression of *MYB28* gene in *Thlaspi caerulescens* [103]. TFs bZIP exhibit an important role in response to HM. Wang et al. [104] determined that 6 h after the effect of $CdCl_2$, the products of *ThbZIP1* gene accumulated in roots, leaves, and stems of the transgenic tobacco plant (see Table 1).

Recently, information about TF involvement in gene expression regulation induced by effect of HMs appeared; however, this information is ambiguous and inconsistent. One of the possible reasons of the complication of TF role in the protective and adaptive responses of plants to the HM effect is connected to their inclusion in the signal pathways induced by the effect of other abiotic factors [105].

CONCLUSION

Plants developed the ability to adapt to severe environmental conditions; the complex effect of stress factors is frequently observed in natural conditions. Plants that experience one abiotic stress often adapt more to the second stress [106, 107]. Moreover, plants that are able to successfully resist several stresses demonstrate an evolutionary advantage over plants resistant to individual environmental factors [108]. In every respect, plants often do not develop different protection mechanisms for every type of abiotic stress; therefore, the same systems connected to degradation are activated in response to hypothermia, drought, salinity, and HMs. The effect of abiotic stress factors results in the activation of the expression of hundreds and even thousands of different genes of protective proteins, the part of which has not been annotated yet. The major part of these proteins complicates practical selection and the use of appropriate target genes. An alternative option is the use of TF genes for these purposes, which are one order less than the quantity of protective proteins. TF genes discussed in the article and presented in Table 1 can be used for the development of stress-resistant transgene and genetically edited plants as well as for the marker-assisted selection of agricultural crops.

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