Chapter 1
Halophyte Responses and Tolerance to Abiotic Stresses

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Abstract Different anthropogenic activities result in the contamination and degradation of the agricultural ecosystem. Improper disposal of industrial waste, use of excess chemical fertilizers, and mining are major sources of soil contamination. These adverse conditions exert a negative effect on crop growth and yield, while a group of plants, known as halophytes, exhibit greater tolerance. These plants are native to such adverse environments and can withstand different abiotic stresses such as salinity, drought, toxic metal stress, and hypoxia. Halophytes grow luxuriantly in saline soils, which make them suitable for saline agriculture. In addition, they are a

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good source of salt-responsive genes and value-added products. Many halophytes show common biochemical and physiochemical responses to salt stress, whereas under multiple stresses, different mechanisms operate. The accumulation of osmolytes such as proline, selectivity in K:N, the exclusion of sodium and vacuolar compartmentalization, the induction of antioxidant molecules (enzymatic and non-enzymatic) are the most common features of halophytic adaptation to stress. The comparative study of halophytes and glycophytes revealed that the former are well equipped with cross-tolerance mechanism and are well prepared before stress imposition. It is also reported that pretreatment/priming with salinity or other stresses in early developmental stage of halophytes improves their salt tolerance at later stage. This observation suggests that halophytes might have stress memory, which helps them to respond better to stress conditions. In this article, we present a current perspective of the general tolerance mechanism and the responses of halophytes to different abiotic stresses such as salt, drought, toxic metal, and combination of these. Understanding the mechanism of such abiotic stresses alone and in combination will help to identify potential halophytes for re-vegetation or possible breeding for redevelopment of salt-affected agricultural lands.

Keywords Halophytes · Abiotic stress · Multiple stress · Salinity · Drought · Toxic metals

1.1 Introduction

Of the world's total land area, 6% is plagued by excess salinity, mainly in arid and semi-arid areas (Flowers et al. 2010). In agriculture, regional salinity problems are increasing owing to low precipitation, high evaporation, naturally saline soil, poor waste management, and saline water irrigation (Hamed et al. 2013). Usually, plants' response to salinity stress alone differs from their natural biotope behavior in comparison with combined stress (Mittler 2006). It was suggested that plants enhance the negative effect of a first stress in the presence of a second stress (Mittler 2006). Hence, increasing plants' tolerance toward stresses requires multiple stress research (Mittler and Blumwald 2010). The salinity tolerance of halophytes predominantly depends upon uptake control and compartmentalization of Na^+, K^+, and Cl^- (Flowers and Colmer 2008; Shabala and Mackay 2011). Halophytes survive not only in a saline habitat, but also in drought, heat, and an alkaline habitat (Hamed et al. 2013). Along with these stresses, halophytes are also exposed to various biotic stress such as pathogen attack and abiotic stress, for example, toxic pollutants including pesticides, noxious gases (SO_2, NOx, O_3), soil acidification, excessive use of fertilizers, heavy metal and intensified UV-B irradiation (Flowers and Colmer 2008). When combined abiotic stress affects halophytes, they usually show tolerance against combined stress (Hamed et al. 2013). Combined stress tolerance is a complex phenomenon to explain because of multitude of events that take place at various stages of plant development.

Salt-tolerant plants with a phenomenal ability of completing their life cycle under saline conditions are known as halophytes (Flowers and Colmer 2008; Grigore et al. 2014). Development of morphological, anatomical, and physiological characteristics during evolution has enabled halophytes capable of growing under high salt conditions (Flowers and Colmer 2008; Grigore et al. 2014). Because of the wide range of stress tolerance environments, halophytes cannot be classified easily, but a few definitions of halophytes are available (Huchzermeyer and Flowers 2013). They are defined as plants capable of accomplishing their life cycle in a living environment with a salt concentration greater than 0.5% NaCl (Xu et al. 2016). Another definition is that they are exposed to salt stress and able to survive for at least a life cycle in an environment that is lethal to a large population of plants (Xu et al. 2016). Halophytes classified on the basis of salt requirement are obligate halophytes, facultative halophytes, and habitat-indifferent halophytes (Braun-Blanquet et al. 1933; Cushman 2001). Obligatory halophytes require salt for their growth, but facultative halophytes can grow in salt-devoid soil in a similar manner to habitat-indifferent halophytes, but differ because they like to grow in salt-devoid soil, but they are also able to survive under saline conditions (Braun-Blanquet et al. 1933). Another classification divides halophytes into reversible extremophytes, irreversible extremophytes, and mesophytes (Grigore et al. 2014). Extremo-halophytes are able to grow massively in a saline environment (Grigore et al. 2014). They are further subclassified on the basis of their habitat, which could be reversible or irreversible (Mishra and Tanna 2017). Modern omics techniques have enabled the understanding of salt tolerance mechanisms in these plants (Xu et al. 2016). With more insights into salt tolerance mechanisms, it has become apparent that there is more to tolerance mechanisms than mere salt tolerance (Xu et al. 2016). In this chapter, we present an account of stress tolerance behavior of halophytes under different abiotic stress conditions and in a combined stress regime. The main attention is given to abiotic stress factors, such as drought, salinity, flood, heavy metal and nutrient deficiency, which are usually lethal to plants other than halophytes.

1.1.1 Flooding

There are potential conditions of submergence of plants in flood water (Armstrong 1980). Complete submergence of plants results in to reduced O_2 supply to plants because diffusion of gases in water is 10,000 times slower in comparison with air (Armstrong 1980). Under dark conditions, O_2 is deficient, which can inhibit tissue respiration, which finally becomes anoxic (Gibbs and Greenway 2003). Internal O_2 level everyday based on CO_2, O_2, and incident light at the site of submergence (Pedersen et al. 2004; Winkel et al. 2013). The amount of CO_2 uptake by shoots for photosynthesis is also reduced because of submergence, mainly under circumstances where there is high resistance across the leaf cuticle (Mommer et al. 2005). In succulent halophytes, internal O_2 production is mainly based on O_2 production during daytime photosynthesis and anoxic when it is dark at night (Pedersen et al. 2006;

Colmer et al. 2013). In association with other problems of exchange of gases under submergence, halophytes also have to maintain an osmotic potential difference between tissues and floodwater, which could lead to swelling of tissues (Flowers and Colmer 2008). In that situation, to constrain such excessive swelling, a strong epidermis may be required, which greatly reduces the rate of gaseous exchange, already diminished because of the gas diffusion pathway and the relatively low surface area to volume (SA/V) ratio of succulent stems (Konnerup et al. 2015). Salicornioideae stem succulents habitually occupy saline, often flooded, habitats around world (Wilson et al. 1993; Shepherd and Wilson 2007). Perennial halophytes, stem succulent species largely endemic to Australia, contain the genus *Tecticornia* (Wilson et al. 1993; Shepherd and Wilson 2007). At ephemeral inland salt lakes, where the environment is distinguished by high soil salinity and episodic flooding punctuated by durations of drought, many *Tecticornia* species are known to grow (Wilson et al. 1993; Shepherd and Wilson 2007). Species zonation was found on the margins of ephemeral salt lakes in Australia in *Tecticornia* communities (English and Colmer 2011, 2013). Usually, *Tecticornia* field distribution has a different tolerance of flood, salinity, and drought, but an elevation in particular plant establishment may depend on the ability of submergence stress tolerance at low marsh conditions (Konnerup et al. 2015).

The SA/V ratio differs among species of succulent halophytes. Plants with thicker stems are more tolerant than others, explained by the internal O_2 dynamics of plants under submergence stress (Colmer et al. 2013). The major barrier is the supply of oxygen to stem tissue under darkness and submergence in the epidermis with the *T. medusa* stem being hypoxic throughout (Konnerup et al. 2013). Oxygen production in photosynthesis builds up owing to the low permeability of the epidermis; for example, *T. medusa* has a less permeable epidermis, but gas films on *T. auriculata* contribute to obtaining a better gas exchange initially after submergence stress, compared with *T. medusa*, in which gas films are absent (Pedersen et al. 2006). Therefore, low epidermis permeability and a low S/A ratio result in different oxygen patterns when there is a manipulation in the presence of light and submergence (Pedersen et al. 2006). Built-up respiratory carbon dioxide does not occur to the same extent in adequate species as they have thin leaves and a more penetrable epidermis without cuticles, which allows them to exchange gases with the surrounding water (Armstrong 1980; Colmer 2003). In waterlogged or submerged plants, the aeration of roots by O_2 diffusion is uncommon (Pedersen et al. 2006). Stem-succulent halophyte species experience problems during the night under submergence stress owing to O_2 depletion (Flowers and Colmer 2008). The O_2 depletion occurs because of the great fluctuation, as during the day time stem-succulent halophytes are voluminous and have low epidermal permeability (Konnerup et al. 2015). The survival of stem-succulent halophytes under submergence stress is associated with carbohydrate conversion, resistant osmotic stress, and the organized production of new tissue after the flood is over (Bailey-Serres and Voesenek 2008). To assist the survival of the plant, either in an environment susceptible to prolonged deep floods or during a short transient flood, the plant resumes better growth after the flood water has receded, which is considered a quiescence response (Bailey-Serres and Voesenek 2008).

1.1.2 Heavy Metals

In the earth's crust, heavy metals are present as a natural component (Lutts and Lefèvre 2015). However, anthropogenic activities have led to the acceleration of heavy metal accumulation in the environment (Han et al. 2013). Various industrial and agricultural activities, for example, mining, smelting, burning of fossil fuel, and the excessive use of fertilizers, pesticides, fungi, and sewage sludge in agricultural practices are responsible for rapidly increasing heavy metal pollutants such as Cu, Cd, Pb, and Zn (Ernst and Nelissen 2000; D'Amore et al. 2005). These pollutants not only pose a serious threat to the environment, but also affect the health of living beings and disrupt the food chain (Sirguey and Ouvrard 2013). In the rhizosphere, through microbial activity, many organic pollutants can be converted into harmless compounds, but heavy metals cannot degrade and hence remain in the soil for long periods of time (Batty and Dolan 2013). These toxic compounds affect various plant species by inhibiting their growth, influencing the water status, photosynthesis, and inducing over-synthesis of reactive oxygen species (ROS), which is responsible for various physiological disorders that finally leads to plant death (Vázquez et al. 1994). There are some exceptional plant species known as hyper-accumulators. These hyper-accumulators display a higher shoot concentration of heavy metals than roots and these have the ability to absorb and also to translocate heavy metal (Vázquez et al. 1994; Yang et al. 2004).

Overproduction of ROS leads to oxidative stress (Demidchik et al. 2010). This oxidative stress is the major cause of oxidative damage to proteins, nucleic acids, and lipid peroxidation, which may also lead to programmed cell death (PCD) (Demidchik et al. 2010; Nikalje et al. 2017a, b, c; Demidchik 2015). Transition metals in response to oxidative stress generate hydroxyl radicals (Zepeda-Jazo et al. 2011; Rodrigo-Moreno et al. 2013), which activate plasma membrane Ca^{2+} and K^+ channels, and lead to Ca^{2+} influx and K^+ efflux (Demidchik 2015). Halophytes need proper regulation of Na and K concentrations inside their cells, exhibiting a defense response to hydroxyl radicals (Flowers and Muscolo 2015). In *Zygophyllum fabago*, the significance of K relocation in cells of photosynthetically active tissues in response to heavy metal toxicities were studied (Lefèvre et al. 2014). The accumulation of reduced form of transition metals such as Cu, Mn, and Fe is favored by anoxic conditions in some cases (Rodrigo-Moreno et al. 2013). In apoplast and cytosol through the Fenton reaction, transient metals in the presence of H_2O_2 catalyze the production of hydroxyl radicals (Rodrigo-Moreno et al. 2013). Essential components of the plant antioxidant defense systems are Cu and Fe, which are part of superoxide dismutase (SOD) (Bose et al. 2014). When Cu and Fe become over-absorbed, they may result in metabolic disturbance such as loss of chloroplast integrity, remodeled plastid membrane, and also inhibits photosynthetic electron transport (Bose et al. 2014). Further ROS overproduction is generated owing to the disruption of electron transport (Bose et al. 2014). Cu and Zn toxicities are important factors that result in secondary oxidative stress, but Cu and Zn are not involved directly in ROS synthesis (Lutts and Lefèvre 2015). Glutathione, ascorbate, and α-tocopherol are some of the antioxidants present in plants (Bose et al. 2014; Ozgur et al. 2013). Among antioxidant enzymes, Catalase and peroxidase remove H_2O_2 and, SODs catalyze the disproportion of superoxide radicals to O_2 and H_2O_2 (Bose et al. 2014; Ozgur et al. 2013). The greater constitutive antioxidant defense activities of halophytes play an important role in heavy metal toxicity, salinity and other stress (Wang et al. 2014).

In response to heavy metal and metalloids such as Cd, Ni and As, *Salicornia brachiata* is able to up-regulate catalase (CAT) and SOD activities (Lefèvre et al. 2010). The expression of the *CAT1*, *GST*, and *PrxQ* genes responsible for enzymes activity is increased by cadmium (Cong et al. 2013). In shoots of *Suaeda salsa* in response to Zn, Pb or a combination of both metals, only CAT gene expression level increased significantly in contrast to activities of antioxidant enzymes SOD, glutathione peroxidase (GPxS), and catalase increased in response to Zn and Zn+Pb (Bose et al. 2014; Jithesh et al. 2006). SOD activities play a significant role in the protection of halophytes from extreme environmental changes (Bose et al. 2014; Jithesh et al. 2006).

Glutathione by phytochelatin synthase enzymatically synthesizes phytochelatin and low-molecular-weight polypeptide with general structure (γGlu-Cys)n Gly 'n' varying from 2 to 11 (Lutts and Lefèvre 2015). These polypeptides help to reduce damage under heavy metal stress conditions (Lutts and Lefèvre 2015). In *Avicennia germinans*, on exposure to a polluted environment, shows a high level of tolerance due to the overexpression of the *AvPCS* in response to high concentration of Cu^{2+} and Cd^{2+} within few hours (Tennstedt et al. 2008). This over-expression triggers a tolerance mechanism during long-term exposure, and remains transient (Baena-González et al. 2007). Proteins are found in almost all plants, animals, and microbes, that bind to metal and microtubules rich in cysteine (Cobbett 2003). According to the location and distribution of cysteine residue, plant microtubules are divided into four types (Cobbett 2003). Microtubules bind metals efficiently, which leads to metal tolerance. In *Bruguiera gymnorrhiza*, Zn, Cu, and Pb up-regulate genes encoding type 2 microtubules (*MT2*) (Lutts and Lefèvre 2015). Such results were also obtained in *Avicennia marina* and transgenic *E. coli* LB4 (Huang and Wang 2009). Expression of gene coding *MT2* has a differing impact according to the various elements (Huang and Wang 2010). As in *Prosopis juliflora*, Cu and Cd stress cannot change the expression of *PjMT2*, but Zn up-regulates the expression of *PjMT2* (Usha et al. 2009). Similarly, in *Salicornia brachiata*, expression of *SbMT2* is unaffected by Pb and is up-regulated in the presence of Zn and Cu (Chaturvedi et al. 2012).

Halophytes lead to osmotic stress owing to the high NaCl concentration in soil, but to maintain internal osmotic pressure and water uptake, various organic compounds accumulate and maintain the water gradient (Flowers and Colmer 2008). These compounds protect cellular structures and enzymes (Lutts and Lefèvre 2015). Halophytes are able to synthesize protective compounds rapidly in response to ion toxicity, which describes the ability of halophytes to tolerate heavy metal stress

(Rastgoo and Alemzadeh 2011). An accumulation of proline in cytosol is frequently associated with vacuolar Na^+ sequestration (Lutts and Lefèvre 2015). This not only results in osmotic function protecting the protein quaternary structure and stabilizing the cell membrane through direct interaction with phospholipid (Rastgoo and Alemzadeh 2011). In *Aeluropus littoralis*, proline content increased heavy metals such as Cd, Co, Pb, and Ag (Lutts and Lefèvre 2015). In a facultative halophyte, *Mesembryanthemum crystallinum*, Cd exposure caused accumulation of proline and total soluble sugars (Lefèvre et al. 2009). In a similar manner, some amino acids such as histidine, glutamine, alanine or asparagine form complexes in response to metal stress (Sharma and Dietz 2006). In *Suaeda salsa*, in response to Cd and Zn, branch chain amino acids such as leucine, isoleucine, valine, glutamine, glutamate, tyrosine, threonine, arginine, phenylalanine, and tryptophan content increased (Lefèvre et al. 2009). For methionine and GSH/PC synthesis, cysteine is required and acts as a central metabolite in antioxidant defense and metal sequestration (Liu et al. 2011). However, whether these accumulations are related to metal tolerance or protein degradation is unclear (Wu et al. 2013). In different halophyte plant species, heavy metal stress and NaCl in combination may trigger the accumulation and synthesis of quaternary ammonium compounds, such as glycine betaine, resulting in the maintenance of membrane integrity, protecting other cellular structures, stabilizing macromolecule structures, and protecting chloroplasts and Photosystem II (Wu et al. 2013). In leaves of *Atriplex halimus*, over-synthesis of glycine betaine in response to Cd was observed (Bose et al. 2014; Ozgur et al. 2013; Lefèvre et al. 2009). *Sesuvium portulacastrum*, a metallo-protectant halophyte, also accumulates trans-4-hydroxy-proline betaine and 3,5,4-trihydroxy-6,7 dimethoxyflavone 3-glucoside (Adrian-Romero et al. 1998; Nikalje et al. 2018). This mechanism differs according to variation in species, such as in *S. salsa*, glycine betaine can decrease on exposure to Cd, while choline increases (Liu et al. 2013). Synthesis of Polyamines (PAs) and small aliphatic amines during plant development is considered to have myriad biological functions in response to ion toxicities. They also act as protective molecules to repair and protect stress-induced injuries by forming a direct interaction with numerous cell structures and biochemical responses in *Atriplex halimus* (Lefèvre et al. 2014; Lutts et al. 2012).

1.1.3 Salinity

Almost 72% of the Earth's surface is covered with saline water dominated by Na^+ and Cl^- (Flowers and Colmer 2015). In ocean water, usually 19 g of Cl^- and 11 g Na^+Kg^{-1} with substantial concentration of Mg^{2+}, $SO_2{}^-$, K^+ and Ca^{2+} are found (Flowers and Muscolo 2015). But the essential nutrients $H_2PO_4{}^-/HPO_4{}^{2-}$ and $NO_3{}^-$ required for plant growth are in very low supply (Flowers and Colmer 2015). Even in such diverse conditions, there are a few exceptional plants such as halophytes that can still survive (Flowers et al. 2010). Hence, halophytes are considered the flora of saline environments (Saslis-Lagoudakis et al. 2015). The salt tolerance capacity of halophytes develops early in some lineages and in many other origins (Saslis-Lagoudakis et al. 2015). Salt tolerance is observed in a few current species, which indicates that the trait has been gained and lost, or various salt tolerant species are becoming extinct throughout evolution (Saslis-Lagoudakis et al. 2015). Phylogenetic analysis can tell us about the macroevolution of salt tolerance, for example, C_4 photosynthesis metabolism has evolved and increased multiple stress tolerance in plants (Saslis-Lagoudakis et al. 2015). The halophyte species are still evolving and relatively new, but have some common features among them (Flowers and Muscolo 2015). This describes recent advancement in halophytes evolution and systematics (Flowers and Muscolo 2015). Their management of salt tolerance is mainly based on the relationship between salt and water. Halophytes are able to reduce the ion concentration of the solution in the xylem owing to which the quantity of salt delivered to the leaves is assimilated by growth and ion excretion through salt glands (Munns and Tester 2008). The ion regulation through the xylem is usually found in all plants to tolerate salinity stress, but halophytes are capable of Na^+ and Cl^- exclusion at high salt concentrations (Bennett et al. 2009). Ion retrieval is the removal of Na^+ from xylem sap as it rises to the leaves and leads to a genotypic difference in the “apparent exclusion” of Na^+ from entering leaves (Munns and Tester 2008). Mangroves growing in tidal wetland show a range of 90 to 99.6% of external Na^+ as a degree of “exclusion” (Reef and Lovelock 2015). Such a high range of exclusion in mangroves is achieved by anatomical adaptation that decreases and prevents apoplastic movement of solution from outside the root to the xylem, guards the cell membrane, and their transporters may be determined ions that pass into the xylem. Halophytes can tolerate multiple stresses (Flowers and Colmer 2015).

In a solute compartmentalization model of salt tolerance, it was suggested that osmotic adjustment occurs firstly with the ions (Na^+ and Cl^- mostly) in their environment, but under high concentrations of toxic salts the potential disturbance of metabolism results in ions becoming concentrated in vacuoles, relative to cytosol (Konnerup et al. 2015). Whether concentrations of Na^+ and Cl^- are toxic when halophytes are exposed to supra-optimal saline condition is not clear. To decrease growth and eventual death, other factors contribute, such as low cytoplasmic K^+, cellular dehydration, mineral deficiency, reduced stomatal conductance, which limits the net photosynthesis rate, hormonal imbalance, elevated ROS production, and energetic requirement for either ion transport or the synthesis of compatible solutes (Slama et al. 2015). Diverse compatible solutes (amino acid, quaternary ammonium compound, tertiary sulfonium compound, sugars, and sugar alcohols) also explain the role of osmolytes in the cellular compartmentalization model (Flowers et al. 2015). These osmolytes/organic solutes explain the main halophytes families found, their synthesis pathways, and the importance of osmotic adjustment (Flowers and Colmer 2015). Osmolytes act as chemical chaperones and scavengers of hydroxyl radicals and also describe osmotic regulation and transport, which can participate in salt tolerance by enhancing the use of transgenics or by exogenous application to increase these compounds in plant tissue (Flowers and Colmer 2015). Halophytes reduce stomatal opening by generating ROS, which ultimately maintains water transport to diminish the net salt uptake in shoots (Uzilday et al. 2015). Hence, the water–water cycle enzyme may prevent excessive ROS accumulation in chloroplasts to protect photosynthesis machinery (Hou and Bartels 2015). The main factor behind salt tolerance is the ability of halophytes to regulate Na^+ and Cl^- uptake while maintaining cytoplasmic K^+ and Mg^+ concentrations required for essential enzyme activation (Bose et al. 2015).

1.1.4 Combined Stress [Salt + Drought]

Plant transpiration, or soil evaporation in plants, is increasing because of a rise in the surface temperature resulting from global climate change (Brown and Pezeshki 2007). Halophytes show positive effect of salinity under drought or water scarcity, such as *Sesuvium portulacastrum, Zygophyllum xanthoxylum, Atriplex halimus, Ipomoea pes-capra*, and *Bruguiera cylindrica* (Slama et al. 2007, 2008; Ma et al. 2012; Atreya et al. 2009). Under the combined stress of salinity and water scarcity, the higher leaf Na^+ concentration, increased stomatal conductance (g_s), and net photosynthesis rate (P_n) leads to the inference that Na^+ can enhance photosynthesis and also perform osmotic adjustment for the improvement of water status (Slama et al. 2007; Martínez et al. 2005). Various species show differential involvement of Na^+ in total osmotic adjustment, such as under the combined stress condition of salt and drought (Slama et al. 2007). *Atriplex halimus* shows a negligible contribution of Na^+ in total osmotic adjustment (Zribi et al. 2012). Different species have different approaches to dealing with Na^+. For example, in *Atriplex halimus*, absorbed Na^+ accumulates in trichomes or large bladder cells, but in *Sesuvium portulacastrum*, Na^+ is sequestered in the vacuoles of parenchyma cells (Slama et al. 2007, 2008). In *Sesuvium portulacastrum*, Na^+ acts as an osmoticum, because under combined drought and salinity, the stress level of proline accumulation is higher than with salinity alone and with drought alone (Hamed et al. 2013) suggesting that there might be a correlation between proline and water potential, i.e., the level of proline increases when the water potential is low (Slama et al. 2007). Under combined stress, proline improves plant tolerance through mechanisms that provide the multiple functions of proline (ROS), scavenging, protein stabilization, and the regulation of cellular redox potential (Szabados and Savouré 2010; Glenn et al. 2012). Another mechanism for increasing tolerance toward combined stress is reduced stomatal conductance, leading to increased water use efficiency (WUE), which results in a slow growth rate, but accelerated carbon fixed per unit of water transpired (Glenn and Brown 1998). This mechanism has been reported in *Atriplex canescens, Atriplex lentiformis*, and *Atriplex halimus* (Zhu and Meinzer 1999; Nemat Alla et al. 2011).

1.1.5 Combined Stress [Salinity + Flood]

Large saline areas are unusually wet land habitats such as coastal zones and salt marshes (Flowers and Colmer 2008). To survive in these habitats, plants have to tolerate both tidal flooding and high salinity, because, owing to these stress conditions, root respiration becomes restricted (Baena-González et al. 2007), which leads to decrease in the activity of H^+-ATPase and inhibits Na^+ and K^+ intake (Barrett-Lennard 2003; Shabala et al. 2014). Exclusion of toxic compounds, such as CO_2, ethylene, hydrogen sulfide and carboxylic acid can accumulate in plant tissue in response to reduced O_2 and reduces the uptake of essential nutrients, such as NH_4^+ and Ca^{2+} (Greenway et al. 2006; Bradley and Morris 1990; Rengel 1992). Despite combined flood and salt stress, there are some halophytes, e.g., *Spartina*, that show high productivity. *Spartina* can increase net primary productivity up to 40 tons dry weight (DW) ha^{-1} $year^{-1}$ (Mishra and Tanna 2017). Barrett-Lannard listed data on waterlogging and salinity interactions for two species, i.e., *Atriplex amnicola* and *Casuarina* sp. (Barrett-Lennard 2003). Further data on a large number of halophytes (15 species) was added by Colmer and Flowers (Flowers and Colmer 2008). Several species show reduced growth when both waterlogging and salinity were imposed (Hamed et al. 2013). A well-known indicator of a wet land ecosystem is *Phragmites australis* (common reed) because it shows an efficient Na^+ exclusion mechanism from leaves and a high K^+:Na^+ selective ratio under hypoxic conditions over salinity (Gorai et al. 2010). There are some other similar species, e.g., *Melilotus siculus* and *Puccinellia* shoots. Hence, a high value of intrinsic membrane potential is associated with a high H^+ pumping rate, which describes more about K^+ retention in their roots under combined stress conditions (Jenkins et al. 2010). The importance of K^+ retention by roots and shoots for tolerance to combined salinity and hypoxia is explained by comparative studies between halophytes in contrast to water logging (Jenkins et al. 2010). Flower and co-workers used *Suaeda maritima* as a model halophyte for salinity and flood tolerance studies (Flowers 2004). The plant *S. maritima* showed reduced growth, but it is tolerant and survives under saline flooding conditions (Hamed et al. 2013). Research also revealed that *S. maritima* showed increased antioxidant capacity under both natural and controlled saline flood conditions, which was also compared with well-drained conditions (Hamed et al. 2013). Further insights described the contribution of lactate production by roots to tolerate flooding when *S. maritima* was compared with nonhalophyte species such as *Arabidopsis*, tomato, soybean, and tobacco. The former halophyte showed high production of lactate in roots (Teakle et al. 2013). In *S. maritima*, a large amount of lactate is stored in the root vacuoles (concentration of ~120 mM) along with sodium (concentration of more than 200 mM), leading to sodium lactate solution, which prevents vacuole acidification (Teakle et al. 2013). Unlike *S. maritima*, in some other halophyte species, such as *Limonium*, formation of lactate is continuous, but lactate concentration is much lower because most of the lactate is secreted into medium found by Rivoal and Hanson (Flowers and Colmer 2015). To prevent lowering of cytoplasmic pH, it was important for lactate to transport out of cytoplasm (Bazihizina et al. 2012). Some plants show reduced growth; others were unaffected, but rarely stimulated. Owing to various tolerance traits, such as salt exclusion, K^+:Na^+ selectivity and antioxidant capacity are amplified in most of the reported species, whereas pH activity and lactose production are important in *S. maritima* roots (Hamed et al. 2013).

1.1.6 Combined Stress [Salt + Metal]

A site for the accumulation of industrial and urban effluents contaminated by heavy metals is natural saline soil (Ghnaya et al. 2005; Zaier et al. 2010). Owing to repeated irrigation with sewage sludge or poor quality water, the use of pesticides and phosphorous fertilizers in agricultural soil leads to metal contamination (Hamed et al. 2013). Some halophytic species are accumulators and some are hyper-accumulators of certain metals such as *Sesuvium portulacastrum*, which can tolerate and accumulate high levels of cadmium and lead in aerial parts (Ghnaya et al. 2005; Zaier et al. 2010). In a similar manner, *Mesembryanthemum crystallinum* is a copper hyper-accumulator because it accumulates 3500 μg g^{-1} DW of copper in its tissues. *Sesuvium portulacastrum* produces a higher biomass than *Mesembryanthemum*; hence, *Mesembryanthemum* is a poor candidate for phytoremediation of contaminated soil (Thomas et al. 1998). *Atriplex halimus* has high biomass, but accumulates low concentrations of lead and cadmium; however, it is a viable candidate for use in phytoextraction in arid and saline soils (Manousaki and Kalogerakis 2009). One more suggested suitable species for phytoremediation because of its high translocation rates of cadmium and lead toward above ground tissue is *Halimione portulacoides* (Lutts et al. 2004). *Salicornia maritima* can accumulate reasonable levels of copper and zinc and tolerates moist or dry saline soil, but it is not a metal hyper-accumulator (Reboreda and Caçador 2007). The high metal tolerance of halophytes is associated with salt tolerance traits that include an antioxidant system, and osmoprotectant synthesis, such as proline, which scavenges free radicals and leaf surface excretion by using specialized salt glands (Milić et al. 2012). The major advantage of halophytes is that they can grow and accumulate metal in saline soil (Jithesh et al. 2006; Thomas et al. 1998). In the presence of optimal salinity, when exposed to cadmium stress *Sesuvium portulacastrum* showed improvement in growth and decreased the cadmium accumulation in roots and shoots (Manousaki and Kalogerakis 2011). In contrast, the quantity of cadmium extraction from plants is higher under combined (salinity and heavy metal stress) than under cadmium alone (Manousaki and Kalogerakis 2011; Ghnaya et al. 2007). It was suggested that Na^+ might indirectly contribute to the tolerance of *Sesuvium portulacastrum* from combined stress by osmotic adjustment (Ghnaya et al. 2007). It was found that the most toxic form of cadmium (Cd^{2+}) was removed in favor of another form bound to chloride anion and phytochelatins on NaCl treatment (Ghnaya et al. 2005). A comparison of leaves of Cd+NaCl-treated plants and NaCl-treated alone showed high proline and polyamine concentrations in leaves under Cd+NaCl conditions, which could have helped *Atriplex halimus* to tolerate cadmium inside leaf tissue (Hamed et al. 2013). Salinity reduces the harmful effect of cadmium in halophytes such as *Kosteletzkya virginica* by reduced oxidative stress and altering the hormonal status through reduced ethylene and abscisic acid accumulation (Han et al. 2013).

1.1.7 Combined Stress [Salt + Nutrient Deficiency]

Usually, Na^+ and Cl^- are dominant in saline soil. Seawater has a dominant ion concentration around 500 mM and sodic soil with pH >8.5 has CO_3^{2-} and HCO_3^- as dominant anions (Reboreda and Caçador 2007; Debez Huchzermeyer et al. 2011). Seawater contains 11 mineral nutrients needed by plants in sufficient concentrations for the growth of crops, but deficient in N and PO_4 (Hamed et al. 2013; Debez et al. 2011). Halophytes grow on seawater with supplied N and PO_4^{2-} and show similar biomass production to that of plants grown on full-nutrient solution such as *Suaeda fruticosa* and *Spartina alterniflora* (Zribi et al. 2012). Hence, in the next section the combined stress of N or PO_4^{2-} deficiency with salinity is discussed.

1.1.8 Combined Stress [Salinity + Nitrogen Deficiency]

Nitrogen (N) is an essential plant growth element. Higher plants absorb N in two major forms, i.e., NO_3^- (nitrate) and NH_4^+ (Bennett et al. 2009). However, in halophytes, the form of N used under high salt conditions varies among species and with both NH_4^+ and NO_3^- (Lu et al. 2005). *Suaeda maritima* shows high nitrate reductase activity in low-marsh (waterlogged) in comparison with high-marsh plants (drained) (Britto and Kronzucker 2002; Lewis et al. 1989; Leidi et al. 1991). As plants response to NH_4^+ has not been studied, the concept is unclear (Mahmood and Kaiser 2003). It was found that the contribution of nitrate in osmotic adjustment is greater than chloride in *Suaeda physophora* in an intertidal zone, even though the soil has a low nitrate concentration and high salinity (Wetson and Flowers 2010). Under low N and high NaCl conditions, some halophytes, such as *Salicornia bigelovii*, *Phragmites australis*, *Glyceria maxima*, and *Spartina alterniflora*, show that ammonium is beneficial for their growth (Song et al. 2006). *Suaeda salsa* accumulates high NO_3 even in soils with low NO_3 content and regulated Cl at low level at intertidal zone. In addition, the PSII machinery remains intact under high salinity, which is an important characteristic of this plant (Song et al. 2009). When NH_4^+ was dominant, K^+ regulated growth in *Salicornia bigelovii*. Owing to comparative inhibition, Na^+ absorption was suppressed by increased NH_4^+ and consequently K^+ was selectively absorbed (Kudo and Fujiyama 2010; Munzarova et al. 2006; Hessini et al. 2009). In the case of *Leptochloa fusca*, a comparison of NH_4^+ and NO_3^- nutrients revealed that there was considerable root growth reduction and a strong modified concentration of divalent cation in shoots that did not affect its salt tolerance (Hessini et al. 2013). Some halophytes avoid inhibition comparing Cl^- and NO_3 by an improved mechanism of utilizing NH_4^+ and overcoming NH_4^+ toxicity (Amtmann 2009). Some halophytes under saline conditions, show beneficial effects of NH_4^+ by utilizing salt-affected soil because they have salt and NH_4^+ tolerance and use NH_4^+ instead of NO_3^- as essential N source (Hamed et al. 2013).

1.1.9 Combined Stress [Salt + Phosphorous Deficiency]

Usually in alkaline, calcareous soil, an aquatic ecosystem has a high pH and the concentration of P is very low (Mahmood and Kaiser 2003). Plants require a substantial amount of P for living cells, but inorganic phosphate acts as an obstacle, owing to the indirect uptake of P from the environment (Hamed et al. 2013). Pi is usually immobile and not uniformly distributed, and is therefore not readily available to roots (Hamed et al. 2013). In seawater, there is little light and the ammonium level is elevated with a low P concentration and increased vulnerability of the seagrass *Zostera noltii* (Touchette and Burkholder 2000). To facilitate the acquisition of external Pi, consumption of Pi is restricted, and to maintain cellular Pi homeostasis, there is an adjustment in internal recycling carried out by the adaptive processes of plants (Raghothama and Karthikeyan 2005). Under inadequate Pi conditions, Pi homeostasis was maintained by the accelerated acquisition of external Pi and conversion and the remobilization of internal Pi (Raghothama and Karthikeyan 2005). The alteration of metabolic pathways and reallocation and recycling of internal Pi among different organs or cellular compartments led to the conversion and remobilization of internal Pi (Brun et al. 2008). A combination of salinity and P nutrient on halophytes show very complex and contradictory outcomes (Hamed et al. 2013). The interaction between salinity and P nutrient is majorly dependent upon plant species, developmental stage of plant, composition, salinity level, and concentration of P in substrate (Hamed et al. 2013). In *Hordeum maritimum*, P deficiency and salinity stress are applied separately, which leads to restricted whole plant growth and nutrient uptake with a clear effect of P-deficient stress rather than salinity (Zribi et al. 2012). Plants show a significant increase in root growth and root:shoot DW ratio rather than correspondence of the total well-known root adaptation response to mineral deficiency under P-deficient stress (Hamed et al. 2013). When NaCl is added to *Hordeum maritimum*, P-deficient plants show remarkable improvement in photosynthesis activity, capacity for osmotic adjustment, selective absorption of K^+ over Na^+, and antioxidant defense (Hamed et al. 2013).

1.2 Cross Tolerance

In response to single or multiple stresses, plants generally activate a common type of response, which is known as cross-tolerance (Hamed et al. 2013). Halophytes have evolved cross-tolerance mechanisms to manage stressful conditions and develop stress anticipation (Dhar et al. 2013). The signaling cascade of cross-tolerance is independent on the number of pathways activated. At the final stage, more than two pathways may result in the same response, where they may have interacted with each other or operated independently (Knight and Knight 2001). *Thellungiella* is tolerant to both oxidative and salt stress, which indicates possible cross-talk between these two stressors (Taji et al. 2004). Stress sensors such as calcium, calcineurin B-like interacting protein kinases, Ca^{2+}-dependent protein kinases, mitogen-activated protein kinase cascade, and transcription factors are the main components of cross-talk (Chinnusamy et al. 2004). Several halophytes show cross-tolerance against combined stressors (Hamed et al. 2013). The evolved signaling system involves antioxidants, hormones, and oxidant molecules; they show improved tolerance to many stressful conditions (Munne-Bosch et al. 2013).

1.3 Stress Memory

There is a difference among three kinds of stress responses given by plants, such as a negative response, which results in stress damage, a neutral response exhibiting assimilation, and an improved response, which exhibits additional sensory memory (Walter et al. 2013). After exposure to stress, the plant maintains a stress memory “imprint” that improves the plants’ response (Bruce et al. 2007). The accumulation of transcription factor or signaling protein, epigenetic change involving chemical change in DNA (DNA methylation and acetylation), histone modification, or the accumulation of small RNA are considered possible mechanisms of the stress imprint (Hamed et al. 2013). The mechanism has not yet been revealed, but research into this aspect is underway. Long stress memory in plants pre-exposed to salinity, drought or cadmium results in decreased oxidative stress in the halophyte *Cakile maritima* when subsequently exposed to salinity (Hamed et al. 2013). There are plants that continue for several weeks after relief of the first stress that allow plants pre-exposed to stress to either protect or scavenge ROS more efficiently than plants that have not been pre-exposed (Ellouzi et al. 2011). In stress memory, hormones such as salicylic acid, abscisic acid, and jasmonic acid also play important roles. In *C. maritima*, exposure to high salt concentration and increased level of jasmonic acid result in a strong response in correlation with low H_2O_2 and malondialdehyde level (Jaskiewicz et al. 2011). Stress pre-treatment alleviates salt-induced oxidative stress and reduces the jasmonic acid level in leaves (Ryals et al. 1996). Upon cellular oxidation, the metabolic priming effect of drought and cadmium is similar to salt stress pre-exposure, signifying an effective cross-tolerance response in the above-mentioned species (Ryals et al. 1996). The ability of an organism to use its present environment to trigger gene expression and lead to physiological change to adapt further to the environment is referred to as anticipation (Hamed et al. 2013). The concept of anticipation and memory has significance in the response of plants to pathogenic infection. Plants acquire systemic immunity to further infection after local infection by a pathogen (Hamed et al. 2013). This systemic immunity requires salicylic acid accumulation in tissue distal from the infectious site and is called systemic acquired resistance (D'Amore et al. 2005). Some exogenous applications of salicylic acid trigger abiotic and biotic stress resistance mechanisms with some salicylic acid analogs such as benzo (1, 2, 3) thiodiazole 7-carbothionic acid S-methyl ester (Conrath 2009).

1.4 Conclusions and Future Prospective

Halophytes have the capability to survive under harsh conditions because of their developed adaption mechanisms, not only toward salinity, but also to other abiotic stresses (Table 1.1, Fig. 1.1). These tolerance mechanisms help plants to tolerate a wide range of abiotic stresses. Tolerance mechanism involved in abiotic stress include ion toxicity, water stress, oxidative burst, osmotic adjustment, and homeostasis. Interaction between salinity and other abiotic stresses leads to physiological and biochemical amplification of certain traits, which are usually associated with salinity, such as proline accumulation and antioxidant capability. Halophytes are considered as a source of new traits and genes for tolerance to multiple stressors because of their ability to tolerate various forms of abiotic stresses. There is already a growing concern about the scarcity of water and increased demand for food. Therefore, there is a need to utilize saline soil for the production of food crops, and secondary metabolites which can be made are possible by analysis of the response of halophytes to combined stress. This could provide several relevant tools for environmental and agricultural practices. For the development of economic and environmental sustainability, such approaches are required that are purely based on appropriate farming practices and the identification of multiple stress-tolerant species.

Table 1.1 List of halophytes subjected to a combination of abiotic stresses and showing high tolerance to other abiotic stresses

Combination of abiotic stress	Tolerant halophyte species	References
Salinity and drought	*Cakile maritime*	Ellouzi et al. (2013)
	Bruguiera cylindrica	Atreya et al. (2009)
	Sesuvium portulacastrum	Slama et al. (2008)
	Atriplex halimus	Slama et al. (2007)
	Atriplex hortensis	Glenn et al. (2012)
	Atriplex canescens	Glenn et al. (2012)
	Atriplex lentiformis	Glenn et al. (2012)
	Zygophyllum xanthophyllum	Ma et al. (2012)
	Ipomoea pes-carpra	Hamed et al. (2013)
Salinity and flood	*Suaeda maritima*	Wetson et al. (2012)
	Phragmites australis	Gorai et al. (2010)
	Puccinellia ciliate	Teakle et al. (2013)
	Thinopynum ponticum	Jenkins et al. (2010)
	Melilotus siculus	Teakle et al. (2013)
	Lotus tenuis	Teakle et al. (2006)
	Tecticornia pergranulata	Colmer and Voesenek (2008)
	Limonium	Hamed et al. (2013)
Salinity and heavy metal	*Sesuvium portulacastrum*	Ghnaya et al. (2005)
	Mesembryanthemum crystallinum	Thomas et al. (1998)
	Atriplex halimus	Manousaki and Kalogerakis (2009)
	Halimione portulacoides	Reboreda and Caçador (2007)
	Salicornia maritima	Redondo-Gómez (2013)
	Spartina densiflora	Kholodova et al. (2005)
	Spartina alterniflora	Golldack et al. (2014)
	Kosteletzkya virginica	Han et al. (2013)
Nutrient deficiency and salinity		
Nitrogen deficiency and salinity	*Suaeda maritime*	Wetson and Flowers (2010)
	Suaeda physophora	Song et al. (2006)
	Salicornia bigelovii	Kudo and Fujiyama (2010)
	Phragmites australis	Munzarova et al. (2006)
	Glyceria maxima	Munzarova et al. (2006)
	Spartina alterniflora	Hessini et al. (2009, 2013)
	Leptochloa	Mahmood and Kaiser (2003)
Phosphorus deficiency and salinity	*Zostera noltlii*	Lin et al. (2009)
	Crithmum maritimum	Nieman and Clark (1976)
	Hordeum maritimum	Zribi et al. (2012)

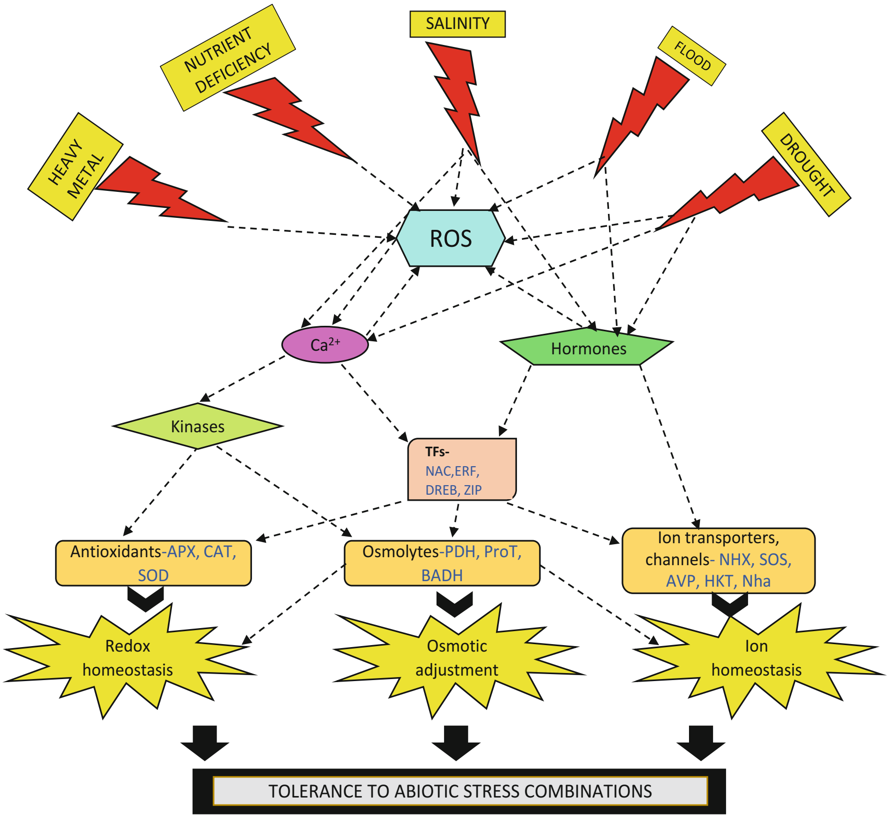

Fig. 1.1 Diagrammatic representation of abiotic stress responses and components involved in the adaptation mechanism of halophytes

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