Chapter 4
Plant Molecular Adaptations and Strategies Under Drought Stress

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4.1 Introduction

Growth and development of plants can be significantly influenced by several environmental factors. Among them, drought is one of the main abiotic factors limiting the productivity of crops. Furthermore, as an aggravate aspect, drought is increasingly growing in dimension of severity in many regions of the world [1]. Thus, the development of crops tolerant to drought will be significantly advantageous in regions where such stress frequently occurs.

Stress is an altered physiological condition caused by factors that tend to disrupt the equilibrium of an organism. In plants, the water deficit caused by drought reduces growth and development, arising from the reduction of water content, diminished leaf water potential and turgor loss, closure of stomata, and decrease in cell enlargement and growth (Fig. 4.1a) [2]. Other effects of drought that limit plant growth and crop productivity include the reduction of photosynthesis, osmotic stress-imposed constraints on plant processes, and interference with nutrient availability as the soil dries [3].

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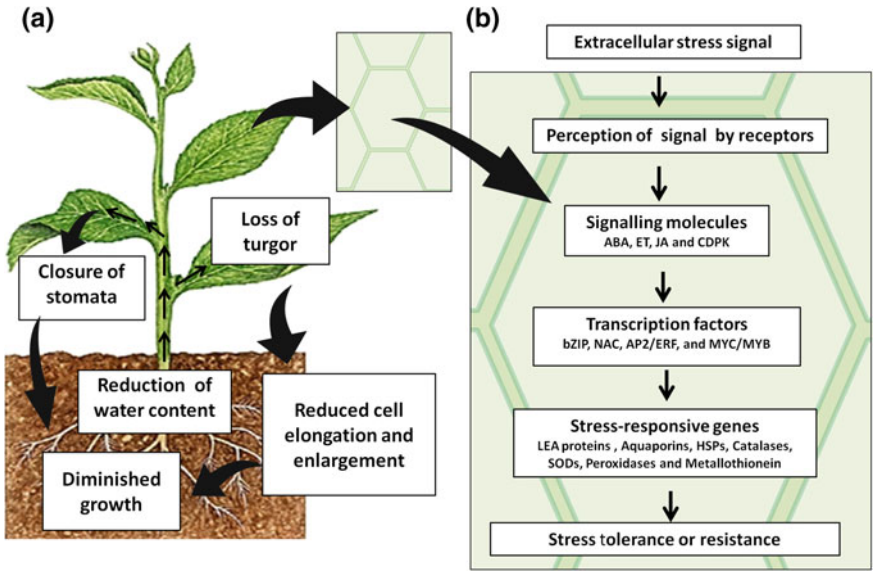

Fig. 4.1 Adaptation of plant to drought involves morphological, cellular, and molecular alterations to prevent injury to the plant. **a** Some important causes of growth reduction in plants under drought stress. **b** Molecular mechanisms that regulate the expression of stress-responsive genes of plant under abiotic stress

As a response to stress caused by diverse environmental factors the higher plants have evolved adaptive mechanisms at the physiological, cellular, and molecular levels [4]. The response of a plant to abiotic stress, first involves the perception of the extracellular stress signal by receptors of the cell, followed by many stress regulatory networks, including signal transduction and transcriptional regulation of stress-responsive gene expression that result in physiological response of tolerance or resistance of the plant to stress [3]. Thus, as depicted in Fig. 4.1b, at the molecular level the response of the plant to abiotic stress, such as drought, comprises the participation of signaling molecules such as hormones, transcription factors, and stress-responsive genes coding for proteins with protective roles against stress, including LEA proteins and peroxidases. Therefore, the elucidation of a molecular pathway for plant response to stress is essential to understanding how plants respond and adapt themselves to diverse abiotic stress.

Molecular knowledge of stress regulatory networks is likely to pave the way for engineering plants that can withstand and give satisfactory economic yield under drought stress. The specific importance to crop plants is not whether they survive stress, but whether they show significant yields under stress conditions [1, 2].

Comprehensive research has been done on identification of many molecules involved in regulatory networks of plant response to stress, such as signaling molecules (hormones, phosphatases, and protein kinases), transcription factors (bZIP, NAC, AP2/ERF, and MYB/MYC), and stress-responsive genes (LEA

proteins, aquaporins, HSPs, catalases, SODs, peroxidases, and metallothioneins; Fig. 4.1b) [5]. Furthermore, some key genes of these stress regulatory networks have been important candidates for the development of transgenic plants tolerant to drought [6].

4.2 Transcriptional Regulation of Gene Expression

According to the mechanism of plant response to stress, the stress signal is detected by the cell and transduced by different transduction components resulting ultimately in transcription of stress-responsive genes [3]. Therefore, as part of the molecular adaptive mechanisms of plants to stress, the regulation of gene expression involves changes in transcript levels of gene-coding proteins that can directly or indirectly provide stress tolerance to the plant. Stress-responsive genes with potential for engineering of plants tolerant to drought include genes coding for LEA proteins [7, 8] and aquaporins [9, 10]. The main roles of these proteins in providing drought tolerance are presented in this chapter.

It is well known that the transcriptional regulation in eukaryotic organisms involves the interaction of *cis*-acting regulatory elements that are conserved DNA sequences found in the promoter gene with regulatory proteins, also known as transcription factors. By interaction with *cis*-acting elements, these regulatory proteins can activate and/or repress the transcription of the target gene, whose product can play roles in various biological processes, including tolerance to abiotic stresses. Thus, due to essential roles of certain transcription factors in regulating downstream stress-responsive genes, their genes have also been useful in providing stress tolerance in transgenic plants [6, 11, 12, 13, 14, 15].

In addition to the binding transcription factors, some c*is*-acting regulatory elements can also act as response elements for signaling molecules of stress regulatory networks, such as hormones. An example is the ABA Response Element (ABRE), a *cis*-acting element found in the promoter gene responsive to abscisic acid (ABA), which is accumulated under osmotic stress conditions caused by drought, and has a key role in stress responses and tolerance [14, 15]. Other signaling molecules of stress regulatory networks comprise protein kinases that can regulate the activity of transcription factors by mechanisms of phosphorylation [16, 17].

Within the intricate and complex stress regulatory networks, several signaling molecules, transcription factors, and *cis*-acting elements found in drought regulons have been identified in many plants. In the last decade, *Arabidopsis thaliana*, a genetic model plant, has been extensively used for unraveling the molecular basis of stress tolerance. Arabidopsis also proved to be extremely important for assessing functions for individual stress-associated genes due to the availability of knockout mutants and its amenability for genetic transformation [4, 5, 18].

Advances have been made in the development of drought-tolerant transgenic plants, including rice, tomato, soybean, maize, barley, and Arabidopsis [6, 19, 20, 21], among others. Such genetically engineered plants have generally been developed

using gene-encoding proteins that control drought regulatory networks. Stress signaling networks in drought responses are composed of intracellular signaling systems, transcriptional regulatory complexes, and intercellular communication systems [22, 23]. These proteins include transcription factors, protein kinases, receptor-like kinases, enzymes related to osmoprotectant or plant hormone synthesis, and other regulatory or functional proteins [6]. Major transcription factor families of plants, such as bZIP, NAC, AP2/ERF, and MYC orchestrate regulatory networks underlying drought stress tolerance [5].

4.2.1 Signaling Molecules

Acclimation of plants to changes in their environment requires a new state of cellular homeostasis achieved by a delicate balance between multiple pathways. Hormones, phosphatases, and protein kinases are crucial components within the stress-induced signaling network that regulates a multitude of biochemical and physiological processes [24].

The hormone ABA is a major molecule facilitating signal transduction during drought stress response. This master ABA-responsive transcription factor regulates a diverse array of genes that coordinate cellular responses to the drought stress. Such cellular responses include stomatal closure, induction of stress proteins, and accumulation of various metabolites for the protection of cells against water-deficit stress [23, 25]. Kuromori et al. [25] have demonstrated that specific cells in vascular tissue synthesize ABA and transport the molecule to target cells. Bauer et al. [26] have proposed that ABA is autonomously synthesized in guard cells. Drought stress signals can also be propagated through ABA-independent pathways [23]. Plant genes responding to ABA contain the ABRE in their promoters. ABRE binding factors (AREB/ABF) are basic leucine zipper (bZIP) transcription factors that bind to ABREs and regulate osmotic stress tolerance in an ABA-dependent manner [14, 15].

Other hormones, such as jasmonic acid (JA) and ethylene (ET), are also involved in facilitating signal transduction during drought stress [27]. Major JA and ET signaling hubs such as Jasmonate Zim (JAZ) proteins, Constitutive Triple Response1 (CTR1), Mylocytomatosis Oncogene Homologue 2 (MYC2), Ethylene Insensitive 2 (EIN2), EIN3, and several members of the APETALA 2-Ethylene Response Factor (AP2/ERF) transcription factor gene family have complex regulatory roles during stress adaptation [6, 27, 28]. JA is implicated in promoting stomatal closure. It was proposed that drought stress prevents the conversion of precursor 12-oxo-phytodienoic acid (OPDA) to JA. OPDA then acts either independently or together with ABA to promote stomatal closure, leading to increased drought tolerance [27, 29]. In contrast, the ET has been implicated in both stomatal opening and closure [30].

Drought stress signaling can be triggered by accumulation of calcium-dependent protein kinase (CDPK). Often this process is a result of early osmotic stress-induced

Ca^{2+} spiking/oscillation, which leads to CDPK activation and drought-responsive gene transcription. Additionally, they can be a consequence of stress-responsive selective proteolysis or phospholipid hydrolysis [31]. A positive regulatory effect of CDPKs in drought stress signaling may be explained by the enhanced expression of ABA-responsive genes [32].

4.2.2 Transcription Factors

Genes induced during stress conditions not only protect cells from stress by the production of important metabolic proteins (functional proteins), but also regulate the genes for signal transduction in the stress response (regulatory proteins), such as the transcription factors (TFs). TFs are sequence-specific DNA-binding proteins able to activate and/or repress transcription. They are responsible for the selectivity in gene regulation and are often expressed in tissue-specific, development-stage–specific or via stimulus-dependent pathway. Overexpression of key TF genes has been shown to impart stress-tolerant phenotypes in several studies [6, 13, 14, 15].

4.2.2.1 AP2/ERF

The APETALA2/ethylene responsive element (AP2/ERF) superfamily is a large group of plant-specific transcription factors containing at least one DNA binding domain, named the AP2 domain and divided into three separate families, namely the ERF, AP2, and RAV families [33, 34]. This domain was first identified in the Arabidopsis homeotic gene APETALA 2 [35], and a similar domain was found in tobacco ethylene-responsive element binding proteins (EREBPs) [36].

The conserved DNA binding domain characteristic of the AP2/ERF superfamily is composed of 60 amino acid residues that confer a typical three-dimensional conformation organized into a layer of three antiparallel beta-sheets followed by a parallel alpha helix. Following a general rule, AP2-containing TFs can be roughly classified as activators or as repressors depending on whether they activate or suppress transcription of specific target genes [33].

AP2/ERF genes were identified in tobacco [37], rice [38, 39], grape [40], Arabidopsis [41], wheat [42], apple [43], and potato [44]. These genes resulted in improved tolerance against pathogen attack and osmotic stress [37], drought, low temperature, salinity [39], cold, and heat [41]. Due to their plasticity and specificity of individual members of this family, AP2/ERF transcription factors represent valuable targets for genetic engineering and breeding of crops [33].

Dehydration responsive element binding proteins (DREB2) proteins are members of the AP2/ERF family of plant-specific transcription factors. Among the eight *DREB2* genes in Arabidopsis, *DREB2A* and *DREB2B* are highly induced by drought, high salinity, and heat stress, and function as transcriptional activators in the ABA-independent pathway [6]. The yield of transgenic rice plants expressing

DREB1A under drought stress conditions was increased in comparison to the nontransgenic plants [38]. Likewise, in transgenic potato plants overexpressing *StDREB1* and *StDREB2*, the level of drought tolerance was significantly greater than in the wild-type control plant.

The results suggest that the StDREB1 and StDREB2 as AP2/ERF transcription factors may play dual roles in response to drought stress in potato [44].

4.2.2.2 bZIP

The basic leucine zipper (bZIP) is an important group of transcription factors in plants [45]. In plants, they are involved in important processes such as pathogen defense, abiotic stress signaling, hormone signaling, and energy metabolism, as well as development, including flowering, senescence, and seedling maturation [46, 47]. bZIP genes were identified in Arabidopsis [48], soybean [49], tomato [50], sorghum [51], maize [47], and rice [46].

The name of the bZIP family is derived from the basic region/leucine zipper domain found in all its members. This domain consists of an uninterrupted α-helix comprising a basic region (BR) which is necessary and sufficient to bind the DNA, followed by a C-terminal leucine zipper (LZ) motif responsible for the dimerization. The bZIP family was subdivided according to sequence similarities and functional features resulting in 10 groups. Although many bZIPs can form homodimers, bZIP members classified in different groups can be combined through heterodimerization to form specific bZIP pairs with distinct functionalities [47, 52].

About 75 members of the bZIP TFs family were identified in Arabidopsis, and they were divided into more than 10 groups. Many of the well-studied group A bZIP TFs play a central role in ABA signaling. The ABA-responsive element binding protein (AREB) subfamily of bZIPs is upregulated by drought stress. For example, the ABA responsive element (ABRE) binding proteins/factors (AREBs/ABFs) *AREB1/ABF2*, *AREB2/ABF4*, *ABF1*, and *ABF3* are mainly expressed in vegetative tissues and all except *ABF1* are key regulators of ABA signaling that respond to drought stress [53]. Overexpression of *AREB2/ABF4* or *ABF3* in Arabidopsis conferred ABA hypersensitivity, reduced transpiration, and enhanced drought tolerance [54], whereas overexpression of an activated form of *AREB1/ABF2* also showed increased ABA sensitivity and drought tolerance [55].

bZIP regulators have been explored as potential candidates for application in the improvement of drought tolerance in crops [53]. For example, the Group A TF OsABF1 from rice [50] and SlAREB from tomato [56] both enhanced tolerance to drought and salt stress. In maize, the expression level of ZmbZIP37 was increased under drought stress, implying a possible regulatory role in response to such stress [47].

4.2.2.3 MYB/MYC

The proteins of MYC/MYB families are found in both plants and animals playing many varied functions. In plants, these families participate in the ABA-dependent pathway of stress signaling for the upregulation of the abiotic stress responsive genes. Many *MYB* and *MYC* genes have been studied for their involvement in the regulation of abiotic stress response, such as drought stress [28, 57].

MYB TFs contain the MYB domain involved in DNA binding. A MYB domain is usually composed of one to three imperfect repeats, each with about 52 amino acid residues which form three α-helices; the second and the third ones are involved in the formation of a helix–turn–helix (HTH) fold [58]. MYC TFs are members of the basic helix–loop–helix (bHLH) domain that is a highly conserved amino acid motif. This motif defines these groups of transcription factors. The bHLH domain consists of 50–60 amino acids that form two distinct segments: a stretch of 10–15 predominantly basic amino acids (the basic region) and a section of roughly 40 amino acids predicted to form two amphipathic α-helices separated by a loop of variable length (the helix–loop–helix region) [59].

MYC and MYB proteins play important roles in many physiological processes under normal or stress conditions and both MYC/MYB TFs participate in the ABA-dependent pathway of stress signaling for the upregulation of the abiotic stress-responsive genes [28, 60, 61]. MYB is a large TF family in plants. There are over 198 and 183 MYB genes in *Arabidopsis* and rice, respectively, where many of them are regulated by drought [62, 63].

Katiyar et al. [62] reported that 65 % of *MYB* genes expressed in rice seedlings were differentially regulated under drought stress. In Arabidopsis, 51 % of *AtMYB* genes were upregulated by drought whereas 41 % are downregulated by such stress [62, 64].

In *Arabidopsis*, many MYB genes are responsive to abiotic stress. For example, *AtMYB2* functions in the ABA-mediated drought stress response and *AtMYB102* is a key regulatory component in responses of *Arabidopsis* to osmotic stress, salinity stress, and ABA application [65]. In addition, *AtMYB96* modulates ABA signaling in response to abiotic stresses in *Arabidopsis* [66].

The rice *OsMYB4* was reported to play a positive role in cold and drought tolerance in transgenic plants of Arabidopsis, tomato, and apple [67–69]. *OsMYB55* was shown to be involved in tolerance to high temperature through enhanced amino acid metabolism [70]. In a recent study, molecular characteristic features of *OsMYB2* have clearly been indicating its regulatory role in salt, cold, and dehydration tolerance in rice [71].

Among *MYC* genes, *MYC2* is an ABA- and drought-responsive gene and therefore earlier studies have focused on the role of MYC2 in ABA signaling. Indeed, MYC2 overexpressing plants and the myc2 mutant show increased and reduced ABA sensitivity, respectively. Furthermore, transactivation assays show that MYC2 is capable of activating the expression of the ABA response gene Responsive to Dessication22 (*RD22*), showing that MYC2 is a positive regulator of ABA signaling [72].

Transgenic plants overexpressing both MYC2 and MYB2, a drought-inducible MYB TF, showed reduced electrolyte leakage following mannitol treatment, suggesting that MYC2 can contribute to stress tolerance [72]. In contrast, a recent study found an increased drought tolerance in the myc2 mutant based on smaller relative biomass reduction observed under drought conditions than in wild-type plants [73]. Therefore, the role of MYC2 in abiotic stress tolerance is not as conclusive as its role in ABA signaling [28]

4.2.2.4 NAC

The NAC family of plant-specific TFs is one of the largest in the plant genome [74]. The NAC transcription factor contains a highly conserved N-terminal DNA-binding domain and a diversified C-terminal domain [75] and based on the motif distribution, the NAC domain can be further divided into five subdomains (A–E) [76]. The NAC domain was originally characterized from consensus sequences from petunia NAM and Arabidopsis ATAF1, ATAF2, and CUC2. Therefore, NAC was derived from the names of the first three described TFs containing the NAC domain, namely no apical meristem (NAM), ATAF1-2, and cup-shaped cotyledon (CUC2) [77].

NAC family genes have been identified by genome-wide analysis from various plant species, such as Arabidopsis [76], rice [78], poplar [79], and soybean [80]. NAC proteins play essential roles in diverse aspects of plant development, such as pattern formation in embryos [81] and lateral root development [82]. The NAC TFs function as important components in complex signaling progresses during plant stress responses. Considering the relatively large number of NAC TFs from different plants and their unknown and diverse roles under complex environmental stimuli, it remains a considerable challenge to uncover their roles in abiotic stress [83].

There is increasing evidence demonstrating that NAC family transcription factors are involved in responses to various biotic and abiotic stresses, including drought, salinity, cold, bacterial and fungal pathogens, and low-oxygen stress [83, 84]. The expression of three Arabidopsis NAC genes, *ANAC019*, *ANAC055*, and *ANAC072 (RD26)*, was induced by drought, high salinity, and ABA, respectively. Overexpression of these three genes remarkably enhances tolerance to drought stress [85].

Others Arabidopsis NAC genes, such as *ATAF1* (*ANAC002*) and *ATAF2* (*ANAC081*), together with *ANAC102* and *ANAC032* were phylogenetically classified into a small subfamily (ATAF) [76, 86]. *ATAF1* was initially reported to play a negative role in response to drought stress by functional analysis of *ataf1* null mutants [87]. However, studies reported by [88] showed that the overexpression of *ATAF1* conferred an enhanced drought tolerance, revealing a positive role of *ATAF1* in plant drought response.

Understanding the complex mechanism of drought and salinity tolerance is important for agriculture production. Many *NAC* genes have been shown to be

involved in plant responses to drought and salinity stress. In transgenic rice, the *Os01g66120/OsNAC2/6* and *Os11g03300/OsNAC10* genes were found to enhance drought and salt tolerance [16, 89], and *Os03g60080/SNAC1* increased grain yield (21–34 %) under drought stress [90].

Plant response to abiotic stresses is via both ABA-dependent and ABA-independent signal transduction pathways, where ABA can act as a signaling molecule of regulatory networks of plant response to stress. Arabidopsis overexpressing *MlNAC5* exhibited hypersensitivity to exogenous ABA and enhanced tolerance to dehydration stress. A higher ABA sensitivity may stimulate stomatal closure to retain water and increase drought tolerance in plants [91], as was found in Arabidopsis and maize [88, 92].

Much progress in NAC TF functional research has been attained over the past decade. However, most of these advances are related to the involvement of biotic stress. Thus, the identification of NAC functions in biotic and abiotic stresses will remain a substantial challenge in the coming years.

4.3 Drought-Responsive Genes

4.3.1 Late Embryogenesis Abundant Proteins

A class of proteins widely involved in plant response to drought is called late embryogenesis abundant (LEA) proteins, first discovered in late stages of embryo development in plant seeds [93]. Under dissection conditions, there is an improved accumulation of mRNA molecules coding for LEA [94]. The increase of this expression is correlated to an improvement in abscisic acid levels, whose induction is associated with increased drought tolerance [95].

LEA proteins are members of a large group of glycine-rich proteins that act in ion sequestration [96]. There are several groups of LEA proteins distributed through different classifications based mainly on different motifs present in the amino acid sequence of each protein [97, 98]. In *Arabidopsis thaliana*, 51 genes encoding LEA proteins clustered into nine families [99].

LEA proteins are mainly low molecular weight (10–30 kDa) proteins and are mainly composed of hydrophilic amino acids ordered in repeated sequence (e.g., Gly and Lys) in higher plants, forming hyperhydrophilic domains and allowing thermal stability [100]. Most LEA proteins are randomly coiled in solution, cytoplasmic, and hydrophilic proteins [97], although some called atypical present a preponderance of hydrophobic content. These proteins may also be included in the group of intrinsically disordered proteins [101].

The differential expression of genes coding for LEA proteins in response to drought has been reported in several species of plants [102–104]. Furthermore, studies have detected overexpression of the LEA protein contributes to the resistance of *E. coli* cells against drought [105, 106].

Changes in conformation of these proteins have been reported at the cellular level, considering increased expression of LEA proteins under dehydrating conditions [107, 108]. Other reports have assessed their role in water retention as hydration buffers [109], as molecular chaperone [110], in the protection of cell membrane [111, 112], and sequestration of reactive oxygen species [113]. The heat tolerance is a common feature of all proteins of this family [105]. Several in vitro studies have shown activity of the LEA proteins in protecting other enzymes against dissecting-induced aggregation [114–116].

The role of LEA protein expression in generating drought-tolerant plants has also been ratified. For instance, [8] verified the role of LEA protein in water-stress protection by overexpression of the *HVA1* gene from barley into rice plants. In this study, an increase of growth rate stability under conditions of water deficit was detected in transgenic plants, as well as better recovery of growth, compared to control plants. Also in rice, the *OsLEA3-1* gene was overexpressed in lineages at field conditions, which had higher grain yield than the wild-type under drought stress [7]. A higher survival rate in transgenic *Arabidopsis* plants for *BnLEA4-1* gene [117] was also observed, and the expression of the *TaLEA* gene improved cell membrane protection in transgenic poplar [118].

Transgenic plants of *Salvia miltiorrhiza* overexpressing the *SmLEA* gene showed reduction of water loss under dehydrating conditions [106]. Overexpression of the *SiLEA14* gene of foxtail millet improved resistance to osmotic stress, as well as contributed to the increase of free proline and soluble sugar content, which are metabolites related to defense against water stress in plants [119]. Under conditions of drought stress, [120] observed that, compared to control plants, Arabidopsis transgenic plants overexpressing the *JcLEA* gene had higher relative water content and less damage to the cell membrane, as well as a higher increase in glucose accumulation, which contributed to the stability of the internal milieu of the plant cells.

These results demonstrate that the prospecting of genes coding for LEA proteins is fundamental to better understanding of endogenous mechanisms of plant defense against dehydration conditions and molecular breeding.

4.3.2 Aquaporins

The protein family called major intrinsic (MIP) includes aquaporins that constitute a family of proteins that act to regulate the movement of water through intracellular and plasma membranes of plants and animals. Aquaporins may also be referred to as water channels and contribute to the translocation of water molecules [121, 122], as well as solutes (urea, boric acid, and silicic acid) and gases (ammonia and carbon dioxide) [123].

These proteins are expressed in nearly all plant tissues and their high expression occurs in organ development and contributes to the maintenance of cell turgidity [124]. The activity of aquaporins in membranes and the change of their abundance

can control the rate of water transport along the transcellular pathway, influencing the movement of guard cells or cell expansion [125].

There are five existing subgroups for aquaporins, which vary according to cell location: plasma membrane intrinsic proteins (PIP), vacuolar membrane (tonoplast) intrinsic proteins (TIP) [126], nodulin-26–like intrinsic membrane proteins (NIPs), small basic intrinsic proteins (SIPs) [127], and the X intrinsic proteins (XIPs) [128].

The aquaporins' molecular weight ranges from 21 to 34 kDa, consisting of six membrane-spanning α-helices connected by five loops (A to E) and N- and C-termini facing the cytosol [129]. Several studies performed thus far have reported the important role of aquaporins in response to drought in plants. For instance, Xu et al. [130, 131] demonstrated that TaTIP2;2 acts as a negative regulator of salinity and drought stress. Moreover, these authors observed the response of this protein is independent of abscisic acid, in accordance with the expression of other TIP proteins, whose expression is generally not induced by hormonal regulation.

According to Khan et al. [132], the overexpression of JcPIP2;7 might help in faster water uptake through outer water channels, leading to faster imbibition thus accelerating germination even under normal conditions. The JcTIP1;3 probably is internally localized to the vacuolar membrane. Thus, as with other TIPS, such protein functions more in maintaining cell turgidity and might interact intricately with the cellular developmental and stress signaling machinery.

Li et al. [60, 61] observed through *GoPIP1* overexpression that the protein GoPIP1 could modify the water movement, changing the stomatal aperture (faster water loss through leaves). Therefore, its overexpression had a negative impact on plant growth under drought stress, supporting the proposition that, under drought stress, a general increase in water transport is harmful in most plant tissues and cells, as observed for studies reporting overexpression of other aquaporins [133, 134].

On the other hand, Lian et al. [9] detected that, compared to the wild-type plant, the transgenic lowland rice (overexpressing the RWC3 aquaporin) exhibited higher root osmotic hydraulic conductivity, leaf water potential, and relative cumulative transpiration, improving drought tolerance and corroborating other studies reporting aquaporins upregulate drought tolerance [135–137].

Zhou et al. [10] verified that *TaAQP7* generates an increase in drought stress tolerance in transgenic tobacco by improving the ability to retain water, reduce reactive oxygen species accumulation and membrane damage, and enhance the antioxidants' activities. In *Arabidopsis thaliana,* [138] detected that MaPIP1;1 contributed to increased drought tolerance associated with decreased membrane injury and improved osmotic adjustment (MaPIP1;1-overexpressing transgenic plants have maintained higher levels of proline).

The information presented above confirms the importance of studies related to aquaporins, which are essential for plant breeding focused in the maintenance of water balance in plants.

4.3.3 Heat Shock Proteins

Heat shock proteins (HSPs), also known as heat stress proteins, were identified initially in response to high temperatures and are present in prokaryotes and eukaryotes. The increased expression of HSPs is related to defense mechanisms against injuries caused by dehydration, as the decrease in cellular volume that promotes the crowding of cytoplasmic components. This crowding generates an increase of molecular interactions that can cause protein denaturation and membrane fusion [139].

The association of HSPs with membranes can contribute to drought-induced changes in cellular architecture and help in the maintenance of normal membrane-associated processes during drought stress [140, 141]. It is known that, at the cellular level, these proteins respond to various stresses and act in normal cells as molecular chaperones. This role was confirmed by means of heterologous expression in *E. coli* and subsequent purification of recombinant protein, [142–144]. Thus, HSPs contribute to reducing the impact of protein denaturing conditions and contribute to the maintenance and/or restoration of protein structure and its homeostasis [145].

According to the molecular weight (15–42 kDa), there are five major families of HSPs: the Hsp70 (DnaK), chaperonins (GroEL and Hsp60), the Hsp90, the Hsp100 (Clp), and the small Hsp (sHSP) family [146]. Studies have shown differential expression in response to drought for HSPs of different molecular weights [104, 123, 147]. There is a significant increase in induction of HSP expression when there is a combination of different stresses, such as the combined effect of drought and high temperature [148].

The regulation of genes encoding HSPs is strongly related to the heat stress transcription factors (HSTF). The overexpression of genes coding for these transcription factors have been reported to induce drought resistance in transformed plants [11, 12]. These regulatory proteins are usually located in the cytoplasm, where they are found inactivated. The activation takes place by means of stress conditions and consequent oligomerization, as well as recompartmentation to the nucleus. This enables the occurrence of binding to promoter sequences of genes encoding HSPs [149].

Several studies have reported the widespread importance of HSP expression in response to drought. Sun et al. [150] and Cho and Hong [151] verified that AtHSP16.6A and NtHSP70-1, respectively, can participate in the regulation of water flow during drought. Moreover, Sato and Yokoya [141] detected that rice transgenic seedlings with higher expression levels of sHSP17.7 showed growth recovery potential after submission to drought.

In addition, *GHSP26* gene product might act as a factor in the signal transduction pathway of a drought stress response from the nature of early induction [140]. In *Arabidopsis thaliana*, Zhang et al. [136, 137] verified that ectopic expression of cytosolic sHSP 17.1 generated more biomass and less water loss, as

well as flowered earlier and recovered more quickly and robustly after being rewatered.

Recently, it was found that in transgenic sugarcane plants overexpressing the EaHSP70 protein there was a drastic increase (2000-fold or more) in the upregulation of the HSP70 gene compared to the control plants. In this study, in addition to increased tolerance to drought, the upregulation of abiotic stress-responsive genes (DREB2, DNA helicase 45, LEA, RD29, ERD, ERF, Cor15, and BRICK) was more than 100-fold in each transgenic event when compared to control plants. Thus, the authors suggest that the expression of these genes might be one of the reasons for its enhanced drought tolerance [152].

4.4 Molecules with Antioxidative Activity (Protection Against ROS)

Drought stress drastically affects various physiological traits in plants. It is known that the downregulation of photosynthesis due to drought stress is mainly the result of a reduction in stomatal conductance, although the photosynthetic apparatus is not significantly affected [153]. It is generally observed from the first stages of water shortage due to limited CO_2 diffusion through stomata. The limitation of CO_2 assimilation in water-stressed plants causes the overreduction of the photosynthetic electron chain. Consequently, plants are exposed to an excess of light energy that leaves cannot dissipate and which cannot be converted into biochemical energy. Then there is a redirection of photon energy and that leads to the production of reactive oxygen species (ROS) and finally to a substantial oxidative damage [154, 155]. This state is so-called oxidative stress.

ROS are partially reduced forms of atmospheric oxygen and under normal conditions their production in plant cells is tightly controlled by the scavenging system [156]. The main ROS are superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (OH^-), and singlet oxygen (O). They are present in all plant cells because of aerobic lifestyle [157, 158].

In plant cells chloroplasts, mitochondria, and peroxisomes are important intracellular generators of ROS. It is now widely accepted that the production of these species at a higher level results in a loss of balance between the production ROS and their removal [159, 160]. If not effectively and rapidly removed from plants, excessive levels of ROS are responsible for various stress-induced damages to macromolecules and cellular structure including RNA and DNA damage, enzyme inhibition, protein oxidation, membrane lipid peroxidation, and ultimately cell death. Then, their scavenging is necessary to protect the subcellular components and for maintenance of normal growth and development [154, 157, 160, 161, 162].

Plants have evolved a complex system of antioxidant molecules to prevent oxidative injury. The antioxidant defense mechanism plays an important role by delaying or preventing the oxidation of cellular oxidable substrates. Antioxidants

exert their effects by scavenging ROS, activating a battery of detoxifying proteins, or preventing the generation of ROS [157]. This network is composed of over 150 genes encoding ROS-producing proteins, with enzymatic and nonenzymatic molecules [163]. The well-known enzymatic antioxidants comprise superoxide dismutase (SOD), catalase (CAT), and peroxidases (glutathione peroxidases, GPX; ascorbate peroxidase, APX). These enzymes are present in practically all subcellular compartments. Usually, an organelle has more than one enzyme able to scavenge a single ROS [164]. Furthermore, they also possess numerous low molecular weight antioxidant nonenzymatic compounds. Glutathione, flavonoids, alkaloids, carotenoids, and polyamines are the main nonenzymatic components [154, 155, 157, 160, 161, 165]. Together, all these molecules act as the main defense against ROS produced in various parts of plant cells [162].

The extent of oxidative stress in a cell is determined by the amounts of superoxide, H_2O_2, and hydroxyl radicals. Therefore, the balance of SOD, APX, and CAT activities will be crucial for suppressing toxic ROS levels in a cell. Changing the balance of scavenging enzymes will induce compensatory mechanisms. For example, when CAT activity was reduced in plants, scavenging enzymes such as APX and GPX were upregulated. Unexpected effects can also occur. When compared to plants with suppressed CAT, plants lacking both APX and CAT were less sensitive to oxidative stress [158, 166].

However, it is known that ROS also act as signaling molecules that can trigger cell responses. In this context, focus has been on H_2O_2, the most stable ROS. H_2O_2 generated in chloroplasts can function directly as a signaling agent. To act in this function, H_2O_2 must be able to rise rapidly to a threshold concentration and remain high enough for a sufficient time so that it can oxidize the molecules involved in the cell-signaling events. Then enzymes that scavenge ROS must play two roles: in an active state, they keep ROS concentrations at safe levels. In a deactivated state, ROS concentrations reach critical levels for activation of signaling components [167].

4.4.1 Enzymatic Molecules

4.4.1.1 Superoxide Dismutase

Superoxide dismutases belong to a family of metalloenzymes that protect cells from the harmful effects of superoxide radical (O_2^-) by catalyzing its dismutation into molecular oxygen and hydrogen peroxide (H_2O_2) [168, 169]. Depending on the metal in their active site, SODs are classified into four groups: CuZnSODs, NiSODs, FeSODs, and MnSODs. Each SOD group displays a distinct subcellular distribution and structural features [170, 171].

They are important for early metabolic cellular defense, acting as the first line of defense against ROS. The resultant H_2O_2 can be detoxified to oxygen and water by CAT or APX, which occur mainly in peroxisomes [130, 131, 153]. The balance

between SODs and the different H_2O_2-scavenging enzymes in cells is considered to be crucial in determining the steady-state level of O_2^- and H_2O_2. This balance, together with the sequestering of metal ions by ferritin and other metal-binding proteins, prevents the formation of the highly toxic HO radical [165].

Recent studies have demonstrated the main role of different SODs under drought conditions. In *Pennisetum glaucum,* different abiotic stresses were able to induce a CuZnSOD. In addition, when expressed in bacteria, it conferred enhanced tolerance to oxidative stress [172]. Under salinity stress, *Arabidopsis* increased the expression of two FeSODs [173]. Sales et al. [174], studying sugarcane plants, observed that SOD improves the metabolism of plants subjected to water deficit. In transgenic plums with the overexpression of CuZnSOD, the tolerance to salt and drought stress was enhanced [175].

Some studies reported to SODs a role against structural damages. The overexpression of CuZnSOD in transgenic tobacco improved tolerance against drought stress, alleviating the cellular and tissue damages produced by water stress conditions [176]. Shafi et al. [177] reported in *Arabidopsis* that the expression of CuZnSOD genes positively regulates secondary cell wall biosynthesis and promotes plant growth and yield under salt stress, showing the importance of SOD to the development of plants under stress conditions. Ambiguous results were also reported. Drought stress triggered in Arabidopsis a downregulation of CuZnSODs, but an upregulation of FeSODs [171].

4.4.1.2 Catalases

Catalases (H_2O_2 oxidoreductase; CAT) are tetrameric heme-containing enzymes, mostly localized in peroxisomes that are bound by a single membrane and contain hydrogen peroxide-generating oxidases. They are also localized in glyoxysomes and mitochondria and are apparently absent in the chloroplast. They serve as efficient scavengers of ROS, mainly in the removal of excessive H_2O_2 generated during developmental processes or by environmental stimuli into water and oxygen in all aerobic organisms [162, 178]. Catalases play an important role in biotic/abiotic stress, to avoid oxidative damage. Plant catalases are composed of a multigene family and have been reported in many plant species [179]. Plant peroxisomal proteins including catalases require particular peroxisomal targeting signal (PTS) for import into peroxisomes. The catalase activity levels is inversely correlated with the cellular H_2O_2 amounts of plants [178].

There are two main routes for H_2O_2 metabolism in cells: its removal by peroxidases and by catalases. Peroxidases require a small reducing molecule to act as a regenerating cofactor. On the other hand, catalases mainly catalyze a dismutation reaction in which a first oxidizing molecule of H_2O_2 is transformed to water and a second reducing H_2O_2 is then converted to O_2. Thus, no additional reductant is required. Catalases are encoded by three genes [172].

Considering the key role of CAT in photorespiration, many authors focused on the role of the CAT catalysis pathway under both drought and salt stress. Indeed,

the maintenance of CAT activity in leaves of drought-stressed plants likely allowed the removal of photorespiratory H_2O_2 produced when plants were subjected to the water deficit of salinity [175].

Transgenic plants expressing CAT had increased tolerance against drought stress. However, studies have reported that the expression of either SOD or CAT alone led to no change in response to drought stress. These contradictory findings may be due to the complex network of plant antioxidant defenses and raise the possibility that a higher tolerance to oxidative stress might be achieved by pyramiding or stacking genes in a single genotype. The antioxidant effects of the two enzymes are directly linked through their converting superoxide to H_2O_2 and H_2O_2 to oxygen and water, sequentially [130, 131]. The combination of the two upregulated genes was reported as improving the drought stress responses. In cassava, the removal of ROS was enhanced by overproduction of both CAT and CuZnSOD, delaying the postharvest physiological deterioration of storage roots [130, 131].

In potato, the single overexpression of a catalase controlled the H_2O_2 levels and delayed the leaf senescence (related to oxidative damage) [178]. The catalase induction can also be triggered by other abiotic stresses, such as heavy metal and hyperosmotic stresses, as shown by [179].

On the other hand, low levels of catalases allow the accumulation of H_2O_2 in cells. Michelet et al. [167], working with knockdown mutants of *Chlamydomonas reinhardtii*, downregulated catalase activity and reported high levels of H_2O_2. For the authors, this concentration seems to be necessary to activate H_2O_2-dependent signaling pathways stimulating the expression of H_2O_2 responsive genes. However, high levels of H_2O_2 cannot be maintained for long periods, because the deficiency in catalases can also promote cell death, as reported by [180] in *Arabidopsis*.

4.4.1.3 Peroxidases

Plant peroxidases can be grouped into three classes based on their structural and catalytic properties. Class I peroxidases include intracellular enzymes, such as microbial cytochrome C peroxidase, bacterial catalase-peroxidases, and APX in plants, bacteria, and yeast. Class II peroxidases, including lignin peroxidase, are extracellular fungal peroxidases. Class III peroxidases are secreted into the cell wall or the surrounding medium and the vacuole [181].

In the complexity of the regulation network of plant antioxidant defenses, APX is an antioxidant enzyme that plays a key role in drought stress responses and following recovery from drought [175]. They are found in higher plants, chlorophytes, red algae, and members of the protist kingdom [164]. They have multiple locations and are among the most important key enzymes that scavenge potentially harmful H_2O_2 from the chloroplasts and cytosol of plant cells [176]. There are two main isoforms: APX1 and APX2. APX1 is constitutively expressed in roots, leaves, stems, and other plant tissues, and its expression is significantly upregulated in response to a large number of biotic and abiotic stresses [163]. APX2 is also involved in the response of plants to abiotic stress. Expression of APX2 is almost

undetected in many plant tissues and is significantly upregulated in roots in response to wounding and oxidative stress and in roots and shoots in response to salinity and osmotic stress [163]. The main hydrogen peroxide-detoxification system in plant chloroplasts is the ascorbate–glutathione (ASC–GSH) cycle, in which APX is a key enzyme. APX utilizes AsA as specific electron donor to reduce H_2O_2 to water [164].

The ROS-scavenging enzymes in plants have been widely studied and the results have demonstrated that, in response to environmental stress, APX activity generally increases along with other enzyme activities, such as CAT and SOD. In addition, the balance of APX, GPX, and CAT activities, representing the main enzymatic H_2O_2 scavenging mechanism in plants, is crucial for the suppression of toxic H_2O_2 levels in a cell. As reported above, the enzymes APX, GPX, and CAT are able to scavenge H_2O_2 with different mechanisms. If the balance of scavenging enzymes changes, compensatory mechanisms are induced (i.e., APX and GPX are upregulated when CAT activity is reduced in plants) [162, 175]. Weisany et al. [162] reported in soybean that abiotic stresses, such as salinity and drought, could increase the production of both enzymes: CAT and peroxidases (APX and POD).

In transgenic plums with the overexpression of APX, the tolerance to salt and drought stress was enhanced (Xing et al. 2015). Sales et al. [174], studying sugarcane plants, observed that APX improves the metabolism of plants subjected to water deficit. In *Arabidopsis*, [163] showed that deficiency in APX2 resulted in a decreased tolerance to light stress, which is related to drought stress. Also, these plants produced more seeds under heat and drought stresses, suggesting the activation of protection mechanisms of reproductive tissues from heat and drought damage. Some peroxidases are strongly induced by both abiotic and biotic stresses. Choi and Hwang [181] reported it in *Capsicum annuum*: PO2 was induced by drought, salt, cold, and infection by a fungal pathogen. Plants without PO2 were more susceptible to these stresses. In *Arabidopsis*, when the peroxidase was overexpressed, the plants were more tolerant to all stresses.

On the other hand, in wheat, different isoforms can be expressed in different levels under abiotic stress (up- and downregulated), as well the same isoform can also be differentially regulated in different wheat genotypes [182].

4.4.2 Nonenzymatic Molecules

4.4.2.1 Glutathione

Glutathione (γ-glutamyl cysteinyl glycine) is an abundant, ubiquitous, and main low molecular weight thiol in all aerobic organisms. The presence of cysteine confers its biological properties mainly as antioxidant function through its involvement in cell redox homeostasis [183, 184]. It is a tripeptide constituted of glutamate (Glu), cysteine (Cys), and glycine (Gly), and is represented by the formula g–Glu–Cys–Gly. GSH exists either in a reduced form (GSH) with a free thiol

group or in an oxidized form (GSSG) with a disulfide between two identical molecules. The presence of Cys in the chemical reactivity and high water solubility of the thiol (-SH) group of GSH confer its biological properties and make it a crucial metabolite to perform multiple functions including growth, development, and plant responses to drought stress [185, 186]. GSHs also function with GSTs to detoxify a range of herbicides by tagging electrophilic compounds for removal during oxidative stress [178]. Among the nonenzymatic antioxidants, GSH is considered the most important intracellular defense against ROS and/or their reaction products-induced oxidative damage in plants [187].

It has long been recognized that GSH is oxidized by ROS as part of the antioxidant barrier that prevents excessive oxidation of sensitive cellular components. Unlike the oxidized forms of many other primary and secondary metabolites that can also react with ROS, GSSG is rapidly recycled by the glutathione reductases (GRs) in key organelles and the cytosol. A main characteristic of glutathione is its high concentration in relation to other cellular thiols. In general, glutathione accumulates to millimolar concentrations, with tissue contents well in excess of free cysteine. A second key characteristic of the glutathione is its high reduction state. In the absence of abiotic stresses, tissues maintain measurable GSH [184].

Plants of *Arabidopsis* treated with GSH showed more tolerance to drought stress [178]. On the other hand, when a GR gene (the GSH recycler) is not expressing, plants increase their sensitivity to abiotic stress, as reported by Wu et al. [188]. Also, GSH has supplemental functions in plants. Ramírez et al. [189] showed its protective role against iron deficiency in the same above-mentioned species.

4.4.2.2 Flavonoids

Flavonoids are a vast class of plant polyphenolic secondary metabolites encompassing more than 10,000 structures, showing a common three-ring chemical structure (C6–C3–C6). The main classes of flavonoids are anthocyanins (red to purple pigments), flavonols (colorless to pale yellow pigments), flavanols (colorless pigments that become brown after oxidation), and proanthocyanidins (PAs) or condensed tannins. These compounds are widely distributed in different amounts, according to the plant species, organ, developmental stage, and growth conditions [190]. The multiplicity of the functional roles of flavonoids in plant–environment interactions is consistent with their presence in a wide array of cells and subcellular compartments [191].

Flavonoids have the capacity to absorb the most energetic solar wavelengths (i.e., UV-B and UV-A), inhibit the generation of ROS, and then quench them once they are formed [192]. There is evidence corroborating the hypothesis that they have antioxidant functions in higher plants that are challenged with a range of environmental stresses, constituting a secondary ROS-scavenging system in plants suffering from severe excess excitation energy to the photosynthetic apparatus [191, 193] and also preventing the generation of ROS [190].

The biosynthesis of flavonoids is upregulated as a consequence of UV radiation and in response to a wide range of other abiotic and biotic stresses, ranging from nitrogen/phosphorus depletion to salinity/drought stress [194]. For instance, Agati et al. [191] have reported that root-zone salinity stress had a very similar effect on flavonoid metabolism to that exerted by UV radiation in *Ligustrum vulgare*. This shows that flavonoid pathway genes (*FLS*-flavonol synthase and *F3'H*-flavonoid 3′-hydroxylase) are also upregulated under salt/drought stress conditions.

The biosynthesis of antioxidant flavonoids increases more in stress-sensitive species than in stress-tolerant species; stress-sensitive species present a less effective first line of defense against ROS under stressful conditions and are subsequently exposed to a more severe "oxidative stress" [191].

Some studies have shown the antioxidant function of flavonoids. It was reported in wheat leaves that the expression of flavonoid biosynthesis genes and accumulation of flavonoid in response to drought stress improve the stress tolerance [195]. In addition, flavonoids with radical scavenging activity mitigate against oxidative and drought stress in *Arabidopsis thaliana* [196].

4.4.2.3 Carotenoids

Carotenoids are isoprenoids containing 40 carbon atoms and 3–13 conjugated double bonds in their skeleton [197]. They are synthesized by photosynthetic organisms and some nonphotosynthetic bacteria and fungi. In plants, they are synthesized in plastids, where they play different functions [198]. Carotenoids such as b-carotene, lycopene, and lutein are important in the food and oil industries because of their powerful antioxidant activities [199].

They play a main dual role in photosynthetic organisms: first, they serve as accessory pigments in the photosystems, increasing light absorption in the blue spectral domain (420–500 nm). Carotenoids are synthesized in plastids and accumulate as red, orange, and yellow pigments in flowers, fruit, and roots [197, 199]. Second, they protect the photosynthetic apparatus against toxic ROS produced by plant abiotic stresses, especially singlet oxygen ($^1O_2$), being considered to be the first line of defense of plants against O_2 toxicity. The second occurs either via a physical mechanism involving thermal energy dissipation or via a chemical mechanism involving direct oxidation of the carotenoid molecule. The latter mechanism can produce a variety of products (aldehydes, ketones, endoperoxides, and lactones) resulting from their direct oxidation by O_2, all being potential antioxidant candidates [197, 200].

One such molecule, the volatile β-carotene derivative β-cyclocitral, triggers changes in the expression of $^1O_2$-responsive genes and leads to an enhancement of photo-oxidative stress tolerance [197]. Additional protective functions of carotenoids include stabilization of membrane lipid bilayers, scavenging of free radicals and protection against membrane lipid peroxidation [201].

In sweet potato, the expression of the *Or* gene, responsible for the accumulation of carotenoids, increased in response to abiotic stress. Also, plants transformed with this gene exhibited increased antioxidant activity, showing the possible role of carotenoids in oxidative stress [199]. In *Arabidopsis*, oxidative stress induces the oxidation of carotenoids, and its products change the expression of many responsive genes to this kind of stress, increasing the tolerance of these plants [197].

Ruiz-Sola et al. [198], studying *Arabidopsis*, reported that the presence of high concentrations of salt in the growth medium rapidly triggers a root-specific activation of the carotenoid pathway. It shows the probable participation of carotenoid molecules in salt/drought stress. Finally, in *Brassica rapa* and *Brassica oleracea*, enzymes involved in carotenoid oxygenase (a key enzyme involved in the metabolism of carotenoids) pathways may be activated as multifunctional stress signaling factors under abiotic stress treatment conditions [199].

4.4.2.4 Polyamines

Polyamines (PAs) are essential solute compounds for cell survival. They are small, flexible, organic polycationic compounds of low molecular weight that are present in almost all cells and most living organisms, except some archaeal methanogens and halophiles [202]. PAs are present in all compartments of the plant cell, including the nucleus. The main PAs are: diamine putrescine (Put), triamine spermidine (Spd), tetramines spermine (Spm), and its isomer thermosspermine (tSpm). They can all be found in free and conjugated forms [203].

PAs have key roles in a variety of regulatory and cellular processes such as cell division and elongation, root growth, flower and fruit development, replication, transcription, translation, membrane and cell wall stabilization, chromatin organization, ribosome biogenesis, and programmed cell death [204]. Current evidence points to the occurrence of intricate crosstalk between polyamines, stress hormones, and other metabolic pathways required for their function. The identification of molecular mechanisms suggests that some PAs conjugate to hydroxycinnamic acids, and the products of PA oxidation (hydrogen peroxide and γ-aminobutyric acid) are required for different processes in plant development pathways during the lifespan of plants and participate in abiotic and biotic stress responses [205].

Among the different classes of compatible solutes, polyamines stand as one of the most effective against extreme environmental stresses, which include drought, salinity, low temperature, oxidative stress, and metal toxicity. In tobacco, the response to heat/drought stress involved a transient increase in the levels of free and conjugated Put and in the levels of free Sp, norspermidine (N-Spd) and Spm [206].

PAs partially reversed the NaCl-induced phenotypic and physiological disturbances in *Citrus aurantium*. The expression of PA biosynthesis and catabolism genes was systematically upregulated by PAs. In addition, PAs altered the oxidative status in salt-stressed plants as inferred by changes in ROS production and redox status accompanied by regulation of transcript expression and activities of various

antioxidant enzymes [207]. In *Arabidopsis*, the polyamine spm protects from heat stress-induced damage by increasing expression of heat shock-related genes [203].

4.5 Conclusions and Future Perspectives

The understanding about cellular and molecular mechanisms of plant response to stress is essential to development of genetically engineered plants focused on acquisition or increasing of tolerance against abiotic stresses such as drought, allowing better insights into the high complexity of molecular strategies used by plants to their adaptations under adverse conditions. These adaptations contribute to a considerable reduction of productivity losses of plants with agronomical importance. Thus, this chapter presented efforts of scientific research to unveil the participation of several genetic components (such as signaling molecules, transcription factors, stress-responsive genes, and enzymatic and nonenzymatic molecules with antioxidative activity) in the drought stress response and its relationship with endogenous defense mechanisms of plants.

How the manipulation of gene expression, mainly by the overexpression of certain genes, can contribute to reach the plant tolerance to drought was also discussed. There is great importance in the achievement of more scientific studies for further identification of new components involved in the drought response. Such studies will promote a better understanding about the role of different genes and proteins whose contribution to tolerance is already well described, especially knowledge about the combined effect of several gene products related to this response, culminating in the generation of tolerant plants at the field level with high-yield production.

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