

Halophytes and Heavy Metals: Interesting Partnerships



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1 Introduction

The continuous progress in industrial, urban, and agricultural aspects of human activities in recent years has resulted in chemical pollution of the environment (Gavrilescu et al. 2015). Presence of toxic metallic elements in soil and water has increased to a level that endangers human health (Kelishadi et al. 2014). In order to combat this pollution, wide range of techniques mainly for removal of heavy metal has been developed. Conventional physicochemical remediation being expensive, labor-intensive, and detrimental to both microbiological and soil ecosystem, is now replaced by modern, alternative techniques (Fasenko and Edwards 2014; Singh and Santal 2015). Modern techniques involve microorganisms (bioremediation) and plants (phytoremediation) to transform or remove toxic elements from the environment (Kang 2014; Mani and Kumar 2014; Gavrilescu et al. 2015). In recent times, phytoremediation has emerged as the most viable and useful technology for soil cleanup in numerous heavy metal-polluted locations. Phytoremediation as the method of choice holds certain advantages such that it is less expensive, promotes biodiversity, reduces erosion, and provides significant reduction of the volume of contaminated material for disposal (Lee 2013; Wan et al. 2016). Several plant species have been studied as the candidates of choice for phytoremediation.

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Halophytes are able to survive even at higher concentrations of sodium and chloride ions that would be toxic to most of the crop species (Nikalje et al. 2017a, b). Mechanisms of adaptation that allow halophytes to survive high salt concentrations are not exclusive to sodium and chloride but also confer tolerance to other toxic ions, including heavy metal ions. It has been recently shown that halophytes have the ability to transform heavy metals into nontoxic compounds making some halophytes excellent candidates for phytoextraction and phytostabilization (Liu et al. 2018; Nikalje and Suprasanna 2018; Nikalje et al. 2019b).

2 Heavy Metals and Toxicity

Heavy metals are those metals with relatively high densities, ranging from 3.5 g/cm^3 to above 7 g/cm^3 . These metals are generally non-biodegradable, have long-term persistence in soil, and easily get accumulated in living bodies. Above certain concentrations and over a narrow range, the heavy metals turn out to be toxic. For example, Cd content in plants ranges between 0.2 and 0.8 mg kg^{-1} and becomes toxic when concentrations reach $5\text{--}30 \text{ mg kg}^{-1}$. Even at lower concentrations, they are capable of causing various diseases and disorders (Alloway 2013). The most common heavy metal contaminants are of As, Cd, Cr, Cu, Hg, Pb, etc. The toxicity caused by metal ions is categorized into three processes: (1) generation of reactive oxygen species, which further results in oxidative stress, (2) direct interaction with proteins, and (3) displacement of essential cations in specific binding sites (Sharma and Dietz 2009). Heavy metals form OH^- from H_2O_2 through the Haber–Weiss and Fenton reactions. These radicals are capable of damaging cells through lipid peroxidation (Sharma and Dietz 2009). The oxidized lipids interfere with protein function through uncontrolled hydrophobic interactions (Farmer and Mueller 2013). The accumulation of heavy metals in plants causes wide range of negative effects on their growth and development. The photosynthetic machinery of plants is highly sensitive to metal toxicity. Cadmium is found to be severely affecting the chlorophyll content, photosynthetic rate and intracellular CO_2 concentration of plants (Dong et al. 2005). Other heavy metals like copper (Cu), manganese (Mn), nickel (Ni), and zinc (Zn) decrease the photosynthetic efficiency of PS II in *Elodea densa* and *Thalassia hemprichii*, resulting in poor chlorophyll content of plants (Maleva et al. 2012; Li et al. 2012). Metal toxicity results in the reduction of chlorophyll pigments, photosynthesis rate, PS II quantum yield, stomatal conductance, and CO_2 assimilation, further causing changes at cellular and tissue levels (Singh et al. 2016). Nickel (Ni) is found to be affecting several enzyme activities such as amylase, protease, and ribonuclease, thus retarding seed germination and growth of many crops. Toxic concentration of Ni in soil causes other detrimental effects on plants such as reduction in plant height, root length, fresh and dry weight, chlorophyll content, and enzymatic activity of carbonic anhydrase and increased malondialdehyde content (MDA) and electrolyte leakage (Siddiqui et al. 2011). Lead (Pb) toxicity has strong effect on seed morphology and physiology. It affects seed germination and

development, root elongation, transpiration rate, chlorophyll content, and amount of water and proteins present in plant, causing alternated chloroplast, obstructed electron transport chain, and inhibition of calvin cycle enzymes, impaired uptake elements like Mg and Fe, and poor stomatal efficiency (Pourrut et al. 2011). Arsenic toxicity in plants results in oxidative stress by generating reactive oxygen species (ROS) and inhibiting antioxidant defense system of tissues (Hartley-Whitaker et al. 2001).

Nitrogen metabolism plays a crucial role in plant growth and development and is affected by metal toxicity. The metals induce protease activity and thus reduce the activity of nitrate metabolizing enzymes such as nitrate reductase, nitrite reductase, and ammonia assimilation enzymes such as glutamine synthetase, glutamine oxoglutarate aminotransferase, and glutamate dehydrogenase (Chaffei et al. 2003). The nitrate metabolism is severely affected by cadmium, inhibiting the uptake of nitrate and its transportation (Lea and Mifflin 2004) ultimately leading to altered primary nitrogen assimilation pattern.

At cellular level, chromium hampers cell cycle, inhibits cell division, and thereby reduces root growth of plants (Sundaramoorthy et al. 2010). The expression of a cyclin-dependent kinase (CDK) is found to be reduced due to Cd toxicity which further results into altered transition of G1 to S phase and progression of cell cycle (Pena et al. 2012). Copper (Cu) alters distribution of auxin by modulating PIN1 proteins, resulting in inhibition of primary root elongation (Peto et al. 2011). Cd toxicity resulted in overexpression of Gpx (a thioredoxin-dependent enzyme in plants) and reduced activity of glutathione reductase (GR), thus modulating the level of thiol during the germination (Smiri et al. 2011). Further, high concentration of Cu ions resulted in oxidative stress by up-regulating antioxidant and stress-related proteins like glyoxalase I, peroxiredoxin, aldose reductase, and regulatory proteins like DnaK-type molecular chaperone, UlpI protease, and receptor-like kinase in plants (Shethy and Ghosh 2013).

3 Halophytes: Responses to Heavy Metals

Halophytic plants are able to cope up with several abiotic constraints occurring simultaneously in their natural environment. These plants are naturally present in the environment and are characterized by an excess accumulation of toxic ions, mainly sodium and chloride ions. Studies revealed that halophytes are able to tolerate other stresses including heavy metal toxicity. The tolerance to salt and heavy metals is partly based on common physiological mechanisms (Przymusinski et al. 2004). It is assumed that halophytes and heavy metal-tolerant plants possess both specific and general functioning mechanisms of tolerance towards numerous abiotic factors (Shevyakova et al. 2003a, b). One such study on the halophyte *Mesembryanthemum crystallinum* suggested that salinity stress overlaps with copper toxicity to some extent, as several integrated mechanical and chemical signals are responsible for stress-related responses (Thomas et al. 1998).

The halophytic plants have developed different strategies to survive and complete their life cycles in highly saline conditions. This includes controlled uptake of Na^+ and Cl^- ions, their compartmentalization into vacuoles, and protection of sensitive organelles such as nuclei or chloroplasts by production of different stress proteins. Production of osmolytes such as proline, glycine, betaine, and carbohydrates is another important feature for salinity tolerance (Shevyakova et al. 2003a, b). Proline plays significant functions during metal stress by performing three major actions, namely, metal binding, antioxidant defense, and signaling (Sharma and Dietz 2006). It is also accumulated in response to Cd, Cu, and other heavy metals (Shevyakova et al. 2003a, b; Lefevre et al. 2009; Nedjimi and Daoud 2009). Presence of cadmium triggered the oversynthesis of glycinebetaine, which is an efficient osmoprotectant synthesized in Chenopodiaceae family (Lefevre et al. 2009). Heavy metal stress induces both secondary water stress and oxidative damage to cellular structures, and the ability of halophytes to synthesize these osmoprotectants is involved in coping up with heavy metals (Lefevre et al. 2009; Shah et al. 2001; Verma and Dubey 2003; Nedjimi and Daoud 2009). These osmolytes play a crucial role in protecting macromolecular subcellular structures and mitigate oxidative damage caused by free radicals produced in response to the stress (Szabados et al. 2011). Under control conditions, the amount of osmolytes is high in halophytes as compared to glycophytes, which makes halophytes well prepared during stress condition and more tolerant than glycophytes (Slama et al. 2015; Nikalje et al. 2017c).

Antioxidant system enables halophytes to cope with heavy metal stress better than other common plants (Shah et al. 2001; Verma and Dubey 2003). A facultative halophyte *Mesembryanthemum crystallinum* responds to cadmium stress by activation of the peroxidase system, which decreases the damaging effect of reactive oxygen species (Shevyakova et al. 2003a, b). Besides tolerance mechanisms, halophytes have evolved number of secondary mechanisms to handle excess salt as well as toxic ions (Table 1). At the leaf level, they have developed salt glands, salt bladders, trichomes, or succulent tissues to remove the excess of deleterious toxic ions from photosynthetically active tissues and regulate plant tissue ion concentration (Lefevre et al. 2009). Leaves of *Tamarix smyrnensis* are found to be covered with salt glands, which accumulate and excrete Cd and Pb on the surface of the leaves suggesting that this salt-tolerant plant uses its salt excretion mechanism to

Table 1 Example of halophytes and their modified structures for tolerance

Halophytic plant	Modification	References
<i>Mesembryanthemum crystallinum</i>	Bladder cells	Agarie et al. (2007)
<i>Limonium bicolor</i>	Secretory cells	Feng et al. (2014)
<i>Aeluropus litoralis</i>	Cuticular chamber	Barhoumi et al. (2008)
<i>Chloridoid grasses</i>	Bicellular salt gland	Amarasinghe and Watson (1998)
<i>Suaeda salsa</i>	Succulent leaves	Song and Wang (2015)
<i>Limonium bicolor</i>	Salt glands	Yuan et al. (2016)
<i>Porteresia coarctata</i>	Secretory hairs	Dassanayake and Larkin (2017)

excrete excess metals on its leaf surface as a possible detoxification mechanism (Manousaki et al. 2008; Kadukova et al. 2008).

Metal excretion through trichomes has been observed in a number of other estuarine and salt marshy halophytes such as the *Armeria maritima* (Neumann et al. 1995), *Avicennia marina* (MacFarlane and Burchett 1999, 2000) *Avicennia germinans* (Sobrado and Greaves 2000), and *Spartina alterniflora* (Windham et al. 2001; Weis and Weis 2004).

4 Mechanism of Metal Tolerance

Halophytes have evolved a number of tolerance mechanisms against heavy metal ion toxicity, which include (a) avoidance or exclusion that minimizes the cellular accumulation of metals; (b) excretion of toxic ions through specialized structures and tolerance, which allow plants to survive; and (c) accumulating high concentrations of metals in vacuoles (Nikalje et al. 2018).

Based on the above mechanism, these plants are categorized into three groups: (a) metal excluders, (b) excretors, and (c) accumulators or hyperaccumulators (Dahmani-Muller et al. 2000).

4.1 Metal Excluders

The halophytes that effectively limit the levels of heavy metal translocation within their system and maintain relatively low levels in their shoot over a wide range of soil levels are referred to as metal excluders (Baker and Walker 1990). Heavy metal excluders are the plants which have high levels of heavy metals in the roots but have shoot/root quotient which is less than 1 (Boularbah et al. 2006). These metal excluders can survive on highly contaminated soil, and their uptake of heavy metals is quite low even at higher concentration of heavy metals (Wenzel et al. 2003). In the presence of toxic metal Cu and Cd, growth performance of propagules and 6-month-old seedlings of *Bruguiera gymnorhiza* was examined, and it was found that older mangrove seedlings showed more tolerance because of their more efficient exclusion mechanism (Wang et al. 2013). Several adaptation mechanisms including avoiding the uptake of metals actively and exclusion of ions resulted in tolerant *A. marina* against Pb toxicity (Burchett et al. 2003). In soil contaminated with heavy metal ions, *Atriplex* showed increased concentration of heavy metal ion in shoots and roots, suggesting an exclusion strategy for metal tolerance (Senock et al. 1991; Kachout et al. 2012). The metal transporters like ATPases, cation diffusion facilitator, multidrug and toxin efflux, natural resistance-associated macrophage proteins, and zinc-iron permease play an important role in metal transport (Williams et al. 2000). Transformation of a protein, ACHMA1, isolated from *Atriplex canescens* showed enhanced tolerance to copper and other abiotic stresses in yeast (Sun et al. 2014).

The metal hyperaccumulator *T. caerulescens* shows increased expression of FDR3 which is a member of MATE family protein under metal stress in roots (Kramer et al. 2007). Metal hyperaccumulation has also been shown to be mediated by 200 times enhanced expression of metal transporter genes in hyperaccumulators compared to related non-accumulator plants (Verbruggen et al. 2009; Leitenmaier and Küpper 2013).

4.2 Excretion

Few halophytes use excretion as one of the methods for the removal of excess salt ions from their tissues. The modification in morphological and physiological features of plant, especially of roots and glandular tissue, is crucial for metal accumulation, transport, partitioning, and excretion in halophytes during metal stress (MacFarlane et al. 2007; Chen et al. 2016). Along with removal of Na⁺ and Cl⁻ ions, other toxic ions such as Cd, Zn, Pb, or Cu are accumulated and excreted by salt glands or trichomes on the surface of the leaves through a process known as “phytoexcretion” (Manousaki and Kalogerakis 2011). Less than 5 % of toxic metal ions are flushed out from plant system by using this mechanism.

Excess of Cd and Pb is excreted out on the leaf surface of the *T. smyrnensis*, though its salt gland showed that it uses its salt excretion mechanism to excrete excess metals (Hagemeyer and Waisel 1988; Burke et al. 2000; Lefevre et al. 2009). Similarly, in *Limoniastrum monopetalum*, leaves excreted Cd and Pb from salt glands (Manousaki et al. 2014). Several other halophytes (*Atriplex halimus*, *Tamarix aphylla*, *T. smyrnensis*, *Armeria maritima*, and *A. marina*) showed the release of toxic elements such as Cd, Pb, or Zn through their salt glands or trichomes (Ruiz-Mirazo and Robles 2011; Lokhande and Suprasanna 2012).

4.3 Accumulation

Some of the plants, referred to as accumulator plants, have the ability to grow on highly contaminated soils, accumulating higher amounts of toxic metals in their tissues without exhibiting any symptoms of toxicity (Baker et al. 1991). Ion accumulators are often known as hyperaccumulators, as they have the capacity to uptake higher concentrations of ions from the soil as an adaptation mechanism. According to definition, a hyperaccumulator must accumulate at least 100 mg g⁻¹ (0.01% dry wt.) of Cd, As, and some other trace metals; 1000 mg g⁻¹ (0.1 dry wt.) of Co, Cu, Cr, Ni, and Pb; and 10,000 mg g⁻¹ (1% dry wt.) of Mn and Ni (Reeves and Baker 2000). Accumulation of toxic ions in plants depends upon the ability to store accumulated excess metals in organs or subcellular compartments where no sensitive metabolic activities take place. The central vacuole is one of the most suitable storage reservoirs for the accumulation of metals in plants (Oosten and Maggio 2015).

Sesuvium portulacastrum accumulated Cs content in leaves ($536.10 \mu\text{g}\cdot\text{g}^{-1}$) than in stem ($413.74 \mu\text{g}\cdot\text{g}^{-1}$) and roots ($284.69 \mu\text{g}\cdot\text{g}^{-1}$) (Nikalje et al. 2019a). Bioaccumulation factor (BAF) is generally used to determine the plant's ability to accumulate metals from soils, defined as the ratio of metal concentration in plants to that in soil (Govindasamy Agoramoorthy et al. 2008; Qiu et al. 2011). Chelation of the metal cation by ligands and sequestration of metals away from sites of metabolism in the cytoplasm are two crucial mechanisms needed for plants to be a hyperaccumulator. Till date, about 400 plant species are found to be metal hyperaccumulators, and some of these are now used in field applications (Zaier et al. 2010; Mariem et al. 2015).

5 Metal Uptake and Mechanisms of Transport

Plants take up ions from soils in response to concentration gradients induced by selective uptake of ions by roots or by diffusion of elements in the soil. The level of accumulation of elements differs varies on the plant species, the age and growth stage of the plant, seasonal variations, metal speciation and bioavailability in the environment, and metal characteristics (Cacador et al. 2000).

5.1 Forms of Metal Uptake and Root Exudates

The oxidation state of metal ions and coordination of these ions with the environment directly affect their absorption, translocation, and detoxification in root tissues (Salt et al. 2002). For example, mobility of inorganic arsenic in the form of arsenite (As III) is lesser than that of inorganic arsenate (As V); however, the former is more toxic to the environment (Jose et al. 2009).

Few plants release different soluble organic substances from their roots, including both low-molecular-weight (LMW) organic acids and high-molecular-weight (HMW) polysaccharides and other organic substances which form complexes with heavy metals in the soil (Bertin et al. 2003). The compound thus formed affects the availability of the heavy metals (Bertin et al. 2003). Root exudates like oxalate and malonate from halophyte *Juncus maritimus* form complex with heavy metals (Pb, Cr, Cu, Zn, Ni, and Cd). The complex so formed is able to increase metal bioavailability in polluted estuarine environments (Mucha et al. 2005). Application of citric acid around the rhizosphere of *Halimione portulacoides* plants showed enhanced Cd uptake and decreased Ni uptake (Duarte et al. 2007).

Thus, the complexes, either organic or inorganic, have the ability to affect the metal uptake by plants. Metal complex having hydrophilic ligands has the ability to enter the xylem vessels through an apoplastic pathway from the tips of the root where the Casparian bands are absent or poorly developed (Lutts and Lefevre 2015). Depletion of free metal ions from the rhizosphere results in the dissociation of metal

complexes in this area, further causing an enhanced diffusion flux and metal uptake (Degryse et al. 2006). Thus, these dissolved complexes have the ability to increase metal uptake; however, the magnitude of this increase depends on the concentration and lability of the complexes so formed.

Few plant roots are found to be associated with arbuscular mycorrhizal fungi which showed interference with heavy metal absorption (Liao et al. 2003). Halophytic plants like *Arthrocnemum macrostachyum* and *Sarcocornia fruticosa* showed reduced plant uptake of toxic metals especially Pb, whereas in *Aster tripolium* increased Cd and Cu accumulation was observed (Carrasco et al. 2006; Carvalho et al. 2006). Presence of anoxic conditions in wetlands causes dominance of a reduced form of heavy metals in soil which is scarcely available to the plants (Weis and Weis 2004).

5.2 Heavy Metal Movement Across Roots

Plants uptake and mobilize As (V) by phosphate transport channels (Tripathi et al. 2007). As (V) being similar to phosphate ion competes with it for root uptake and often interferes in different metabolic processes like ATP synthesis and oxidative phosphorylation (Tripathi et al. 2007). Chromium ion enters into the plant system either by reduction or by formation of complex with root exudates, which increase its solubility and mobility through the root xylem (Bluskov et al. 2005). Zayed and Terry (2003) reported that Cr(III) enters in the plant system by passive mechanism, whereas uptake of Cr(VI) is inhibited by SO_4^{2-} and Ca^{2+} ions. In halophytic plant *Suaeda salsa*, uptake of Cd ion is regulated by Ca ion transporters or channels present in root cell plasma membranes (Li et al. 2012).

5.3 Transport and Accumulation of Heavy Metals

Accumulation of heavy metals in plant system is the final step of metal absorption, which is directly influenced by the transpiration rate and shoot relative growth rate (Lutts and Lefevre 2015). Cr ions, poorly translocated to aerial parts, are mobilized and accumulated inside tissues depending on its chemical form (James and Barlett 1983). Bioaccumulation factor (BF) is defined as the ratio of the metal concentration present in plant tissues to that in the soil. This parameter is generally used to determine the efficiency of metal accumulation in plants. The transfer factor (TF) stands for the ratio of metal concentration in shoot to that of roots (Sousa et al. 2008). Halophytic plant *Arthrocnemum macrostachyum* accumulates Cd at high concentration with a BF exceeding the critical value of 1 and lower TF value. The values for BF and TF decrease with high external concentration of pollutant (Redondo-Gomez et al. 2010).

Studies using x-ray absorption spectroscopy on tumbleweed showed that Cd ion binds to oxygen in the roots, oxygen and sulfur groups in the shoots, suggesting the role of small organic acids in Cd transport (de la Rosa et al. 2004). These organic acids act differently on different heavy metal ions. Presence of citric acid improves the translocation of Cd ion but drastically reduces translocation of Ni in the halophyte *Halimione vulgaris* (Duarte et al. 2007). Halophytic plant *Sesuvium portulacastrum* showed higher amount of Pb translocation from the root to the shoot in comparison to glycophyte *Brassica juncea* in presence of citric acid (Ghnaya et al. 2013).

The presence of chloride influences heavy metal ion mobility in the soil as well as within the plant system. Presence of Cl^- in soil facilitated the translocation of Cd to the shoot by enhancing the Cd flow into the xylem (Wali et al. 2014). External application of NaCl into the medium containing Cd–lipid complexes promotes the release of bounded Cd from lipids resulting in the formation of soluble Cd–Cl complexes in the medium (Girault et al. 1998).

In few halophytic plants, significant proportion of Na^+ gets accumulated in the mucilage (Ghanem et al. 2010). Generally, heavy metal gets concentrated in compartments exhibiting low metabolic activity, such as cell walls or vacuoles as an efficient mechanism of tolerance (Carrier et al. 2003). Halophytic plant *Halimione portulacoides* had more than 65% of the absorbed heavy metals accumulated in the root cell wall, and almost 50% of metals, which are accumulated in the leaves, are retained by cell wall polymers only (Sousa et al. 2008). Heavy metals are preferentially accumulated in the epidermis and in vascular bundle of collenchyma in hyper-accumulating species *Noccaea (Thlaspi) praecox* (Vogel-Mikus et al. 2008).

The chemical nature of heavy metal sometimes influences its redistribution in tissues. *N. praecox* showed reallocation of essential mesophyll cations (Fe, Mn and Zn) with increased Cd concentrations in the environment (Pongrac et al. 2010). *Zygophyllum fabago* was able to protect its photosynthetically active tissues against Cd or Zn toxicity through the accumulation of Cd or Zn ions in less metabolically active tissues by reallocating few essential elements such as K (Lefevre et al. 2014).

6 Cross-Tolerance and Augmenting Uptake of Heavy Metals Through Salinity

Halophytic plants have the ability to withstand a number of stress conditions by undergoing various adaptations including the development of cross-tolerance (Dhar et al. 2013). When a plant is exposed to any stress condition, it activates a number of responses in order to withstand that stress. Cross-tolerance is defined as a biological phenomenon by the virtue of which a plant, which is resistant to one stress, is able to develop tolerance to another form of stress (Foyer et al. 2016; Nikalje et al. 2019b). During cross-tolerance, two or more different types of pathways activate a signaling cascade. These different signaling pathways may operate independent of each other giving same kind of response in the end or interact with each

other to give a final response (Knight and Knight, 2001). This could be either additive regulatory pathway, negative pathway, or competitive pathway (Capiati et al. 2006). The common mechanism of salt and metal tolerance of halophytes is shown in Fig. 1. Elements like stress sensors, calcium channels, CDPKs, MAPKs cascade, and transcription factors are included in cross talks (Chinnusamy et al. 2004). Besides these, hormones, oxidants and antioxidants are also involved (Munne-Bosch et al. 2013).

Halophytic plant *Thellungiella salsuginea* withstands both high salinity and oxidative stress, which has provided information on plant's ability for cross talk between combined stresses (Taji et al. 2004). Further, the gene *ThCBL* encoding for calcineurin B-like protein, gene *ThC4PT1* encoding for cyclophilin, and gene *ThZF1* encoding for Cys-2/His-2 transcription factor are involved in cross talk against different stresses in *Thellungiella salsuginea* (Amtmann 2009). *Kandelia obovata* is highly tolerant to cadmium. Under Cd stress, *KoFSD2* and *KoCSD3* genes were significantly expressed in roots of *Kandelia*, and overexpression of *KoFSD2* improved cadmium tolerance in transgenic tobacco by maintaining lower O_2^- and H_2O_2 levels (Pan et al. 2019).

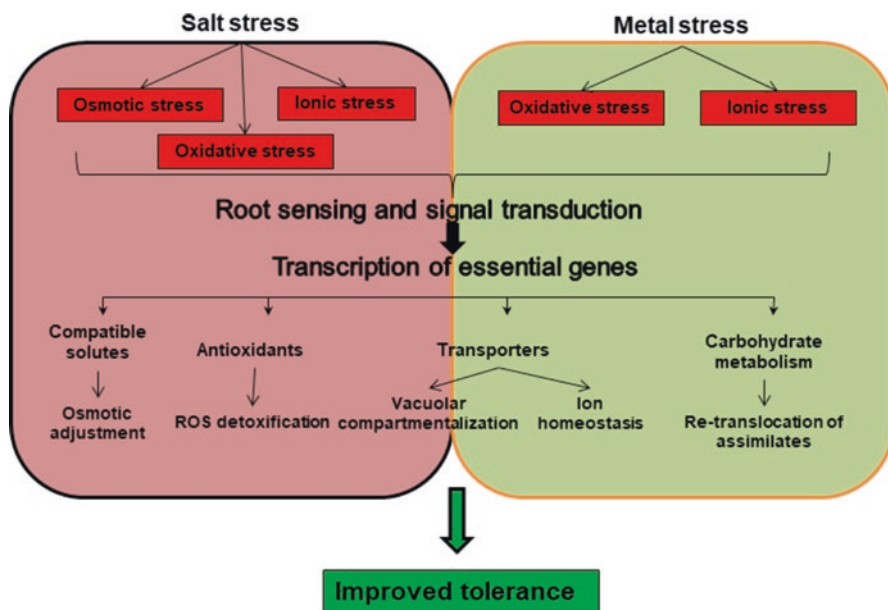


Fig. 1 Mechanism of salt and metal tolerance in halophytes: salt and metal toxicity both induce oxidative and ionic stress in halophytes. Being the first organ which comes in contact with stress-causing factors, the roots sense and induce cascade of signal transduction events. This leads to induction of ion transporters, antioxidant molecules, compatible solutes, carbohydrate metabolism, etc. The compatible solute carries out osmotic adjustment; antioxidants detoxify ROS by scavenging of free radicals. Transporters help in vacuolar compartmentalization and ion homeostasis, while carbohydrate metabolism helps in re-translocation of assimilates. The cumulative effect of all these stress responsive factors improves tolerance to both salt and metal tolerance in halophytes

7 Applications of Halophytes in Restoration of Metal-Contaminated Soils

Halophytes can grow in land with poor quality, which enables their use for phytoremediation of soils with poor fertility resulting in lower operational costs. Selection of plants suitable for restoration of contaminated soil is one of the crucial factors in phytoremediation, keeping in mind that plant selected should not translocate the metals into their aerial parts, provide sufficient cover of vegetation that stabilizes low levels of metals in soils, and prevent metals from mobilizing or leaching into groundwater. The applications of halophytes in restoration of metal-contaminated soil are shown in Fig. 2 and Table 2.

Halophytes like *Atriplex halimus*, *Atriplex nummularia*, *Mesembryanthemum crystallinum*, *Sesuvium portulacastrum*, *Tamarix smyrnensis*, and *Salicornia* sp. have shown their potential in phytoremediation and their value-added products (Lutts and Lefevre 2015; Muchate et al. 2016; Nikalje et al., 2018; Nikalje et al. 2019a,c). Annual halophyte like *Chenopodium botrys* is found to be effective in removing heavy metals, especially Cd, removing six times more than Cd removed by the hyperaccumulator *Noccaea caerulescens* (Mazharria and Homaeed 2012). Leaves of halophytic plant *Tamarix gallica* showed accumulation of As, mostly in its polysaccharidic fraction of cell wall components (Sghaier et al. 2016). Xerohalophytic plant *Atriplex atacamensis* has the ability to absorb and accumulate high concentration of As mainly in its roots. The absorbed As(V) gets quickly

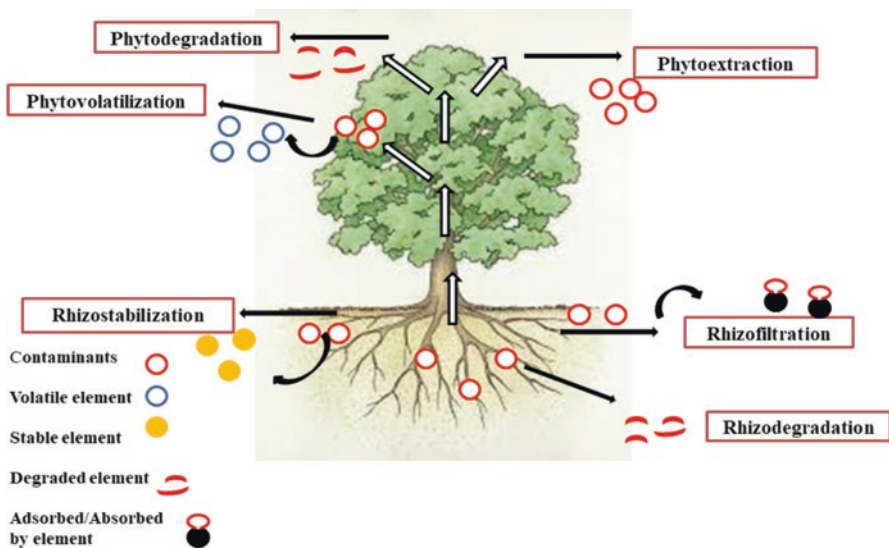


Fig. 2 Applications of halophytes in restoration of metal-contaminated soils: halophytes imply different strategies to cope up with toxic metals, namely, rhizodegradation, rhizofiltration, rhizostabilization, phytoextraction, phytodegradation, and phytostabilization. These strategies can be utilized for restoration of saline and metal-contaminated soils

Table 2 Examples of halophytes and heavy metal accumulation

Halophytic plant	Heavy metal	References
<i>Halimione portulacoides</i>	Cu, Cd, and Pb	Reboreda and Caçador (2008)
<i>Atriplex halimus</i>	Cd and Zn	Lefèvre et al. (2010)
<i>Atriplex hortensis</i> and <i>Atriplex rosea</i>	Cu, Pb, Ni, and Zn	Kachout et al. (2012)
<i>Atriplex atacamensis</i>	As	Vromman et al. (2011)
<i>Sesuvium portulacastrum</i>	Cd and Pb	Ghnaya et al. (2007)
<i>Sesuvium portulacastrum</i>	As	Lokhande et al. (2011)
<i>Sesuvium portulacastrum</i>	Cs	Nikalje et al. (2019a, b, c)
<i>Mesembryanthemum crystallinum</i>	Cu	Shevyakova et al. (2003a, b)
<i>Tamarix aphylla</i>	Cu and Zn	Lutts et al. (2004)

reduced to As(III) either enzymatically by arsenic reductase or non-enzymatically by glutathione, which further reacts with thiols as a strategy of detoxification (Zhang et al. 2012; Smith et al. 2010; Verbruggen et al. 2009; Zhao et al. 2010).

Often the plants that accumulate toxic metals in aerial parts when harvested, make the soil devoid of or lessened with soil contaminants and this conditioning allows cultivation of other crops. Halophytic plant *Sesuvium portulacastrum* has the ability to accumulate salts and heavy metal ions (chromium, cadmium, copper, zinc) from tannery effluent. From ternary samples *Sesuvium* accumulated high amount of Cr (49.82 mg), Cd (22.10 mg), Cu (35.10 mg), and Zn (70.10 mg) per gram dry weight of leaf samples (Ayyappan et al. 2016). Rabhi et al. (2010) assessed potential of *Sesuvium portulacastrum* for desalination of saline soil. Their results showed that *Sesuvium* has the ability to reduce both salinity and sodicity of saline soil, it can accumulate high amount of Na⁺ ions (872 mg per plant), and the phytodesalinated soil can be utilized for cultivation of *Hordeum vulgare* crop. Some organic pollutants also concomitantly contaminate some of heavy metal-contaminated sites. Halophytes like *Spartina alterniflora* has been found to increase bioremediation of oil-contaminated salt marshy areas (Tate et al. 2012). Muchate et al. (2016) evaluates the potential of *S. portulacastrum* for desalination purpose and found considerable lower soil electrical conductivity (2.2 dS m⁻¹) and increased biomass in 90 days. Increased biomass can offer scope for production of value-added products. Halophytes hold an additional advantage for phytoextraction applications. Since they can be cultivated with saline water easily, this is a desirable feature because of lack of high-quality irrigation water needed for cultivation in arid regions. The plant *Tamarix smyrnensis* showed total Cd removal from soil increased from 9.4 µg in the absence of salt to 19.7 µg at 0.5% NaCl (Manousaki et al. 2008). These salt-tolerant plants are viewed as promising candidates for the immobilization or the removal of heavy metals not only from regular soils but also from saline soils, suggesting their application in decontaminating saline soils polluted with metals (Manousaki et al. 2008; Manousaki and Kalogerakis 2009; Nedjimi and Daoud 2009) and mine tailings in semiarid areas (Lutts and Lefèvre 2015).

8 Conclusions

Heavy metal accumulation in soils has become a major environmental issue and strategies are in place for remediation of such soils. Being endowed with natural saline habitat, halophytes have shown remarkable metal tolerance ability. The basic strategies against salt and metal toxicity are exclusion, excretion, and accumulation of metal/salt ions. This has been shown to be based on their common physiological and molecular responses to both salt and metal stress. In addition, accumulation of compatible solutes, osmolytes, induction of antioxidant enzymes helps plant in maintaining osmotic balance. In some halophytes, it is proved that supplementation salt improves metal tolerance. This may be because of an efficient cross-tolerance mechanism and augmentation of uptake of heavy metals through salinity. This phenomenon is reported from only few halophytes like *Sesuvium portulacastrum*. There is a need to direct more concerted efforts on screening more halophyte species to prove such an observation. The ability of halophytes to combat with both metal and salt ions is becoming successful in environmental cleanup and restoration of contaminated soils. Further research needs to be directed on optimization of growth conditions and tolerance level of candidate halophyte species to metal and salt at field level.

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