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REVIEW

Understanding the Transcription Factor Mediated Regulatory Mechanism Towards Abiotic Stress Response in Cereal Crops

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Abstract

Cereal crops are critical to global food security and are valued for their adaptability and nutritional value. However, they are increasingly threatened by abiotic stresses such as water scarcity, high soil salinity, severe climatic conditions, and nutrient deficiencies. This review focuses on the central role of transcription factors (TFs) in the response of cereal crops to these environmental challenges. TFs, such as the DREB family, the bZIP family, and the WRKY family, emerge as central players in this intricate regulatory network. They initiate or inhibit the activation of stress-responsive genes by binding to specific cis-regulatory elements located in gene promoters and enhance the resilience of cereal crops to various abiotic stresses. For example, DREB1/CBF TFs alleviate cold stress, NAM, ATAF1/2, and CUC2 (NAC) factors combat salinity stress, and WRKY TFs modulate responses to drought, salinity, and cold stress by initiating vital physiological processes, including osmotic regulation, antioxidant defense, and ion homeostasis, ultimately promoting stress tolerance. Genetic engineering strategies that overexpress these stress-responsive genes and TFs hold great promise for enhancing crop resilience and productivity in the face of climate change. In addition, this review also emphasizes the potential of epigenetic modifications, such as DNA methylation and histone modifications, to fine-tune the control of genes that respond to abiotic stresses. These findings benefit agriculture by addressing global food security challenges.

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Statement of Sustainability: The manuscript emphasizes the importance of transcription factors (TFs) in orchestrating the responses of cereal crops to environmental challenges and reviews the specific functions of different TF families in combating various abiotic stresses. The manuscript highlights the physiological processes regulated by TFs, including osmotic regulation, antioxidant defense, and ion homeostasis, and suggests the potential of genetic engineering strategies to overexpress stress-responsive genes and TFs, which contributes to several SDGs, such as Zero Hunger (SDG 2), in the face of frequent environmental changes that aim to end hunger, achieve food security, and promote sustainable agriculture. By increasing the resilience and productivity of cereal crops, this review can help ensure an adequate and stable food supply.

1. Introduction

Cereal crops are a group of grasses grown for their edible grains or seeds. Some common examples of these types of crops are *Oryza sativa* (rice), *Zea mays* (corn), *Triticum aestivum* L. (wheat), *Hordeum vulgare* (barley), etc. (Sahoo et al., 2019). Cereals are the most widely cultivated crops in the world, and this is because they possess several important characteristics. These include multiple nutritional values, essential components of animal feed, boosting the economies of many nations through agricultural production, trade, and industrial applications, etc. (Sahoo et al., 2020). In the case of nutritional and caloric values, grains are cultivated worldwide because they serve as a staple food for many people around the world. They can survive in high, low, and moderate temperature areas and are therefore abundant in almost every region of the world. This level of diversity is due to several cellular pathways and genes that control their metabolism (Samal et al., 2021). During climate change, abiotic factors induce stress in these crops, which tend to hinder their activities. During this phenomenon, crops undergo genetic changes that result in morphological differences and poor performance, making abiotic stress a major issue for cereal crops (Bodinga et al., 2023). Abiotic variables that can adversely affect plant growth, production, and yield include a variety of stresses and abiotic components such as temperature extremes, drought, salinity, and flooding, and cereal crops are susceptible to these phenomena (Radha et al., 2023).

Drought stress, caused by inadequate water availability, can result in stunted growth, reduced grain filling, and even crop failure. Salinity stress, caused by high soil salinity, can impair water uptake and nutrient absorption, leading to reduced crop productivity (Hu and Xiong et al., 2014). Flooding can lead to oxygen deprivation in the root zone, resulting in root damage and reduced nutrient uptake. Nutrients such as potassium (K), phosphorus (P), and nitrogen (N) are key factors in plant growth, and a deficiency of these nutrients can inhibit their rate of growth and development. Periods of extreme heat, prolonged drought, heavy rainfall, and severe weather events have increased in frequency and severity and pose significant challenges. For example, heat stress during flowering can lead to reduced pollen viability and poor grain set, resulting in yield loss. Lack of water during the reproductive period of the plant can lead to wilting, reduced grain filling, and smaller grain size. At the zenith of abiotic stress effects, cereal crop production begins to decline, affecting global food security (Akhtar et al., 2012). Some recent findings on the effect of abiotic stress on cereal crop yield are indexed in Table 1. During stress, cereal crops use multiple signaling pathways to inhibit the induced stress. The way they do this is through specialized transcription factors (TFs). TFs are specialized proteins that interact with precise DNA sequences within promoter regions to control gene expression, in this case, to inhibit abiotic stress (Zhang et al., 2019). The mechanisms of these transcription factors vary from one cereal crop to another, depending on the genes and conditions involved. TFs are often considered as molecular switches (Solis et al., 2022). This review aims to explain in detail the mechanisms of how transcription factors control genes in cereal crops to inhibit abiotic stress.

Table 1. Some recent findings on the effect of abiotic stress on the yield of cereal crops.

Abiotic Stress(s)	**Cereal Crop**	**Year of Study**	**Effects on Yield**	**Region**	**Reference**
Salinity	Rice	2021	Growth retardation and less germination	-	Solis et al. (2022)
Drought	Rice	2023	Reduced pollen fertility and biomass production	South and Southeast Asia, Latin America	Radha et al. (2023)
Heat and osmotic stress	Wheat	2022	Reduce grain size and weight 6% yield loss	-	Annum et al. (2022)
Salinity	Wheat	2021	Affect the physiological process	-	Soni et al. (2021)
Drought	Maize	2022	Decrease in pollination and grain set	-	Ali et al. (2022)
Chilling injury	Maize	2022	Premature leaf senescence	-	Ali et al. (2022)
Drought and waterlogging	Maize	2021	25-30% yield loss	-	Salika and Riffat (2021)
Drought	Barley	2023	Less grain filling	-	Alamholo and Tarinejad (2023)
Short-term heat stress	Barley	2021	Pollen abortion	-	Schindfessel et al. (2021)
Drought	Sorghum	2022	Seed setting and grain filling	India	Banerjee and Roychoudhury (2022)
Drought and heat stress combined	Sorghum	2021	Reduced seed set and pollen viability	Sub Saharan Africa	Ndlovu and Maphosa (2021)
Drought	Pearl millet	2021	60-40% yield loss	Sub-Saharan, Africa	Numan et al. (2021)
Dryland salinity	Pearl millet	2023	30% reduction in ground plant biomass	Parts of Africa and Asia	Gunguniya et al. (2023)
Drought	Oats	2022	Shrinkage of grain and loss in yield	China	Zhang et al. (2022)

2. Structure of Transcription Factor (TF)

TFs consist of three main domains: DNA binding domain, activation domain, and protein interaction domain (Figure 1). DNA binding domain has two main parts and is composed of Helix-turn-helix (HTH): which is composed of alpha and beta helices that are connected by turn, Basic Leucine Zipper (bZIP): this sub-domain facilitates the binding of leucine zipper and other sub-domains (Solis et al., 2022). The activation domain consists of the acidic domain (acidic zone and machinery of the transcription factor), the proline-rich active domain (proteins and coactivators), and the serine-threonine-rich activation (serine and threonine). Protein-protein interaction consists of the coiled-coil domain (alphas helices zone), tetratricopeptide repeat (TPR) (repeats of a 34-amino acid motif) that act as a scaffold for the assembly of protein complexes, and WD40 repeat domain is composed of many repeats of a 40-amino acid motif (Alamholo and Tarinejad, 2023).

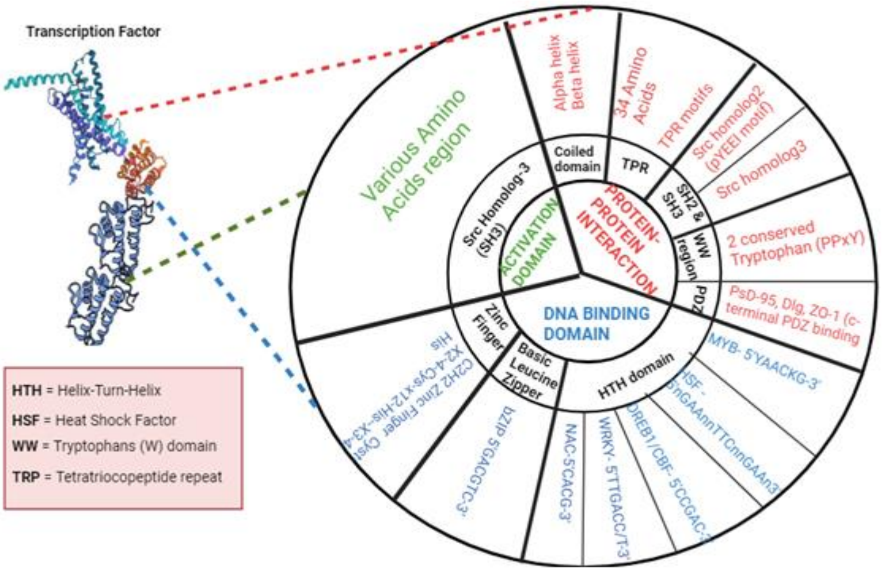

Figure 1. Structure and composition of a transcription factor.

3. Abiotic Stress in Cereal Crops

Common stresses include drought, temperature extremes, salinity, flooding, and limited or absent nutrients (Figure 2). Drought causes water deficiency in the soil and plant tissues, resulting in low root water uptake, reduced transpiration rates, and disrupted photosynthesis (Alamholo and Tarinejad, 2023). Drought stress affects cereal crops by reducing cell expansion, leaf area, and biomass accumulation, resulting in stunted growth and reduced yield. Physiologically, drought stress triggers various responses in plants, including stomatal closure to avoid leaf dehydration, accumulation of osmoprotectants to maintain cell hydration, and activation of antioxidants to remove free radicals to avoid cell damage (Solis et al., 2022).

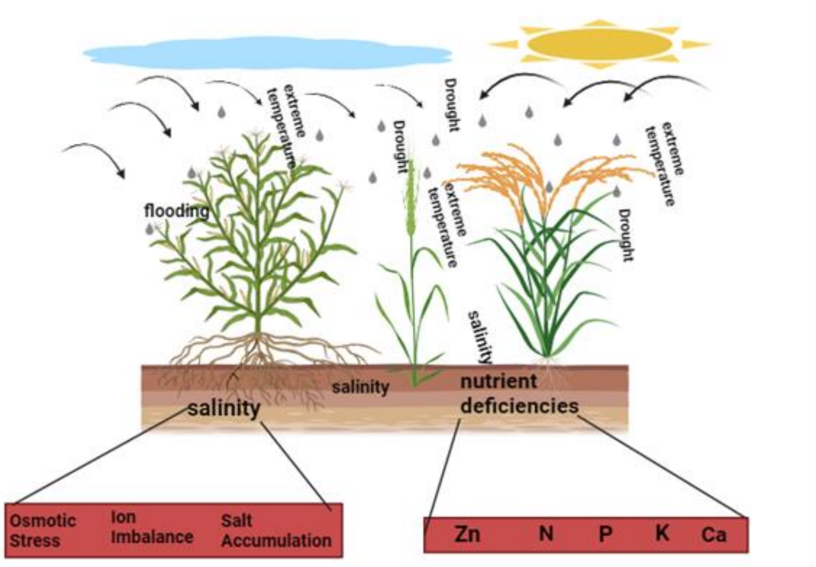

Figure 2. An illustration of how stress is induced in cereal crops.

Salinity can lead to reduced water uptake, ion toxicity, and osmotic stress. This affects cereal crops by inhibiting seed germination, reducing root growth, and impairing nutrient uptake. In response, plants accumulate compatible solutes, such as proline and glycine betaine, to maintain their osmotic balance and activate ion transporters to regulate ion concentrations in various plant tissues (Hu and Xiong, 2014). Cold and high temperatures can cause cell damage, low photosynthetic activities, and decreased nutrient uptake. protein hydrolysis, membrane damage, and oxidative stress. It is beneficial to understand the molecular mechanisms to find the genes that respond and the regulatory systems that control them (Solis et al., 2022). This information facilitates the improvement of stress tolerance in crop varieties through genetic engineering and breeding or breeding initiatives.

4. TFs in Abiotic Stress Response

Numerous genes have been identified as key players in the response of cereal crops to abiotic stress. For example, the DREB group of TFs can modulate the expression of genes associated with both high salinity and low water content (Hu and Xiong, 2014). Similarly, a class of gene regulators known as basic leucine zipper (bZIP) uses light signaling in response to several abiotic stresses (Akhtar et al., 2012), while another group of transcription factors, such as WRKY, are associated with controlling these responses in response to biotic or abiotic stresses and have been found in maize, barley, rice, and wheat (Zhang et al., 2022). Upon exposure to stress, the levels of specific stress-responsive transcription factors are often altered. Targeted genes are involved in response to stress when a transcription factor binds elements known as cis-regulatory sequences in their promoter regions to initiate a pathway that induces abiotic stress by repressing these targeted genes (Banerjee and Roychoudhury, 2022). Activation occurs when the transcription factor recruits other proteins, such as RNA polymerase, to the promoter region, leading to the initiation of transcription and subsequent expression of genes (Solis et al., 2022). The process by which transcription factors bind to cis-regulatory sequences is highly specific, as each transcription factor recognizes a specific DNA sequence motif. This specificity allows precise control of how a gene is expressed in response to abiotic stress (Samal et al., 2021). Different sets of target genes can be activated or repressed by different transcription factors depending on which cis-regulatory regions they recognize, due to their distinct properties such as DNA-binding domains (Alamholo and Tarinejad, 2023). Examples of such domains are the APETALA2/Ethylene-Responsive Element Binding Factor (AP2/ERF) domain in the DREB family, the bZIP domain in the bZIP family, and the WRKY domain in the WRKY family. The bZIP factor, for example, is associated with drought resistance in wheat and binds to a specific cis-regulatory element within the promoter of the gene and modulates various physiological and biochemical processes such as osmosis, scavenging of free radicals, and opening and closing of stomata to control how water enters and exits leaves (Soni et al, 2022).

5. Molecular Mechanisms of TF-mediated Abiotic Stress

Drought stress activates the dehydration-responsive element-binding (DREB) and myeloblastosis (MYB) transcription factors in cereals (Samal et al., 2021). However, elevated soil salinity can cause osmotic stress and ion imbalances in plants. These bind to cis-elements (Table 2) on genes activated by the stress response and initiate their transcription. Cis-elements in this region include; dehydration-responsive element/C-repeat (DRE/CRT), which is activated by DREB, and MYB/MYC cis-elements, which are myeloblastosis oncogene-like transcription factor/myelocytomatosis oncogene (MYB/MYC) TFs, resulting in the control of genes that respond to drought stress as well as those involved in osmoprotectant synthesis and antioxidant defense (Zhang et al., 2022). Salinity stress also triggers the activation of specific TFs in cereal crops (Sahoo et al., 2019).

Some abiotic stress-related TFs are described in (Table 3). This situation triggers a group of TFs, such as NAC TFs, which modulate the salinity stress response by binding to cis-elements, known as NAC recognition sequence (NACRS), of target genes to initiate ion homeostasis, adjust the osmotic balance, and enhance antioxidant defense. Through this action, NAC TFs contribute to the improvement of salinity tolerance in cereal crops (Zhang et al., 2022). NAC is an acronym representing the first three members of the group of TFs that control these processes. They are No Apical Meristem (NAM), Arabidopsis Transcription Activation Factor 1 and 2 (ATAF1&2), and Cup-Shaped Cotyledon 2 (CUC2). For example, extreme temperatures activate the C-repeat binding factor/dehydration-responsive element-binding protein-1 (CBF/DREB1) TF in cereals to inhibit cold stress through a mechanistic interaction with CRT/DRE cis-elements (Alamholo and Tarinejad, 2023).

Table 2. Genes and cis-elements in the promoter region, and their recognition sequences.

Genes	Cis-element / Sequences of Gene	Name of Cis-element / Sequence	Reference
RD29A	DRE; TACCGACAT & ABRE; ACGTGG/TC	Dehydration-responsive element (DRE) & ABRE	Samal et al. (2021)
RD22	RYACGTGGYR	ABRE	Bodinga et al. (2023)
RD29B	TACCGACAT	DRE	Radha et al. (2023)
RAB18		ARABIDOPSIS THALIANA DROUGHT-INDUCED 8	Zhang et al. (2019)
Amy3D (amylase) promoter of rice (O.s.)	CTACGTGGCCA	Like ABRE; G box-related element	Zhang et al. (2019)
Wheat histone H3	GGACGCGTGGC	Response to ABA element and desiccation	Solis et al. (2022)
Wheat (T.a.) Em gene	GGACACGTGGC	ABRE	Alamholo and Tarinejad (2023)
Wheat histone H3	GGACGCGTGGC	Synthetic element (hex-3) related to response to ABA and desiccation	Radha et al. (2023)
Maize anthocyanin promoter	AGTTGAATGGGGGTGCA	(Anthocyanin regulatory element)	Samal et al. (2021)
Maize (Z.m.) rab28	ACGCGCCTCCTC	ABA	Bodinga et al. (2023)
Barley alpha-amylase gene (Amy 1/6-4)	GGCCGATAACAAACTCCGGCC	GARE (gibberellic acid responsive element)	Radha et al. (2023)
Barley (H.v.) HVA1 gene	CCTACGTGGCGG	ABRE1and ABRE2	Zhang et al. (2019)
iso1 (encoding isoamylase1) promoter	AAAACTAAGAAAGACCGATGGAAAA	Sugar-responsive element	
Barley HVA1 gene	ACGCGTGTCCTC	ABRC3 (ABA response complex 3) of HVA1 consists of CE3 and A2; ABA responsive element; stress response	Alamholo and Tarinejad (2023)
EPB-1	GTAACAGAATGCTGG	GAMyB Putative binding site of the transcription factor,	Radha et al. (2023)
HY5AT	TGACACGTGGCA	development of root and hypocotyl	Banerjee and Roychoudhury (2022)
RTBV promoter	CAGAAGATA	GATA motif binding factor	Zhang et al. (2022)

Table 3. Transcription factor-mediated gene regulation in cereal crops.

Transcription Factor	Genes Regulated	Abiotic Stress	Outcome of Gene Regulation	Cereal Crop	Reference
DREB1/CBF	RD29A, COR47, KIN1, COR6.6,	Drought, Cold	Drought tolerance	Wheat	Samal et al. (2021)
MYB	RD22, RD29B, RAB18	Drought	Enhanced drought tolerance	Wheat, maize rice	Bodinga et al. (2023)
NAC	SNAC1, SNAC2, OsOAT	Salinity stress	Salinity tolerance	Rice, maize, wheat	Radha et al. (2023)
CBF/DREB1	COR genes, antifreeze proteins	Extreme temperature	Cold tolerance	Rice, maize, Wheat	Zhang et al. (2019)
HSF	HSP genes	Heat stress	Heat tolerance	Rice, maize, Wheat	Zhang et al. (2019)
MYB	MYB2, MYB44	Drought, UV-B	Activation of stress-related genes	Sorghum	Solis et al. (2022)
WRKY	WRKY22, WRKY46	Salinity, Pathogens	Salinity, Pathogens tolerance	Barley	Alamholo and Tarinejad (2023)
bZIP	bZIP28, bZIP53	Extreme temperature, drought	Heat, drought tolerance	Maize	Radha et al. (2023)

6. TF-mediated Abiotic Stress in Cereals: Case Studies

Transcription factor-mediated responses to abiotic stress in cereals have been the subject of extensive research, with notable case studies providing valuable insights. The following case studies illustrate the importance of TFs in conferring abiotic stress resistance in cereals, offering promising avenues for crop improvement and agricultural sustainability in the face of changing environmental conditions.

6.1. RD29A, COR47, KIN1 and COR6.6 Genes Mediated Drought Tolerance in Wheat

RD29A (Responsive to Dehydration 29A) is a stress-responsive gene up-regulated by DREB1/CBF TFs under low temperature and low water content in wheat. It functions in the synthesis of osmoprotectants and the regulation of ion transporters. Osmo-protectants are small organic molecules that help plants maintain cellular osmotic balance (Annum et al., 2022). Their nature as compatible solutes allows them to accumulate in the cell without interfering with cellular processes. Osmo-protectants include proline, glycine betaine, and sugars such as trehalose and sucrose can be synthesized in response to stress (Soni et al., 2021). This complex process also involves the activation of several enzymes and metabolic pathways. The enzyme proline dehydrogenase is responsible for the synthesis of proline from glutamate, while enzymes such as betaine aldehyde dehydrogenase and choline monooxygenase synthesize glycine betaine from choline (Annum et al., 2022). The synthesis of sugars such as trehalose and sucrose involves the activation of specific sugar biosynthetic enzymes (Soni et al., 2021).

COR47 (Cold-Regulated 47) is another gene that is activated to inhibit cold stress in wheat. It encodes a protein that prevents freezing damage in plant cells by stabilizing cell membranes to prevent ice crystal formation. It has been proposed that COR47 acts as a cryoprotectant by binding to and stabilizing the lipid bilayer of cell membranes (Annum et al., 2022). This helps to maintain membrane integrity and prevent leakage of cellular contents that can occur during freezing and thawing cycles, while the KIN1 (short infusion) gene functions in osmotic adjustment, which is essential to prevent dehydration in plants under drought conditions. RD29A may be involved in the regulation of ion channels and transporters that control the uptake and efflux of ions such as (K^+), (Na^+), (Ca^{2+}), and (Cl^-) in plant cells. The exact mechanisms are still under investigation (Soni et al., 2021).

6.2. WRKY22 and WRKY46 Genes Mediated Salinity Tolerance in Barley

WRKY DNA-binding protein 46 (WRKY46) helps activate the plant's immune response and increases its resistance to various pathogens (Nazir et al., 2022). However, it minimizes damage to plants caused by high salt concentrations. In the presence of salt, there is an imbalance of ions inside and outside the cell, causing toxicity and subsequent cell damage (Alamholo and Tarinejad, 2023). channels, such as those responsible for the uptake and efflux of sodium (Na^+) and potassium (K^+). Meanwhile, WRKY22 can activate the expression of the potassium transporter HKT1, known for its strong attraction to potassium ions and its role in maintaining potassium homeostasis, and prevent sodium accumulation in the cytoplasm or by causing cellular dehydration through osmotic regulation (Schindfessel et al., 2021).

6.3. COR Gene Mediated Cold Tolerance in Rice and Maize

COR genes can respond to cold stress. The OsCOR413im gene in rice encodes a protein that is triggered by low-temperature conditions and helps to stabilize cell membranes. Its full name is *Oryza sativa* Cold-Regulated Protein 413 and is located in the mitochondria (Ndlovu and Maphosa, 2021). One proposed mechanism is that the OsCOR413im protein interacts with lipids in the cell membrane, particularly phospholipids, and helps maintain their proper arrangement and organization (Ndlovu and Maphosa, 2021). This interplay could prevent the lipids from shifting from a state characterized by liquid crystalline properties to a more solid, gel-like state, which can occur at low temperatures and lead to membrane rigidity (Ali et al., 2022). In maize, the *Zea mays* Cold-Regulated Protein 413 or ZmCOR413 genes are induced during cold stress and are involved in membrane stabilization and protection against freezing-induced damage.

Antifreeze genes such as the ZmAFP1 gene, which encodes a protein that inhibits ice crystal growth and increases cold tolerance, have also been identified in maize (Ndlovu and Maphosa, 2021). In wheat, the TaCOR14b gene is induced by cold stress and encodes a protein with cryoprotective properties that protects plant cells from freezing-induced damage, and the TaAFP2 gene has also been identified to confer cold tolerance by inhibiting ice crystal growth (Ali et al., 2022).

6.4. bZIP28 and bZIP53 Genes Mediated Heat and Drought Tolerance in Maize

Basic leucine zipper 28 or bZIP28 is a transcription factor that is functional in the unfolded protein response (UPR) during stress in the endoplasmic reticulum (ER). bZIP28 undergoes multiple post-translational modifications that result in its subsequent translocation to the nucleus where it interacts with specific DNA sequences known as ER stress response elements (ERSEs) in the promoter region (Soni et al., 2021). As a result, protein folding enzymes including protein disulfide isomerases (PDIs) and chaperones such as heat shock proteins (HSPs) are induced (Ali et al., 2022).

These proteins ensure that proteins are properly folded and prevent the accumulation of misfolded or unfolded proteins, which can be toxic to cells under stress (Ndlovu and Maphosa, 2021). Superoxide dismutase (SOD) and catalase are two proteins that function to remove reactive oxygen species (ROS) and protect cells from oxidative damage caused by heat stress. Both the bZIP53 and bZIP28 genes modulate these proteins under drought stress to produce osmoprotectants that maintain cellular osmotic balance and protect against dehydration (Banerjee and Roychoudhury, 2022).

7. Future Trends in TFs Mediated Cereal Crops Improvement

WRKY and DREB/CBF transcription factors DRE/CRT cis-acting element in the promoter regions of stress-responsive genes to enhance tolerance to drought stress. The conservation of this mechanism allows the transfer of knowledge and strategies for improving drought tolerance (Banerjee and Roychoudhury, 2022), as it is used by the majority of cereal crops. WRKY TF is used by cereal crops to modulate multiple abiotic stresses such as drought, salinity, and cold temperatures (Wang et al., 2023). In an event where environmental climate change creates situations characterized by intense multiple effects on the environment that cause prevailing abiotic stress in cereal crops, it becomes imperative to enhance TFs and genes associated with abiotic stress response using genetic engineering methods (Radha et al., 2023). This will increase the concentration of osmoprotectants to maintain cellular osmotic balance and protect against dehydration in case of drought. Regarding antioxidant protection, enzymes such as superoxide dismutase (SOD) and catalase (CAT) will scavenge free radicals to prevent oxidative damage, and TF such as DREB/CBF will be engineered to be overexpressed (Samal et al., 2021). In addition, epigenetic modifications such as DNA methylation and histone modifications can affect the ability of TFs to bind sites in response to stress (Zhang et al., 2019). These modifications may directly or indirectly affect the composition of chromatin and the activity of genes to influence abiotic stress in cereal crops. For example, in rice, DNA methylation has been shown to modulate genes that respond to stress (Zhang et al., 2019). During drought stress, the promoter regions of these stress-responsive genes can become hypermethylated, leading to transcriptional repression and reduced stress tolerance (Samal et al., 2021). However, DNA methylation regulates the accessibility of transcription factor binding sites by adding or removing methyl groups to cytosine residues of DNA (Soni et al., 2021). Meanwhile, hypermethylation of promoter regions of stress-responsive genes under drought stress can lead to transcriptional repression and reduced stress tolerance (Samal et al., 2021). However, this occurs because DNA methylation can directly block the binding of TFs to their target sites on DNA, preventing the initiation of gene expression. Histone modifications, which include processes such as acetylation, methylation, phosphorylation, and ubiquitination, can regulate the accessibility of TF binding sites. Similarly, histone methylation can either activate or repress gene expression, depending on the specific lysine residue and the degree of methylation (Alamholo and Tarinejad, 2023).

8. Conclusion

TFs in cereal crops are regulators of genes that respond to stress, and activating or repressing their expression levels can enhance the ability of plants to cope with environmental stresses. The identification and characterization of specific TFs involved in these processes have provided valuable insights into the molecular mechanisms of abiotic stress tolerance in cereals. A more detailed understanding of their regulatory networks and interactions with other genes is still needed. TFs serve as central nodes in these interaction networks, integrating signals from different stress-responsive genes and orchestrating their expression. Furthermore, the integration of omics technologies allows the identification of novel TFs and the genes they target.

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