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Review Article

Genes Acting on Transcriptional Control during Abiotic Stress Responses

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Abiotic stresses are the major cause of yield loss in crops around the world. Greater genetic gains are possible by combining the classical genetic improvement with advanced molecular biology techniques. The understanding of mechanisms triggered by plants to meet conditions of stress is of fundamental importance for the elucidation of these processes. Current genetically modified crops help to mitigate the effects of these stresses, increasing genetic gains in order to supply the agricultural market and the demand for better quality food throughout the world. To obtain safe genetic modified organisms for planting and consumption, a thorough grasp of the routes and genes that act in response to these stresses is necessary. This work was developed in order to collect important information about essential TF gene families for transcriptional control under abiotic stress responses.

1. Introduction

Plant breeding is "*the art and science of changing the characteristics of the plant in order to produce desired characteristics*" and has been successfully practiced since of the beginning of civilization [1, 2]. Currently, their priorities and focus are the increase of yield in the same area. With population growth, the demand for food is increasing. However, large and small crop yields oscillate annually, because of several abiotic stresses, causing the increase in world food prices and food deficit.

In some developmental stage, a stress or a combination of abiotic stresses can cause irreversible damage to plants. In rice, for example, cold can be drastically harmful during grain filling, depending on the temperature and time of exposure [3]. Also, water restriction at flowering can significantly reduce grain production in wheat cultivars [4]. Salinity, at higher concentrations, can inhibit germination and reduce the production of biomass, whereas low soil pH can lead to accumulation and mineral imbalance, all greatly affecting yield [5].

Abiotic stresses lead to a series of morphological and physiological, biochemical, and molecular changes that dramatically affect plant productivity [6]. In field conditions, a stress is always associated with other stress. For example, aluminum toxicity is always associated with other mineral imbalance [7, 8] and drought in most cases is associated with heat or salinity [9]. When plants receive any sign of stress, signaling is activated in the membrane, which will awake different intermediate stress genes. These genes could be members of the MAP Kinase cascade, or calcium-dependent, which has the function to activate transcription factors that will bind to different types of protective genes [10, 11]. These protective genes will drive the accumulation of macromolecular and damage repair proteins, cellular protection protein, osmotic homeostasis, and/or ionic homeostasis proteins. Many of these will be performing excretion of metals to the apoplast or reallocation of ions that can be found in excess; others will modulate proteins that lose their function in stress without the aid of these modulators. Other genes will provide the accumulation of osmoprotectants to prevent the loss of water; finally, we can see that a very large number of genes will act against abiotic stresses. Drought, salinity, high temperature, and oxidative stress are often interconnected and may induce cell damage and even, in this case, denaturation of structural and functional proteins [12]. Similarly, genes that act against these stresses have a specific

regulation; however, they usually induce the same defense response [12–14].

Genes linked to the processes of abiotic stresses tolerance are divided into three classes: genes involved in signaling cascades and transcriptional control, the genes that have direct roles in the protection of membranes and proteins, and genes involved in ion uptake and transport [12, 13].

Many reports involving genetic expression and transformation have been conducted mainly with model plants, in order to obtain better tolerance to abiotic stresses. These are of great importance, because it is possible to have a better understanding of the defense mechanisms that plants may have facing a stressful condition and thus increase crop productivity, avoiding losses to farmers and consumers.

Thus, this review will report the main families of transcription factors that act against abiotic stresses, covering a paramount process of mechanism defense that is responsible for the activation of pretranscription protection responses.

2. Transcription Factors

Transcription factors (TFs) are commonly defined as proteins that recognize and bind, alone or with the interaction of other proteins, DNA sequences of promoters, to regulate transcription, by activating or inhibiting the expression of particular genes [15]. They interact with *cis*-acting elements in the promoter region of genes, activating or disabling the transcription, therefore regulating gene expression. TFs are ranked and grouped into families according to their DNA binding conserved domain. However, those TFs who do not own conserved domains but interact with TFs with domains to form transcriptional complexes are also described as transcription factors [15].

With the sequencing of the *A. thaliana* genome [16], nearly 2000 TFs divided into ca. 30 families could be identified, half of them being unique to plants [17, 18]. This number is much higher than in animals [19] supporting the idea that transcriptional regulation in plants is much more significant than in animals and humans. There is about 1500 TF involved in stress response, corroborating with the idea that the transcriptional regulation involved in abiotic stress in plants is extremely complex [20]. It is known that there are several pathways that respond independently to environmental stresses, suggesting an intricate gene regulatory network [21]. But it is known that a large number of TFs that are involved in abiotic stress responses function independently. Thus, this review will focus on these TF families, as well as their use in crop improvement programs, through engineering stress technology.

2.1. Zinc-Finger (ZFPs). In *A. thaliana*, 600 ZFP genes were identified [22]. These belong to zinc-finger family TFs that have a sequence motif of cysteine and/or histidine that coordinates zinc atoms to form specific peptide structures. They have an EAR repressor domain that is important in the regulation of genes against biotic and abiotic stresses [23].

Research with mutants in several plant species shows the importance of this family of transcription factors against various abiotic stresses. In rice, *OsISAP1* gene, which has a zinc-finger domain, was isolated and it was identified that it has a high rate of transcription after stress by cold, salinity, dehydration, and heavy metals. Overexpression in tobacco led to an increased tolerance to cold, salinity, and dehydration [24]. In *A. thaliana*, the expression of *Zat12* indicated that it produces transcripts during oxidative, osmotic, saline, and heat stress. When the same gene had its constitutive expression by genetic transformation, a high number of transcripts of genes responsive to oxidative and light stress were affected [25].

Also in *A. thaliana*, when the gene *rhl41* was placed in front of a constitutive promoter, it showed efficiency in tolerating high rates of brightness and increased the leaf anthocyanin and chlorophyll contents, playing a key role in acclimatizing plants under intense change in light intensity [26]. AZF1, AZF2, AZF3, and STZ proteins, possessing a repressor domain, were effective in repressing the expression of other TFs. AZF2 and STZ were strongly induced when plants were subjected to dehydration, salinity, cold, and ABA stress [27].

2.2. MYB and MYC. This TFs family is abundant in plants, with about 200 members. Phylogenetic analyses indicated a clear division between monocots and dicots [20]. The MYB domain is composed of one to three imperfect repeats, with 52 amino acid residues that adopt three α-helices [28]. The third helix of each repeat is the helix that makes direct contact with DNA [29]. Members of the MYB family are involved in processes including primary and secondary metabolism; cell fate and identity; developmental processes; and responses to biotic and abiotic stresses [30]. MYBs participate in the ABA-dependent signaling stress pathway and are activated only after ABA accumulation. *AtMYB60*, *AtMYB96*, and *AtMYB44* act in the ABA signaling cascade regulating stomata movement in response to abiotic stresses, the first two being also activated in drought stress and disease resistance [31–33]. *AtMYB13*, *AtMYB15*, *AtMYB33*, and *AtMYB101* are all involved in ABA-mediated responses to environmental stresses [34].

Recently, it was demonstrated that overexpression of a member of the MYB family in *O. sativa* and *A. thaliana*, *OsMYB2P-1*, gave an excellent tolerance to low levels of Pi, and a better reallocation of Pi when it is found in high concentrations on the soil, showing the importance of this TF in combating this stress [35]. *AtMYB102* is involved in routes of osmotic dehydration, injuries, and salt stress [36]. *AtMYB15* is upregulated by salt and cold and, in freezing conditions, it acts as a repressor of the expression of CBF genes [37]. It was also demonstrated that overexpression of the same gene resulted in increased tolerance to salt and drought [38].

2.3. NAC. The NAC family of TFs is largely described in plants, with about 150 members identified in rice [39]. They contain a diversified C-terminal domain and a highly conserved N-terminal [40] and were firstly characterized from petunia (NAM protein) and *A. thaliana* (AtaF1, Ataf2, and Cuc2 proteins) [41]. NAC TFs recognize the *cis*- element NACRS [42] that is a drought responsive element.

It is known that the rice genes *ONAC19*, *ONAC55*, *ONAC72*, and *ONAC045* are induced by drought [43], and *ONAC045* also by high salt, low temperature, and ABA treatment [44]. In Brassicas, the gene *BnNAC* is induced in response to wounding, insect feeding, cold shock, and dehydration [45]. In soybean, some NAC genes that act against stresses were identified. *GmNAC2*, *GmNAC3*, and *GmNAC4* are induced by osmotic, ABA, JA, and salinity stresses [46]. In wheat, the gene *TaNAC4* is induced by cold, salt, ABA, MeJa, ethylene, and wounding stresses, suggesting a cross talk between pathogen and abiotic stresses [47].

2.4. bZIP. The bZIP family of TFs is extremely abundant, having homologues in several species, including 17 in yeast, 56 in humans, 75 in Arabidopsis, 89 in rice, 92 in sorghum, 125 in maize, and 131 in soybean [48, 49]. The bZIP domain, fairly conserved, consists of a double structure, forming a α-helix, the same as the one providing the name of the family [50]. It has a hydrophobic portion at the C-terminus, creating an amphipathic helix. The DNA adherence occurs through two subunits that attach via hydrophobic interaction of the helix, creating a structure called zipper [51]. The preferred binding sites are the *cis*-elements A-box (TACGTA), C-box (GACGTC), and G-box (CACGTG) [52]. The family is subdivided into ten groups, according to their genetic similarity and not to the function of each protein [48, 49].

The role of bZIP proteins in response to biotic stress is widely known. Several proteins bZIP, of the type TGA, act as regulators of SA signaling. Members of this family bind to NPR1 genes that are key components in the SA defense signaling pathway [53, 54].

Another bZIP protein, from *A. thaliana,* is coded by *AtbZIP10*, which interacts with *LSD1.* This gene is a negative regulator of cell death and protects plant cells from oxidative stress [55]. Studies report that bZIP proteins act in abiotic stress. The rice gene *OsISAP1*, a bZIP family, when overexpressed in tobacco, conferred tolerance to cold, dehydration, and salt stress at the seed germination [24]. Another rice TF, *OsbZIP71*, was strongly induced by drought, PEG, and ABA treatments and repressed by salt treatment, suggesting that this gene may play an important role in ABA mediated drought and salt tolerance [56].

2.5. WRKY. Members of the WRKY family of TFs act as transcriptional regulators in biotic and abiotic stresses, specific to plants and protists [37]. This family has a conserved domain of 60 amino acids with the WRKYGWK sequence at the N-terminus. They possess cysteine and histidine residues binding a zinc atom, which forms a finger type structure [37, 57]. Reports on WRKY family genes in diverse plant species showed that they respond to various abiotic stresses. In rice, OsWRKY89 increased tolerance to UV irradiation and fungal infection [58], and *OsWRKY45* is upregulated by cold, heat, salt, and dehydration [59]. The overexpression of *OsWRKY11* enhanced heat and drought tolerance [60]. Soybean genes *GmWRKY21* and *GmWRKY54,* when cloned in *A. thaliana*, conferred salt and drought tolerance [61]. *AtWRKY25* and *AtWRKY33* showed importance in salt tolerance in *A. thaliana* while *AtWRKY45* is involved in ABA synthesis and tolerance to drought [58, 62]. In tobacco, the knockout of *NbWRKY* produced chlorosis and senescing phenotypes [63]. These results demonstrate that WRKY family genes play a role against abiotic stresses in different metabolic pathways.

2.6. HSPs. The last family of TFs to be discussed in the "fight" against abiotic stress is the HSF family (heat shock factor) in which members bind to the promoter region of some chaperones, also known as heat shock proteins (HSPs) [64]. These TFs are located in the cytoplasm when in their inactive state [65, 66] and have a C-terminal portion and 3 N-terminal portions, besides the amino acid leucine [67].

The overall structure and recognition of HSFs are conserved in both kingdoms, even with different size and sequences. Near to the N-terminal binding domain (DBD) DNA is formed by a set of three helices (H1, H2, and H3) and a segment of four antiparallel β sheets. The inner portion of the β-sheet is highly conserved and hydrophobic. On the other hand, the outer portion is composed of nonconserved and hydrophilic domains [68, 69]. The hydrophobic portion ensures perfect placement of H2-T-H3 portions, which are responsible for recognizing the promoters of HSPs, the HSE (heat stress promoter element) [70].

In the HSFs structure, one can still find the oligomerizing domain (OD or region HR-A/B), which is connected to the DBD by a region of variable length of amino acids. A pattern of hydrophobic amino acids in the region HR-A/B leads to forming a helical filament. Their description is based on the conservation of the oligomerizing domain: *HsfA*, *HsfB*, and *HsfC* [71].

There are several differences among the structures of HSFs: class B has a more compact HR-A/B region, while the classes A and C are elongated [71]. Class A is characterized by the presence of an AHA transactivator domain in the C-terminal domain, while classes B and C do not. This suggests a role for transcriptional activation of class A, while classes B and C act as coactivators or repressors [72–74]. An exception is the HSFs of the *A3* and *HsfA8* class that do not have AHA domain. The first has a pattern of tryptophan residues, which also act as activators and class that do not have the AHA domain [71]. An exception to class B HSFs was identified in *HSFb5* that does not have the tetrapeptide repressor [75]. The DO differences confer distinct patterns of heterooligomerization [71]. The HSFs structures still have nuclear localization signal (NLS) and nuclear export signal (NES).

In mammals, only 4 HSFs were characterized [75, 76], and in *D. melanogaster* and *S. cerevisiae* only one has been described [77]. This strongly contrasts with plants, where surveys report at least 21 HSFs in *A. thaliana* [78], 30 in corn, 24 in *Brachypodium*, 25 in rice, 27 in tomato, and 52 in soybeans [71], supporting the idea that, in plants, there were several duplications, which make HSFs extremely complex. Each class has its own regulatory network; however, all cooperate in the regulation of various functions and stages of stress [65, 79].

The interaction of these HSFs with HSPs involved with environmental stresses is widely studied. Several studies

with mutants (mainly *A. thaliana*) are helping to elucidate the specific functions of these HSFs. These studies usually employ the techniques of silencing the domain by merging it with a repressor or making use of constitutive promoters when overexpression is needed. *HsfA1* mutants in tomato, which had gene expression regulated by the 35S promoter (cauliflower mosaic virus, CAMV), display a 10-fold increase in expression when compared to the control, and the mutants that were cosuppressed by RNAi demonstrated the need of *HsfA1* for the control of heat stress [80].

HsfA2 A. thaliana mutant, also with constitutive expression, resulted in a thermotolerance, osmotic, and salt tolerant stresses, suggesting the involvement of this gene in various stress regulatory networks [81]. Aiming at clarifying the influence of genes in class B in *A. thaliana*, the knockout of *AtHsfB1* and *AtHsfB2b* resulted in plant resistance when exposed to the fungus *Alternaria brassicicola.* [82].

Studies with rice mutants also demonstrate the performance of HSFs as the response to abiotic stresses. Overexpression of *OsHsfA7* mutant in rice and *A. thaliana* promoted a tolerance of 42°C, resulting in the survival of more than 50% of the mutants when stressed, twice the value of the results obtained by the control WT [83]. Another report confirmed the higher expression of HSPs and HSFs under heat stress in rice, showing that the regulation of abiotic stress induces a very large range of genes and several HSPs act together in different cascades to combat the problems of abiotic stress [84].

These studies emphasize the importance of transcription factors, indicating HSFs in the regulation of metabolic pathways responsive to abiotic stresses. One can observe that TFs can regulate multiple defense mechanisms, thus being considered of great importance in breeding programs that aim mechanisms of tolerance to abiotic stresses.

3. Conclusion and Perspectives

Around 70% of yield losses in major crops occur due to abiotic stresses. There has been a tremendous effort to clarify the stress response pathways, such as the elucidation of the function and characterization of various genes and gene families, directly or indirectly responsible for fighting stresses.

The combination of genetic engineering techniques, together with the understanding of the mechanisms developed by plants to supply a certain kind of aggression, will provide advanced strategies in order to fight with the various types of stress and thereby obtain genetic gains sufficient to meet world demand for food.

The diversity and specificity of TFs make key components for triggering signaling cascades and the understanding and knowledge of the field are fundamental to the generation of new technologies that may be useful in breeding programs, such as overexpression of TFs that can bind specific promoter of genes that interact directly in a stress response, or the manipulation of specific transcription factors to increase the tolerance to determinate stress.

So, one must consider transcription factors as important candidates in breeding and crop improvement programs, since they are the keys to unlock the needed variability that will lead to the next generation of plants and push yield plateaus beyond the critical points needed by our growing population.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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