

Review

Exploring the Adaptive Responses of Plants to Abiotic Stresses Using Transcriptome Data

Muhammad Haseeb Javaid, Ali Raza Khan, Abdul Salam , Asifa Neelam, Wardah Azhar, Zaid Ulhassan and Yinbo Gan *

Zhejiang Key Lab of Crop Germplasm, Department of Agronomy, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310058, China; 11916140@zju.edu.cn (M.H.J.); 11616094@zju.edu.cn (A.R.K.); 11916126@zju.edu.cn (A.S.); asifaneelam@yahoo.com (A.N.); 11716101@zju.edu.cn (W.A.); 11616086@zju.edu.cn (Z.U.)

* Correspondence: ygan@zju.edu.cn; Tel.: +86-571-8898-2204

Abstract: In recent decades, global climate change and heavy metal stress have severely affected plant growth and biomass, which has led to a serious threat to food safety and human health. Anthropogenic activities, the rapid pace of urbanization, and the use of modern agricultural technologies have further aggravated environmental conditions, resulting in limited crop growth and productivity. This review highlights the various adaptive transcriptomic responses of plants to tolerate detrimental environmental conditions, such as drought, salinity, and heavy metal contamination. These stresses hinder plant growth and development by disrupting their physiological and biochemical processes by inducing oxidative stress, nutritional imbalance, and osmotic disturbance, and by deteriorating their photosynthetic machinery. Plants have developed different strategies to safeguard themselves against the toxic effects of these environmental stresses. They stimulate their secondary messenger to activate cell signaling, and they trigger other numerous transcriptomic responses associated with plant defense mechanisms. Therefore, the recent advances in biological sciences, such as transcriptomics, metabolomics, and proteomics, have assisted our understanding of the stress-tolerant strategies adopted by plants, which could be further utilized to breed tolerant species. This review summarizes the stress-tolerant strategies of crops by covering the role of transcriptional factors in plants.

Keywords: abiotic stress; transcriptomic; crops



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1. Introduction

Abiotic stresses have always been a major concern for agronomic crops in terms of yield reduction. Plants are vulnerable to abiotic stresses, which include drought, salinity, and the accretion of heavy metals. The data have portrayed an alarming situation, with a crop yield reduction of 70% caused by abiotic stresses, which is considered the major constraining factor to crop productivity [1,2]. Natural resources are diminishing, which poses a serious question to agriculture stakeholders: how can food demand be managed for a rapidly growing population? Plants are always at the verge of risk when grown under natural conditions and often encounter abiotic stresses [3]. Under such conditions, plants have developed some strategies that they adopt according to the prevailing conditions. Some plants can escape, whilst others try to avoid the lethal effects of the stresses [4]. However, some plants adopt a tolerant mechanism. Nevertheless, among all the mentioned strategies, they have to lose a certain amount of yield, but the tolerant mechanism is somehow less destructive for plants in comparison to other adopted strategies. Scientists have revealed that this process is very complex and engages with multiple processes, such as extensive modifications to metabolic and biochemical levels, which lead to the alteration of morpho-physiological pathways [5]. Furthermore, some changes in transcription and translational processes have also been noted.

According to WHO, globally, 55 million people are affected by drought, and it is estimated that by 2030, 700 million people will be at the risk of displacement due to drought [6,7]. Water, indeed, is the most indispensable element for plants. From emergence to growth, plants mainly rely on moisture to proceed activities. Water shortage at any stage during growth for a long period causes destabilization in their structure and shortens their life cycle [8]. Plants adopt different approaches due to exiguous water conditions and generate two types of signals, i.e., (I) osmotic stress and (II) oxidative damage. Plants have to endure detrimental effects during oxidative damage, which directly deteriorate cellular components, including protein, nucleic acid, and lipids, and disrupt metabolic activities. Plants, being smart organisms, have natural mechanisms to tackle stresses [9]. They anticipate the threat and trigger their defense system for revival by allocating available nutrients and energy. Furthermore, they are competent enough to adjust their transpiration rate accordingly by various modifications [10]. In addition to this, the role of some phytohormones has been acclaimed by scientists. Abscisic acid is said to be a preeminent phytohormone that can control stress signaling at transcription levels, which is responsible for the closing of stomata under water-scant environs [11].

After drought, salinity is a serious problem that reduces plant production by various means. It not only affects quantity but also causes great damage to the quality of agricultural products [12]. According to a recent appraisal given by stakeholders, salinity affects 20% of the total arable land around the globe [13]. It is considered the major hindrance to crop production worldwide, particularly for productive land near the sea. FAO (2016) estimated that the salinity problem due to global climate change could cover 33% of the total cultivated land in the near future [14].

Climate change can be described as a phenomenon of various environmental problems [15]. Increased anthropogenic activities and climatic changes have resulted in an increase in heavy metal accumulation causing injurious effects on living organisms [16]. Since the industrial revolution, the accretion of heavy metals has increased periodically, especially those that are hazardous, such as Cd, Cr, Pb, Al, Hg, and Ti [1,17,18]. It has been reported that even a small amount of heavy metal causes toxicity to plants. Some of the common symptoms are as follows: growth reduction, blocked photosynthesis, amended nutrient assimilation, disturbed water balance, reduced biomass accumulation, and triggered senescence as well as chlorosis [19]. The internal system of plants collapses after facing such trauma, and they die. Furthermore, the abundance of heavy metals in nature is more hazardous for human health as declared by health officials. They enter our food chain via plants and cause fatal diseases [20,21].

A plethora of complex events happen in plants when undergoing abiotic stress. In these complicated mechanisms, some changes are initiated at various levels, including transcriptional modifications and translational and post-translational changes [22–24]. Some events may lead to an alteration in metabolic and biochemical processes, hence causing major physiological and morphological changes. ‘Omic’ means to ascertain all biological activities, such as genes, ions, proteins, metabolites, and transcription factors, in a sample by using high-throughput technologies as shown in Figure 1. In 1902, Professor Hans Winkler first used the Latin suffix ‘-ome’ as the genome to reveal hereditary material in chromosomes. This suffix was further used in the following years in metabolome, transcriptome, and proteome to identify biological activities. In subsequent years, omics technologies expanded with the development of new levels, including ionomics, lipidomics, and phenomics. The advancement in omics technologies has revealed new aspects for researchers to understand plant responses in abiotic stresses. In this review, we focus on the plant stress-tolerant mechanisms concerning omics approaches (transcriptomics). This review endeavors to contribute advanced knowledge to the scientific community committed to investigating abiotic stresses and their tolerant mechanisms.

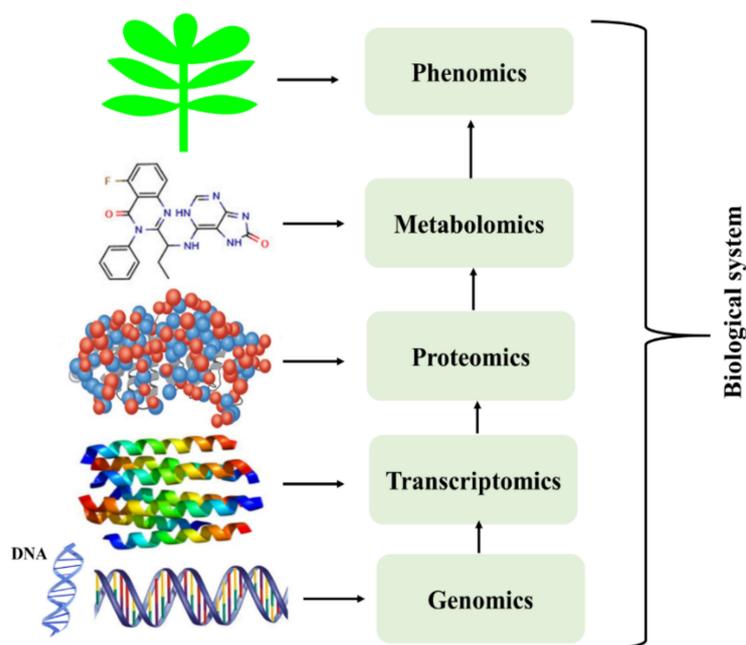


Figure 1. Omics approaches.

2. Plant Response to Abiotic Stresses: Physio-Biochemical and Molecular Perspectives

Being sessile in nature, plants are more vulnerable to abiotic stress factors, including salinity, drought, and heavy metals, which arrest their growth attributes and cause massive losses to agricultural production. Thus, improving plant tolerance potential to these extreme environmental conditions is a prerequisite and one of the key aims in crop improvement programs [25].

2.1. Drought Stress

In response to drought stress, plants re-organize their entire growth cycle and major physiological attributes, which include osmotic potential, relative water content, and transpiration, as well as leaf water potential [26]. As a result of a meagered water supply to leaves, plants progressively reduce the imperative activities of photosynthesis, which is linked to impairments in nitrogen and carbon assimilation [27].

Furthermore, impairments in the metabolism of photosynthetic pigments reduce the efficiency of chlorophylls, which have key roles in harvesting sunlight [10]. Ultimately, chloroplast structures are distorted and negatively affect the photosynthetic efficiency of plants. Under water-scarce conditions, the reduction in intercellular CO₂ diffusion to carboxylation sites (which favors the reduction in electron transport chains) is the main cause of limited CO₂ concentration, which lessens the photosynthetic rate and causes stomatal closure. Therefore, water losses due to a reduction in the intake of CO₂ can be carried out by limiting diffusion actions [27].

Water shortage leads to the unavailability of important mineral nutrients even in fertile soil, causing reduced absorbance of important nutrients leading resulting in a lower diffusion from the soil to the plants roots [28]. Under these damaging effects, roots become disorganized by losing their efficiency to take up water and nutrients, leading to a reduction in plant productivity.

A limited water supply causes an imbalance in reactive oxygen species (ROS) and the scavenging system, which mediates oxidative stress, the peroxidation of lipids and proteins, and membrane damages in the cellular organelles of plants. The elevated ROS levels govern the enhanced photorespiration by reducing the capacity of CO₂ fixation. Plants activate their internal defense system (enzymatic and non-enzymatic antioxidants) to scavenge drought stress. However, severe drought conditions restrict the efficiency of anti-

oxidative defense systems [29]. Various osmoprotectants have been reported to scavenge drought stress by maintaining turgor strength, which facilitates stomatal conductance; thus, there is a higher uptake of CO₂ in leaves and water intake by roots. The involvement of biosynthetic osmoprotectants and the regulation of various transcription factors enhance the accumulation of osmoprotectants [30].

2.2. Salinity Stress

Salt stress is one of the major constraints to the sustainability of the agriculture sector, and it limits crop production by disrupting plant physio-biochemical and molecular functions. Salt stress imposes osmotic, ionic, and secondary stressors. Salt mediates an ionic imbalance, which is a major hindrance that affects nutrient accessibility, and it enforces oxidative damage, which leads to limited water supply from roots to shoots. Salts are intruders in soil environs and actively threaten overall growth characteristics by, for example, lowering the germination percentage and growth and obstructing vegetative, development, and reproductive ontogeny [31–33].

Salt stress limits plant growth traits (leaf area, number, length/height, etc.) and biomass production and it suppresses the soluble sugar and protein levels, the rates of seed germination, and crop yield. Among the key physio-chemical processes, photosynthesis, stomatal conductance, and transpiration rates are severely affected by salt stress [34,35]. Salinity minimizes the water potential, osmotic potential, extra ROS production (abnormalities in cellular structures), and ionic homeostasis [36]. Plants respond to salt stress by the modulation of physio-biochemical, anatomical, and molecular traits; by the regulation of ionic homeostasis and antioxidant defense machinery (enzymatic and non-enzymatic antioxidants); by the synthesis of osmoregulators; and by the compartmentalization and involvement of metabolites and phytohormones. These attributes help plants to modulate osmoticum, up-regulate defense genes/proteins, tackle ionic toxicities, and scavenge the extra accumulation of ROS by salt stress [31]. Further exploration of transcriptomic, proteomic, and metabolic studies may enhance our understanding concerning the salt tolerance mechanisms in plants. Some emerging tools, such as genetic engineering, can be beneficial to produce salt-tolerant plant species.

2.3. Heavy Metal Stress

Since the industrial revolution, the natural ecosystem has been badly disrupted. The release of heavy metals from industries in a bulk amount accumulates in soil environments, which causes severe damages to the life cycle of plants. These heavy metals jeopardize a plant's functioning via different mechanisms [37–45]. Firstly, they restrict the absorption of essential nutrients at root surfaces by replacing them with toxic metal elements [1]. Secondly, they disrupt the structure of a functional protein by interacting directly with the sulfhydryl group (-SH), which inactivates its functioning [46]. Furthermore, they collapse the function of binding sites by replacing the position of essential cations. Finally, the production of ROS has been found to be devastating for macromolecules [23] and, thus, stunts plant growth. The over-accumulation of heavy metals in soil–plant systems impairs overall plant growth traits, such as plant length, biomass, leaf necrosis, and chlorosis; restricts the seed germination rates; cripples the photosynthetic apparatus; interferes with water and nutrient uptake metabolism; causes leaf senescence and DNA damages; enhances the rigidity of the cell wall; and cross-talks with biomolecules, causing alterations in the cell cycle or division. The extra accumulation of heavy metals in plant tissues overproduces ROS generation, which severely targets cellular organelles, causes the peroxidation of lipids, and impairs their functions [47,48]. Plants develop various strategies to respond and handle the abnormalities caused by heavy metals, such as the enhancement of ionic homeostasis; antioxidant enzyme activities; the accumulation of osmolytes; the induction of membrane transporters; and the biosynthesis of chaperons, chelators, complexes (phytochelatin and metallothionein), and organic acids [49]. Advances in omics technologies can help further

our understanding of the molecular characterization of the genes, proteins, and metabolites involved in enhancing the heavy metal tolerance in plants.

Furthermore, scientists are actively engaged in finding the infrastructural alterations that take place in plant morphology, physiology, and biochemical processes upon exposure to abiotic stresses. They have examined multiple behaviors and responses of plants under different types of stresses with various concentrations as shown in Figure 2. It has been demonstrated that plants, for example, sense the ability of external stress and prompt the transmission of signals into cells. The interaction between plants and abiotic stress at their highest exposure has been proven lethal. To maintain an internal cell balance to external threats, plants have to respond accordingly. Researchers think that some changes emerge at a transcriptomic level, which could be used as a learning tool to cope with these abiotic stresses.

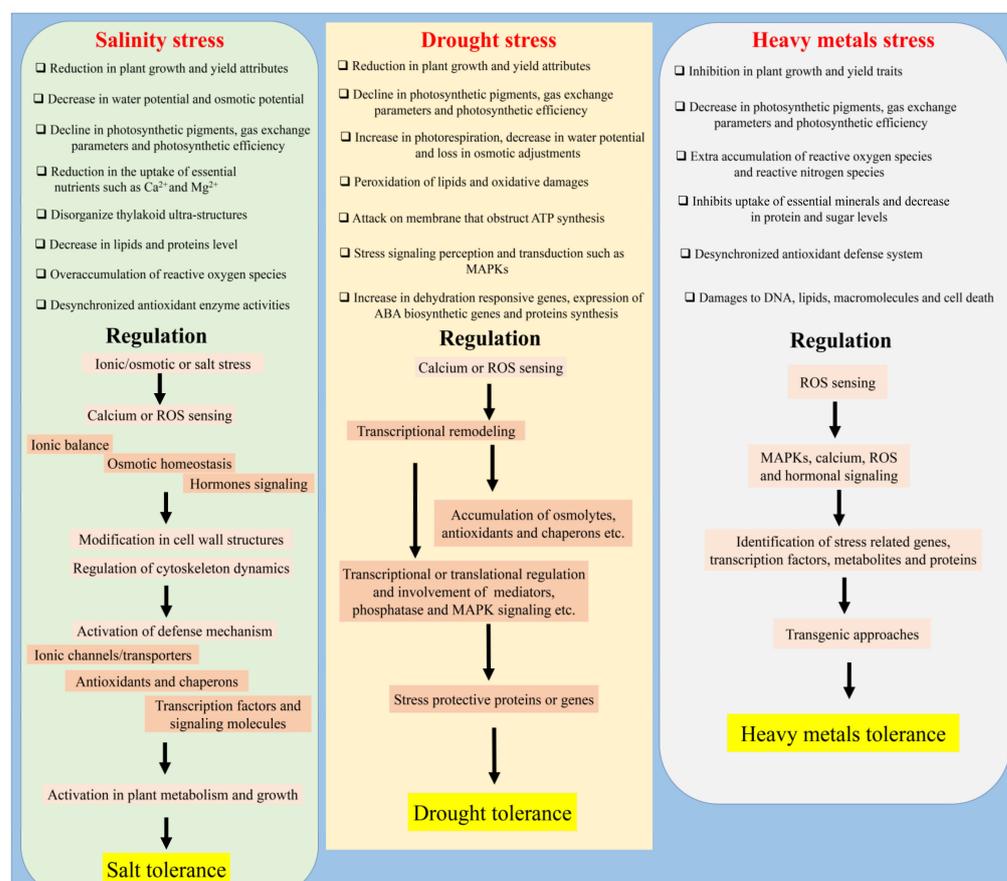


Figure 2. Schematic diagram illustrating the salt, drought, and heavy metal stress responses and their regulation to enhance plant tolerance against these environmental stressors.

3. Transcriptomics

It is a matter of great concern to understand and investigate the basic mechanisms of abiotic stress and the way of adaptation, which requires intensive research for the betterment of the scientific community [50]. The regimentation of multiple gene expression determines the plant stress tolerance ability. In plants, a set of gene expressions is induced by various stressors [51]. Moreover, they also initiate various proteins to associate the signaling pathways that deliberate the tolerant mechanism [52]. These genes are categorized into regulatory genes and functional genes. The regulatory group of genes is responsible for the encoding of several transcription factors (TFs), which actively regulate multiple stress-responsive genes in a collective and separate manner, hence forming a gene network [53]. On the contrary, the genes pertaining to the functional group are engaged in the coding

of metabolic compounds, for instance, sugar, sugar alcohols, and amines; all of these compounds actively participate in inducing stress tolerance in plants [54].

The TFs are also known as trans-acting factors, especially in the promoter region of eukaryotic genes, where they bind to cis-acting elements. Furthermore, they take part in the regulation of biochemical and physiological processes in the cell at the transcriptional level [55]. Studies based on scientific credentials indicate that a single TF is liable for handling the expression of multiple target genes through the particular binding capability of a TF with a cis-acting element of its target genes [56]. They play a very important role in signaling the transduction network and bringing the perception of stress signals, and they are further involved in the expression of stress-responsive genes [57]. Regulon (a group of genes that regulate as a unit under one regulatory protein) is interpreted as a transcriptional regulatory system, in which transcriptional factors have a DNA-binding domain that intermingles with cis-regulatory elements of its target gene promoters through the protein–protein interaction domain; this helps the other regulators to form the oligomerization of transcriptional factors [58]. Previously, a total of 3337, 2450, 1611, and 1922 transcription factors were reported in maize, sorghum, rice, and *Arabidopsis thaliana*, respectively [59].

3.1. Role of Transcriptome in Drought

Drought is considered as a major environmental stress that negatively affects crop productivity and growth [60,61]. A study revealed that non-ethylene receptor histidine kinases, such as AHK1/ATHK1, are known to have an optimistic role in regulating the abscisic acid (ABA-related) drought response; on the contrary, non-ethylene receptor kinases, also known as cytokine receptors (CKs), containing AHK2, AHK3, and CRE1, have a negative participation in drought stress [54]. Experimental results based on an analysis revealed that ATHK1 plays a constructive role against drought in both vegetative stages and seed formation, and its over-expression enhances tolerance against drought stress [62].

Furthermore, a MAPK cascade minimally composed i.e., MAP kinase kinase kinase (MAP3K, MEKK, and MAPKKK), MAP kinase kinase (MAP2K, MAPKK, MKK, and MEK) and MAP kinases (MAPKs/MPKs) [63,64]. Their activations are dependent on the phosphorylation process; as a result, phosphorylate substrates are formed in the cells that include transcription factors and proteins. The genome of *Arabidopsis thaliana* has 10 MAPKKs, 20 MAPKs, and 80 MAPKKKs [65–67]. Under drought stress, some MAPKinases were shown to be up-regulated via the transcriptional process, while others were activated post-translationally [68]. Furthermore, Chini et al. [69] demonstrated that ADR1, a CC–NBS–LRR gene (homologue of serine/threonine protein kinases), was observed to give the information about dehydration tolerance with responsive gene expression.

Similarly, another family of protein kinases includes SNF-1-like kinases, which are further classified into three families (SnRK1, SnRK2, and SnRK3). Their activations are dependent on the phosphorylation of serine or threonine [70]. In different plant species, various SNF-1-like kinases were anticipated, and they have indispensable roles concerning dehydration or ABA [71]. In *Arabidopsis*, Open Stomata1 (OST1) protein kinase is predicted and acts as a positive and negative regulator in ABA-induced stomatal closure and as a substrate of protein phosphatase 2C (PP2C) HAB1. Moreover, it is reported that the activation of OST1 is a result of the ABA-bound receptor, which inhibits protein phosphatases [72].

Furthermore, phosphatases are categorized into two main groups on the basis of substrates, namely, phosphoproteins (serine/threonine) and phosphatases (PPases). Among these mentioned categories, the role of serine/threonine PP2Cs, along with *ABI1*, *ABI2*, and *HABI*, has been found to be negative in ABA signaling. A further analysis of *ABI1* and *ABI2* mutants reported that these were present in guard cells for the activation of ABA of Ca²⁺-permeable channels requiring three steps: first, the action of *ABI1*; then, ROS production; and, finally, the action of *ABI2* [73]. The studies based on tyrosine phosphatases (PTPases) indicated that it has a crucial role in the following functions: the downstream signaling of Ca²⁺; the closing of stomata; and assisting in the process of dephosphorylation, resulting in ion flux from stomatal opening and guard cells [74].

In addition, various phospholipid-derived messengers were studied for drought tolerance, including inositol 1, 4, 5-triphosphate (IP3), phosphatidic acid (PA), and diacylglycerol (DAG) [75,76]. The most imperative secondary messenger is phospholipase D (PLD); it splits phospholipases into phosphatidic acid (PA); this contains the Ca²⁺-binding domain, which further activates phospholipase C (PLC) [76]. Furthermore, PLDs were studied to induce ABA in drought in different plant species [77,78]. Gampala et al. [79] reported that PLDs play an indispensable role in stomatal closure by interacting with ABA effectors and that they are also involved in the ABA-dependent pathway. Transgenic studies revealed that this messenger is converted to phosphatidic acid and takes part in ABA sensitivity; stomatal closure; and, ultimately, drought tolerance [80].

Simultaneously, Ca²⁺ sensors have been noted to actively participate in drought signaling [81]. The *Arabidopsis thaliana* CDPKs (AtCPK1, AtCPK10, and AtCPK34) phosphorylate both F2KP nitrate reductase (NR) peptides [82]. In *Arabidopsis thaliana*, AtCPK1 acts as a positive regulator in drought tolerance [83]. However, AtCPK10 actively takes part in ABA signaling pathways and the response to drought [84]. CDPKs are known as calcium-dependent protein kinases. Despite this, calmodulin is another Ca²⁺ sensor that is a Ca²⁺-binding protein; it is activated by increasing calcium concentration, and specific kinases are activated to modulate its concentration. Moreover, Bouche et al. [85] discovered a family of calmodulin-binding transcription activators under drought stress in *Brassica napus*. Calcineurin B-like protein (CBL) is also a Ca²⁺-binding protein. In *Arabidopsis*, 10 CBLs were identified, and, among them, CBL1 was induced by drought. Albrecht et al. [86] illustrated the supportive role of CBL1 in deliberating drought tolerance.

3.2. Role of Transcriptome in Salinity

Under saline conditions, salt stress induces the accumulation of ROS, specifically hydroxyl radical ([•]OH), which further activates ROS-NSCC and GORK potassium (K⁺) efflux channels. Moreover, a sodium (Na⁺) influx to the cytosol of the cell induces GORK channel activation [87]. However, salinity tolerance is referred to as the capability of a plant to retain cytosolic K⁺ and sequester Na⁺ in cell vacuoles or exclude it into the root. Leaf mesophyll K⁺ retention is related to overall plant salinity tolerance [88,89]. This action is carried out through the activity of K⁺ channels/transporter genes [87,90]. Plants also adjust their osmotic pressure to tolerate salinity by the up-regulation of P5CS and the down-regulation of ProDH and MYB60. P5CS1 and P5CS2 are involved in the encoding of delta1-pyrroline-5-carboxylate synthase enzymes, which regulate proline biosynthesis. These genes are expressed in stressed conditions, specifically under salt stress, while ProDH catalyzes the degradation of proline to produce glutamic acid [91,92]. Furthermore, the expression of the TAS14 gene encodes a group 2 LEA protein called dehydrin, which is induced by osmotic stress and ABA. The expression of this gene provides a long-term tolerance to drought and salinity by a reduction in osmotic potential and accumulation of sugar and K⁺ [93]. Moreover, the expression of MYB60 is directly involved in stomatal movement, regulated by ABA. Its induction apparently facilitates the stomatal opening [93,94]. Under the initial state of stress, this gene can induce root growth. In contrast, in a severe state of stress, its expression is inhibited, resulting in stomatal closure and a decrease in root growth [95]. This shows that rapid signals are generated from roots to shoots, which pre-activate the tolerant mechanism before stress is induced in plants [96,97].

In salinity stress, H₂O₂ waves are generated for rapid root-to-shoot signaling [31,98,99], resulting in the exclusion of sodium from shoots [100]. H₂O₂ and calcium are considered as universal signal molecules that are capable of transferring a stimulus after sensing [98] through OSCA hyperosmolarity-gated calcium channels and plasma membrane NADPH oxidases (NOXs) [101]. Schmidt et al. [102,103] demonstrated that the H₂O₂-mediated salt-responsive ERF1 (SERF1) transcription factor belonging to the ethylene-responsive gene class was involved in root-to-shoot signaling in rice under salinity. A misleading response can occur due to the wrong H₂O₂ wave, because it interrupts signal transduction

and the activation of genes associated with salinity signaling (SERF1 and DREB2A), turgor maintenance (P5CS2), and ion homeostasis (NHX1 and TPKb).

Goyal et al. [104] identified 77 transcription factor families, and, among them, WD-40, bZIP, PHD, MYB-HB-like, zinc finger, bHLH, CCHC (Zn), and C₂H₂ were the most abundant in salt stress. The WD-40 gene was expressed in several plants, and it improves salt tolerance in transgenic aspen hybrid *Populus* (*Populus davidiana* × *Populus bolleana*) [105], and SiWD40 in foxtail millet [106]. The over-expression of *OsMYB3R-2 MYB* and *OsMYB48-1* genes has been shown to increase salt tolerance in *Arabidopsis* and rice, respectively [31,107]. Similarly, the over-expression of GST and PODs was also reported to improve stress tolerance and play a vital role in scavenging H₂O₂ in tobacco and soybean [96,108]. Thioredoxin (Trx), peroxiredoxin (POD), and glutathione peroxidase (GPX) are involved in ROS detoxification and are also up-regulated with various stress-responsive genes, including sulfur assimilation (ATPS, APR, and AKN) [109]. The commencement of sulfate to adenosine 5'-phosphosulfate (APS) is involved in sulfur assimilation by ATP sulfurylase (ATPS), which is phosphorylated by APS kinase (AKN). Afterward, adenosine 5'-phosphosulfate (APS) is reduced to sulfite and further reduced to sulfide by APS reductase (APR). It is integrated into cysteine, which is a precursor of glutathione (GSH).

3.3. Role of Transcriptome in Heavy Metals

Research based on a transcriptome analysis of plants indicates that upon exposure to heavy metals, some induced transcriptional factors tend to regulate correlative transcriptional processes [110,111]. The first regulatory gene named FER, which was reported by Du et al. [112], was suggested to be involved in the uptake of Fe in tomato. Under Fe stress in *Arabidopsis*, FER-like deficiency-induced transcription factor (FIT), which is the functional analog of FER, was found to play a requisite role [113]. Moreover, various subgroups of the bHLH family (AtbHLH38, AtbHLH39, AtbHLH100, and AtbHLH101) are also up-regulated in *Arabidopsis* under Fe stress [114]. Yuan et al. [115] proposed that heterodimers are formed by the interaction of AtbHLH38 or AtbHLH39 with FIT. Under Fe deficient conditions, two major genes, ferrous transporters, and ferric chelate reductase significantly regulate Fe uptake. These genes are induced by transcription factors that are directly activated by heterodimers [116]. IRT1 has been demonstrated to be a crucial ferrous transporter in *Arabidopsis*. While transporting Fe under deficiency, other heavy metals, such as Zn, Co, Ni, Mn, and Cd, were also transported and accumulated [117,118].

An *Arabidopsis* transcriptomic study explained the expressions of some other transporters, which are activated by the interaction of FIT with AtbHLH38 or AtbHLH39. These transporters are iron-regulated transporter 2 (IRT2), heavy metal ATPase 3 (HMA3), and metal tolerance protein 3 (MTP3); they are involved in maintaining the concentration of Fe in Cd stress [110,119]. A transcriptome analysis of *Oryza sativa* revealed that Cd stress stimulates the myelin basic protein (MBP) kinase gene and OsMAPK2. Heavy metal stress induces the activation of different mitogen-activated protein kinases (MAPKs) [120]. Kintlová et al. [121] identified the *HvPCR2* gene in barley as one of the most responsive genes to a Cd stimulus. Li et al. [122] conducted a *Populus* × *canadensis* comparative transcriptomic study and found 35 TFs from 11 TF families in response to Cd stress, of which 16 were up-regulated while 19 were down-regulated.

One study used the alfalfa plant for the phytoremediation purpose of Ni and showed a high expression of genes related to peroxiredoxin-1C, glutathione-S-transferase (GST), and phytochelatins (PCs). These genes were linked to anti-oxidative and cell damage prevention responses, as well as Ni detoxification via their binding to PCs, forming Ni-PC complexes [123]. A transcriptomic study of weeping willow (*Salix babylonica*) revealed 2002 DGEs, of which 1165 and 837 were identified in roots and shoots, respectively. Additionally, 107 TFs were identified from DGEs, which mostly belong to the NAC and ERC families [124].

Dehydration-responsive element-binding protein (DREB) belongs to the ethylene response factor (ERF) family of TF and have been introduced in various transgenic plants,

which exhibited the tolerance against different abiotic stresses [125]. DREB is also responsible for controlling the osmotic potential, which reduces the flow of heavy metal-polluted water, hence curtailing the threats against toxic effects to plants [126]. It is important to investigate the involvement of genes and their mechanisms, as it further assists scientists in modifying plants in a genetic way to cope with such extreme environmental stresses in a better way [50,127].

4. Conclusions and Future Perspectives

Climate change and agriculture productivity are directly linked. It is the leading cause of several environmental stresses, including drought, salinity, and metal toxicity in soil and the environment. An increase in these environmental stresses is a major global concern for crop productivity and food security. The deleterious effects of these environmental stresses hamper plant physiological, biochemical, and molecular mechanisms, including ROS scavenging, metabolic energy supply, signal transduction, redox homeostasis, glycolysis, and the biosynthesis of carbohydrates and nucleotides. Moreover, increased intrusions have led to environmental contamination with a toxic concentration of heavy metals/metalloids. Furthermore, the uptake of these toxic metals/metalloids leads to their enhanced accumulation in food, which causes serious health problems in human beings. These emerging threats are devastating for global crop production; thus, a comprehensive understanding of the biological processes is required to cope with toxic metals/metalloid toxicity in the emerging technological era, and it is important to develop climate-smart plants that are adaptive to extreme environments.

In plants, the stress tolerance pattern against abiotic stress is more complex to develop and engineer as compared to biotic stress due to the involvement of various signaling pathways [128]. Therefore, the expression of a gene(s), with the combination of some proteins and metabolites, is preeminent concerning the signaling and regulatory pathways that are involved in stress tolerance. Stakeholders are continuously working to improve the genetic structure of plants and achieve significant progress; however, the complexities of the various mechanisms that are involved in stress tolerance capabilities are still under examination. With the technological advancements in operating tools and omics approaches, scientists are systematizing genetic codes into improved combinations that will be more effective against abiotic stresses. Therefore, more studies should be carried out by adopting the multidisciplinary approaches of omics technology, i.e., transcriptomics, metabolomics, and proteomics, to modify important cash crops against the future threats of abiotic stresses.

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