Chapter 7
Molecular Mechanisms of Osmotic Stress Recovery in Extremophile Plants: What Can We Learn from Proteomics?

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Contents

Abstract During their life cycle, plants are often exposed to phases of high salinity and dehydration stress. Extremophile plants have evolved mechanisms of stress tolerance allowing them to survive or recover from extremely adverse conditions such as water deficit stress and soil salinity. Plant adaptability environmental constraints are linked with deep modifications in proteomic profile, with relevance in abiotic tolerance. Research in extreme drought and high salinity tolerance in resurrection plants and halophytes, respectively, provided some insights into stress tolerance and stress recovery through dynamic changes in protein abundance. Identified proteins under drought and salinity conditions cover a wide range of biological functions: photosynthesis, energy metabolism, protein synthesis, protein folding and degradation and defence response. Proteins related to antioxidant metabolism and scavenging of oxygen radicals were found with higher abundance in halophytes and resurrection plants enabling them to cope with stressful conditions. Comprehensive data from recent proteomics studies confirming the relationship between stress tolerance and specific protein abundance are summarized in this paper.

Keywords Drought · Salinity · Halophytes · Resurrection plants · Recovery · Proteomics

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7.1 Introduction

Plants are frequently subjected to a variety of abiotic stresses which negatively affect plant performance and yield crop. Drought and salinity are major constraints limiting plant growth resulting in a huge restriction of world crop production (Barnabas et al. 2008; Athar and Ashraf 2009). Many studies revealed that plant responses to abiotic stresses through a network of regulatory mechanisms with specific characteristics for various species (Rodziewicz et al. 2014). According to Munns (2002), primary responses to water deficit stress and salinity have been considered typically similar. Indeed, these two constraints share dehydration that reaches, more or less intensely, all plant parts (Chaves et al. 2009). Nevertheless, under long-term salt stress, plants are responding not only to dehydration but also to ion toxicity (Chaves et al. 2009). Both soil salinity and water stress have been considered as transient conditions. Thus, fast and efficient recovery from these stresses may play a crucial role in plant stress adaptation (Chen et al. 2016). Nevertheless, previous investigations focused on plant stress response and ignored to evaluate plant recovery aspects after stress release. Recently, more attention has been devoted to stress release in plants (Perrone et al. 2012; Fang and Xiong 2015), which is considered as a major component of stress tolerance. The active management linking between different adaptive strategies at physiological and metabolic levels that result in dynamic changes in protein abundance can explain the ability of extremophile plants to alleviate and recover from the detrimental effects of a variety of biotic and abiotic stresses (Ghosh and Xu 2014; Kumari et al. 2015). These changes can be best explored using proteomic approach since proteins are the central players of an extensive range of cellular processes (Ghosh and Xu 2014). This powerful tool allows global investigation of plant proteomes at different levels and can be useful to compare and analyse proteome changes under stressful conditions (Fernandez-Garcia et al. 2011). The ability of extremophile plants to preserve healthy tissue and recover following stress relief (salt stress and water shortage) is a key feature for stress tolerance. Several model plants adapted to high salinity (halophytes) or prolonged period of water shortage (resurrection plants) have developed efficient adaptive strategies leading them to resist and continue their growth and development processes (Abreu et al. 2013). Halophytes and resurrection plants are of great importance for proteomic studies to further understanding the plant their tolerance to salt and drought stresses, respectively (Dinakar and Bartels 2013; Griffiths et al. 2014; Kumari et al. 2015). In this paper, we highlight at proteomic scale plant responses to salinity and drought that indicate a capacity for stress recovery and adaptability, resulting in improved stress tolerance.

7.2 Drought Stress

The drought has a major impact on plant growth and crop productivity mainly in arid and semiarid regions throughout the world (Gallé et al. 2007). According to the United Nations Food and Agriculture Organization (FAO), drought covers up to 26%

of the earth's land (Pitman and Lauchli 2002; Rehman et al. 2005). Water is the main constituent of all living organisms and required by all known life forms, as a medium for biochemical activities (Xiong and Zhu 2002; Moradi et al. 2018). Drought is a prolonged period of water scarcity, preventing normal plant growth and leading to extensive damage of crops. Most of higher plants are unable to survive under drought conditions (Dinakar and Bartels 2013). Their relative water content is around 85–100% under actively growing conditions and can withstand only moderate dehydration conditions 59–30%. Below 30% of water content, these plants cannot survive (Höfler et al. 1941). By contrast, a small group of vascular angiosperm plants has evolved unique mechanisms to preserve vital cellular components during severe dehydration and thus can tolerate severe water loss. These plants are known as resurrection plants which were used as model plants for studying desiccation tolerance due to their ability to adjust their water content with the relative humidity in the environment (Dinakar and Bartels 2013). The survival water deficit strategies include the rapid downregulation of growth process and the inhibition of water loss resulting in a quick and efficient photosynthetic capacity re-establishment following a rainfall event (Griffiths et al. 2014). The aptitude of resurrection plants to maintain healthy tissues and to restore plant growth through the strong reactivation of many metabolic pathways is a crucial trait of dehydration tolerance (Griffiths et al. 2014). Since desiccation tolerance is controlled by many mechanisms which can be measured at different levels, a combination between different approaches (physiology, proteomics, metabolomics and genomics) should be informative in order to elucidate mechanisms allowing plant adaptation to drought conditions. For its great importance and impact on drought response and adaption, more attention is paid in this paper on proteomics to examine the impact of drought on plant growth and survival.

7.3   Proteomic Analysis of Resurrection Plants

Here, we focused on specific protein families (proteins associated to photosynthetic process, energetic metabolism, stress and defence, protein folding and degradation, etc.) and protein modification that have been strongly linked and characterized as relevant to allow adaptation to limiting water conditions. In the last decades, proteomic approaches involved in the drought response in plants have been extensively studied. However, there are only few proteomic studies in resurrection plants which are limited to some species. Proteome changes upon drought stress confirm that the abundant proteins in the hydrated tissues are related to photosynthetic function and regulation and carbohydrate metabolism (Dinakar and Bartels 2013; Fig. 7.1). In fact, suppression of the photosynthetic electron transport chain is often observed as a consequence of the excess excitation energy related to the enhanced generation of reactive oxygen species (ROS) (Ghosh and Xu 2014). Different research findings on proteome field revealed that the impairment of photosynthetic process and subsequent recovery are key responses found during drought and after water deficit stress release, respectively (Ingle et al. 2007; Wang et al. 2010; Oliver
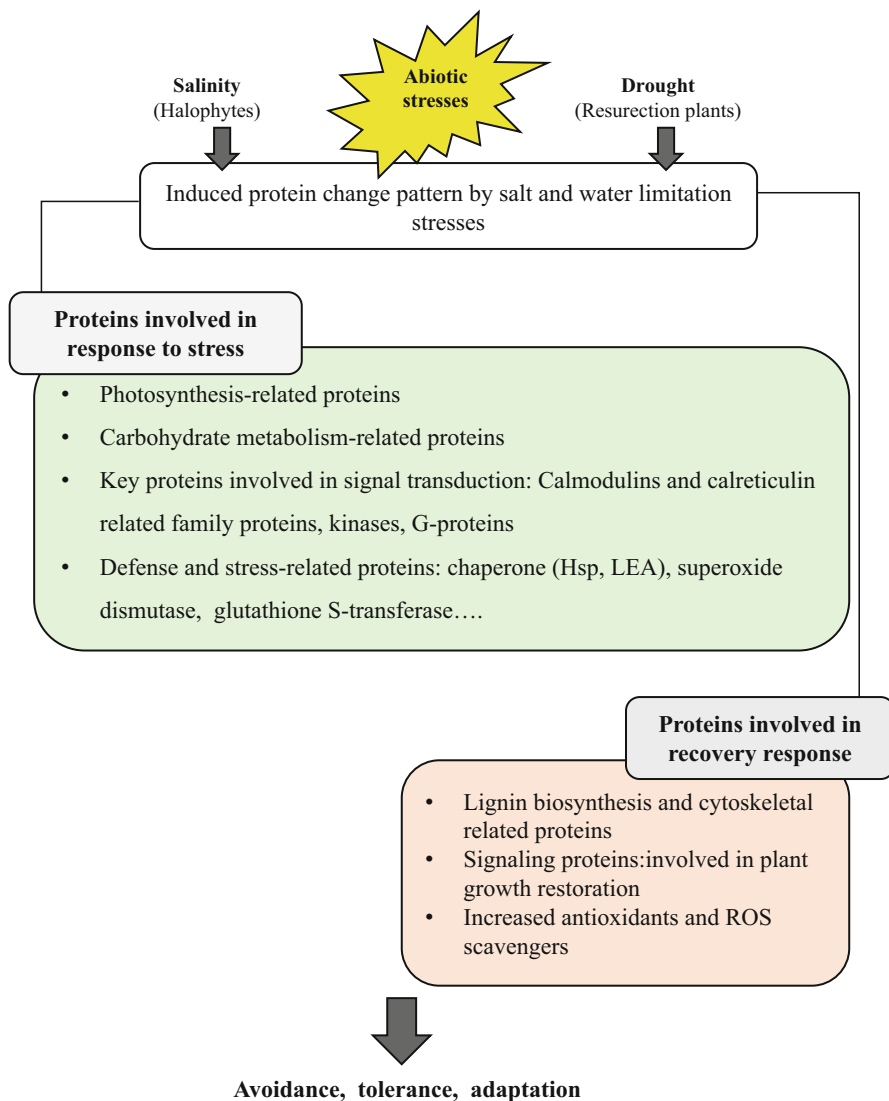
Fig. 7.1 Hypothetical summarizing scheme of proteome change pattern in extremophile plants highlighting the synergism of responses to osmotic stresses (salinity and drought) and during subsequent recovery

et al. 2011). Water scarcity is associated with cell homeostasis and impairment of photosynthetic apparatus (Chaves et al. 2009). The main reason is CO_2 diffusion reduction due to stomata closure (Cornic 2000; Chaves et al. 2009). Proteome changes during dehydration have been elucidated in a relatively drought-tolerant

Populus euphratica by Bogeat-Triboulot et al. (2007). Enhanced abundance of proteins involved in photosynthesis and energy metabolisms such as ATP synthase subunit, ATPase subunit, RuBisCo activase and components of oxygen-evolving complex (OEC) was noticed under water deficit stress conditions. Moreover, an upregulation of proteins related to glycolysis such as GAPDH and PGK was noticed. By contrast, photosynthesis-related proteins (RuBisCo large subunit, chlorophyll a-/b-binding protein and oxygen-evolving complex protein) were downregulated in *Selaginella tamariscina* during dehydration (Wang et al. 2010). Ingle et al. (2007) related photosynthesis impairment in *Xerophyta viscosa* upon drought at 35% relative water content with decreased abundance of photosynthetic proteins such as the two components of luminal oxygen-evolving complex of PSII (PsbO, PsbP), the PSII stability factor HCF136, the α-subunit of the F-ATPase and the transketolase, a Calvin cycle-related enzyme. Similarly, several related proteins to chromatin structure and function, such as the SNF2P protein (an enzyme involved in ATP-dependent chromatin remodelling) in the model resurrection plant *Sporobolus stapfianus*, were found to be enhanced under water deficit stress (Oliver et al. 2011). According to Abreu et al. (2013), such modifications may play an important role on gene expression changes allowing drought adaptation. During dehydration, similar protein profile was shown by Jiang et al. (2007a) in the resurrection plant *Boea hygrometrica,* who related increased abundance of putative ATPase subunits matching a vacuolar H^+-ATPase A subunit to preparation for rewatering. During dehydration, late embryogenesis abundant (LEA) proteins are excessively accumulated in resurrection plants indicating its key role in defence mechanism (Alamillo and Bartels 1996; Ndima et al. 2001). LEA proteins which are known to be synthesized and accumulated in embryo tissue upon desiccation process were identified for the first time in cotton seeds (Baker et al. 1988). It seems that LEA proteins have a great potential to improve crop tolerance to adverse environmental conditions (water deficit stress, salinity and cold). The crucial role of these proteins in cellular protection or mitigation effects of drought stress via ion sequestration and preserving minimum tissue water requirements was well documented (Chakrabortee et al. 2007). Different researches were in accordance to indicate the protective roles ensured by the high accumulation of LEA proteins inresurrection plants during water deficit stress (Michel et al. 1994; Ndima et al. 2001). Phosphorylation of LEA proteins was often described under water limitation, such as in *Zea mays* embryo LEA proteins (Goday et al. 1988) and in *Craterostigma plantagineum* (Röhrig et al. 2006).

Proteome analysis conducted in the resurrection plant *Selaginella tamariscina* revealed downregulation of proteins related to photosynthetic process, energy metabolism, defence- and stress-related proteins and cellular biogenesis under drought conditions (Wang et al. 2010). Antioxidant and energy metabolism-associated proteins were upregulated in *B. hygrometrica* indicating the activation of protective mechanisms in response to dehydration, leading to scavenging ROS, cell wall remodelling proteins, sucrose accumulation, etc. Hence, one can conclude that resurrection plants are able to cope with dehydration through the rapid and efficient accumulation of stress-protective proteins (Dinakar and Bartels 2013).

7.4   Salt Stress

Soil salinity has been considered a major threat affecting crop yield in drylands of the world (Munns 2002). It is estimated that 80 million ha of cultivated lands suffer from salinity problems (Zhang et al. 2012). However, the degree of salt damages depends on the plant age, the duration and the timing of stress (Atteya 2003; Lafitte et al. 2007; Ashraf et al. 2008). Besides, changes in soil salinity can occur in association with many factors: time and space (Epstein and Rains 1987), soil management, water properties, irrigation technique and climate change (de Lacerda et al. 2005). These fluctuations can affect crop adaptability to salt stress, by enhancing or reducing salinity impact on plant responses. The primary salinization of water naturally occurring increase salinity input by evapo-concentration, decrease freshwater input or increase freshwater extraction (Himabindu et al. 2016). By contrast, secondary salinization due to anthropic activities can generate more accented problems (Chaves et al. 2009; Himabindu et al. 2016). For their survival and growth re-establishment during stress period and subsequent recovery, respectively, plants respond by an adjustment in their metabolic pathways (Ghosh and Xu 2014). The mobilization of the metabolic machinery towards plant acclimation and survival occurs via a complex network based on the interaction of physiological, cellular and molecular events developing in the same time and rapidly (Chaves et al. 2009). In high-salt environments, in addition to osmotic stress imposed by water deficit, plants endure ion-specific stress (Blumwald et al. 2000; Shabala and Mackay 2011). Therefore, excessive soil salinity is found to cause dehydration, ion toxicity and nutrient deficiency, along with a suite of metabolic changes, affecting development of salt-sensitive plants and even some tolerant species (Wang et al. 2003; Flowers 2004; Sobhanian et al. 2011). Dehydration caused by salinity is associated with an impairment of photosynthesis, production of reactive oxygen species (ROS), solute accumulation and ion injury (Ashraf and Harris 2004). Understanding plant responses to individual or combined effects of drought and salt stress can play a determinant role in preserving plant productivity and phyto-resources grown under these conditions (Chaves et al. 2009). Adequate management techniques as proteomic approach have become a powerful tool allowing to better understand plant responses to adverse conditions and to improve resource use efficiency by plants (Rodziewicz et al. 2014).

7.5   Proteomic Analysis in Halophytes

Severe osmotic imbalance developed from excessive concentrations of salt leads to harmful modifications at various levels in cellular components (Vinocur and Altman 2005). To counter the adverse effects of salinity, halophytes respond by effective

coordination between various adaptive mechanisms responsible for delivering salinity tolerance. To cope with salt stress, plants respond with increase or decrease the abundance of proteins which protects them and avoids the damaging effects of salt stress (Kumari et al. 2015). Hence, more attention has been given to halophytes which play a key role in proteomic research leading to elucidate their salt-adaptive mechanisms with the possibility of cloning genes and transferring the tissue tolerance trait to glycophytes (tobacco, rice, *Arabidopsis*) (Tang et al. 2011). Proteomic studies conducted in several halophytic species such as *Suaeda aegyptiaca* (Askari et al. 2006), *Salicornia europaea* (Fan et al. 2011), *Cakile maritima* (Debez et al. 2012), *Aeluropus littoralis* (Azri et al. 2016), *Thellungiella halophila* (Wang et al. 2013) and *Halogeton glomeratus* (Wang et al. 2015) have identified numerous salt-responsive proteins which fulfil a vast diversity of functions (Fig. 7.1): photosynthesis, carbohydrate and energy metabolism, cell growth and division, protein synthesis and folding, stress and defence, etc. (Zhang et al. 2012).

Photosynthesis-related proteins are differentially changed under saline conditions. RuBisCo a Calvin cycle enzyme, is implicated in the first major stage of carbon fixation process and the competing photorespiration pathway (Spreitzer and Salvucci 2002). Sengupta and Majumder (2009) found that RuBisCo (large subunit and small subunit) was upregulated in *Porteresia coarctata* leaves. However, RuBisCo LSU and RuBisCo SSU activity has slightly reduced in *Aeluropus lagopoides* (Sobhanian et al. 2010). According to Askari et al. (2006), plants need adequate photosynthetic rate to deal with salt stress. Increased CO_2 assimilation was also observed in some halophytes such as *Suaeda aegyptiaca* and *Suaeda salsa* when grown under saline conditions, activating numerous photosynthetic enzymes. The preservation of adequate photosynthetic rate under such conditions in *Suaeda aegyptiaca* was strongly related to enhanced abundance of reaction centre proteins (D1 and D2). Impairment of energy metabolism during salt stress can be related to the high amount of needed energy by plants for their growth and development. This energy is mainly produced through glycolysis process, TCA cycle, ATP synthesis and electron transport chain (ETC) (Chitteti and Peng 2007; Du et al. 2010; Manaa et al. 2011). In a study conducted by Wang et al. (2009), several glycolytic and Krebs cycle enzymes and ATPase isoforms were found to be with higher abundance in *Salicornia europaea* subjected to salt. Other proteins involved in the glycolytic pathways (triosephosphate isomerase, glyceraldehyde-3-phosphate dehydrogenase, PGK and enolase) showed enhanced relative abundance in *Aeluropus lagopoides* (Sobhanian et al. 2010). In addition, an increased accumulation of mitochondrial F1-ATPase beta subunit, ATP synthase CF1 alpha subunit and F1-ATPase, involved in ATP synthesis, has been reported by Wang et al. (2008a) in *Physcomitrella patens* in response to salt stress. According to Zhang et al. (2013), the control of ATP metabolism is an adaptive strategy to deal with high salinity.

Under salt stress, reactive oxygen species (ROS) are abundantly accumulated (Polle 2001), as a result of osmotic stress and nutrient imbalance (Munns and Tester 2008). An excessive generation of ROS may exceed the plant antioxidant defence

system, resulting in oxidative stress that may disturb cell homeostasis and, consequently, may be implicated in programmed cell death activation (Dat et al. 2000). An efficient antioxidant defence machinery involving enzymatic and non-enzymatic systems has found to appear at a high level to scavenge ROS and to adapt to high salt levels. According to Xiong and Zhu (2002), the capacity to reduce oxidative damage seems to be an adaptive trait to enhance stress tolerance. Proteomic studies on several salt-responsive species (*Solanum chilense,* canola and *S. europaea*) showed a higher abundance of SOD in response to salt stress (Wang et al. 2009; Zhou et al. 2011), revealing its crucial role in defence response. Increased SOD levels were also noticed in *Tangut nitraria* (Cheng et al. 2015). However, its activity was induced in *Puccinellia tenuiflora* treated with 50 mM NaCl but significantly diminished when exposed to 150 mM NaCl (Yu et al. 2011). *Suaeda aegyptiaca* plants exposed to salt treatment, levels of antioxidant enzymes such as cytosolic isoform of Cu/Zn-SOD, GPX, quinone oxidoreductase, stromal isoform of APX as well as enzyme cyanase involved in degradation of cyanide ions were induced (Askari et al. 2006). Different studies have indicated that the salinity tolerance is strongly related to the antioxidative defence activity (Abogadallah 2010; Gupta and Huang 2014). Moreover, to avoid the risk of protein misfolding or unfolding which may result in non-functional proteins, cells produce proteins with chaperone functions such as chaperones, like heat-shock proteins (HSPs), as well as cytosolic, chloroplastic and mitochondrial chaperonins (Kosová et al. 2011; Kumari et al. 2015). The effect of salinity on HPS70 which are involved in various cellular processes was well discussed by Cheng et al. (2015) and Sobhanian et al. (2010). Changes in proteins involved in signal transduction were also observed under adverse conditions, including salinity (Zhang et al. 2013). These comprise receptors situated in the plasma membrane (PM) or in the cytoplasm, G protein, calcium-sensing proteins and phosphoproteins involving activation of kinase cascade (Ghosh and Xu 2014). Different families of Ca^{2+} signalling-related proteins were identified in plants, such as calmodulin (CaM) and calreticulin (CRT) (Cheng et al. 2009; Li et al. 2010) which were found to be upregulated by salt stress. The key role of calmodulins (CML) in the transduction of stress-response signals is reported in many studies. Increased tolerance to water shortage and salinity conditions was observed in the transgenic *Arabidopsis* expressing rice CML (OsMSR2) (Xu et al. 2011). The calreticulin (CRT), another Ca^{2+-} binding protein, which is involved in calcium signaling in the endoplasmic reticulum (Qiu et al. 2012), is differentially accumulated in response to salt stress (Jiang et al. 2007b; Aghaei et al. 2008). Moreover, increased number of 14-3-3 proteins was often observed in plants exposed to high salinity, such as GF14a and GF14b in rice (Malakshah et al. 2007), 14-3-3-like protein A in wheat (Wang et al. 2008b) and 14-3-3 proteins in sugar beet (Yang et al. 2012). These proteins may play a key role in plant development (Roberts 2003) since they are known as positive regulators of the electrochemical gradient across the plasma membrane (Denison et al. 2011).

7.6 Recovery Aptitude in Extremophile Plants Dictates Survival

Recovery aptitude after salt/water stress may be strongly related to the severity and duration of applied stress. Under continuous drought conditions, yield loss is unavoidable (Chen et al. 2016). In their natural biotopes, crops are exposed to continuous cycles of drought and rehydration (Perrone et al. 2012). After stress release, plants require to resume rapidly their growth. The recovery phase is very complex that linked the readjustment of distinct processes to repair detrimental effects caused by water deficit stress leading to plant growth restoration (Chen et al. 2016) (Fig. 7.1). Generally, plants exposed to moderate stress quickly re-establish after water deficit stress release as compared to plants subjected to acute dehydration. In the latter, only 40–60% of the maximum of photosynthetic process is restored 1 day following stress release, and photosynthesis re-establishment endures few days, without always recovering maximum levels (Grzesiak et al. 2006; Gallé et al. 2007). Rewatering (for 10 days) of *Populus euphratica*, subjected previously to drought stress, was associated with increased abundance of some photosynthetic-related proteins, such as RuBisCo activase and proteins of the water-splitting complex (Bogeat-Triboulot et al. 2007). Hence, as soon as water shortage is relieved, plants start the stress-release cycle that can be distinguished by an active adjustment of proteome profile. For example, increased abundance of actin isoform B was found in different parts of soybean seedlings (leaf, hypocotyl and root) exposed to water deficit stress and following stress release (Mohammadi et al. 2012), indicating that actin may play a critical role in repairing injured membranes. Similarly, accumulation of proteins related to lignin biosynthesis, an important component of plant cell wall, was usually described under drought conditions. Modification in the cell wall is known to maintain cell osmotic balance and protective membrane integrity, which is of great importance to plant drought stress adaptability (Ghosh and Xu 2014). Among these proteins, caffeoyl-CoA 3-O-methyl-transferases and class III plant peroxidases showed enhanced abundance in roots of wild watermelon and maize plants (Yoshimura et al. 2008; Degenhardt and Gimmler 2000), during rewatering conditions.

Contrary to drought stress, few studies are trying to evaluate plant response to recovery phase after salt stress mitigation in the root environment, while the soil salinity has been considered a transient condition (Amzallag 1997; Pardossi et al. 1998). As for water limitation, modification in the cell wall was also observed following recovery from salt stress (Fig. 7.1).

Different cytoskeleton-associated proteins were commonly altered during water deficit stress and rewatering conditions, such as actin (Xu et al. 2010; Cao et al. 2017), profilin (Cao et al. 2017), tubulin (Peng et al. 2009; Pang et al. 2010) and other proteins associated with cytoskeleton dynamics. These alterations were found to be strongly related with other physiological responses, such as morphological

response. In fact, the downregulation of profilin in *Amygdalus mira* roots resulted in a significant reduction of filamentous actin number leading to actin disorganization. These modifications were concomitant with the morphological aspect of *Amygdalus mira* roots which became shrivelled and brown (Cao et al. 2017).

7.7   Conclusion

Both salinity and drought are considered among the primary causes of plant loss worldwide. This review provides information of plant responses to salinity and water limitation at a proteomic level leading to elucidate adaptive mechanisms of salinity and drought tolerance in halophytes and resurrection plants. It seems that proteins may play a critical role in making these plants tolerant by minimizing ionic and osmotic effects. We can conclude that generally under abiotic stresses such as salinity and dehydration, proteins and metabolites related to photosynthesis are downregulated in tolerant species. Activation of various defence mechanisms together with upregulation of energy metabolism-related proteins and accumulation of high levels of osmoprotective compounds was often observed in these plants. At the recovery phase, rearrangement of proteome repertoire was found following salinity and drought stress, thus leading to repair injuries caused by drought and salinity. Future investigations on plant recovery aptitude are expected to improve our understanding of plasticity, enabling halophytes and resurrection plants to tolerate abiotic constraints to which they are exposed.

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