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PROTEIN METABOLISM IN PLANTS UNDER ABIOTIC STRESS: AN OVERVIEW

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ABSTRACT

Plants are frequently subjected to several abiotic environmental stresses under natural conditions causing profound impacts on agricultural yield and quality. Tolerance and acclimation of plants are always related to significant changes in protein, cellular localization, post transcription, and post-translational modifications. This review discusses the different stress-induced protein response pathways that help plants to survive under stressful conditions. In a nutshell, this paper provides an overview of several modifications, synthesis, degradation, and metabolism of protein in plants to cope up with the abiotic stresses such as drought, submergence, cold, and heat to revive again to normal growing conditions.

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1.1 BACKGROUND

Alterations in global climatic change invite stress (Fukao and Xiong, 2013); any environmental factor can adversely affect plant growth, development, crop quality, and finally yield as well (Kosová *et al.*, 2011). The major abiotic stresses like drought, heat, low temperature and salinity show dominant effects in the agriculture system worldwide. Plants acclimatize leading to escape stress where survival is in metabolically dormant phases (such as seeds) or activate stress response to the altered environment via changes in transcriptome, proteome, and metabolome and ultimately resulting in changes in gene expression (Levitt, 1962). Gygi *et al.* (1999) and Bogeat *et al.* (2007) suggest changes at transcript level do not correspond with protein level for gene expression. Since proteins are the components directly affecting plant stress response thus, this review investigates the plant proteome changes which is highly important for identifying plant response to stress. Along with the enzymes responsible for catalyzing changes in metabolite levels, elements for transcription and translation activities, also constitute proteins. Changes in protein accumulation during stress and plant phenotypic response to stress are directly related and determine plant tolerance to stress. Kosova *et al.* (2011) stated knowledge of the plant stress tolerance mechanism at the protein level is crucial to understand plant reaction under stress conditions.

Undoubtedly, metabolism is centralized in signaling, physiological regulation, and defense mechanisms when plant growth is affected in an adverse environment. At the same time, biosynthesis, concentration, transport, and storage of primary and secondary metabolites are also affected as feedback. In response to abiotic stressors, metabolic adjustments involve fine adjustments in amino acids, carbohydrates, and amine metabolic pathways. Different experiments showed that metabolic activities respond faster to stress than transcriptional activities, which enables the identification of tolerance traits due to the collection and integration of metabolic data concerning abiotic responses that may be transferable to cultivated crop species (Fraire-Velazquez and Emmanuel, 2013).

Stress intensity and its duration is essential for plant stress response which is distinguished on several stages, such as an initial alarm phase, an acclimation phase, a maintenance phase, and an exhaustion phase. It creates shock on a non-acclimated plant in the initial phase with decreased plant stress tolerance; an acclimation phase leads to the establishment of new homeostasis in plant metabolism which is maintained under stress conditions in the maintenance phase. However, if stress persists for a longer duration and plants fail to maintain their induced homeostasis environment, finally end up in the exhaustion phase. Stressed environment ceases, fortunately, the plant enters a recovery phase with re-manufactured cellular homeostasis under non-stressed conditions. Here, every stage that occurred for plant response to stress could be attributed to its specific proteome composition, and the recovery stage where the plant establishes new homeostasis is an active process requiring extra energy (Kosová *et al.*, 2011). Thus, every activity that the plant shows against stressed conditions for its tolerance is preserved at the proteome level. The composition of protein at each step is specific and different from those in normal conditions.

In the following review, different studies and findings dealing with metabolic responses and changes in proteomes against various factors of abiotic stress: cold, heat, drought, flood, and water-logging are discussed and summarized.

1.2 ABIOTIC STRESSES AND ITS IMPACT ON AGRICULTURE

These days, agriculture possesses a great challenge to ensure food supply insufficiency while maintaining high productivity and quality standards. Nevertheless, despite increasing demographic demands, climate changes with alteration in weather patterns are threatening crop productivity globally (Fraire-Velazquez and Emmanuel, 2013). Unfavorable climate change causes changes in agro-ecological conditions and indirectly affects the growth and distribution of incomes as well, ultimately increasing demand for agriculture production (Schmidhuber and Tubiello, 2007). Major growth stressors such as different factors of adverse climate, for instance, drought, extreme temperature (heat, freezing), irradiance, and soil contamination by high ion concentration are responsible for limiting crop productivity and quality worldwide (FAO, 2011). These effects of adverse scenarios could cope up with the flexibility of biodiversity (genes, species, and ecosystems) in increasing the ability of crop plants to adapt to abiotic stresses. According to FAO (2007), the use of cultivated plants is promoted by Food and Agriculture (FAO) of the United Nations for the selection and propagation of crop varieties adapted or resistant to adverse conditions. Also, global programs, such as Global Partnership Initiative for Plant Breeding Capacity Building (GIBP) propose to choose and disseminate crops and cultivars with tolerant ability to abiotic stresses for sustainable use of plant genetic resources for food and agriculture (GIBP, 2012).

1.3 PLANT RESPONSES TO ABIOTIC STRESS

Plants have evolved and developed a wide variety of highly sophisticated and efficient mechanisms to sense, respond and acclimatized to a wide range of environmental changes; and respond by activating tolerance mechanisms at multiple levels of organization (molecular, tissue, anatomical, and morphological), through the adjustment of membrane system and cell wall architecture, altering the cell cycle, rate of cell division, and by metabolic tuning (Atkinson and Urwin, 2012). Many molecular genes are induced and repressed by abiotic stresses at the molecular level involving a precise regulation of extensive stress-gene networks (Delano-Frier *et al.*, 2011; Grativol *et al.*, 2012; Shinozaki and Yamaguchi-Shinozaki, 2007) and their products may function in stress response and tolerance at the cellular level. Proteins involved in multiple protein functions, such as biosynthesis of osmoprotectant compounds, detoxification enzyme systems, proteases, transporters, and chaperones act as the first line of direct protection from stress. Moreover, regulatory proteins, for instance, transcription factors, protein phosphatases, and kinases, and signaling molecules activation are essential in the regulation of signal transduction and stress-responsive gene expression (Krasensky and Jonak, 2015, Wang *et al.*, 2009).

Generally, observed tolerance responses towards abiotic stress in plants are composed of stress-specific response mechanisms and adaptive responses that confer strategic advantages in adverse conditions. In energy maintenance, general response mechanisms related to the central pathway are involved, including calcium signal cascades (Pan *et al.*, 2012), reactive oxygen species signaling elements (Ahmad *et al.*, 2010; Loiacono and De Tullio, 2012), energy deprivation signaling (energy sensor protein kinase, SnRK1) (Baena-Gonzalez and Sheen, 2008), and induction of these central pathways are observed during plant acclimation towards different stress. Hey *et al.* (2007), Ghillebert et al. (2011) and Cho *et al.* (2012) presents an example, where protein kinase SnRK1, despite being a central metabolic regulator of the expression of

genes related to energy-depleting conditions, also get activates when plant face different sorts of abiotic stresses such as drought, salt, flooding or nutrient deprivation. SnRk1 kinases alter over a thousand stress-responsive gene expression allowing the re-establishment of homeostasis by repressing energy-consuming processes, thus promoting stress tolerance (Cho *et al.*, 2012; Baena, 2010). Optimization of cellular energy resources is essential during stress for plant acclimation; and partially arrested energetically expensive processes, such as reproductive activities, translation, and some biosynthetic pathways. For instance, in maize during salt stress and potassium deficiency stress, nitrogen, and carbon assimilation are impaired; also, the synthesis of free amino acids, chlorophyll, and protein are affected (Good and Zaplachinski, 1994; Qu *et al.*, 2011, Holcik and Sonenberg, 2005). After cessation of the energy-expensive process, energy resources can be redirected to activate protective mechanisms (Dhaubhadel *et al.*, 2002).

1.4 PLANT STRESS TOLERANCE AND RESISTANCE

Plants, sessile organisms, are continuously confronted with several detrimental factors rising from an ever-changing environment, and to cope up with these problems, they have developed sophisticated and delicate defense mechanisms. In fact, diverse defense signals including the production of reactive oxygen species (ROS), change in redox potential or cellular level of calcium ion, disruption of ion homeostasis, and membrane fluidity adjustments are activated (Gilroy *et al.*, 2016, Choudhury *et al.*, 2017). Once external stress is sensed via specific receptors, a foreign signal is induced into intracellular downstream signaling pathways including the activation of protein kinase or phosphatase, stimulation of downstream target proteins, and biosynthesis of phytohormones for the control of plant growth/development (Sheikh *et al.*, 2016, Akimoto-Tomiyama *et al.*, 2018).

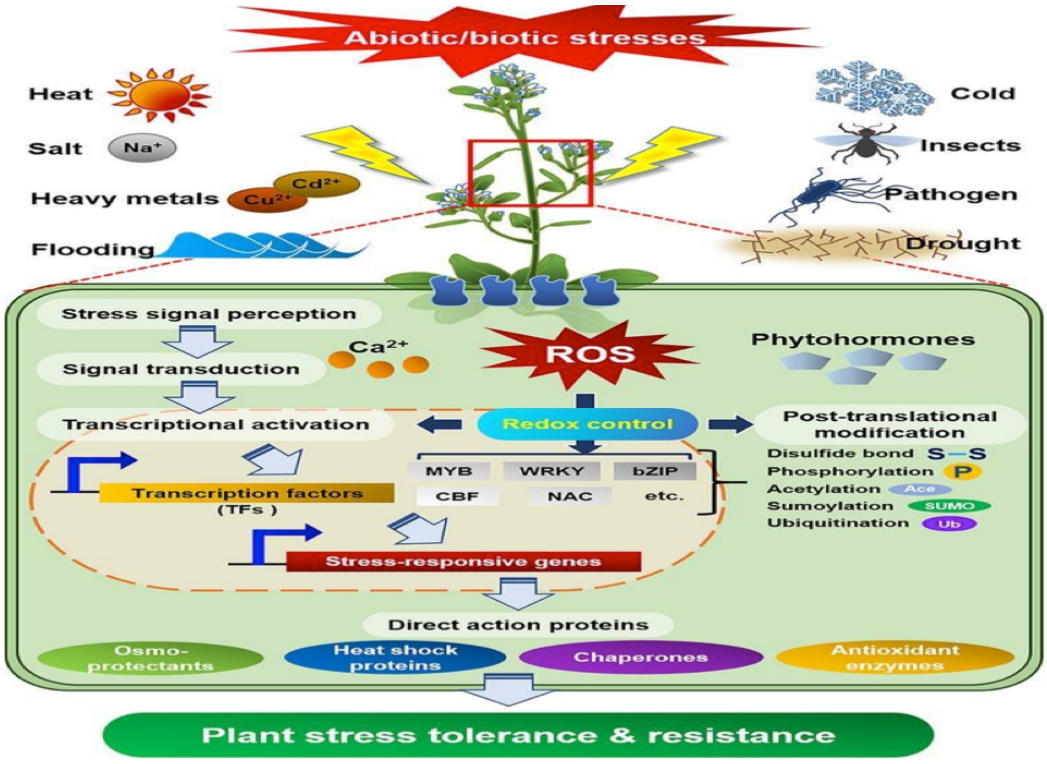

Figure 1: Defense signaling in plants against diverse abiotic external stresses

1.5 ROLE OF AMINO ACID DURING STRESS

Gene expression can be adversely affected by salinity, drought, and temperature stress, and many genes coding for enzymes involved in cellular metabolism are differentially expressed upon stress, thus modeling some stress-related transcription factors to induce changes in stress-associated metabolite levels (Krasensky and Jonak, 2015).

For the synthesis of secondary metabolites and signaling molecules, several amino acids can act as precursors, for instance, polyamines are derived from Arg (Alcázar *et al.*, 2006), Met synthesized the plant hormone ethylene (Amir, 2010), and conversion of Lys to N-hydroxy pipecoline is necessary for immune signaling (Chen *et al.*, 2018, Hartmann *et al.*, 2018). Moreover, several aromatic amino acids, such as Phe, Tyr, and Trp, or intermediates of their synthesis pathways produce a broad spectrum of secondary metabolites possessing multiple biological functions and health-promoting properties (Tzin and Galili, 2010). Usually, plants exposed to different abiotic stresses tend to accumulate free amino acids (Aleksza *et al.*, 2017, Huang and Jander, 2017), as exemplified to this response, several researchers (Martinelli *et al.*, 2007, Ranieri *et al.*, 1989, Showler, 2002) reported extensive accumulation of amino acid in response to drought stress in maize, cotton, tomato, and the resurrection plant. Also, recent studies conducted by Barros *et al.* (2017), Hildebrandt (2018), Hirota *et al.* (2018), Huang and Jander (2017) suggest increment in free amino acids as a result of autophagy and abscisic acid-induced. Similarly, plants surviving in the stressed environment can use amino acids as an alternative for mitochondrial respiration substrates during inadequate carbohydrate supply due to a decrease in photosynthesis rates (Araújo *et al.*, 2011, Hildebrandt, 2018). Although ambiguity remains for the specific role of catabolic pathways, the degradation pathways for Lys and the branched-chain amino acids Val, Leu, and Ile have already been identified as crucial factors for dehydration tolerance for Arabidopsis (Pires *et al.*, 2016). And, soon after reviving of plants to favorable growth conditions, reprogramming their metabolism to switch back for survival and active growth is necessary, thus Batista-Silva *et al.* (2019) concludes in his paper metabolic adjustments to the stress conditions as well as plant's efficiency of resuming its growth and seed production after stress release will also affect plant fitness and crop yield ultimately.

Members of the AP2/EREBP (Apetala2/ethylene-responsive element-binding protein) family of transcription factors, CBF/DREB1 proteins (C-repeat binding factor or dehydration responsive element binding proteins), such as CBF1/DREB1B, CBF2/DREB1C, and CBF3/DREB1A play a key role in the transcriptional response under osmotic stress (Shinozaki and Yamaguchi-Shinozaki, 2007, Thomashow, 2010). Liu *et al.* (1998), Kasuga *et al.* (1999) Gilmour *et al.* (2000) and Gilmour *et al.* (2004) stated improved tolerance of Arabidopsis to freezing, drought, and/or salt stress via over-expression of these transcription factors, and Gilmour *et al.* (2000), Gilmour *et al.* (2004), Cook *et al.* (2004), Achard *et al.* (2008) supported above researchers confronting plants over-expressing of CBF/DREB1 accumulated higher levels of proline and soluble sugars (glucose, fructose, sucrose, and raffinose) when grown under normal growth conditions and during cold acclimation. The conclusion made by Cook *et al.* (2004) and Maruyama *et al.* (2009) suggested the overall metabolic profile of CBF3/DREB1A over-expressers grown at normal growth temperatures resembled that of cold-exposed plants.

2. PROTEOMIC OVERVIEW ON ABIOTIC RESPONSES IN PLANTS

The biological research of abiotic stress in plants can be studied in a broad range of transcriptomic and proteomic based, provides comprehensive information, during and following stress condition, on alteration of gene expression and proteome profile (Hakeem *et al.*, 2012), the study about 30 min to 1 day after induction and time-lapse between transcriptomic and proteomic suggest the more than 50% of gene responsive to flood, heat and other stress were found to encode transcription regulators (Kilian *et al.*, 2007).

2.1 PROTEIN METABOLISM IN PLANT ROOTS AND SHOOTS DUE TO DROUGHT STRESS

Due to prolonged water deficit in the soil causes drought, that vastly affects the metabolism and physiological function in growing plants especially roots and, responsive for water supply from soils to leaves and photosynthesis respectively. Most of the proteomic evidence has been noticed due to drought conditions, six steps predominantly occur in the responsive drought stress. Signaling and sensing receptor, yet not especially but drought-responsive photoreceptor, phytochrome C1, found in maize, phytochrome gene (i,e., PHYA, PHYB, and PHYE) in Arabidopsis, believed to regulate the transcription of light-responsive genes by modulating the activity of several transcription factors and involved in suppressing drought tolerance. Other signaling cascades, G protein subunits (alpha and beta), small G protein (e.g., Ras-related protein Rab7 and Ras-related nuclear protein Ran), and a Ran-binding protein 1 (play important role in cell cycle and DNA synthesis), regulates positive role in drought stress (Zhang *et al.*, 2008), involved in vesicle trafficking, intercellular signaling, polar growth, plant hormone signal cross talk and stress response (Ma *et al.*, 2007). The PgRab7 gene was up-regulated by dehydration in *P. glaucum* - (Choudhary *et al.*, 2015), while overexpression of the peanut AhRabG3f exhibited enhanced tolerance to drought stress in transgenic peanut (*Arachis hypogaea* L.) (Song *et al.*, 2012) but the negative role in Arabidopsis. Calcium-binding proteins (CaBs), such as calmodulin (CaM), calcium-sensing receptor (CaSR), calreticulin (CRT), and calcium-dependent protein kinase (CDPK), enhanced the survival of *T. aestivum* (Islam *et al.*, 2015), and several protein kinases (e.g., serine/threonine-protein kinase, germinal center kinase (GCK)-like kinase MIK, receptor-like protein kinase HERK 1-like, phototropin family protein kinase, and salt-inducible protein kinase), implies their role in drought response signaling pathway, in addition, the Phosphorylation level of protein phosphatase 2C (PP2C), act as a negative regulator for plant drought tolerance in the abscisic acid (ABA) signaling pathway, which can inhibit the activity of SnRK, leading to a decrease of the phosphorylation of its substrates in the signaling cascade (Li *et al.*, 2009). Similarly, 14-3-3 protein availability fluctuation shows the drought condition and reported that drought stress can directly alter the abundance of 14-3-3 proteins (Li *et al.*, 2015). In addition, overexpression or silencing of the 14-3-3 protein genes can modulate drought tolerance of transgenic plants (e.g., Gossypium hirsutum and Arabidopsis) (Sun *et al.*, 2011, Sun *et al.*, 2014).

The role of phytohormones plays important role in signal transduction pathways such as drought-increased ethylene-responsive transcription factor (ERF) in Gossypium herbaceum (Deeba *et al.*, 2012) and some members of the drought-responsive auxin-binding protein (ABP) family in Q. robur (Sergeant *et al.*, 2011), Z. mays, and polar clones (Bohler *et al.*, 2013). Under drought stress, ERF gene was induced in G. herbaceum (Jin *et al.*, 2008, Jin *et al.*, 2009), and its overexpression in various plants, such as sugarcane SodERF3 overexpression in tobacco, tomato TERF1 in rice,

and Brassica rapa BrERF4 in Arabidopsis, can improve plant drought tolerance. BpERF11 was found to negatively regulate osmotic tolerance in Betula platyphylla (Zhang *et al.*, 2016). ABP members such as ABP2, ABP20, and ABP19a are found in response to drought stress, additionally, TRIP-1 was phosphorylated by the brassinosteroid (BR)-insensitive I (BRI-1) protein, drought-increased TGF-β-receptor interacting protein 1 (TRIP1) was found in Sporobolus stapfianus (Oliver *et al.*, 2011) triggered the BR signaling pathways in water deficit condition.

Gene expression plays an important role in the transcriptional regulatory networks, requires chromatin structure modification i.e., histone, a major protein of chromatin and regulates the expression and high mobility group protein (HMG), involved in cell cycle progression. Several histones such as histone H1 was found to be decreased in drought-sensitive Z. mays cultivar but increased in a drought-tolerant one (Benesova *et al.*, 2012) and H2B histone H1 was decreased in a drought-sensitive Z. mays cultivar but increased in a drought-tolerant one (Benesova *et al.*, 2012).

Similarly, the phosphorylation level of HMG was significantly decreased in a drought-tolerant wheat cultivar but increased in a drought-sensitive one (Zhang *et al.*, 2014) that reduced its binding to DNA, inhibiting replication and transcription (Zhao *et al.*, 2009).

Several RNA processing-related proteins changed over the stress condition, representing the critical for plants to cope up. Five glycine-rich RNA binding proteins (GR-RBPs) increased with drought and three GR-RBPs decreased with drought which binds to RNA molecules for transcriptional gene regulation and is suspected to function in the regulation of specific gene expression. For instance, transgenic rice consisting of GR-RBPs gene shows higher yield and drought recovery rate as compared to wild rice (Yang *et al.*, 2014), besides overexpressed in Camelina sativa, reduced the drought-tolerant (Kwak *et al.*, 2016). Similarly, S-like Ribonucleases (RNases) specialized function as stress regulation, defense against microorganisms, phosphate scavenging, and even nitrogen storage, increased in rice under drought (Salekdeh *et al.*, 2002).

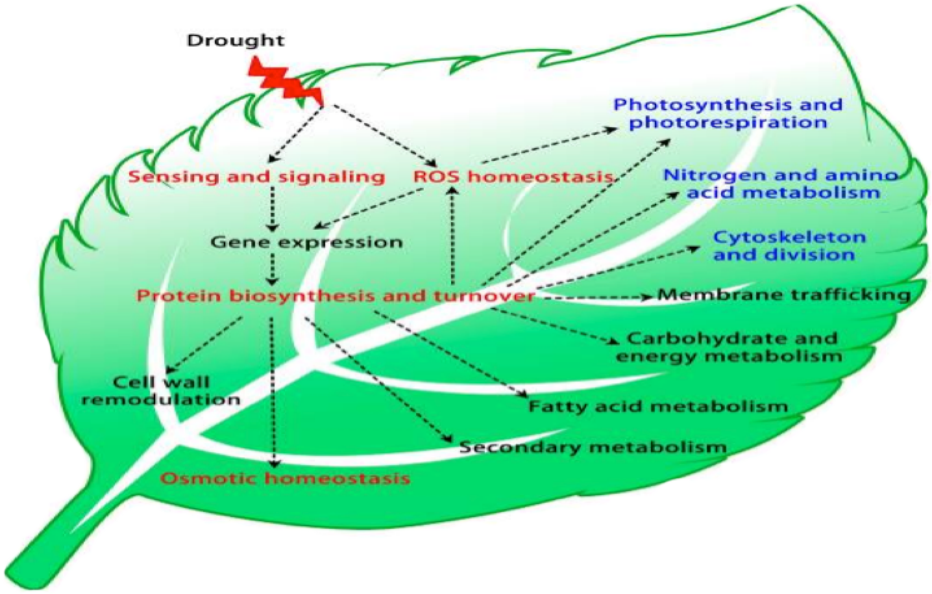

Figure 2: protein metabolism response on drought condition in plant leaves

Additionally, an intron splicing related protein, and maturase K (MatK) and multiple organelle RNA editing factor 9, involved in RNA editing in mitochondria and plastids, was found to fluctuate in *B. napus* with the extension of drought stress (Koh *et al.*, 2015) indicates the transcriptional regulation.

The most fundamental metabolic process to cope up with drought stress, a plant can attribute to protein synthesis and turnover. Several proteins are involved in protein biosynthesis, such as ribosomal protein (RP), elongation factor (EF), translation initiation factor (TIF), tRNA synthetase (TRS), and ribosome recycling factor (RRF), beneficial to protein synthesis, besides protein folding and processing varies cultivars and species. Instances, peptidyl-prolyl cis-trans isomerases (PPIases) were significantly increased in *G. max* (Mohammadi *et al.*, 2012), *T. aestivum* (Ford *et al.*, 2011), *O. sativa* (Pandey *et al.*, 2010), and *Q. robur* (Sergeant et al., 2011), but decreased in a drought-sensitive cultivar of Phaseolus vulgaris (Zadraznik *et al.*, 2013). Protein disulfide isomerases (PDIs) were found to be high in barley and *B. napus*, but low in *Agrostis stolonifera*, *Q. robur*, and poplar. In addition, ER-luminal binding protein (BiP), trigger factor-like protein (TIG), common heat shock proteins (HSPs), and other molecular chaperones (i.e., calnexin, endoplasmin) were found to be increased, while T-complex protein and HSP70-HSP90 organizing protein were found to be decreased in the leaves of drought-treated plants. This protein helps in maintaining the normal protein folding, repairing, and renaturation of the stress-damaged protein, whereas HSP popularly functions in protein folding in Arabidopsis and yeast for improving the drought tolerance (Gao *et al.*, 2010).

Protein degradation, the process of removing the abnormal, damaged protein and maintenance of a certain level of regulatory proteins during drought, includes the components such as - ubiquitin/26S proteasomes, small ubiquitin-like modifier (E3 SUMO) ligase, and proteases/peptidases (ATP-dependent Clp protease, cysteine proteinase, zinc metalloprotease, aspartic proteinase, serine carboxypeptidase and aminopeptidases (APs)). This component shows positive response in *P. vulgaris* (Zadraznik *et al.*, 2013) *Hordeum vulgare* (Ghabooli *et al.*, 2013), *B. napus* (Koh et al., 2015), and Medicago sativa (Aranjuelo et al., 2011) under drought condition, involved in ubiquitination, exhibited significantly increased values in drought-tolerant and decreased in drought-sensitive leaves.

Due to drought conditions, it interrupts the normal cellular mechanism to produce ROS. Plant evolve diverse mechanisms to keep ROS homeostasis in cells, including anti-oxidative enzymes eg. SOD (first defense mechanism by converting O2 into H2O2) and CAT (convert H2O2 into H2O and O2), and chemical antioxidants (e.g. glutathione and ascorbate). The diverse abundance of SODs in cytosolic, peroxisomes as well as in chloroplast helps in the drought-tolerant and avoidance. For instance, increment of cytosolic Cu-Zn SODs drought avoidance CT9993 and drought tolerance IR62266), while chloroplast Cu-Zn SODs were increased in CT9993, but decreased in IR62266 (Salekdeh *et al.*, 2002), additionally in a cultivar of Malus domestica, Cu-Zn SOD decreased and Fe SOD increased. Similarly, in Ascorbate-Glutathione (AsA-GSH) pathways, the ascorbate peroxidase (APX) reduces H2O2 to H2O using ascorbate (AsA) as an electron donor, then the oxidized AsA is restored by monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) (Miller *et al.*, 2010). GR catalyzes the reduction of glutathione disulfide (GSSG) to the sulfhydryl form GSH and works out for the drought-tolerant. In addition, some protein that involved in glutathione-mediated ROS scavenging: glyoxalase (GLO),

phospholipid hydroperoxide glutathione peroxidase, glutamate-cysteine ligase (GCL), glutaredoxin (Grx), and monothiol. GLO catalyzes the detoxification of methylglyoxal, whereas GCL, the first enzyme in GSH biosynthesis pathways found in drought-stressed B. napus (Koh *et al.*, 2015). Additionally, Prx/Trx also catalyzes the reduction of H2O2, whose abundance responds to drought. The Trx-linked enzyme, methionine sulfoxide reductase (MSR), which is involved in the conversion of methionine sulfoxide to methionine, protects the cells and tissues from oxidative stress. Besides, Glutathione Peroxidase/Glutathione S-Transferase pathways, GPX catalyzes the reduction of H2O2 using Trx (Foyer and Shigeoka, 2011), and GST catalyzes conjugation reactions between GSH and several xenobiotics, playing a key role in the degradation of radical oxygen species (ROS). To cope with drought, GPXs were found to increase in *Boea hygrometrica* (Jiang *et al.*, 2007), E. elongatum (Gazanchian *et al.*, 2007), and B. napus (Koh *et al.*, 2015).

There will be an occurrence of pathogen when left plant for water deficit condition, but some pathogenesis-related protein viz. chitinase, disease resistance protein (DRP), polyphenol oxidase (PPO), oryzacystatin, pathogen defense-related protein 10 (PR10), and disease resistance gene analog PIC15 increased in the response to drought conditions. These proteins act on the pathogen by acting on insect exoskeleton and fungi cell walls, catalyzing the oxygen-dependent oxidation of phenols to quinones' during plant defense, acting as cysteine proteinase inhibitor in the phytocystatin family of proteinase inhibitors. e.g. The over-expression of the oryzacystatin gene was found to be linked to improving total SOD and guaiacol POD activities resulting in increased tolerance to drought in Tobacco.

Osmotic regulation will be hindered due to - exposure to water deficit, but important osmotic homeostasis-related protein viz. embryogenesis abundant (LEA) protein, dehydrin (DHN), and betaine aldehyde dehydrogenase (BADH), which function as cellular protectants to stabilize cellular components, protein structure through detergents and chaperone-like properties, act as calcium buffer. LEA proteins were also increased in *Z. mays* (Benesova *et al.*, 2012) and *B. napus* (Koh *et al.*, 2015) under certain drought conditions.

Cell division and cell wall formation decreased due to decrease in phosphorylation of several proteins (cell division cycle protein, division protein ftsZ1, and cyclin A2) when exposed to drought which implies the suppression of cell growth. Cytoskeleton and cell wall components require cell division, morphogenesis, and signal transduction, while cytoskeleton protein viz. actin, kinesin motor protein, tubulin, profilin, actin depolymerizing factor, and fibrillin to check the cell growth during stress. Additionally, the translationally-controlled tumor protein homolog (TCTP), is a Ca2+ binding protein, which protects against stress and apoptosis, cell growth, and microtubule organization, which was significantly drought-increased in *H. vulgare* (Ghabooli *et al.*, 2013), *T. aestivum* (Zhang *et al.*, 2014, and *B. napus* (Koh *et al.*, 2015), which would facilitate plant adaptation to drought stress.

Cell wall extensibility was directly affected by water loss, while cell wall polysaccharide synthesis/hydrolysis, lignin biosynthesis, and cell wall loosening in leaves were drought-responsive enzymes. Two enzymes, glycosylated polypeptide, and pectin acetylesterase are involved in polysaccharides synthesis, another two enzymes xylanase inhibitor and polygalacturonase inhibitor, are involved in polysaccharide hydrolysis inhibition. Three lignin biosynthesis related proteins, phenylalanine ammonia-lyase (PAL), caffeic acid 3-O-methyl-

transferase, and caffeoyl-CoA O-methyl-transferase, catalyze the transformation of phenylalanine to cinnamylate of lignin biosynthesis, while two cell wall structural proteins (i.e. glycine-rich protein and fasciclin-like arabinogalactan protein) increases cell wall synthesis by supplying UDP-glucose directly to the cellulose synthases and/or callose synthases in response to drought (Amor *et al.*, 1995). Hence, improve the mechanical strength for minimizing water loss and cell dehydration. Another important activity of cell wall loosening/expansion, important aspect in the adaptation to drought, which was related enzymes, polygalacturonase/pectin depolymerase (PG) in *O. sativa* (Pandey *et al.*, 2010) and xyloglucan endotransglycosylase (XTH), where PG degrade pectin, while XTH can cleave and reform the bonds between xyloglucan chains to regulate cell wall rigidity.

Membrane trafficking localized in mitochondria, plasma, and vacuole. Two mitochondrial protein carriers (dicarboxylate/tricarboxylate carrier (DTC) and 2-oxoglutarate/malate carrier protein (OMC)), catalyze the transport of various metabolites (eg., dicarboxylates, tricarboxylates, amino acids, and keto acids), plays important role in gluconeogenesis, nitrogen metabolism, as well as biotic stress (Spagnoletta *et al.*, 2006). Another, Remorin, aquaporin and PEG, plant-specific plasma membrane protein have importance in plant-microbe interaction and signal transduction (Lefebvre *et al.*, 2010). Additionally, the vacuolar H+-pyrophosphatase (V-PPase), vacuolar-ATPase (V-ATPase), and ABC transporter ATPase, are crucial in generating H+ gradient by translocating H+ into the vacuoles that provide a driving force for the accumulation of ions and other solutes in the vacuole and function for abiotic stress.

Photosynthesis inhibition is the primary detrimental effect due to drought stress, and related protein decrease. To cope with this situation, drought increased protein involved in the photoreaction and Calvin cycle in leaves. Light-harvesting chlorophyll a/b-binding proteins (LHCB), involved in ABA signaling partially by modulating ROS homeostasis, besides, an abundance of sedoheptulose-1,7-bisphosphatase (SBPase) and carbonic anhydrase (CA), catalyzes the reversible hydration of CO2, and influence internal conductance (Majeau *et al.*, 1994) and abundance of the protein involved in photorespiration, significantly increases and decreases glycolate oxidase, glycine dehydrogenase, serine glyoxylate aminotransferase, and serine trans-hydroxymethyltransferase, aminomethyltrans-ferase (AMT) and glycine dehydrogenase to adapt the drought stress. The mechanism in photorespiration can protect photosynthesis from photoinhibition and prevent ROS accumulation in green tissues.

Involvement in carbohydrate and energy metabolism is an important step to cope with drought conditions. Phosphoglucomutase (PGluMs), Fructose-bisphosphate aldolase (FBPA) in glycolysis and aconitate hydratases in TCA cycle increased in drought condition which inhibits helps in the accumulation of sugars as osmolyte or energy source for recovery, while the increase of glycolysis and TCA may act as a strategy for providing energy during the activation of stress defenses, especially when the photosynthesis was inhibited. The change in mitochondrial electron transport chain and ATP synthesis related protein implies the ability to enhance energy production to maintain physiological activity and inhibit stress damage.

Due to the drought condition, nitrogen assimilation decreased in the reduction of nitrate reductase (NR), glutamine synthetase (GS), and glutamate synthase (GOGAT), which was the main reason for yield reduction. Similarly, the decline of aspartate aminotransferase (AST) and alanine

aminotransferase (ALAT), indicate that drought stress inhibits the amino-acid metabolism and synthesis of other metabolites. At the same time, S-adenosyl-l-methionine (SAM) cycles were generally increased in leaves, including drought-increased. 5-methyltetrahydropteroyltrigluta-mate-homocysteine methyltransferase (MetE), S-adenosyl-l-homocysteine hydrolase (SAHase), S-adenosylmethionine synthase (SAMS), and methionine synthase (MS) which implies that it enhance the methionine and osmo-regulant metabolism for plants to cope with drought stress.

Acetyl-coenzyme A carboxylase carboxyl transferase, acyl carrier protein, enoyl-acyl carrier protein reductase, and lipoxygenase 6 involved in fatty acid biosynthesis, and enzymes thiolase I, thiolase II, and acyl-CoA dehydrogenase used for fatty acid degradation. Greater composition of unsaturated fatty acid in membrane lipids contribute to superior leaf dehydration tolerance and maintain membrane integrity and preserve cell compartmentation under water stress, in addition, two flavonoid biosynthesis related proteins (i.e., chalcone isomerase (CHI) and dihydroflavonol-4-reductase) involved in secondary metabolism were also changed in response to drought.

2.2 PROTEIN METABOLISM UNDER FLOODING AND SUB-MERGE STRESS CONDITION

Deprivation of the soil oxygen due to consequence of flooding and forced the plant to shift from aerobic to anaerobic respiration (Hossain *et al.*, 2009), which regenerate NAD+, through ethanol fermentation by selectively synthesizing flooding-inducible proteins involved in sucrose breakdown, glycolysis, and fermentation (Bailey and Voesenek, 2008). Several glycolysis-related proteins, including fructose-bisphosphate-aldolase, phosphogly-cerate kinase (Hashiguchi *et al.*, 2009), glyceraldehyde-3-phosphate dehydrogenase (Komatsu *et al.*, 2010), enolase (Nanjo *et al.*, 2013), sugar isomerase, phosphofructo-kinase (Oh and Komatsu, 2015), and pyruvate kinase (Nanjo *et al.*, 2011) are increased in soybean under flooding stress, indicate the glycolysis and fermentation pathways activation, initiating for plants protecting plant from flooding induced damage, whereas decrease of fructose-1,6-bisphosphate aldolase and sucrose-fructan 6-fructosyl transferase in wheat show response to flooding stress. Othersides, fermentation under anaerobic conditions influences the accumulation of fermented related proteins such as alcohol dehydrogenase (ADH) and pyruvate carboxylase, and indicates activation of the alcohol fermentation pathways, to cope with the hypoxic condition. The conversion of acetaldehyde to ethanol by ADH with concurrent reoxidation of NAD+ for the continuation of glycolysis. The fermentation related enzyme pyruvate decarboxylase, and aldehyde dehydrogenase increase to accelerate the energy production via non-oxidative pathways, even growth is suppressed.

On the other hand, flooding stress induces impair-ment of the electron transport chain in plants. Protein related to complexes II. IV and V of the electron transport chain decreased in abundance and while, succinate-semialdehyde dehydrogenase, 2-oxoglutarate dehydrogenase, and gamma-amino butyrate are significantly increased, that are required for energy production via non-oxidative pathways (Komatsu *et al.*, 2011). Oxaloacetate produced in the TCA cycle stimulates phosphoenol pyruvate synthesis and provides the indirect simulation for the continuation of glycolysis. Reduction of Energy metabolism-related proteins, including citrate synthase, glutamate dehydrogenase, and adenosine kinase, in wheat roots under waterlogging stress (Haque *et al.*, 2011). In addition, energy-related proteins such as -

beta-amylase, malate dehydrogenase, fructose-1,6-bisphosphatase, and phosphoenolpyruvate carboxykinase are decreased in response to flooding stress, indicating that gluconeogenesis is suppressed in wheat under these conditions (Chen *et al.*, 2014). RuBisCo subunit binding protein alpha subunit and RuBisCO activate degraded and senescence in high ROS condition and decreased the chlorophyll content, resulting in decrease in net energy production.

ROS is recognized as a toxic byproduct of aerobic metabolism and controlled by antioxidants and anti-oxidative enzymes. The plant development of a well-organized scavenging mechanism to overcome ROS toxicity likely led to the use of reactive molecules as signal transducers in plant cells. ROS production in cellular organelles, such as plastids, mitochondria and peroxisomes, involved in signaling cascades controlled by production and scavenging of ROS intermediates (Komatsu *et al.*, 2014). ROS scavengers, such as peroxidase, APX, cytosolic APX, and superoxide dismutase (SOD), linked to biophoton emissions and decreased photosynthesis are beneficial for normal metabolism and cell signaling.

Cell wall modification related proteins viz. polygalacturonase inhibitor-like and expansion-like B1-like proteins and cell wall synthesis related proteins such as cinnamyl-alcohol dehydrogenase and cellulose synthase-interactive protein-like protein abundance response under water logged condition. Flooding stress induces the assimilation of methionine and promotes cell wall hydrolysis, thereby restricting growth so, under the waterlogged stress, cell wall synthesis related proteins decrease, cell wall loosening related protein increase and cell wall lignification is suppressed.

Proteolysis, protein folding and storage plays an important role in removing the flooding damage induced by non-active proteins (Komatsu *et al.*, 2012). Heat shock proteins act as molecular chaperones in preventing protein aggregation, translocation of nascent chains across membranes, assembly or disassembly of multimeric protein complexes, and targeting proteins for lysosomal or proteasomal degradation (Komatsu *et al.*, 2012). The ubiquitin/proteasome-mediated proteolysis of enzymes involved in glycolysis and fermentation pathways may be negatively controlled under the hypoxic condition caused by flooding stress (Komatsu *et al.*, 2012).

Post recovery protein metabolism is less studied but studied by Salavati *et al.* (2012) Gro-EL-like chaperone ATPase, 26 S proteasome regulatory subunit 7, 26S regulatory subunit S 10B, and cyclophilin were decreased in seedlings recovering from flooding stress, whereas globulin-like protein, Kunitz trypsin protease inhibitor, and peptidyl-prolyl cis-trans isomerase 1 were increased, and soybean root recovers from flooding by altering cell structure, strengthening cell wall lignification, and scavenging toxic ROS.

2.3 COLD STRESS

One of the major abiotic stresses is cold or low temperatures (LTs) that severely affect plant growth and survival. Chilling or freezing with temperatures <20˚C and <0˚C respectively can induce ice formation in plant tissues which causes cellular dehydration (Chinnusamy *et al.*, 2007). To be able to withstand this adverse condition, plants adopt several strategies, such as production of more energy via activation of primary metabolisms, levelling up of antioxidants content and chaperones, and maintenance of osmotic balance by altering membrane structure (Prasad, 1996).

2.3.1 PROTEIN METABOLISM IN COLD STRESS

Several articles and reviews deal with the metabolic responses of plants at low temperature, where some attempted correlating metabolic and biochemical responses with cold tolerance. Steponkus (1984) noted correlative studies of biochemical changes does not enable understanding of cold acclimation (CA) leading to increased freezing tolerance and till date no new approaches in molecular biology and genetics have been extensively enlisted on study of cold-tolerance and injury mechanisms. However, few studies of CA started focusing on some of the more rapid plant physiological and molecular responses subjected to LTs, which revealed that within the hours of LT exposure, plant and algal cells can rapidly initiate to alter membrane lipid composition (Dickens and Thompson, 1981, Lynch and Thompson, 1984), RNA (Cattivelli and Bartels, 1989), and protein content (Marmiroli et al., 1986; Yacoob and Filion, 1986). These findings of rapid biochemical alterations in response to LT convince the rapid induction of freezing tolerance at inductive temperatures and by desiccation and ABA at non inductive temperatures (Siminovitch and Cloutier, 1982) and ABA (Chen and Gusta, 1983). This suggests a possible molecular basis, at minimum, for the adjustment of metabolism to low nonfreezing temperature, and perhaps for freezing tolerance. Also, upon exposure to LT, it consists of repeated observations that a number of enzymes show shifts in isozymic composition, whereas both quantitative and qualitative differences in the protein content is shown by numerous electrophoretic studies between non-acclimated and cold acclimated tissues.

2.3.2 ENZYME VARIATION

Compared to plants maintained at warm temperature, (McCown *et al.*, 1969) reported changes in activity, freeze stability, and isozyme variation in plants subjected to LTs. He mentioned increased peroxidase activity in hardened stems of four widely unrelated woody species when electrophoretic techniques - to separate enzymes from non-hardened and hardened tissues. Here, peroxidase isozymes present in hardened tissues were not found in the other three non-hardened tissues. Similarly, during deacclimation, no change in peroxidases, glucose-6-phosphate, 6-phosphogluconate, and malate dehydrogenases was observed in willow stem (Hall *et al.*, 1970), however, differences were observed in lactate dehydrogenase where the activity increased during deacclimation. Similarity as above findings was illustrated by Roberts (1974), in which an invertase enzyme in wheat leaves undergoes a shift from a lower-molecular weight form to a higher-molecular-weight form at LT. Different kinetic properties are exhibited in larger form functionally replacing small forms in cold-hardened plants (Roberts, 1978). Also, Krasnuk and colleagues (Krasnuk *et al.*, 1975, Krasnuk *et al.*, 1976) observed increased activity of a number of dehydrogenases associated with respiratory pathways, including glucose-6-phosphate dehydrogenase, lactate, and isocitrate dehydrogenase (Krasnuk *et al.*, 1976) during a comprehensive study with alfalfa. Guy (1990) suggests higher amounts of enzyme may increase in activity and soluble protein content indicating the LTs induced readjustments in metabolism to overcome the kinetic constraints caused by the stress.

A more recent study of glutathione reductase from spinach carried out by (Guy and Carter, 1984) demonstrated not only additional isozyme forms in cold-acclimated tissue but also increased activity, freezing stability, and altered kinetic behavior and the activity of this particular enzyme was decreased by freezing/thawing both in vitro and in vivo. However, the enzyme found in cold-acclimated plants was less sensitive than its counterpart from non-acclimated plants to freezing from non-acclimated plants. In contrast, kinetic parameters and freeze/thaw inactivation was observed identical in ferredoxin NADP reductase

from non acclimated and cold-acclimated wheat (Riov and Brown, 1976), whereas activity was increased during CA. Therefore, Guy (1990) illustrated the potential for alterations in enzymes in response to low temperature exposure and the apparent selective basis where such changes can occur.

Ribulose bisphosphate or oxygenase from winter rye is the best-characterized enzyme relative to non-acclimated and cold-acclimated plants. Early *in vitro* studies (Huner and Macdowall, 1976) noted purified enzymes from both non- and cold-acclimated plants demonstrated an increased stability of catalytic activity to denaturants and storage at -25˚C of the enzyme from cold-acclimated plants. Moreover, (Huner and Macdowall, 1978) presented evidence of a stability *in vivo* conformational change during low-temperature adaptation that was not altered by purification of the enzyme. Also, osmotic concentration of the purified enzyme caused a greater degree of aggregation through intermolecular disulfide bond formation of the large subunit from non-acclimated plants (Huner and Carter, 1981). Huner, Palta and Carter (1981) also claimed, similar to rye, the enzyme purified from freezing sensitive and tolerant potato species demonstrated structural differences that paralleled variation in freezing tolerance much in the same way. However, the study still remains in ambiguity for the stable change in conformation, kinetic properties, and differential cryo stabilities of this enzyme from cold-acclimated leaves or cold tolerant potato species. Given that a single chloroplastic gene encodes for a large subunit and does not possess even a minute chance for the synthesis of an alternative cryostable large subunit from another gene. Also, in many plants, always, a small gene family codes the small subunit, a change in the small subunit may possess subtle effects on the cryo stability and other properties of the holoenzyme. Equally possibility occurs in LT - specific post translational processing, although - there is no evidence to support this concept. In addition to isozymic and conformational differences of enzymes in response to LT exposure, Griffith, Huner and Kyle (1984) stated supramolecular interactions can also be affected.

2.3.3 PROTEIN CONTENT

According to Briggs and Siminovitch (1949), accumulation of soluble protein in cold-acclimated cortical bark cells of black locust trees was first correlated with freezing tolerance about 40 years ago. These study may not be explained as simply as stated in past, Siminovitch *et al.* (1968) suggests there are many reasons why some plants might accumulate soluble proteins during CA; but with the exception of a protoplasmic augmentation hypothesis without clear mechanistic rationale for conferring greater freezing tolerance for this hardening response. In temperate deciduous perennials like black locust could provide the nitrogen source for the accumulation of proteins in the cortical cells of the living bark, in expense of nitrogenous materials during senescence (Peumans *et al.*, 1986). Pomeroy and Siminovitch (1970) supported a possible functional role of the increased soluble protein in response to cold tolerance, that an evergreen, red pine, also accumulated soluble proteins during the winter, similarly, cortical bark cells need not to act as vegetative storage in evergreens nevertheless, it cannot be refused that one or more minor components of the total protein content could function in freezing-tolerance mechanisms.

Most of the studies have confirmed the presence of new protein species in cold-acclimated and freezing-tolerant plants. When these plants are compared to non-acclimated plants, subtle shifts in protein content in cold-acclimated tissues involving mostly the appearance and disappearance of minor bands in gel can be observed (Guy, 1990). Existing evidence at

present includes several studies of purified plasma membranes from non-acclimated and cold-acclimated tissue. Uemura and Yoshida (1984) emphasized on declination of more than 20 proteins in cold-acclimated leaf plasma membranes, whereas 11 had increased their concentration, while 26 proteins were new and unique to membranes from hardened tissue, yet increased levels of high-molecular-weight glycoproteins were other alterations included during CA.

2.4. HEAT STRESS

Some defense mechanisms can be triggered in response to several stresses, such as expression of obvious genes which were not expressed under normal situations, resulting in increased synthesis of protein groups (Morimoto, 1993, Feder, 2006). These groups in cases of heat are called Heat Shock Proteins (HSPs), ''Stress-induced proteins'' or ''Stress proteins'' (Morimoto *et al.*, 1994, Gupta *et al.*, 2010).

According to Gurley and Key (1991), declination in normal protein synthesis occurs when exposed to high temperatures, thereby increasing selective translation of mRNAs for characteristic sets of HSPs. Heat responding phenomena in plants generally observed with concomitant reduction in protein synthesis of new or constitutive HSPs. Key *et al.* (1981) observed reduction in total protein synthesis of 400C and above in soybean. The HSPs, in plants, consists an abundant group of low mo1 wt polypeptides with higher molecular weight families (Vierling, 1991), where some of them found to function as chaperones minimizing high-temperature stress damage partially denaturing proteins and preventing breakdown or aggregation. Response towards heat includes increase in binding of ubiquitin to conglomerated high molecular weight protein (Ferguson *et al.*, 1990, Wettem *et al.*, 1990) which both increase and decrease ubiquitin transcripts expression (Burke *et al.*, 1988, Christensen *et al.*, 1992, Garbarino *et al.*, 1992).

2.4.1. ROLE OF HEAT-SHOCK PROTEINS

Levitt (1962) reported, formation and folding patterns of any protein in three dimensional structure determines their function and Dobson *et al.* (1998) favored above statement and confronted with the findings illustrating 50% of principle amino acids sequence is necessary for formation of three dimensional structure which signifies the importance of HSPs in folding of other proteins. As plants were induced in heat stress, HSPs protects cells from injury and facilitates their recovery and survival to normal growth conditions (Morimoto and Santoro, 1998). Also, Timperio *et al.* (2008) specified the role of HSps as molecular chaperones during heat stressed conditions, apart from ensuring maintenance of correct protein structure, which is basically different than in non-thermal stress where proteins unfolding is not the primary effect and protection could occur in any ways.

Schulze-Lefert (2004), Panaretou and Zhai (2008), Hu *et al.* (2009), Gupta *et al.* (2010) also focused the general role of HSPs as molecular chaperones, regulating folding and accumulation of proteins as well as localization and degradation in all plant and animal species, thus preventing the irreversible aggregation of other proteins and participate in refolding proteins during heat stress conditions (Tripp *et al.*, 2009).

Different HSPs with their unique role are described below:

Small heat shock proteins (sHSPs)

These contain a common alpha-crystallin domain containing 80–100 amino acid residues contained in the C-terminal region (Seo *et al.*, 2006). The characteristic features of these proteins is degradation of protein having unsuitable folding (Ferguson *et al.*, 1990).

Another attribute that makes it indifferent from other classes is independence of its activity from ATP (Miernyk, 1999). A recent review from Nakamoto and Vigh, (2007) concluded the presence of some indications that sHSPs play a crucial role in membrane quality control, thereby potentially contributing to the maintenance of membrane integrity under stress conditions.

HSP60

This class, called chaperonins, are known to be important in assisting plastid proteins such as Rubisco (Wang *et al*., 2004). Some studies like Lubben *et al.* (1989) pointed out that they might participate in folding and aggregation of proteins that were transported to chloroplasts and mitochondria. These proteins differentiate other proteins, after transcription and before folding, to prevent their aggregation (Parsell and Lindquist, 1993).

HSP70

These HSP70 functions as chaperones, in almost all organisms, for newly formed proteins to check their accumulations as aggregates and folds in a proper way during their transfer to the final location (Su and Li, 2008). Furthermore, cooperation in the activity of HSP70 and sHSPs primarily function as molecular chaperone and play an important role in protecting plant cell from detrimental effects of heat stress (Rouch *et al*., 2004); and Zhang *et al.* (2008) stressed on crucial role played by HSp70 and sHSP17.6 in the development of cross adaptation to temperature stress in grapevines induced by heat acclimation (HA) and cold acclimation (CA).

HSP90

The protein from HSP90 class shares the role in many chaperone complexes and has an important role in signaling protein function and trafficking (Pratt and Toft, 2003). Furthermore, other important attributes retained by these classes include regulation of cellular signals, such as the regulation of glucocorticoid receptor (GR) activity (Pratt *et al*., 2004).

HSP100

What makes it unique from other classes is the reactivation of aggregated proteins (Parsell and Lindquist, 1993) by re-solubilizing non-functional protein aggregates and also by degrading irreversibly damaged polypeptides (Bosl *et al*., 2006; Kim *et al*., 2007). Members of this class are not restricted only to acclimation to high temperatures but also housekeeping functions necessary in chloroplast development are provided by specific members (Lee *et al*., 2006).

3. CONCLUSION AND FUTURE PROSPECTIVE

Abiotic stresses are major limiting factors for plant growth and yields and with various acclimation responses at morphological, physiological, metabolic and molecular level coordinated by complicated regulatory networks comprising genes, phytohormones, ROS, and other signaling components. The abundance of ion channels protein and trans-membrane water found indicated the change in ions/osmotic balances but the phenomenon was not observed in flooding conditions. In addition, the preventive measure against the oxidative damage caused due to ROS levels under abiotic stress, higher abundance of ROS scavengers plays a great role in this matter, whereas abundance of ROS scavengers was low in the flooding condition. On the other hand, protein folding due to molecular chaperone and disease, defense related proteins such as proteolytic enzymes and proteasomal factors under stress, indicating the refolding of denatured proteins and proteolytic elimination of damaged proteins. This review paper showed the different protein metabolism occurs during the metabolic stages, and secondary metabolism associated proteins and escape and tolerate mechanism under different abiotic stress.

At the recovery stages, increased lignin biosynthesis results in enhanced mechanical strength by hardening of the cell wall. Changes in abundance for cyto-skeletons associated proteins, can be overlooked upon compensation against the reduced cell size as well as repairing injuries caused by drought and flood stress. Moreover, the levels of proteins related to de novo proteins synthesis, growth related signaling and secondary metabolism enhanced during flood replenishment of the stress induced effects. These stress induced effects can be recovered by compensatory mechanisms.

Only after proteomic studies, could we be aware about the mechanism involved in abiotic stress conditions. Analyzing the plant response and abundance of protein and stress tolerant crops will lead to better understanding of the mechanism of the plant to overcome the stress and recover. Moreover, some proteins showed dynamic changes depending on plant species and stress intensity, which gives a clear interpretation of the mechanism in stress response. The integration of those findings from physiological, gene expression, and other large scale "omics" will help us to establish molecular networks of stress response and tolerance.

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