Chapter 11
Understanding Abiotic Stress Tolerance in Plants by Proteomic Approach

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11.1 Introduction

Plants inhabit constantly fluctuating environments that can be stress-inducing and challenging for the growth and development of plants. These ecological nuisances include biotic stresses such as pathogenic invasion and herbivore attacks, and abiotic stresses such as extreme temperature (high and low), drought, salinity, depletion of nutrients, and accumulation of extra salts and toxic metals (Fahad et al. 2013; Hesham and Fahad 2020). Water deficiency, excess salt, and high temperature are the main abiotic stresses and pose a universal threat to plant population. These

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environmental stresses have a catastrophic effect on the geographic location of plants and restrict plant yield (food crops) and nutritional security of crop plants (Fedoroff et al. 2010; Mantri et al. 2012). The way a plant disposes itself to these stresses and develops adaptation to the severity of these stress signals is of prime significance. The approach to establish stress tolerance in plants is the current main focus of agricultural researches (Zhu 2016; Fahad et al. 2021a, b, c, d, e). A number of methods have been exploited previously to induce abiotic stress tolerance in crops. Among them, traditional plant-breeding methods have negligible success rate due to the involvement of multiple genes in stress tolerance. As discussed, stress tolerance is a multigene phenomenon, and it is quite exhausting to understand the mechanisms for advanced breeding programs. Recently, many molecular approaches have been considered to uncover the mechanism with which plants sense stress signals and respond to them. The biological advancement has made it possible to fully understand abiotic stress tolerance in plants using throughput sequencing and functional genomics (Mantri et al. 2012). The exploitation of potential genes that can safeguard and maintain the functions of cells to develop plants with abiotic stress tolerance is the ultimate point of future research in agronomy and agricultural science (Valliyodan and Nguyen 2006). In the following sections, we will evaluate the abiotic stresses, plant responses, and approaches in detail to understand the overall mechanism with specific interest in proteomic approaches to understand the role of protein in abiotic stress tolerance in the plant kingdom.

11.2 Abiotic Stress Tolerance in Plants

Environmental stresses pose a threatening pressure to the survival of plants and have been associated with the influence on the physiology, morphology, biochemistry, and molecular biology of plants (Fahad et al. 2014a, b, 2020). The main abiotic stresses posing a serious threat to plant population include extreme temperatures, drought, salinity, depletion of nutrients, and accumulation of extra salts and toxic metals (Zhu 2016). Abiotic stress is completely different from biotic stresses as it is facilitated by nonliving factors, whereas abiotic stresses are established by the living components of the ecosystem, such as virus, bacteria, fungi, insects, and weeds (Atif et al. 2021; Saleem et al. 2020a, b, c). Abiotic stresses in the form of water deficit, waterlogging, harsh temperatures (extreme hot and cold, frost), saline condition, and mineral toxicity adversely influence the rates of growth and development, productivity, crop quality, and other kinetics (Mahmood Ul et al. 2021; Mohammad I. Al-Wabel et al. 2020a, b)). In the future, it is anticipated that limited water availability will further increase abiotic stresses. Among these stresses, cold is one of the proven stresses that could affect crop productivity via interrupting crop quality and postharvest maintenance. To survive the severity of coldness, plants have developed tolerance against freezing/chilling using an effective phenomenon known as cold acclimation. Salt is on the same page when it comes to threatening global agriculture fraternity by depreciating crop production in salt-abundant regions. Two fundamental effects of salt on crops are mediated by osmotic stress and ion toxicity. Under salt stress, the osmotic pressure beneath soil surpasses the osmotic pressure in plant cells due to salt abundance, thereby limiting plant's ability to acquire water and important minerals. Due to continuous fluctuation in climate, there is a significant increase in global temperature and atmospheric CO_2. The occurrence of rainfall is not consistent globally due to variable climate, which is leading toward drought conditions. Plants restrict their shoot growth and metabolic activities as a result of experiencing water deficit. The global deterioration is also heating up the environment that affects agricultural yields along the growth of crops. The rate of seed germination, photosynthesis, and productivity is worsening when crop plants are confronted with heat stress. Other stresses that are being added to the environment are toxins (toxic metals) resulting from the activities of chemical fertilizers, industries, and use of waste water for irrigation purposes (Gull et al. 2019).

11.2.1 Drought Tolerance in Plants

Drought-induced stress is one of the most common and lethal stresses all over the world. Drought has resulted in loss of large amounts of crop productivity (Ashraf 2010). The application of genomics, transcriptomics, and proteomics has identified the stimulation and regulation of many transcripts and proteins associated with stress tolerance, which are included in two separate groups. One group is lined with cascade signaling and transcriptional regulation, while the other group consists of members involved in the protection of membranes. These members provide their services as osmoprotectants, antioxidants, and scavengers of reactive oxygen species (ROS). The subjection of plant to water-deficient conditions during development can trigger certain physiological and development-related processes. The changes in the physiology and biochemistry upon exposure to drought stress include loss of turgidity and variation in fluidity of membranes, along with composition, fluctuation in solute concentration, ad interactions between proteins–proteins and protein–lipids. Decline in photosynthesis, production of organic acids, and changes in sugar metabolism are some of the physiological and biochemical ways of plants to respond. The assessment of gene expression using cDNA technology has nourished our knowledge about the gene hub that is functional in response to abiotic stresses (Valliyodan and Nguyen 2006). Multiple sequences have been identified in *Arabidopsis*, mainly grouped into two classes: responsive to dehydration (rd) and early response to dehydration (erd) genes (Shinozaki and Yamaguchi-Shinozaki 1996). At least four autonomous regulatory systems are involved in gene expression in response to water-limiting stress. Two of them are abscisic acid dependent (ABA), while the remaining two are abscisic acid independent (Shinozaki and Yamaguchi-Shinozaki 2000). A dehydration-responsive element/C repeat (DRE/CRT), a cis-acting element, is invested in abscisic-independent regulatory system. This responsive element also coordinates in cold- and high-salt-induced expression system. Often overexpressing DRE/CRT-binding protein DREB1/CBF in the genetically modified plant *Arabidopsis*, more than 40 stress-sensitive genes were identified. The level of expression of these genes led to the induction of tolerance in *Arabidopsis* against cold, salt, and water scarcity (Seki et al. 2001; Fowler and Thomashow 2002; Maruyama et al. 2004).

There are small-sized molecules that show no toxicity to cells at molar concentration and provide stability to proteins and cell membrane under stress conditions. These neutral molecules are called osmoprotectants and coordinate the cellular functions to withstand under severe effects of the stress (Yancey 1994). Several main crops do not possess the ability to produce these molecules in response to abiotic stress. Hence, it has been postulated that introducing the pathways essential for the formation of osmoprotectants can be a good effort to enhance stress-bearing ability in plants (Rathinasabapathi 2000). Another product known as mannitol, which is produced during photosynthesis in algae and higher groups of plants, accelerates tolerance in water-limiting conditions with the help of osmotic regulation. By manipulation of *mannitol dehydrogenase* (*mtlD*) gene into wheat, a significant amount of tolerance has been generated under water stress condition (Valliyodan and Nguyen 2006). The shielding of enzymes and membranes from ROS is mediated by D-ononitol and myo-inositol in cytoplasm of cell. In genetically modified tobacco plants, the overexpression of *inositol methyl transferase* gene (*IMT1*) isolated from rice plant has resulted in the enhanced tolerance for drought and salt by the production of methylated form of inositol known as D-ononitol (Sheveleva et al. 1997).

Abiotic stresses interrupt the physiological and biochemical pathways, leading to a sharp decline in plant productivity (Fahad et al. 2016a, b, c, d, 2019a, b). The response system of plants varies depending on various genotypes (Wang et al. 2018). The genomic sequences of plants are triggered by transcription factors in conjugation with other transcription-binding sites (Shinwari et al. 2020). These transcription factors bind to the cis-acting elements in upstream of all gene promoters (Ciarmiello et al. 2011). Furthermore, the transcription factors enhance or restrict the functionality of DNA polymerase for gene expression (Riechmann et al. 2000). The transcription factors stimulate genes associated with stress and elevate drought tolerance response. A group of basic amino acids participate to provide resistance in plants to abiotic stresses (Annunziato 2008). In model plant, for example, *Arabidopsis*, there has been the identification of 1533 transcription factors grouped into about 34 families (Riechmann et al. 2000). In recent years, the tolerance response of *Betula platyphylla* (birch) has been evaluated. In this study, 2917 genes linked to stress tolerance were identified using RNA-sequencing approach. Among them, some drought-responsive transcription factor families, ethylene responsive factor, and myeloblastosis oncogene were reported in maximum amount. Moreover, BpERF2 and BpMYB102 transcriptional factors were associated to tolerance in response to water-deficit stress. These two transcriptional factors further triggered a cascade of other stress-related genes and also boosted drought tolerance in the plant (Wen et al. 2019). Sakuma et al. (2002) explained some types of DREB transcription factors in model plant. They predicted that DREB1A and DREB2A attach to a certain six-nucleotide sequence of DRE and enhance drought-associated

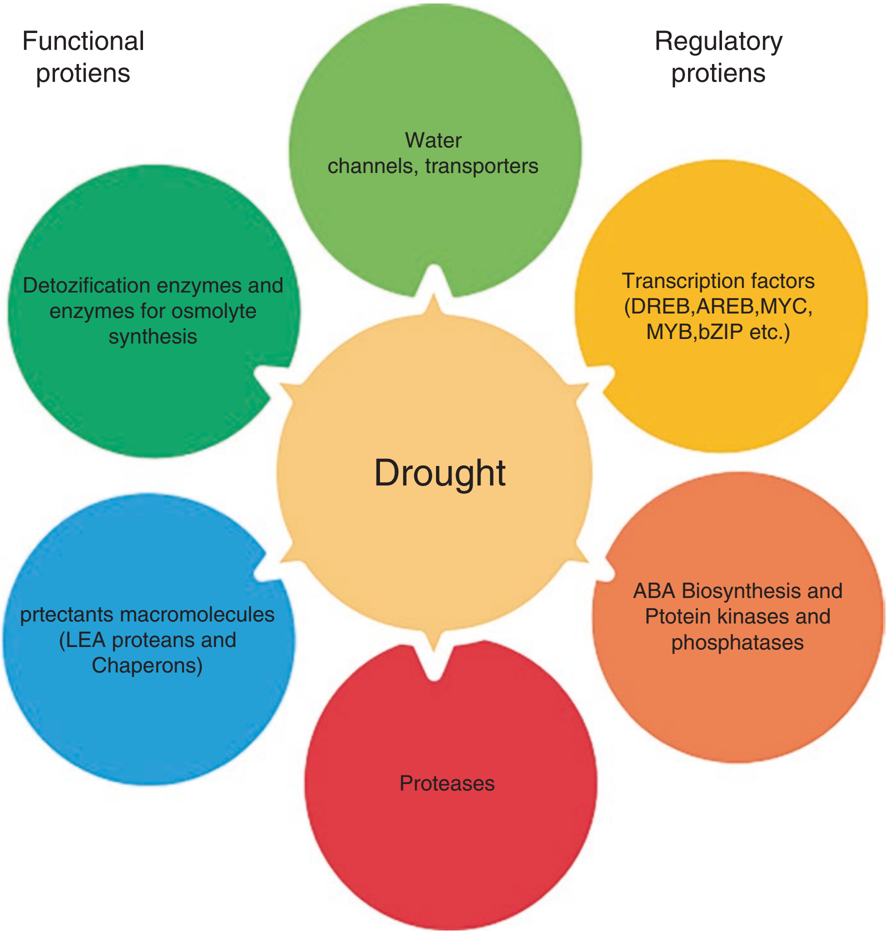

Fig. 11.1 The functions of drought stress-inducible genes in stress tolerance and response. Two types of proteins are produced in response to drought stress. The first group includes function proteins that probably function in stress tolerance, and the second group includes regulatory proteins that function in signal transduction and gene expression of other abiotic stress-related genes. (Shinozaki and Yamaguchi-Shinozaki 2007)

tolerance in *Arabidopsis*. The two main groups of proteins, along with other factors that responded to drought, can be seen in Fig. 11.1.

Studies have proposed in the past that the amount of calcium in cytoplasm elevated in response to certain triggers such as cold, drought, and salt. This calcium influx results in the signal transduction, which is probably linked to a cascade of protein phosphorylation/dephosphorylation. It has been reported that most of the calcium-triggered protein phosphorylation is primarily carried out by members of calcium-dependent kinases (CDPKs) in plants. The gene expression of many CDPK members is also involved in mediating stress signals across some plant species. It is also worth mentioning that a number of transport proteins such as aquaporins and ion channels, which are active during stress regulation, are controlled by CDOKs. The overexpression of *OsCDPK7*, a gene encoding CDPK in rice, increased the stimulation of some stress-responsive genes in reaction to drought/salinity (Saijo et al. 2000).

Aquaporins are trans-membrane proteins mainly responsible for the homeostatic regulation of water in cells. Many researchers have focused on the aquaporins as potential candidates for the integration of drought-tolerance ability into breeding programs (Zargar et al. 2017). The advancement in sequencing technology has made the transcriptome profiling less expensive but effective. The information from the transcriptomes and genomes of hundreds of plants will be supportive to apprehend the phylogenetic distribution and expression of aquaporins in a wide range of species. Some studies proposed that an exposure to dehydration can increase the transcript level of aquaporins, leading to higher water permeability in membrane, mediating water transport, while others assumed that in response to water deficit plants reduce their membrane water permeability to escape the loss of water by down-expression of some aquaporins. The aquaporins located in root tissues also help to avoid stress condition related to water deficiency. The aquaporins in plants' roots are highly regulated and are associated with water-limiting conditions and morphological characterization of the plant. The overexpression of aquaporins is not always a good mechanism in plants. When tobacco plant overexpresses *AtPIP1;2*, the plant gets wilted in drought stress compared to control plants. Moreover, the prominent aquaporin *e HvPIP2;1* when overexpressed in rice resulted in a faster rate of leaf transpiration and decrease in efficiency of water usage (Zargar et al. 2017).

11.2.2 High-Temperature Tolerance in Plants

Global warming has devastating effects on plants due to the lethal effects of higher temperature on the growth and development of plants. The extremity in climatic conditions has resulted in the less productivity and higher chances of famine. According to some reports, India is the main producer of wheat by contributing to 15% of total wheat production, but it is predicted that climatic variation will transpose this production rate into temperature-stressed and negligible seasonal duration. A rise in temperature by 3–4°C could lead to reduction of productivity by 15–35% in Asia and Africa and by 25–35% in the Middle East(Ortiz et al. 2008). In tropical and subtropical regions, the temperature during the growing season may surpass the maximum value of the highest temperature recorded till date (Battisti and Naylor 2009; Varshney et al. 2011). Latin America is supposed to experience blows in temperatures and declines in precipitation all over the continent, particularly in Central America and the Caribbean. In European countries, Southern and Central regions will face increase in temperature, with Spain, Portugal, and Italy suffering the most. Interestingly, the fluctuating climate will significantly enlarge the agricultural production in northern countries, where agriculture is limited due to low temperature (Lotze-Campen and Schellnhuber 2009).

Among all abiotic stresses, the heat stress has an autonomous mechanism of action on the physiology and metabolic pathways of plant cells. The heat-related stress is accompanied by drought and salt stress, but it is obligatory to uncover the independent route of action and biological effects of extreme temperature so that the combined effect of multiple stresses could be apprehended. The vulnerability of plant toward high temperature is dependent on the stage of development and hot conditions that influence the plant in both vegetative and reproductive stages. The affects are also linked to species and genotypes along with interspecific and intraspecific alterations (Barnabás et al. 2008; Sakata and Higashitani 2008). Multiple physiological scratches have been reported in plants upon experiencing rise in temperatures, such as slashing of leaves/stems, abscission and senescence in leaves, and retarded growth in root and shoot and distorted fruits, which ultimately resulted in restricted plant yield (Vollenweider and Günthardt-Goerg 2005). Furthermore, heat stress decreases plant development through changing net shoot assimilation rates and total dry weight of the plant (Wahid et al. 2007).

Plants experiencing higher degree of heat, at least 5°C above their normal growth temperature, demonstrate a unique set of properties of cellular and metabolic responses in order to neutralize the lethal conditions of higher temperatures (Guy 1999). These alterations include modifications in cellular organizations (organelles and cytoskeleton) and membrane activities (Weis and Berry 1988), reinforced by decline in the production of normal protein and incline in the expression of heat shock proteins (Bray 2000). Additionally, the production of phytohormones such as abscisic acid, antioxidant compounds, and certain molecules with protective nature was also reported (Maestri et al. 2002).

One of the proteins that were produced in response to high temperature is heat shock protein (HSP). Recently, the rise in temperature as a result of global warming is the subject of great concern as it has deteriorated the agricultural production in all regions of the world, putting billions of dollars at potential risks (Mittler et al. 2012). Heat stress causes substantial damage to the plants (crops) by affecting protein production, inhibiting main enzymes, and destroying membrane structures. Heat shock instigates oxidative stress, which suppresses plant development and limits yield and nutritional quality. Therefore, plants have acquired molecular chaperons to fold and unfold proteins, and stabilize the assembly of multiprotein complexes and regulation of cell cycle and cellular signaling; the transportation of essential proteins to cellular compartments is also the route of response by plants to ensure protection against the imposing stress or programmed cell death (apoptosis) (Lindquist and Craig 1988).

HSPs, heat shock transcription factor, and molecular chaperons are mandatory for the survival of plants and maintenance of the protein stability under heat shock. High intensity of heat develops heat shock response, which safeguards the plant from cellular injuries and ensures the rehabilitation of cellular and physiological functionalities. These effects also establish a significant level of thermostability in plants. Higher heat exposure also incites the plants to produce ROS and oxidative pressure (Khan and Shahwar 2020). The plants adjust themselves to afford high-temperature stress by adopting certain modifications in plants such as the production of various metabolites like antioxidants, osmoprotectants, and heat shock proteins by changing their metabolic pathways. Further, heat shock also modifies the regulation of genes encoding factors that include osmoprotectants (glycine betaine, proline, trehalose, etc.), phytohormones (gibberellic acids, abscisic acid, brassinosteroids, jasmonic acids, salicylic acid, etc.), detoxifying enzymes, signaling molecules (e.g., nitric oxide), transporters, regulatory proteins, free radical scavengers, polyamines (spermidine, putrescine, and spermine), and protectants in trace elements (silicon, selenium, etc.). These factors mediate signal transduction and transcriptional regulations that have been reported to counteract stress associated with high temperature.

HSPs are stress-associated protein family in cells of almost all organisms synthesized in response to stressful conditions. HSPs are common to both prokaryotes and eukaryotes. Due to the presence of higher conservative sequences, it serves prominent roles in cells. It has been demonstrated that HSPs work in folding, assembling, translocating, and degrading of proteins. There are about five main families of HSPs in plants and animals on the basis of molecular sizes and weights. Some HSPs are localized into cytoplasm and can be found in organelles such as mitochondria, chloroplast, endoplasmic reticulum, and nucleus (Khan and Shahwar 2020). The classification of HSPs on the basis of their cellular location and functions is given in Table 11.1 (Kregel 2002).

Table 11.1 Classification of heat shock proteins on the basis of their cellular location and function

HSP family/ classification	Cellular location/site	Function/role
HSP 20 (sHSPs)	Cytosol. Endoplasmic reticulum, Mitochondria, Chloroplast	Preventing aggregation, co-chaperons
HSP 27 (sHSPs)	Cytosol, nucleus	Microfilament, antipoptotic, stabilization
HSP 60	Mitochondria	Prevents aggregation of denatured protein, refold proteins, proapoptotic
HSP 70 family	Nucleus, cytosol	Antipoptotic
HSP 72 (HSP 70)	Nucleus, cytosol	Molecular chaperons
HSP 72 (Hsc 70)	Mitochondria	Molecular chaperons
HSP 75 (Mhsp 70)	Endoplasmic reticulum (ER)	Molecular chaperons, cytoprotection
HSP 78 (GRP 78)	Cytosol, nucleus, endoplasmic reticulum (ER)	Translocation of protein, regulation of steroid hormone receptors
HSP 100/104	Cytosol	Folding of protein

11.2.3 Low-Temperature Tolerance in Plants

Low temperature, known as temperature from subzero to extremely chilling conditions, is part of natural cycle and inflicts an environmental lockdown on plant's abilities, particularly in cold climates (Janmohammadi et al. 2015). Low temperatures could induce stress in plants via desiccation of cells and tissues when water inside the cells gets frozen (Beck et al. 2004). Low-temperature stress tolerance in plants is a multigenic phenomenon consisting of a network of inducible genes. These genes are related to the synthesis of three types of proteins: structural proteins, regulatory proteins, and osmoprotectants (Breton et al. 2003). While studying low-temperature shock, much of the attention has been given to identify low-temperature-induced proteins and the transcriptional regulation of genes that are responsible for the synthesis of these proteins. Plant response to low-temperature stress is a multifactorial process that is connected to many factors like the stage of development, duration of exposure, intensity of the corresponding stress, thermal rates, and the sites of ice formation where it is produced intracellularly or extracellularly. Low-temperature-tolerant species have adopted different mechanisms to cope with the low-temperature stress. Plants growing over winter can elevate their capacity to afford low temperature, but not chilling temperature, a phenomenon known as cold acclimation (Thomashow 1999). However, it is inappropriate to suggest that even hardy plants possess low temperature/freeing tolerance in all developmental stages. Certain hardy species postpone the transformation of plant from vegetative to reproductive phase until they experience low but nonchilling temperatures, a mechanism known as vernalization that induces the plants to over winter as seedlings (Amasino 2004).

Acclimatization to low-temperature stress is triggered through severe changes in expression of genes that further alter the composition of transcripts, proteins, and metabolites (Thomashow 1999; Chinnusamy et al. 2007). Moreover, some low-temperature-induced protein sequences pass through various types of post-translational modifications such as phosphorylation, ubiquitination, N-glycosylation, SUMOylation, and lipid alterations. These modifications determine the specific aspects of proteins' functionality, such as subcellular localization, stability, and the affinity to associate with other proteins. Hence, it is mandatory to investigate the proteome since, unlike transcript, the proteins are the direct indicators in plant stress response. In the recent decade, efforts have been made to understand the low-stress signaling and regulatory processes underlying cold acclimatization by using proteomics strategies (Weckwerth et al. 2008). In the following sections, the proteome of different crops plants is discussed.

11.2.3.1 Analysis of Wheat Proteome Under Low Temperature

In cold regions, the winter wheat is the most crucial part of agriculture and frost-induced injury during winter and early spring can be disastrous for crops. Plant breeders have sensed the need to introduce wheat cultivars with significant resistance toward winter, but they have negligible success in the development of cultivars that propose enhanced tolerance to freezing conditions. In winter crops, the complete expression of low-temperature-tolerant DNA sequences happens during the vegetative phase. It looks like that developmental genes tend to control genes influencing the transcription and translation of low-temperature-induced genes, a phenomenon recognized as developmental regulation of low-temperature-responsive genes. During cold climate, the wheat vernalization serves a primary role in the acquisition of low-temperature tolerance via inhibition of early transition into reproductive phase prior to the ending of chilling stress (von Zitzewitz et al. 2005).

Low-temperature stress predominantly influences protein synthesis. The participation of RNA-binding proteins in cold acclimation has been apprehended in plants with the help of proteomics (Kosová et al. 2011). A class of RNA-binding proteins known as glycine-rich RNA-binding proteins (abundant in glycine at C-terminal) has been explored in the mediation of low-temperature stress response and can be used as an effective marker for cold tolerance. The synthesis of free and proteinogenic amino acids can be influenced as a result of cold exposure. An enhanced level of several proteins responsible for the biosynthesis of methionine has been reported following cold shocks. Furthermore, the cysteine synthase has been announced as cold stress-responsive protein. In addition to the role of CS in the biosynthesis of cysteine, the protein is also a pacemaker biocatalyst that catalyzes the formation of glutathione. The overgeneration of CS may result in the elevated synthesis of glutathione, which is considered to be associated with tolerance to low temperature (Janmohammadi et al. 2015). Proteome investigation of winter wheat crow after prolonged exposure to cold climate displays a decline in some enzymes catalyzing the biosynthesis of UDP-glucose. Hence, it was presupposed that this may result in the decreased synthesis of cellulose in plants and ultimately could lead to retardation in growth. However, reports on the biochemistry/physiology have shown that low-temperature shocks at the first hour elevated the catalytic activities of b-fucosidase and b-glucosidase, which could in turn intensify hemicellulose turnover with the synthesis of biologically active oligosaccharides that could induce cold tolerance (Zabotin et al. 2009).

11.2.3.2 Analysis of Barley Proteome Under Low Temperature

Barley (*Hordeum vulgare* L.) is one of the widely grown cereal crops in the world, supplementing as a staple food in 1/3 of global population (FAO and Foods 2008). Barley is the most tolerant *Triticeae* species to water stress and salinity. In winter, barley resistance to cold stress is essential for successful overwintering. However, unlike wheat, the proteome reaction to low-temperature stress in barley is less understood. The cold acclimatization process in barley has been investigated based on genomic and transcriptomic. Janská et al. (2011) investigated the translational reaction of barley to periodic low temperature. Their results explored that synthesis of nucleation substances in leaves and crow was downregulated during cold acclimation, while the genes encoding major antifreeze components such as chitinases, glucanases, thaumatin-like proteins, and ice recrystallization inhibition proteins were upregulated. These proteins belong to the class of proteins in plants that enable plants to withstand subzero conditions.

Interestingly, the proteome analysis of barley plants resistant to frost-uncovered (which suffered prolonged cold acclimatization) level of protein variability was higher in leaves as compared to crown and various chloroplast-associated proteins affected, pointing to the tendency to prioritize the protection of photosynthetic machinery (Hlaváčková et al. 2013). This result concluded the presence of unique approaches toward responding to shivering stress in crowns and leaves. Out of all the proteins that exhibited variability at high level, the authors picked out the 33-kDa oxygen-evolving protein of photosystem II and the AAA ATPase in leaves, or the HSP70 and "enhanced disease susceptibility 1" protein in crowns. These findings further stated that these specific proteins might be involved in frost-resistant winter barley, serving as the most distinguished low-temperature-responsive proteins. According to these outcomes, the process of water oxidation during food and energy production in leaves and defense responses in roots is the most forthcoming response to chilling shock. It is the indication of the presence of a complicated connection between chloroplast and cold acclimatization. Those genes that are responsible for chloroplast-localized proteins were also overexpressed, giving green signals about the involvement of plastid-attached proteins in cold tolerance (Svensson et al. 2006). These exemplifications clearly supported the possible assumptions about the response of plants toward decline in temperature of the surrounding and how the plants adapt to extreme climates by regulating its important activities and recruitment of potentially stress-tolerant proteins.

11.2.3.3 Analysis of Rice Proteome Under Low Temperature

Rice (*Oryza sativa* L.) is one of the most consumed cereals and source of sustainable food production in the world. The molecular mechanism underlying cold resistance has been at the center of attention for many decades due to the vulnerability of rice to cold conditions. The cold-induced proteome investigation of the plasma membrane in roots of rice shows that most of the cold-associated proteins were involved in energy generation, cellular signaling, protein formation, cell growth/division, and defense networks (Hashimoto et al. 2009). Furthermore, it has been claimed that variation in membrane permeability in response to chilling temperature resulted in elevated level of cytosolic cations with calcium-dependent membrane-binding proteins such as annexins, which mediate the function of signal processing to low-temperature stress.

Reports of rice seedlings when exposed to short-period low-temperature stress explored that there is a network of low-temperature-responsive proteins (regulatory and functional proteins) serving a potential role in chilling stress tolerance (Yan et al. 2006). Moreover, it has been revealed that a number of proteins become denature in the midst of cold stress. For instance, the injury to enzymes such as glycine dehydrogenase and RuBisCO activase can result in interrupted photorespiration. This mechanism is involved in photosynthetic metabolism and is associated with the recovery of RuBP (ribulose 1,5 bisphosphate) in the Benson–Calvin cycle (Janmohammadi et al. 2015). Cold-responsive proteins are not only restricted to protein metabolism, but are also functional in the biosynthesis of components in the cell wall, free radical-scavenging process, energy generation, and provision of metabolite needed for cold resistance in plants (Cui et al. 2005). In the same study, exposure to cold stress for a short time led to a substantial rise in the level of UDPglucose pyrophosphorylase (UGPase) and sucrose synthase 1; enzymes contribute to Krebs cycle, giving rise to the idea that freeing stress influences the metabolic pathways of carbohydrates. In the meantime, the production of ROS hunting enzymes has been reported as one of the responsive elements during chilling stress. However, the transcriptome of the low-temperature-resistant rice unveiled that, among other genes with antioxidant potential, glutathione peroxidase (GPX) and glutathione S-transferase (GST) were overexpressed in response to low-temperature shock (Zhao et al. 2015). This result may indicate that an integrated regulation of ROS-related enzymes at transcriptional and post-transcriptional levels is most probably active in advancing cold stress tolerance in plants.

An approach to evaluate less-abundant proteins has been used by fractionating these polypeptides with polyethylene glycol (PEG). Using this method, an elevated level of new proteins that included cysteine proteinase, thioredoxin peroxidase, a RING zinc finger protein-like, drought-inducible late embryogenesis abundant protein, and fibrillin-like, was identified in leaves of rice against low-temperature stress (Lee et al. 2007). Neilson et al. (2011) also identified extra-low-abundant proteins such as histones (H2A.3, H2B.9, H3.2, and H4) and vitamin B synthetic proteins mediating response to chilling stress.

Studies in the recent decade have strongly concentrated on the regulatory role of post-transcriptional and post-translational modification of proteins in the low-temperature responses, and hence, there is great fondness in investigating such aspects with proteomic approaches (Miura and Furumoto 2013). In order to investigate the individual mechanism mediating chilling stress, it is believed to be imperative that foundations of proteomic investigation should include comparative analysis of different cultivars of rice.

11.2.4 Heavy Metal Tolerance in Plants

Anthropogenic actions have caused great distress to life on earth. A number of human activities have disrupted the biodiversity around the world with their unplanned and reckless activities. In the same sense, these advanced creatures have contaminated the region with heavy metals, disturbing both the living environment and conditions for plants, animals, and humans. The emergence of such problems is of great concern to the public and governing bodies, and a demand to restore the natural balance is required. The toxicity of contaminants might cause the killing of plants installed for phytoremediation by disrupting different metabolic processes. However, plants survive the severity of metal-induced stress by developing a strategy of tolerance to sustain and survive in contaminated soil. Various studies have focused on the molecular mechanisms involved in the induction of heavy metal tolerance in plants with the help of genomics and proteomics (Macnair et al. 2020).

Plants counteract the environmental contaminants by activating certain genes that are responsible for the synthesis of protein involved in heavy metal stress tolerance. The ions of heavy metals affect the homeostatic regulation of cellular proteins by intervening the folding and trigger aggregation of non-native proteins, affecting the endoplasmic reticulum (ER) and resulting in disturbed cellular activities. However, plants have adopted various survival extinct and enhanced tolerance systems that are used to neutralize heavy metals (Hasan et al. 2017). In cells, the heavy metal ions induce oxidative stress by producing ROS species, which advances DNA deterioration and interrupts the DNA repair strategy of the cell. Moreover, they also handicap membrane integrity, nutrient maintenance, and protein activity (Tamás et al. 2014). When plants are exposed to high concentrations of heavy metals, the cells adopt a complex mechanism of storage and detoxification. This includes the chelation of ions (from heavy metals) with phytochelatins and metallothioneins in the cytoplasm trafficking and sequestration into the vacuole by vacuolar transporters (Zhao and Chengcai 2011).

To escape the destructive effects of heavy metals, plants produce minor cysteine-rich oligomers known as phytochelatins at the start of metal-induced stress. It has been noted that the most peculiar factor in metal-inflicted stress in plants in the synthesis of phytochelatins. Moreover, it is also an established fact that the biosynthesis of the phytochelatins is modulated at post-translational event by metal ions in a variety of plant species. However, the upregulation of phytochelatin synthase gene does not ensure increase in metal stress tolerance in plants (Hasan et al. 2017).

Another important group of proteins associated with metal stress forbearance in plants is intracellular cysteine-rich major metal-binding proteins known as metallothioneins that are recruited by the cells for immobilization, sequestration, and detoxification of metal ions (Capdevila and Atrian 2011). The presence of metallothioneins has been reported in plants since the last few decades; however, the exact physiological roles of these proteins have not yet been fully apprehended (Liu et al. 2015). The anticipated functions of these metallothionein proteins include (a) the homeostatic regulation of essential transition metals, (b) sequestering of lethal heavy metal, and (c) the shielding of cells against oxidative pressure by metal stress (Hossain et al. 2012).

The growth of plants in soil contaminated with heavy metals drives the plants to adjust their physiology by developing metal stress tolerance. Plants overcome these heavy metal stresses through various ways such as synthesis of metal-attaching compounds, metal accumulation in vacuoles, glands-modulated excretions, changes in membrane conformity, and, most importantly, the formation of stress-responsive proteins, including the abovementioned proteins and HSPs (Neumann et al. 1994; Hasan et al. 2017).

11.2.5 Salinity Stress Tolerance in Plants

Each plant has a unique ability of salt tolerance ranging from glycophytes (salt-sensitive species) such as *Arabidopsis* to halophytes (salt-tolerant species) such as Atriplex species (saltbush). Although cereal crops have been claimed as glycophytes, different crops have a separate level of salt tolerance and coping mechanism. For instance, rice shows more glycophtytic characters compared to wheat and barley (Munns and Tester 2008). There can also be considerable genetic variation for salt tolerance within closer species, and this fact can be used to develop salt-tolerant crop breeds (Roy et al. 2011). The collective approaches of functional genomics such as genomics, proteomics, transcriptomics, metabolomics, and ionomics have been exploited to study and analyze abiotic stress tolerance in plants. Investigations of proteins response in plants to saline stress have been carried out in many important species, including cereals like maize (*Zea mays),* rice (*Oryza sativa*), barley (*Hordeum vulgare*), and wheat (*Triticum durum* and *Triticum aestivum*) (Zhang et al. 2012). Proteomic studies of single-cell proteins have been successfully used in mammalian systems where cells can be cultured to enhance the starting materials (Schirle et al. 2003; Diks and Peppelenbosch 2004). However, there are limited examples of single-cell proteins in plants, particularly in cereals, due to the inconvenience in obtaining sufficient materials. Such proteomic evaluation has been demonstrated in guard cell of *Arabidopsis*, trichomes, soybean (*Glycine max*), and tobacco (*Nicotiana tabacum*) trichomes. Proteomic studies of plant tissues in response to salt stress have highlighted rice anthers, rice plasma membranes, and wheat root seedlings (Shelden and Roessner 2013). *Physcomitrella patens* plant shows prominence due to its significant role in the study of plant systematics and evolutionary biology. The high-salt-resilient property makes this plant a unique model to evaluate molecular processes involved in salinity stress response. Proteomic analysis of *P. patens* upon exposure to high-salinity conditions showed that 16 protein spots were downregulated while 49 spots out 65 proteins spots were upregulated. These proteins were related to a diverse set of functions such as energy and metabolic activities, protein biosynthesis, protein degradation, defense cellular behaviors, mitotic division, and signal transduction and transportation. Mainly the overexpressed proteins were involved in defense potentials, protein folding, and homeostatic balancing of ions. Among them, HSP70 is expected to protect from denaturation and degradation due to injury caused by salinity, signally proteins, and phototropin involved in the regulation of H+/ATPase homeostasis and ROS-scavenging proteins, making a potent antioxidative system to safeguard cells from damaged caused by oxidative stress postsalinity exposure in *P. patens* (Wang et al. 2008).

Enhancement in proteomic technology in the term of protein separation and detection and mass spectrometry-based protein analysis has a substantial role in studying plants reflexing under extreme saline conditions (Joseph and Jini 2010). While multiple research groups are active in identifying salt-responsive proteins in plants, a study by Salekdeh et al. (2002) recovered many salt-responsive proteins such as ABA and stress-responsive proteins, ascorbate peroxidase, and several more in the root proteome of both salt-sensitive and salt-tolerant rice genotypes. Most of the proteins were regulated by the salt level in a direct manner (Nohzadeh et al. 2007). The activities of these proteins were seen in photosynthetic activity, metabolic homeostasis, photorespiration, signal transduction, antioxidation, regulation of ions channels, and protein folding. In plants, salt shock proteins (SSPs) are accumulated in response to salt stress that can result in the synthesis of other soluble proteins and bolster the activities of many enzymes (Joseph and Jini 2010). The variation in genomics content (DNA/RNA) of plants upon experiencing saline stress could be accountable for the expression of specified salt shock proteins (SSPs) with molecular weights of 15.28 and 72 kDa in salt-tolerant genotypes, whereas they were entirely absent in vulnerable genotypes (Gomathi and Vasantha,2006). One way to encounter salinity stress is with induction of molecular chaperons. It is interesting in nature that drought, salt, and heat stresses are often unanimous in their effects. Heat shock proteins are a group of proteins consisting of conserved protein families such as HSP100, HSP90, HSP70, HSP60, and other small heat shock proteins (Joseph and Jini 2010)

11.3 Conclusions

The main abiotic stresses in plants and protein-producing mechanisms in plants to tolerate these unfavorable signals were discussed. There are other abiotic stresses evolving with fluctuation in climate that have devastating effects on the plants, particularly crops, and need utmost scientific attention. We should investigate the crops in different geographic regions around the world to understand the significance of abiotic stresses in variable regimes. Moreover, it is also mandatory to use proteomic strategies along with genomics to identify versatile proteins that can provide a grasping view of stress and tolerance interaction in plants so that the main cash crops can be exploited with these potential tolerant proteins to make a balance between agriculture and economy.

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