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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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, Galmès 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 involved 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.
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 AB15, 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 of growth as GRF7. GRFs are a set of transcription factors belonging to the type).

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

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subfamily of non-DREB2, 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, 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-Ya45 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 P450 (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 and salinity stress. 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 (Alqarashi et al. 2018), Nicotiana tabacum (Chen et al. 2019), Populus 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 (Sohbanian 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 gymnorrhiza (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, Sohbanian 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, alterations 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 (Vitámvás 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 polycalcin Ph 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] isofrom X2, vesicle-associated protein 2-2-like isofrom 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, CO2 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 (Kosovà 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 (Kosovà 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 (Kosovà 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 (Park 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 (Chourely 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 100000 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 (PsLEAam), 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 2005, Hossain et al. 2013) 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 dehydrogenases 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$_2$O$_2$ 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 stresses. These activated signaling pathways include those related to hormones, kinase cascades, antioxidants, transcription factors, osmoregulatory 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. 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.

Salinity 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 undiscovered 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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