Hypothermia, drought, salinity, and heavy metals 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 to prevent the negative effects of stress factors. Therefore, understanding the molecular mechanisms of stress response is of great importance in agricultural research.

Keywords: transcription factors; abiotic stresses; hypothermia; drought; salinity; heavy metals; AP2/ERF; WRKY; MYB; NAC; bZIP.
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 APETAL2/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 HcCBF2A 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

<table>
<thead>
<tr>
<th>Family</th>
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<th>Plant species</th>
<th>Effect on plant</th>
<th>Accession number in GenBank</th>
<th>Reference to the source</th>
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<td>EU665428</td>
<td>[17]</td>
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<td></td>
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<td>[95]</td>
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<td>TaWRKY2</td>
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<td>[18]</td>
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<td>[18]</td>
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<tr>
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<td>[70]</td>
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<td>[37]</td>
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<td>M1264449</td>
<td>[37]</td>
</tr>
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<td>HoCBF2A</td>
<td>H. vulgare</td>
<td>Increase of cold resistance</td>
<td>AY785843.1</td>
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</table>
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.

TFs involved in drought resistance regulation

Drought 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 DREB1A 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 regulators 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 CdCl₂, 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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