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REVIEW

Transcriptomic and proteomic profile approaches toward drought and salinity stresses

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Abstract

Drought and salinity, which can alter the water balance, disrupt the ionic equilibrium, and create reactive oxygen species (ROS), are capable of destroying plant tissues. In this study, transcriptomics, proteomics, and metabolomics have been used to elucidate various abiotic stress responses. In transcriptional signaling pathways, abscisic acid (ABA) is one of the plant phytohormones that regulate the stress response. On the other hand, several regulons and factors of transcription contributed in the reaction to osmotic stresses, as well as in ABA-dependent/independent signaling pathways. However, the findings display that intricate molecular reaction of plants under stress conditions may be controlled by complicated regulative networks of gene expression and signal transduction, as well as by the interaction between them. From the point of view of proteomics, protein modifications in response to stress can be considered as a molecular tool to improve the resistance of plants to environmental stresses. These studies have provided new information about the significance of several gene and protein networks involved in the response of plants to salinity and drought, and the induction of tolerance. Moreover, identifying the crucial pathways which are involved in salinity and drought resistance can open doors for the establishment of commercial-resistant crop cultivars, and might be very useful in the next-generation crop breeding strategies to produce plants with salinity and drought-resistant traits.

Keywords: drought, salinity, proteomics, transcriptomics.

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Abbreviations: ABA - abscisic acid; ABF - ABRE binding factor; ABI3 - ABA-insensitive3; ABRE - ABA-responsive element; AREB - ABA-responsive element binding protein; APX - ascorbate peroxidase; bHLH - basic-helix-loop-helix; bZIP - basic leucine zipper; CAT - catalase; CBF - C-repeat binding factor; CE1 - coupling element 1; CE3 - coupling element 3; CRT - C-repeat; CUC2 - cup-shaped cotyledon2, a NAC protein; DRE - dehydration-responsive element; CYP - cytochrome P_{450}; DREB1 - dehydration-responsive element binding protein 1; DRIP1 - DREB2A -interacting protein 1; ERD1 - early-response-to-dehydration1; ERF53 - ethylene response factor 53; DRIP2 - DREB2A-interacting protein 2; ERF53 - ethylene response factor 53; GALP - glyceraldehyde 3-phosphate; GOLGA5 - golgin subfamily A member 5; GST - glutathione-s-transferase; Hsp70 - heat shock protein; LEA - late embryogenesis abundant; MDA - malondialdehyde; MYB - myeloblastosis, a transcription factor family; NAC - NAM, ATAF1,2, CUC2; NAM: no apical meristem, a NAC protein; NF-Y - nuclear factors-Y; P5CR - pyrroline-5-carboxylate reductase; P5CS - Δ1-pyrroline-5-carboxylate synthetase; POD - peroxidase; PTMs - post-translational modifications; RGLGs - ring-type ubiquitin ligases; RD26 - responsive to desiccation 26, also called ANAC072; RDR - ribonucleoside-diphosphate reductase; ROS - reactive oxygen species; SNAC - stress-responsive NAC; SOD - superoxide dismutase.

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Introduction

Drought and salinity are two major environmental threats that plants have to face and that represent a rising threat to agricultural production (Jamshidi Goharrizi *et al.* 2020a). Therefore, concerns about the change in the plant growth environment and the consequent impact on biodiversity, plant resources, and the global security of food have become an important issue in agriculture (Ahuja *et al.* 2010). Salinity as an abiotic threat includes an imbalance in the inflow/outflow of minerals, defects in photosynthetic systems, and a mixture of these symptoms, in addition to the well-known implications of decreased growth, osmotic stress, and ion toxicity (Jenkins *et al.* 2010, Galmés *et al.* 2011, Jamshidi Goharrizi *et al.* 2020c,e). As the region affected by drought and salinity is still expanding, genetic resources with high drought/salinity tolerance must be determined (Jamshidi Goharrizi *et al.* 2020d, Ibrahim *et al.* 2019).

Abiotic stress-responsive gene products can be differentiated functionally into proteins involving in signaling pathways, and transcriptional regulations, and functional proteins, having either regulatory or metabolic functions, for example, those that are involved in osmolyte metabolism, reactive oxygen species (ROS) scavenging and detoxification, proteolysis of the cellular substrate, water uptake and transport of solutes and ions, chaperones, and late embryogenesis abundant (LEA) proteins (Fang and Xiong 2015, Joshi *et al.* 2016). It has been reported that abiotic stress can cause variations in different protein groups such as proteins involved in photosynthesis, the energy pathways, chaperone, transport activity, antioxidant enzymatic and non-enzymatic defense systems, primary and secondary metabolism (saccharides and nitrogen compounds), as well as proteins with unknown function (Pakzad *et al.* 2019, Jamshidi Goharrizi *et al.* 2019, 2020d). Therefore, these studies have remarkable functional and ecological importance in integrating plant resistance to abiotic stresses (Jamshidi Goharrizi *et al.* 2018, 2020f, 2020g).

In this review, we present a detailed overview of vast research improvements on transcriptomic and proteomic mechanisms, regulating adaptation to abiotic stresses.

Transcriptional regulation and gene expression in response to salinity and drought stress

Plants react to damage affected by environmental threats by making alterations to physiological processes and molecular pathways. These alterations help the plants to tolerate the stress and maintain their survival and growth. Drought stress alters the expression of various genes, which are known to show a substantial function under stress conditions. Several genes have so far been identified and characterized (Bray 2000, Todaka *et al.* 2015). Microarray assays carried out by different groups have identified numerous genes, which are either up-regulated or down-regulated under water deficit. On the other hand, many genes are identified that are expressed in response to both drought stress and high salinity, suggesting a connection between drought stress and salt stress (Bray 2000). However, among the strongly up-regulated genes in microarray assays, only 27 genes overlap (Bray 2004). This lack of similarity may be because the probes are applied to the microarray assays at different stages of plant growth and under different stress conditions. Recently, 17 microarray assays have been used in *Arabidopsis*, wheat, barley, and rice by a collaboration called Cross-Species meta-Analysis of progressive Drought (CSA: Drought), during the generative stage of growth. This group found that 225 genes were differentially expressed, and were distributed across experiments and different taxa (Shaar-Moshe *et al.* 2015). The genes that are induced under cellular stress in *Arabidopsis* can be divided into two broad groups, including functional genes and regulatory genes (Yamaguchi-Shinozaki and Shinozaki 2006). Protein coding genes which are necessary for the tolerance of cellular stress are found in the first group, including those encoding LEA proteins, ROS detoxifying enzymes, molecular chaperones, and enzymes responsible for the biosynthesis of sugars and proline. The genes coding proteins that are activated in different signaling pathways are found in the other group. These include protein kinases, ABA signaling components, signaling enzymes of lipid biosynthesis, and various transcription factors (Yamaguchi-Shinozaki and Shinozaki 2006).

As mentioned above, ABA has a considerable function in the drought response by regulating transcriptional networks (Yamaguchi-Shinozaki and Shinozaki 2006). A variety of drought-induced genes are also strongly induced by exogenous ABA treatment. In contrast, there are also numerous genes that are induced under conditions of water deficit but do not change under exogenous ABA. Based on the results reported, the transcriptional response of plants to drought stress can occur by either ABA-dependent or ABA-independent signaling pathways (Yamaguchi-Shinozaki and Shinozaki 2006). Transcription factors can affect the expression of groups of genes *via* specific binding to the promoter regions. Thus, these factors play a significant role in mediating the response of plants towards various stresses, by altering the expression of genes. Regulons describe a set of genes that are governed by the same transcription factor. Many regulons are activated in plants in response to drought and other stresses to improve growth, as shown in *Arabidopsis* (Nakashima *et al.* 2009). ABA-dependent and ABA-independent mechanisms can both modulate transcriptional responses by affecting one or more regulons in response to stress (Nakashima *et al.* 2009).

AREB/ABF regulons

The ABA-responsive element binding protein (AREB) and ABRE binding factor (ABF) are regulons that allow ABA-dependent modulation of gene expression in response to drought stress (Nakashima *et al.* 2009, Yoshida *et al.* 2015). Several genes are affected by water deficiency, and these generally also react to treatment with ABA

(Nakashima *et al.* 2009). Analysis of promoters has shown that many ABA-responsive genes are modulated *via* an ABA-responsive element (ABRE) located in the promoter region. ABRE is a sequence with a conserved 8 bp *cis*-element (PyACGTGG/TC) and a central ACGT sequence (Nakashima *et al.* 2009, Fujita *et al.* 2011). The expression of genes that respond to ABA is not induced by an ABRE version. In order to act as a *cis*-acting element, there is a requirement for additional ABRE copies, or another *cis*-acting element called a coupling element. Specific sequences can act as coupling elements, such as coupling element 1 (CE1) or coupling element 3 (CE3), and dehydration-responsive element (DRE) or C-repeat (CRT), which are the major *cis*-elements in ABA-independent signaling (Shen *et al.* 1996, Narusaka *et al.* 2003). Coupling elements are often rich in GC sequences and are similar to ABRE (Yamaguchi-Shinozaki and Shinozaki 2006). ABRE binding factors (ABFs) were shown to bind to the ABRE element in a yeast one-hybrid assay. ABFs can modulate the expression of genes that respond to ABA (Choi *et al.* 2000, Uno *et al.* 2000). Indeed, AREB/ABFs are a member of the basic leucine zipper (bZIP) family with nine elements in *Arabidopsis.* In addition, every transcription factor of AREB/ABF has multiple domains including one basic domain (bZIP) and four protected domains (Fujita *et al.* 2011, 2013). On the other hand, the type of tissues and the stage of plant life affect the expression of transcription factors. For example, when *Arabidopsis* vegetative tissues are exposed to osmotic stress or ABA treatment, major transcription factors such as AREB1/ABF2, AREB2/ABF4, AREB2/ABF1, and AREB2/ABF3 are mostly expressed in these tissues (Fujita *et al.* 2011). Other transcription factors belonging to this family, such as ABI5, AREB3, DPBF2, and EEL, are also expressed at the seed maturity (Finkelstein and Lynch 2000, Lopez-Molina and Chua 2000, Bensmihen *et al.* 2002). Transgenic plants have been engineered to overexpress AREB1/ABF2, AREB2/ABF4, or AREB2/ABF3 and they demonstrate improved resistance to drought, and also enhanced sensitivity to ABA (Kang *et al.* 2002, Fujita *et al.* 2005). A triple AREB/ABF mutant of *Arabidopsis* called *areb1areb2abf3* showed decreased drought tolerance and lower sensitivity to ABA treatment compared to the wild-type, single, or double mutants (Yoshida *et al.* 2010). Analysis of the transcriptome in the triple mutant in response to osmotic stress revealed decreased expressions of several genes (Yoshida *et al.* 2010). Moreover, it has been suggested that ABF1 has a significant place in gene expression by modulating ABA in response to drought stress. However, ABF1 is expressed at lower levels in comparison with other AREB/ABFs. The *areb1areb2abf3abf1* quadruple mutant plants show higher sensitivity to drought and reduced sensitivity to ABA in comparison with the *areb1areb2abf3* triple mutant.

DREB1/CBF and DREB2 regulons

Dehydration-responsive element binding protein 1 (DREB1) or CBF (C-repeat binding factor), and DREB2 are regulons, which act to regulate ABA-independent gene expression in response to drought stress (Nakashima *et al.* 2009). The *RD29A/COR78/LTI78* gene is expressed under drought and cold in *Arabidopsis*. This gene is known to be expressed after ABA treatment, however, it was also expressed in response to drought and cold stress in mutants that had been engineered to show disturbances in ABA biosynthesis and signaling (Yamaguchi-Shinozaki and Shinozaki 2006). Promoter analysis and expression studies showed that the induction of this gene in response to drought stress was mediated by either ABA-independent or ABA-dependent pathways and by various *cis*-acting elements (Yamaguchi-Shinozaki and Shinozaki 2006). The *RD29A* gene promoter contains a DRE/CRT *cis*-element as well as an ABRE (Yamaguchi-Shinozaki and Shinozaki 1994, 2005). This element is responsible for inducing a number of genes in several plants, including *Arabidopsis*, which are active in ABA-independent signaling pathways under cold and osmotic stresses (Yamaguchi-Shinozaki and Shinozaki 2005). DRE is a *cis*-element containing a conserved 9 bp sequence (TACCGACAT). In addition to ABRE, the expressions of genes that respond to cold and osmotic stresses are also induced by DRE (Yamaguchi-Shinozaki and Shinozaki 1994). Though DREB2A modulates the expression of several genes involved in stress resistance, it slows the growth and reproduction of plants, so the expression of this transcriptional factor is very precisely regulated (Yoshida *et al.* 2014). On the other hand, DREB2A expression is controlled by a regulating factor of growth as GRF7. GRFs are a set of transcription factors with 9 members, of which GRF7, by binding to the DREB2A promoter, suppresses its expression under non-stress conditions in *Arabidopsis* (Kim *et al.* 2003). Knockdown and knockout GRF7 mutants have shown changes in DREB2A expression under control conditions (Kim *et al.* 2012). Moreover, these mutant plants showed increased tolerance to salinity stress accompanied by delayed growth. Microarray assays showed that a large number of genes that had been shown to be responsive to osmotic stress were up-regulated in *grf7* knockout mutants under control conditions. These studies suggested that GRF7 could modulate the expression of genes responsive to osmotic stress *via* regulation of DREB2A expression (Kim *et al.* 2012).

Post-transcriptional regulation has also been shown to be a consequence of DREB2A expression. In contrast to wild-type DREB2A, a DREB2A-CA overexpression mutant demonstrated increased drought tolerance and a small increase in tolerance to cold stress, along with up-regulation of numerous stress-inducible genes (Sakuma *et al.* 2006). Moreover, DREB2A-interacting protein 1 (DRIP1) and DREB2A-interacting protein 2 (DRIP2) both act as ubiquitin E3 ligase which mediates the ubiquitination and subsequent proteasomal degradation of the drought-induced transcriptional activator DREB2A and negatively modulate drought-responsive gene expression (Qin *et al.* 2008). In addition, screening of yeast two-hybrid showed that the domain of DRIP1 is a RING domain (C3HC4 type). Similar to DRIPs and DREB2A, transcription factor ERF53 or ethylene response factor 53 (belonging to the

subfamily of non-DREEB2, with two homologues called RGLG1 and RGLG2 and as an E3 ligase) can affect gene expression in response to salinity and drought stress (Cheng *et al.* 2012). In support of this hypothesis, Cheng *et al.* (2012) reported that the expression of *AtERF53* is strongly increased in response to drought and this overexpression induced tolerance to drought stress in the studied plant. In contrast, under-treatment of plants with ABA, only a moderate increase in gene expression of *AtERF53* was seen (Cheng *et al.* 2012, Hsieh *et al.* 2013). Taken together, these studies suggest that AtERF53 and RGLGs (ring-type ubiquitin ligases) both act together to modulate genes in response to osmotic stress (Cheng *et al.* 2012, Hsieh *et al.* 2013).

NAC regulon

No apical meristem (NAM), ATAF, and cup-shaped cotyledon 2 (CUC2) are members of the large family of transcription factors called "NAC". More than one hundred members of this family have been identified in rice and *Arabidopsis* and categorized into ten classes according to phylogenetic relationships among them (Jensen *et al.* 2010). Based on the results obtained by Nuruzzaman *et al.* (2013), they possess a highly conserved N-terminal DNA-binding domain and a variable C-terminal region which has been found to have a considerable function in the recognition of objective genes. These transcription factors are involved in some growth processes, including the signaling network of plant growth hormones such as auxins and the regulation of shoot apical meristem growth and development (Olsen *et al.* 2005), as well as in the response of plants to environmental and biological stresses. In addition, based on the latter feature, they are known as SNAC or stress-responsive NAC (Olsen *et al.* 2005, Nakashima *et al.* 2012, Nuruzzaman *et al.* 2013).

Another well-known gene involved in response to stresses such as senescence and dehydration, as well as salinity, is the early-response-to-dehydration1 (*ERD1*) gene, but ABA treatment alone does not cause its induction (Nakashima *et al.* 1997). Based on the results reported by Simpson *et al.* (2003), overexpression of *ERD1* in response to abiotic stress such as water shortage is modulated through two *cis*-acting elements in the region of the promoter of *ERD1* including a 14-bp rps1 site 1-like sequence and an MYC-like sequence (CATGTG). Therefore, to express *ERD1*, NAC transcription factors, including ANAC055, ANAC019, and ANAC072/RD26 must bind to the MYC-like sequence in the promoter region of *ERD1*. However, transgenic plants with over-expression of ANAC072/RD26, ANAC055, or ANAC019 revealed increased expression of several genes but did not show up-regulation of *ERD1* (Fujita *et al.* 2004, Tran *et al.* 2004). In addition, based on the results reported, these are categorized in the SNAC sub-category of NAC transcription factors, and their induction is mediated by an ABA-dependent pathway in response to drought stress (Tran *et al.* 2004). For instance, transgenic plants which overexpressed ANAC072/RD26 showed increased resistance to drought as well as enhanced susceptibility to ABA (Fujita *et al.* 2004, Tran *et al.* 2004). Therefore, RD26 (responsive to desiccation 26, also called ANAC072) has a role in the regulation of genes responsive to drought stress in signaling pathways related to ABA (Fujita *et al.* 2004). Similarly, several other NAC factors such as ATAF1, ANAC096, ANAC016, OsNAC10, SNAC1, OsNAC5, and OsNAC6/SNAC2 were also identified and their overexpression led to increased drought tolerance in plants (Wu *et al.* 2009, Xu *et al.* 2013, Nakashima *et al.* 2014, Sakuraba *et al.* 2015). Another type of NACs was also identified as NAC with trans-membrane motif 1-like (NTLs: NTL6 and NTL4) that are activated under drought stress. Null mutants NTL4 and NTL6 in transgenic plants showed drought tolerance, indicating that the two act antagonistically under drought stress (Kim *et al.* 2002, Lee and Park 2012). Therefore, the NAC transcription factors that respond to stress either act to regulate the transcriptional response under both abiotic and drought stress, or are involved in the relationship between the responses to biotic and abiotic stresses (Nakashima *et al.* 2012). Recently, it was reported that in the tolerant and sensitive genotypes of *Triticum boeoticum*, the expressions of TaNAC2 and TaNAC69-1 were significantly different between control and drought stress. However, the increased expression in the most tolerant genotype was much higher than in the most sensitive one. These results suggest a regulatory role of these genes in drought resistance (Nazari *et al.* 2019).

Other pathways in response to drought and salinity stress

There are several other transcriptional pathways, which act in responses to stress. The *RD22* gene in *Arabidopsis* is induced in an ABA-dependent pathway and in response to drought stress (Yamaguchi-Shinozaki and Shinozaki 1993). Though the *RD22* gene is activated by ABA treatment, it lacks the *cis*-ABRE element in the promoter region, so its expression is modulated through two other *cis*-acting elements called myeloblastosis (MYB) and MYC (Abe *et al.* 1997). In support of these reports, it was found that transgenic plants that overexpressed *AtMYB2* and *AtMYC2* showed enhanced sensitivity to ABA and enhanced tolerance to osmotic stress (Abe *et al.* 2003). Therefore, based on these findings, it is suggested that in addition to gene regulation mediated by ABRE, transcription factors such as MYB and MYC can regulate the expression of genes after ABA treatment under drought stress.

The MYB transcription factors contain specific MYB domain within the DNA-binding site (Lindemose *et al.* 2013). Transcriptome data analysis related to the *MYB* gene in the database of *GENEVESTIGATOR* (https://www.genevestigator.com/gv/) proposes that 41 and 51 % of these genes in *Arabidopsis* are down-regulated and up-regulated, respectively, in response to drought stress (Baldoni *et al.* 2015). In addition, transcription factors of MYC belong to the family of the basic-helix-loop-helix (bHLH) transcription factors which contain a specific bHLH domain (Kazan and Manners 2013). Analysis of

transcriptome data of *Arabidopsis* guard cells revealed that several responsive genes to ABA possessed motifs of MYC-binding to specific sites of the promoter (Wang *et al.* 2011). The family of WRKY transcription factors is also involved in the response to drought stress. WRKY transcription factors contain either one or two WRKY domains and can bind to a conserved DNA sequence termed the W box, in order to modulate the expression of a gene (Rushton *et al.* 2010). These transcription factors have roles in different processes, such as response to environmental and abiotic stresses as well as signaling mediated by ABA (Ülker and Somssich 2004, Rushton *et al.* 2010). For example, *WRKY63* (*ABO3: ABA Overly Sensitive3*) gene has been shown to have a positive role in responding to drought stress, while mutant plants with a knockout of the *abo3* gene have shown high sensitivity to ABA during the seedling period, as well as low tolerance to drought stress.

Nuclear factors-Y (NF-Y) are another transcription factors involved in responding to drought and in resistance pathways. For example, in an ABA-dependent signaling pathway, when *Arabidopsis* leaves were exposed to drought, overexpression was found in the *AtNF-YA5* gene. This overexpression, increased resistance to drought as well as decreased water losses in *Arabidopsis* transgenic plants; while mutant plants (*Atnf-ya5*) showed high sensitivity to drought (Wang *et al.* 2008a). In addition, these transcription factors are hetero-trimeric complexes and have three different subunits called -YC, -YA and -YB that connect to a specific site (the CCAAT box) of the promoter in the gene(s) of interest (Wang *et al.* 2008a).

Δ1-pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR) are two enzymes involved in proline biosynthesis. In our previous study (Jamshidi Goharrizi *et al.* 2020f), we observed up-regulation of these enzymes in response to PEG treatment (drought stress) in *Lepidium draba* plants besides wheat under salinity stress (Jamshidi Goharrizi *et al.* 2020b, Pakzad *et al.* 2021). Moreover, the mRNAs of ascorbate peroxidase (APX), peroxidase (POD), and catalase (CAT) were all increased in response to drought stress induced by PEG treatment. Moreover, in our previous study, the expression of the *CYP79F1* gene, a cytochrome P_{450} (*CYP*) gene, was also increased by subjecting *Lepidium draba* plants to salinity stress (Jamshidi Goharrizi *et al.* 2020g).

The interaction of different transcription factors under drought and salinity stress

It has become clear that different transcription factors can act together to modulate the expression of genes in reaction to environmental stresses such as salinity and drought. Protein kinases such as the subclass III SnRK2s have remarkable function in the mentioned process. These proteins are activated *via* both drought stress and ABA (Yoshida *et al.* 2006, Boudsocq *et al.* 2007, Fujii and Zhu 2009). In addition, under osmotic stress, several new proteins have been identified that have a role in the inactivation/activation of these above-mentioned transcription factors (Stecker *et al.* 2014). One of these proteins known in this process is the PP2Cs protein. According to the studies, dephosphorylated PP2Cs could inactivate SnRK2s, but under osmotic stress (drought), inactivated PP2Cs *via* ABA lead to the activation of SnRK2s (Zhang *et al.* 2020).

There are numerous studies showing that AREB/ABFs:DREB/CBFs and AREB/ABFs:NACs interact with each other in various conditions (Lee *et al.* 2010, Jensen *et al.* 2013). For example, the transcription factor ATAF1 of SNAC connects to the NCED3 promoter and therefore can modulate the content of ABA, suggesting that SNACs are likely effective in the ABA-dependent regulation of AREB/ABF regulon of gene expression (Jensen *et al.* 2013). In contrast, the sequences of ABRE have been shown to exist in the region of gene promoter (*SNAC* gene) (Nakashima *et al.* 2012). On the other hand, ABF4 and ABF interact directly with ANAC096, while there is no interaction between ABF4 and ANAC096. Observations have also shown that ABFs work together with ANAC096 to activate genes responsive to drought and also induced by ABA (Xu *et al.* 2013). Sakuraba *et al.* (2015) suggested that ANAC016 could negatively regulate tolerance to drought stress. Moreover, they demonstrated that the expression of AREB1 is suppressed *via* the direct binding of ANAC016 to the region of the AREB1 promoter. Furthermore, other NAC transcription factors may be responsive to drought and could be related to ABA signaling, for instance, NAC019, NAC053/NTL4, NAP, NAC055, and NAC072 (Lee and Park 2012, Zhang and Gan 2012).

Genetic engineering and improving agricultural productivity

Investigating the mechanism of molecular reactions of plants to stress caused by drought and salinity could allow new approaches to overcome these two stressors and improve agricultural productivity throughout the world (Ashraf and Akram 2009, Gupta and Huang 2014). For example, in *Arabidopsis*, the engineering of a specific gene named *MsNHX1* which encodes an antiporter for Na^+/H^+ transport improved osmotic balance but enhanced the malondialdehyde (MDA) content. In rice, an analogous engineered gene encoding Na^+/H^+ antiporter *PgNHX1* resulted in a more elaborated root system (Verma *et al.* 2007). In wheat, an engineered gene called *AtNHX1* as a K^+/Na^+ vacuolar antiporter led to improved grain yield and higher production of biomass along with an improvement in K^+ content as well as reduced Na^+ accumulation in leaves (Xue *et al.* 2004). Interestingly, this engineered gene (*AtNHX1*) showed different functions in *Brassica* and tobacco plants. In *Brassica*, the engineered *AtNHX1* gene resulted in an increase in the content of proline as well as an improvement in growth (Zhang *et al.* 2001); while in tobacco, the mentioned gene is involved in the distribution of sodium ions among different parts of a plant (Zhang *et al.* 2008). Finally, in *Arabidopsis*, the engineered *SOS1* gene as a plasma membrane H^+/Na^+ antiporter resulted in positive changes in the rate of germination, growth of

roots, and content of chlorophyll (Shi *et al.* 2003).

Plants face a wide range of environmental stresses during their life cycle; however, they can develop their tolerance by using evolved mechanisms such as cellular and molecular changes and physical adaptation that begin after stress. Due to the complexity of molecular mechanisms, it seems that understanding the mechanisms of molecular responses to stresses depends on understanding the stresses at the place of their occurrence as well as how information about them is transmitted through the signal transduction pathway. Our knowledge of signaling pathways leading from the stimulus to the final response in plants has increased in recent years. However, the linear signaling pathways are in fact only a part of a more complex signaling network, and there is a great deal of overlap among its branches. For example, many genes can be induced by more than one specific stimulus. Hence, the concept of "cross-talk" and "specificity" can be well seen in complex signaling networks under abiotic stresses. In other words, "cross-talk" refers to any convergence in two signaling pathways caused by different stressors. This convergence may take different forms with different results. For example, convergence between different pathways can lead to the same end or can lead to interaction between pathways for affecting each other's outcome. Interaction between pathways may be negative or positive or may lead to competition for a specific target. Unlike "cross-talk" in the "specificity" phenomenon, there is no convergence between signaling pathways, so a particular stimulus might link to a particular end response, and not to any other final responses. Therefore, it is possible to distinguish between two or more possible outcomes in each part of the signaling pathway. Thus, opportunities for simultaneous occurrence of "cross-talk" and "specificity" may be present within a particular signaling pathway. Consequently, these findings display that intricate molecular reaction of plants under stress conditions can be mediated *via* both signal transduction and intricate regulative networks of expression of the gene and *via* cross-talk between them.

Proteomic analyses of plant responses to salinity and drought

Abiotic stresses have severe effects on plant proteomes: changes in protein relative abundance, localization of proteins in the cells, their post-transcriptional and post-translational modifications, interactions of proteins with other compounds, and biological functions of proteins (Kosová *et al.* 2018). Therefore, in addition to investigating the mechanism of molecular reactions of plants to stresses, several studies compared the responses of halophytes and glycophytes to different stresses using a proteomic methodology, including *Arabidopsis thaliana* (Alqurashi *et al.* 2018), *Nicotiana tobaccum* (Chen *et al.* 2019), *Populous cathayana* (Xiao *et al.* 2009, Chen *et al.* 2011), grass-pea (Chattopadhyay *et al.* 2011, Rathi *et al.* 2018), *Agrostis stolonifera* (Xu *et al.* 2011, Xu and Huang 2018). Other agricultural plants have been evaluated under the mentioned stress conditions in a large number of studies, including *Triticum aestivum* (Peng *et al.* 2009, Jacoby *et al.* 2010, Singh *et al.* 2017, Nazari *et al.* 2020), *Triticum durum* (Budak *et al.* 2013, Capriotti *et al.* 2014), canola (Bandehagh *et al.* 2011, Koh *et al.* 2015), soybean (Sobhanian *et al.* 2010, Hossain and Komatsu 2014, Das *et al.* 2016, Wang and Komatsu 2018), sugar beet (Wakeel *et al.* 2011, Jedmowski *et al.* 2014, Wang *et al.* 2017), peanut (Jain *et al.* 2006, Thangella *et al.* 2018), *Sorghum bicolor* (Kumar Swami *et al.* 2011), *Zea mays* (Zörb *et al.* 2009, 2010, Zenda *et al.* 2018), cucumber (Du *et al.* 2010, 2019), potato (Aghaei *et al.* 2008, Zhang *et al.* 2013), and tomato (Chen *et al.* 2009, Lin *et al.* 2016, Tamburino *et al.* 2017). The proteomic profiles of several halophytes have also been analyzed in response to salinity stress, including *Puccinellia tenuiflora* (Yu *et al.* 2011), *Thellungiella salsuginea* (Pang *et al.* 2010), *Suaeda salsa* (Li *et al.* 2011), *Aster tripolium* (Geissler *et al.* 2010), *Salicornia europaea* (Wang *et al.* 2009), *Bruguiera gymnorhiza* (Wang *et al.* 2014), *Mesembryanthemum crystallinum* (Barkla *et al.* 2009) as well as lower plants as moss *Physcomitrella patens* (Wang *et al.* 2008b) and algae *Dunaliella salina* (Katz *et al.* 2007). Pistachio rootstock was studied under both stresses, salinity and water deficiency (Pakzad *et al.* 2019, Jamshidi Goharrizi *et al.* 2020c).

In glycophytes such as rice, soybean, and potato, studies have shown that excessive salt primarily affects plant roots (Liu *et al.* 2012, Aghaei *et al.* 2008), and significantly alters the expression pattern of salinity-responsive genes and proteins (Yan *et al.* 2003, Hasanuzzaman *et al.* 2013). The proteomic profile of soybean various tissues has also been studied under salinity and showed a down-regulation of the 50S ribosomal protein, which participates in the biosynthesis of total proteins causing reduced plant growth (Aghaei *et al.* 2009, Sobhanian *et al.* 2010, Ma *et al.* 2012). Another study on the proteome of rice roots treated with 150 mM NaCl identified 17 proteins significantly up-regulated and 11 proteins down-regulated (Chitteti and Peng 2007). Glyceraldehyde-3-phosphate (GALP) hydrogenase, ATP synthase beta-chain, and protein kinase were important proteins that were down-regulated, while mannose-binding rice lectin, glutathione-S-transferase (GST), and heat shock protein Hsp70 were up-regulated (Chitteti and Peng 2007). Moreover, pistachio rootstocks exposed to high salinity showed changes in 25 proteins (20 unique proteins as well as 5 proteins with unknown function) in their proteomic profile (Jamshidi Goharrizi *et al.* 2020c). In another study, proteomic profiles of *Hordeum marinum* and *H. vulgare* in response to 300 mM NaCl were analyzed. Based on the results obtained, *H. marinum* increased the content of proteins associated with energy metabolism like glycolysis, ATP metabolism, and photosynthesis-associated proteins showed active compatibility to increased energy necessity for new plant homeostasis. On the other hand, alternations at the proteomic profile in salt-treated *H. vulgare* showed plant tissue damage as demonstrated *via* increased content of proteins associated with apoptosis (Maršálová *et al.* 2016).

Regarding drought stress, the proteomic profile of *Glycine max* roots in response to drought stress shows 45 altered proteins. In the *Glycine max* root proteome, 21

proteins were down-regulated in response to drought stress, while only five proteins were up-regulated (Larrainzar *et al.* 2007). In another study, 36 proteins in wheat were detected to be altered under drought, out of which 33 and 67 % were up and down-regulated, respectively (Caruso *et al.* 2009). In a study of the proteomic profile in barley crown under drought stress, 1 004 proteins are identified including those involved in energy metabolism, protein metabolism, transport and cytoskeleton proteins and stress-related proteins (Vítámvás *et al.* 2015).

In response to salinity, proteins could be grouped into nine different categories including chaperones, transcription factors, calcium-binding proteins, material transport proteins, non-enzymatic antioxidant defense proteins, energy pathway proteins, proteins for replication and repair of DNA, enzymatic antioxidant defense system proteins, and photosynthesis components (Jamshidi Goharrizi *et al.* 2020c). In pistachio rootstock subjected to salinity, ribonucleoside-diphosphate reductase (RDR), Golgi subfamily A member 5 (GOLGA5), and polcalcin Phl p 7-like were up-regulated (Jamshidi Goharrizi *et al.* 2020c). Pakzad *et al.* (2019) in UCB-1 pistachio rootstock found 18 drought-responsive proteins (16 unique proteins as well as 2 unknown function proteins). These proteins were classified into nine groups, including enzymatic antioxidant defense proteins, energy pathway proteins, chaperone proteins, non-enzymatic antioxidant defense proteins, carbohydrate metabolism, material transport proteins, general metabolism, nitrogen metabolism, and photosynthesis proteins (Pakzad *et al.* 2019). In this study, some proteins such as fibroin heavy chain-like, thylakoid lumenal 19 kDa protein, vesicle-associated membrane protein 722-like protein, superoxide dismutase (SOD) [Cu-Zn] isoform X2, vesicle-associated protein 2-2-like isoform X1, vacuolar protein sorting-associated protein 52 A and Golgi subfamily A member 5, were detected to be altered under drought for the first time (Pakzad *et al.* 2019). Furthermore, Zhang *et al.* (2012) reported the proteomics profile of 34 different plants in response to salinity stress. They identified 2 171 different salt stress-responsive proteins that were classified into several categories, including energy metabolism, transcription, CO_2 assimilation/carbohydrate synthesis, cell structure, protein transport, translation, defense interactions, cell division/differentiation, and others. A review of proteins involved in response to salinity and drought stresses is summarized in Supplementary Table 1.

In addition, it is worth mentioning that proteins play a fundamental role in plant stress response leading to stress-adapted phenotype. So, the capability to synthesize multiple functional proteins, *i.e.* protein isoforms and post-translational modifications (PTMs), can be a reflection of the diversity of plant phenotypic responses to environmental stresses. However, different protein isoforms and PTMs derived from a single gene can reveal the same, similar, or entirely different biological functions depending on their cellular localizations and protein-protein interactions (Kosová *et al.* 2018). Indeed, the stress response in plants is a dynamic process with several phases (alarm, acclimation, resistance, exhaustion, and recovery phase) and these phases can be distinguished from each other by a specific proteome composition (Kosová *et al.* 2018). However, relatively small differences in severity/type/time of stress can lead to significant differences in plant proteome indicating stress damage or stress acclimation. Hence, combined stresses that take place in the field have unique effects on the plant proteome which cannot be described as a sum of distinct stresses (Kosová *et al.* 2018).

Photosynthesis and salt stress

In various plants, a range of proteins concerning photosynthesis are activated (indirectly or/and directly) in response to salinity and they are up-regulated or down-regulated (Ahmad *et al.* 2016). The types of proteins that are changed can be different from tissue to tissue and from species to species (Ahmad *et al.* 2016). Therefore, the identification of photosynthesis proteins that are affected by salinity stress can be used to select tolerant cultivars, and also improve salt-sensitive species using modern molecular tools (Ahmad *et al.* 2016). Various proteins involved in protein biosynthesis, detoxification, and energy metabolism are changed when plant tissues are subjected to salinity (Rollins *et al.* 2013, Zhao *et al.* 2013). Moreover, the following proteins in the rootstock of UCB1 pistachio were recognized to change in response to salinity: 50S ribosomal protein L13, RuBisCO large subunit, RuBisCO small subunit, RuBisCO activase 1, and phosphoribulokinase (Jamshidi Goharrizi *et al.* 2020c). In a study of soybean exposed to salinity stress, RuBisCO activase was significantly down-regulated (Parker *et al.* 2006) possibly because of the decreased photosynthetic activity (Sobhanian *et al.* 2010). Recently, Wang *et al.* (2014) reported that 53 proteins either up-regulated or down-regulated in *Kandelia candel* were subjected to salinity stress. The proteins that were up-regulated in this study were responsible for increased salinity resistance in this plant.

Late-embryogenesis abundant proteins and salt stress

Development in plants starts with seed germination and seedling growth and can be affected by various stresses. Late-embryogenesis abundant (LEA) proteins are significantly up-regulated at these stages (Xu *et al.* 1996, Hand *et al.* 2011, Amara *et al.* 2012, Battaglia and Covarrubias 2013). Four LEA proteins were induced under salinity in *Oryza sativa*, but induced proteins were degraded once the salinity was removed (Chourey *et al.* 2003). In soybean plants, the expression of LEA proteins was prompted in response to salinity (Aghaei *et al.* 2009). The engineered *HVA1* gene, a gene encoding LEA protein in barley, is able to improve the growth of rice in response to salinity, in comparison with the wild species (Xu *et al.* 1996) due to the accumulation of HVA1. Therefore, modification of the *LEA* gene family in plants can be a

useful tool to improve/enhance the resistance in plants under salinity (Xu *et al.* 1996).

Oxidative stress and antioxidant proteins under salinity

The proteomic profile of rice roots exposed to 50 and 100 mM NaCl was studied, and it was found that three different proteins were altered, caffeoyl-CoA O-methyltransferase involved in lignin biosynthesis, ascorbate peroxidase, and auxin and salicylic acid response-like protein (Salekdeh *et al.* 2002). In the same study, the amounts of auxin and salicylic acid response-like protein and caffeoyl-CoA O-methyltransferase in the sensitive rice cultivar were much lower than in the salt-resistant cultivar, while both cultivars had a similar response to induced oxidative stress, in terms of increased ascorbate peroxidase activity. Therefore, these proteins are probably able to improve the salt resistance of rice plants (Vincent and Zivy 2007). The root proteomic profiles of two barley cultivars (one salt-tolerant and one salt sensitive) were compared, and 39 proteins are found to be altered, of which 26 are accurately identified. In the resistant barley cultivar, a higher amount of glutathione was produced under salinity, in order to detoxify the ROS generated, while in the sensitive barley cultivar, iron absorption proteins were significantly increased (Witzel *et al.* 2009). In responding to salinity, the proteome of rice roots shows changes in more than 1 100 separate proteins. These proteins are classified into groups concerning nitrogen metabolism, mRNA processing, scavengers of reactive oxygen species, sugar regulation, protein processing, cytoskeleton stability, and energy metabolism (Yan *et al.* 2005). Proteomic analysis of *Arabidopsis* roots showed that 17 proteins related to energy metabolism, defense systems, binding catalysts, signal transduction, cell wall metabolism, and ROS scavenging were significantly changed in response to salinity (Guo *et al.* 2014).

Ion uptake and homeostasis under salinity

Investigation of salt-responsive proteins, especially root proteins, can provide much useful information about salt-resistance mechanisms in plants. The symplastic or apoplastic pathways are the mechanisms of Na^+ entry into plant roots. In this regard, several proteins of transmembrane Na^+ transport, such as HKT and H^+/Na^+ antiporters are involved in the transport of Na^+ (Rus *et al.* 2001, Tester and Davenport 2003). Various proteins are activated against salt stress, many depending on the specific genotype, whereas some others depend on the concentration of salts and time of exposure (Peng *et al.* 2009, Szopinska *et al.* 2011). For instance, an evaluation of the proteomic profile of the plasma membrane of rice plants exposed to salinity stress (Nohzadeh Malakshah *et al.* 2007), showed that 24 proteins were altered, which were involved in controlling K^+ channels, and in different signaling pathways and protein-protein interactions (Hashiguchi *et al.* 2010). An investigation of the proteomic profile of leaves and roots of two wheat cultivars under salinity showed that increased salinity resistance was associated with osmotic/ionic homeostasis and a better efflux of toxic byproducts (Peng *et al.* 2009). In response to different salt concentrations, a large number of proteins (around 88 - 109) were recognized to be altered in the plasma membrane of yeast cells at various time intervals (Szopinska *et al.* 2011). Of these, 12 proteins were detected at medium salt concentration and 20 at both medium and high salt stress (Szopinska *et al.* 2011). In addition, proteins of "t-SNAREs", "Pma1", "ABC amino acid transporters", "P-type HC-ATPase", and "cell wall biogenesis proteins" were detected to be down-regulated under both high and medium salinity (Szopinska *et al.* 2011). It was suggested that these protein expressions changed because of alterations in the plasma membrane morphology and/or ion homeostasis (Szopinska *et al.* 2011).

Photosynthesis and water stress

It is known that the amount and activity of many plant proteins can significantly affect photosynthetic efficiency (Deeba *et al.* 2012, Galvan-Ampudia *et al.* 2013). In *Quercus ilex*, the reduction of some proteins related to photosynthesis and synthesis of ATP was detected in response to drought (Valero-Galván *et al.* 2013). Under water deficit, the expression of glycolytic enzymes decreases. These enzymes in the recovery phase after stress, lead to the accumulation of sugars, which act as a valuable energy source to enhance plant growth (Ahmad *et al.* 2016). Under water stress, the proteomic profile of sugar beet leaves showed major alterations, with pronounced changes being detected in proteins related to photosynthesis, chaperones, oxidative defense system, and redox regulation (Hajheidari *et al.* 2005). In another study in soybeans subjected to drought, the expression of several proteins related to the synthesis of proteins, metabolism of amino acids, carbon metabolism, and cell growth were all decreased (Gil-Quintana *et al.* 2013). In pistachio rootstock, 16.66 % of the altered proteins were involved in photosynthesis (Pakzad *et al.* 2019). In this rootstock, ribulose 1,5-bisphosphate carboxylase/oxygenase was up-regulated 2.42-fold, while ribulose-bisphosphate carboxylase/oxygenase large subunit and the predicted thylakoid lumenal 19 kDa protein displayed a 362- and 133-fold decrease, respectively, in response to drought stress (Pakzad *et al.* 2019).

Late-embryogenesis abundant proteins and drought

LEA proteins are over-produced in responding to drought, especially in drought-resistant plants (Alam *et al.* 2010). A proteomic evaluation of the soybean root proteome under drought, identified an increase in a LEA protein called dehydrin (Alam *et al.* 2010, Nouri *et al.* 2011), which

can also protect against ROS-induced damage (Grelet *et al.* 2005, Hossain *et al.* 2013). Also, *Pisum sativum* late-embryogenesis abundant mitochondrial protein (PsLEAm), which is located within the inner matrix of seed mitochondria was increased, generally only in late seed maturation (Grelet *et al.* 2005). The expression of this protein does not occur in vegetative tissues under non-stress conditions, but in response to severe drought, this protein is expressed in leaves (Grelet *et al.* 2005). In one study, 15 overexpressed proteins were detected in *Medicago truncatula* seeds in response to drought stress. All of these proteins were associated with drought resistance, and 11 of them were identified as LEA proteins (Boudet *et al.* 2006). In maize, some LEA proteins were altered under drought. The LEA Mg3 can control cell shrinkage during dehydration, while another mitochondrial LEA protein (ZmLEA3) normally expressed in seeds, was folded into an α-helix under drought (Amara *et al.* 2012). Usually, this protein protects membranes in response to stress and can protect the inner mitochondrial membrane in response to water deficit (Amara *et al.* 2012).

Oxidative stress and antioxidant proteins under drought

Plants are capable to increase the production of antioxidants to neutralize and remove the ROS that are generated in response to many kinds of stresses. For instance, the accumulation of antioxidant enzymes, such as superoxide dismutase (SOD) in rice (Ali and Komatsu 2006) and soybean (Toorchi *et al.* 2009), and polyphenol oxidase and catalase in rootstocks of pistachio has been reported in response to drought (Jamshidi Goharrizi *et al.* 2020a,d). Several enzyme isoforms and subunits were detected in a proteomic evaluation of *Triticum durum* leaves in response to drought: 15 % of these proteins were related to the removal of ROS, and 6 % were associated with antioxidant defense mechanisms (Caruso *et al.* 2008). In pistachio rootstock, superoxide dismutase, an important ROS scavenging enzyme was up-regulated 2.48-fold in response to drought stress (Pakzad *et al.* 2019). In resistant maize cultivars, several protective proteins such as dehydrins and chaperones were up-regulated in response to drought (Benešová *et al.* 2012). Due to decreased protein synthesis in the sensitive maize genotype, there were lower amounts of antioxidant enzymes (Benešová *et al.* 2012). In the proteomic profile of grapevine in response to water stress, several protein families, concerning antioxidant metabolism, steroid synthesis, and translation were changed (Cramer *et al.* 2013). An investigation of the proteomic profile of two soybean cultivars found that the proteins related to photosynthesis were increased under stresses of drought and heat (alone or in combination), and suggested that these proteins were able to regulate RuBisCO, carbon fixation, electron transport, and the Calvin cycle in stress conditions (Das *et al.* 2016). Additionally, the induction of carbonic anhydrase which produces bicarbonate ions, protons, and carbonic acid from water and carbon dioxide, can help the cells resist high concentrations of hydrogen peroxide produced in response to different stresses (Das *et al.* 2016). Proteomic profiling of sunflower plants subjected to drought showed that energy and defense-related proteins were lower in sensitive sunflower genotypes, whereas they were increased in resistant genotypes (Ghaffari *et al.* 2013). In that study, the authors suggested that improved antioxidant defensive systems, energy usage, and water transport are the main reasons for better plant growth under stress (Ghaffari *et al.* 2013). In *Agrostis stolonifera* subjected to water stress, 56 stress-responsive proteins were identified. These proteins improved drought resistance by increasing membrane stability, ROS defensive systems, maintaining cell pressure potential, and allowing cell wall expansion under drought (Xu and Huang 2012). After stress induction, it has been found that the increased content of H_2O_2 and NO induces an increase in the expression of proteins associated with ROS detoxification, such as FeSOD, MnSOD, and Cu/ZnSOD (Tanou *et al.* 2012). Another study showed that the exogenous calcium was able to enhance the resistance of soybean plants to stress through the increasing activity of antioxidant enzymes, enhanced protein biosynthesis, and redistribution of storage proteins (Yin *et al.* 2015). Using a variety of methods such as metabolomics, proteomics, and transcriptomics, several signaling pathways have been shown to be activated in response to various stressors. These activated signaling pathways include those related to hormones, kinase cascades, antioxidants, transcription factors, osmolyte synthesis, and ROS production (Suzuki *et al.* 2014, Yin *et al.* 2015). Nevertheless, the balance between defense systems of non-enzymatic/enzymatic antioxidant in response to salinity and drought in adapted plants is somewhat different. In most plants, increased ROS accumulation act as a trigger for plants to express proteins designed to restore the cellular redox balance. The evaluation of the plant proteome under induced oxidative stress as a result of exposure to environmental changes can help researchers to understand the pathways that are triggered and could help breeders to improve the tolerance of different crops.

Abscisic acid metabolism under drought stress

Under drought stress, abscisic acid has the main role in the closing of stomata to reduce water loss (Ahmad *et al.* 2016). In a study on the proteomic profiling of *Arabidopsis thaliana* guard cells, the expression of 336 separate proteins was found to be altered under drought (Zhao *et al.* 2008). Among these, 52 have been activated. The protein myrosinase TGG1 which is associated with stomatal regulation and abscisic acid metabolism was included among these 52 proteins (Hashiguchi *et al.* 2010). Furthermore, it is known that the modification of signaling pathways in plants by ABA can increase drought resistance under conditions of water deficit (Nishikawa *et al.* 2008). An evaluation of the *Arabidopsis thaliana* proteome in response to drought showed that the fresh mass of this plant could be improved *via* the prevention of wasting water vapor from the stomata (Nishikawa *et al.*

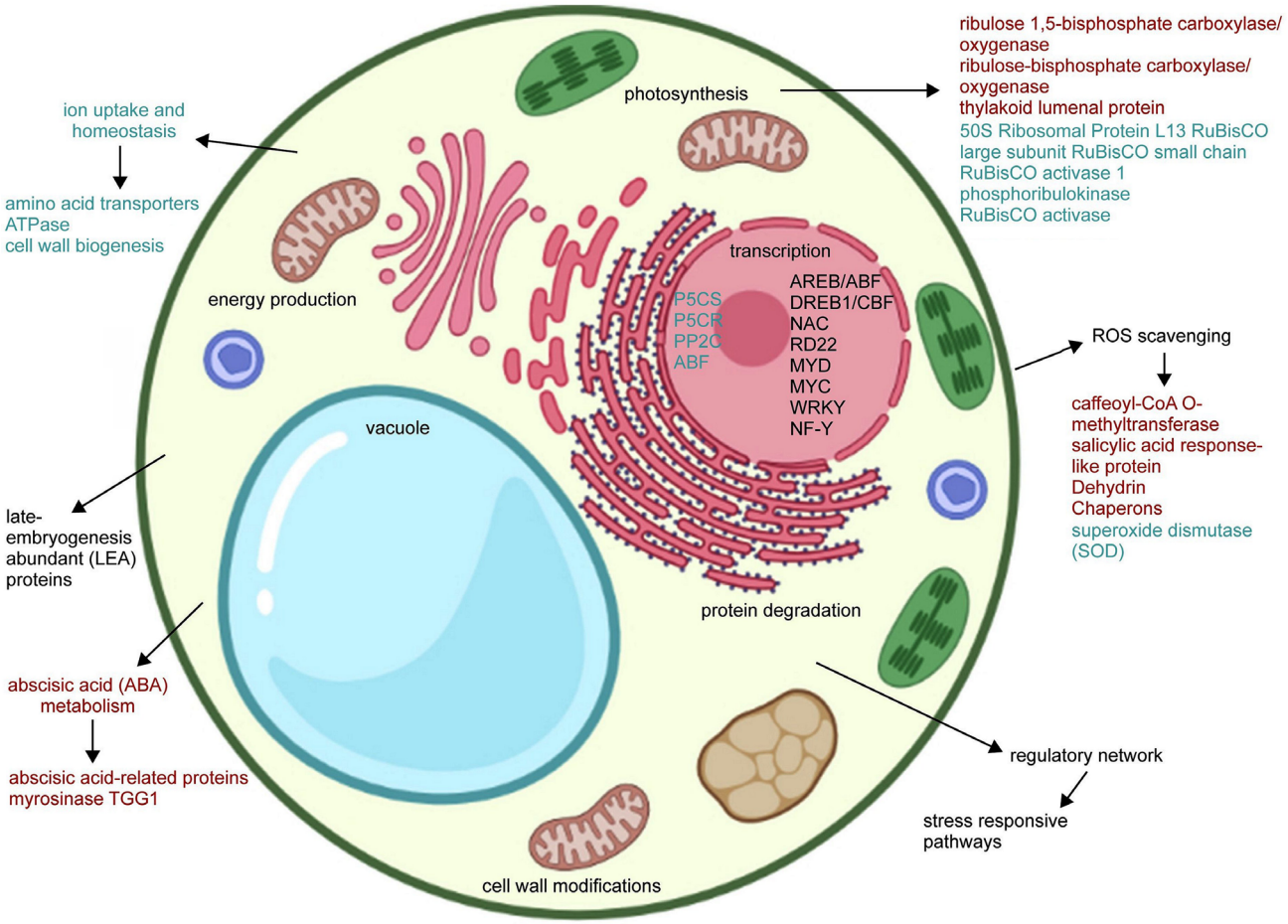

Fig. 1. Comparison between a transcriptomic and proteomic profile in response to salinity and drought stress. Items depicted with black are common between salinity and drought stress, items in red are transcripts and proteins related to drought stress, and items in blue are transcripts and proteins related to salinity stress.

2008). It was shown that sphingosine-1-phosphate, which is controlled by the ABA on the sphingosine kinase activity, was implicated in limiting water vapor loss (Hashiguchi *et al*. 2010). In a recent study on the proteomic profile of the roots of Nesser and Opata wheat cultivars, it was shown that several proteins in the Nesser cultivar were differentially affected by ABA compared to the Opata cultivar (Alvarez *et al*. 2014). This confirmed that ABA-responsive proteins are affected by drought stress and could enhance the tolerance of plants under stress (Alvarez *et al*. 2014). Abscisic acid is considered to be a regulator of stomatal closure in response to water deficit, but few studies have evaluated how the proteome governs ABA accumulation in plants. Furthermore, the identification of abscisic acid-related proteins under drought stress and drought tolerance of different plants needs to be studied more. In summary, Fig. 1 shows a comparison between a transcriptomic and proteomic profile in response to salinity and drought stress.

Summary and conclusions

In summary, proteomics describes protein functions in the cell, especially in response to changing environmental conditions; because many proteins are expressed in control conditions, while under stress conditions, they undergo alterations in their expression. Thus, protein modification is also an effective mechanism that begins in response to stress. On the other hand, it seems that the ability of plants to adapt and successfully cope with stress conditions (drought and salinity) can be related to the up/down-regulation of a number of their proteins, which may be occurred because of changes in gene expressions. Indeed, many proteins play a crucial role, either in signal transduction pathways as response regulators, or in adaptive activities to repair damaged cells, thus allowing plants to improve and survive under abnormal conditions. For instance, the accumulation of hydrophilic proteins belonging to the LEA superfamily in plants can be considered a molecular tool to improve the resistance of plants to different stresses such as salinity and drought. On the other hand, despite constructive modifications in the function of some proteins, undesirable processes are known to occur under salinity

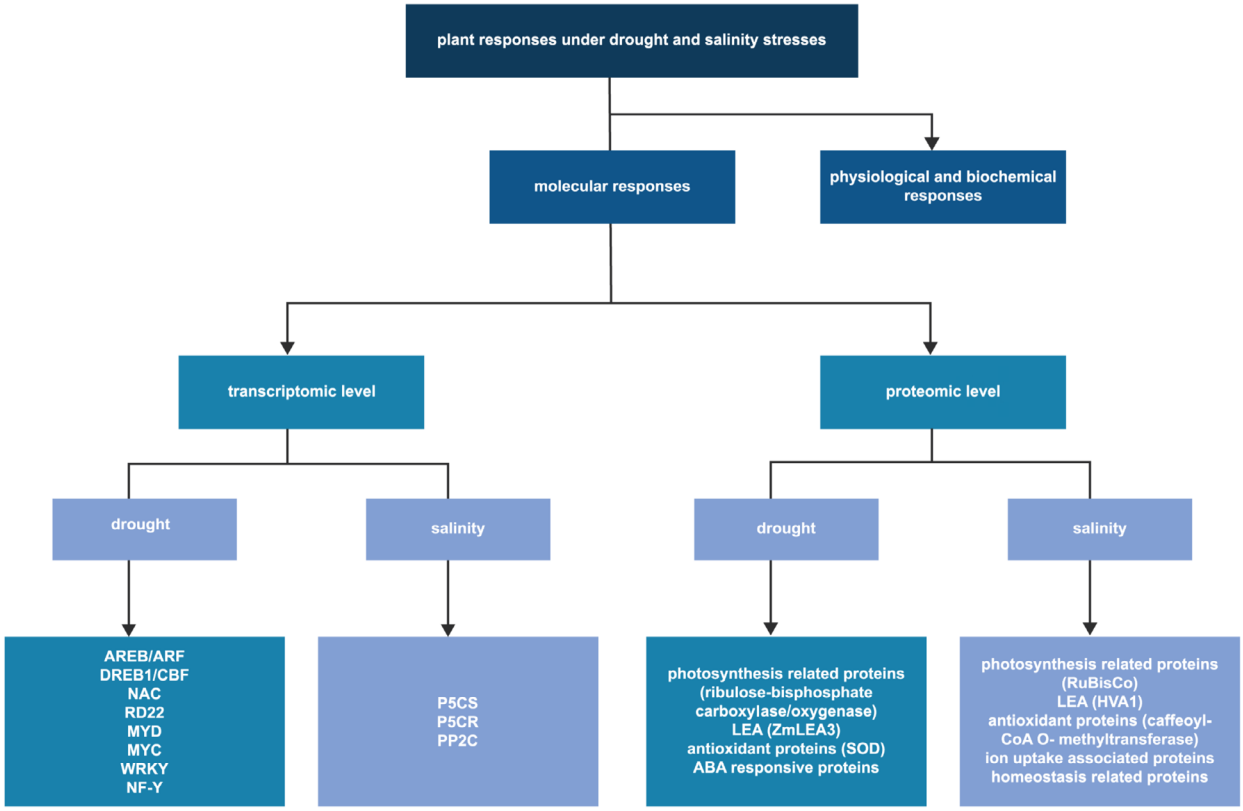

Fig. 2. A diagram representing different responses associated with drought and salinity stresses.

and drought stress, such as membrane irregularities, increased content of toxic metabolites, production of reactive oxygen species, decreased nutrient uptake and decreased cell photosynthesis. In addition, in recent years, proteins have been identified that have an unknown function(s) despite modifications in their gene expression. These proteins are classified as "POFs" (proteins with obscure feature) and have no defined domains or motifs. On the other hand, these "POFs" in plants can not only participate in detected pathways and networks but can also lead to undefined or possibly new functions involved in fundamental or specialized activities and might include novel and undetected networks. Regarding the role of these POFs in response to environmental stresses, the transcripts that encode many "POFs" are expressed in response to abiotic stresses. However, because salinity and drought tolerance are complex traits and are controlled by complicated networks of physiological and biochemical processes, plants use different mechanisms (usually a combination of different mechanisms) to cope with these stresses. Thus, the presence of these proteins, which we term "unknown function" may be essential for new and unknown mechanisms of defense or may play a significant role in signaling pathways of the abiotic stresses response. Fig. 2 depicts a summarized diagram representing different responses under drought and salinity stresses.

Salinity and drought stress are the most important abiotic stresses, especially in dry regions of the world, leading to reduced growth and yield of vital crops. In order to improve the yield of crops growing in saline soil and under abiotic stresses, there is a need for a better understanding of the molecular responses in plants subjected to stress. Recently, in addition to biochemical assays, advanced techniques such as proteomics and transcriptomics have been used to elucidate many of the pathways involved in plant response to stress caused by salinity and drought, and have improved our overall understanding of how to improve tolerance. Proteomics and transcriptomics are powerful tools to reveal how the expression of genes and proteins in plants changes under stresses. The modulation of gene expression has major effects on the growth and physiology of plants. These studies have provided new information about the significance of several gene and protein networks involved in the response of plants to salinity and drought, and the induction of tolerance. Moreover, identifying the crucial pathways which are involved in salinity and drought resistance can open doors for the establishment of commercial resistant crop cultivars, and might be very useful in the next-generation crop breeding strategies to produce plants with salinity and drought-resistant traits.

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