



Halophytic Plants: A Potential Resource That Reduces Water Crisis in Future

18

Ajay Kumar, Neha Yadav, Heena, Naveen Kumar, Mamta, Monika, Sarita Devi, Sunil Kumar, and Sunder Singh Arya

Abstract

In the past few years, global climate change has caused severe drought, soil salinization, irregular rainfall, and other changes to the environment all over the world. These changes have decreased crop yield and upset the balance of ecosystems. Water shortages have been getting worse, and the problem is worse in dry areas. This leads to poverty and other problems in society and the economy. Therefore, for long-term development, an integrated approach is a must. One solution to the water problem could be to employ salty resources to cultivate a variety of commercially relevant halophytes in agronomic field trials, such as vegetable, fodder, and oilseed crops. Halophytes have also been used to bioremediate salt-contaminated soils, and their products may even have pharmaceutical uses. These halophytes have unique physical, biological, and anatomical characteristics that help them live in salty environments. Halophytes can do an excellent job of fixing saline soil because they have many ways to adapt. Ion compartmentalization, osmotic adjustment, ion transport and uptake, succulence, an antioxidant system, regulating redox status, and salt excretion are examples of these. Some halophytes, such as *Spartina townsendii*, *Aster tripolium*, and *Beta vulgaris* sp., exhibit low transpiration, low stomatal resistance, and low CO₂ content inside the plant at their threshold salinity tolerance. These halophytes also

A. Kumar · N. Yadav · Heena · N. Kumar · Mamta · S. S. Arya (✉)
Department of Botany, Maharshi Dayanand University, Rohtak, India

Monika

Department of Environmental Science, Maharshi Dayanand University, Rohtak, India

S. Devi

Department of Botany & Plant Physiology, CCS Haryana Agricultural University, Hisar, India

S. Kumar

Department of Botany, CRM Jat College, Hisar, India

© The Author(s), under exclusive license to Springer Nature Singapore Pte Ltd. 2023

A. Kumar et al. (eds.), *Salinity and Drought Tolerance in Plants*,
https://doi.org/10.1007/978-981-99-4669-3_18

347

have limited (but positive) net photosynthesis. Studies have helped us learn more about how halophytes deal with stress and how they might be used in farming and environmental services. Sodium extrusion, the SOS pathway, which helps keep the balance of ions in the cytoplasm, and vacuolar compartmentalization are all ways that tolerance is achieved.

Keywords

Halophytes · Salt-tolerant · Salinity · Water conservation · Climate change

18.1 Introduction

Sodic soils account for 434 million hectares unfavorable, whereas saline soils account for 397 million hectares of the total 831 million hectares of salt-affected soils (FAO 2000). Due to population pressure, unfavorable environmental conditions, escalating natural disasters, global climate change, agricultural land is rapidly shrinking (Hasanuzzaman et al. 2013a, b). 20% of all irrigated land, or more than 45 million hectares, is affected by salt, and each year, 1.5 million hectares of land is removed from use due to high saline levels (Pitman and Läuchli 2002; Munns and Tester 2008). If this trend keeps up, by the middle of the twenty-first century, half of the world's cropland will be destroyed (Mahajan and Tuteja 2005). Water scarcity is defined as a situation in which water demand exceeds available supply. Water shortage occurs when there is inadequate water to meet both human and environmental water needs at the same time (White 2014). There is a growing global concern over sustainable development, and water is at the center of try more than any other natural resource. Many serious environmental problems with global repercussions are tied to water issues (Gleick 1994, 2000). One-sixth of the world's population resides in arid and semi-arid areas, and these areas also have the largest population densities (World Bank 1999). There is a growing problem in many emerging countries, such as Tanzania, Sudan, Egypt, and Mexico, where a rapidly expanding population is putting a strain on arable land and other resources and pushing people to the periphery, where they must farm on marginal land in dry and semi-arid regions (Ericson et al. 2001; Darkoh 1982; Bilsborrow and Delargy 1990; Findlay 1996). Problems with water scarcity and land degradation develop when more people move to arid and semi-arid regions, leading to even more serious issues with population health, social instability, and poverty (Moench 2002). Consequently, 13–26 million people around the world become environmental refugees every year, with the majority coming from dry and semi-arid regions (Bates 2002). It is become apparent that the issues of poverty, social insecurity, and environmental refugees are all, connected challenges of population increase, water scarcity, and land degradation in arid and semi-arid countries. Now the global issue of salinity and water scarcity can be resolved by multidisciplinary approaches such as development of resistant crops, restoration of degraded land, phytoremediation, and cultivating the wild plants. Halophytes are a type of flowering plants that are capable of

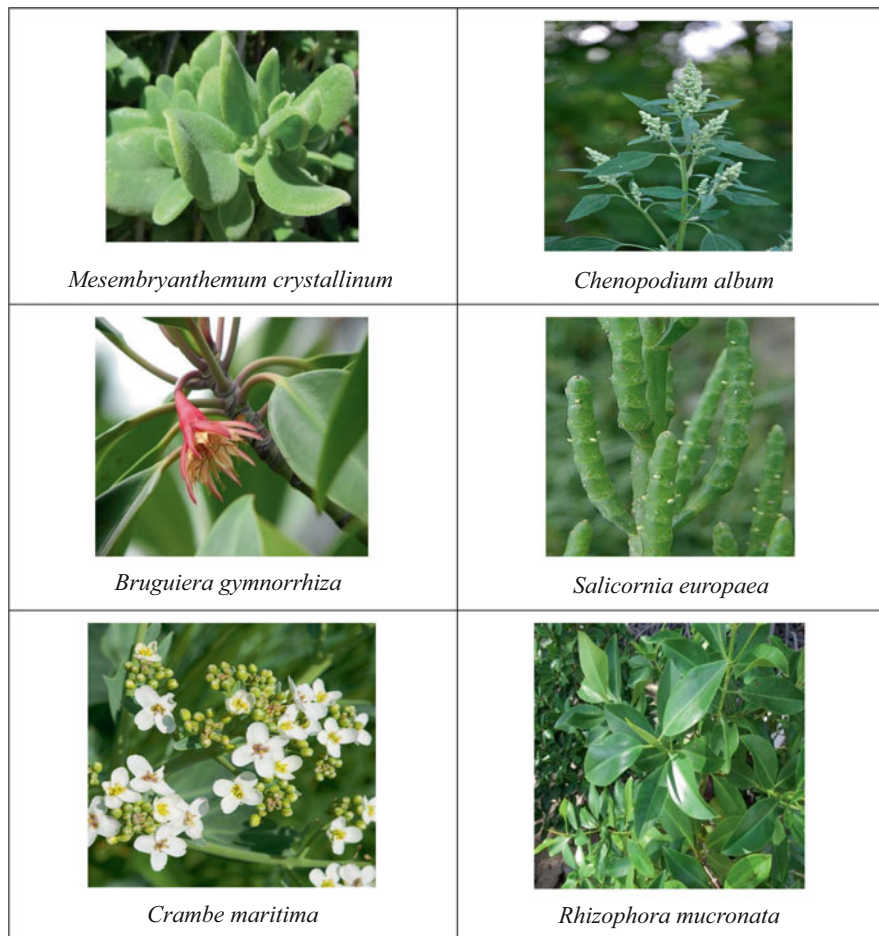


Fig. 18.1 List of major halophytes discussed in this chapter. (a) *Mesembryanthemum crystallinum*, (b) *Chenopodium album*, (c) *Bruguiera gymnorrhiza*, (d) *Salicornia europaea*, (e) *Crambe maritima*, (f) *Rhizophora mucronata* (Hasanuzzaman et al. 2014)

surviving in environments with high salt; hence domesticating them is a realistic alternative. Salinity can be induced by natural (weathering of parent material, flooding of coastal land by tidal water) as well as anthropogenic activities (increase in water table brought on by extensive subsurface water irrigation, poor drainage, etc.) (Hasanuzzaman et al. 2013a, b; Munns 2005; Manchanda and Garg 2008). Halophytes are plants which complete their life cycle in salty conditions (Stuart et al. 2012). Some of the major halophytes are listed in the following (Fig. 18.1).

These halophytes, which flourish in salty conditions, exhibit distinctive morphological, anatomical, and physiological features. In order to successfully alleviate saline soil, halophytes employ a wide range of adaptation processes, including as ion compartmentalization, osmotic adjustment, ion transport and absorption,

succulence, an antioxidant system, the control of redox status, and salt excretion (Lokhande and Suprasanna 2012). Halophytes can be divided into three groups based on their ecological characteristics: obligatory, facultative, and habitat-indifferent halophytes. Obligate grow only in salty habitats. Under highly salinized circumstances, they exhibit adequate growth and development. This category includes a large number of plant species from the Chenopodiaceae family. Facultative halophytes can grow in salty soils, although their best growth occurs in low- or no-salt environments. Some plant species belonging to the family Cyperaceae, Poaceae, and Brassicaceae come under this category. Plants indifferent toward their habitat, are able to survive in salty soils. But they usually grow in soils with less salt. They may live in salty soils and compete with species that are salt-sensitive. Plants' germination, growth, and reproductive capacities are all stunted by high salinity, and other physiological processes, such as cellular homeostasis, metabolism, photosynthesis, respiration, transpiration, membrane characteristics, nutritional balance, enzyme activity, and hormone control are all adversely impacted. In addition, increased salinity causes the production of reactive oxygen species (ROS), which can ultimately lead to the plant's death in extreme stress situations (Mahajan and Tuteja 2005; Hasanuzzaman et al. 2012). These halophytes have evolved unique morphological, anatomical, and physiological processes that allow them to thrive in salty conditions. Because of their varied adaptation mechanisms, such as osmotic adjustment, ion compartmentalization, ion transport, absorption, antioxidative systems, redox status maintenance, succulence and salt inclusion or excretion, halophytes are able to efficiently remediate saline soil (Lokhande and Suprasanna 2012). Coastal saline soil, mangrove forest soil, wetland, marshy land, lands of arid and semi-arid regions, and agricultural fields are a few of the places where some halophyte species thrive. These plants can be grown in high salinity soil and water, can replace more traditional crops, and provide useful products like food, fuel, fodder, fiber, medicinal oils, and fiber for textiles (Lokhande and Suprasanna 2012). It is also possible to use halophytes as a major plant species with the potential for desalination, regeneration of saline soils, and phytoremediation.

18.2 Factors Responsible for Water Crisis

1. Large quantities of potable water are primarily and readily available in the countries that are located in the northern hemisphere, whereas developing countries, which are home to approximately 40% of the world's population, have a much more limited supply.
2. The usage of water has increased by more than 600% over the course of the last century. This indicates that the rate of growth is twice as rapid as the rate of population increase. As a result, by the year 2025, it is anticipated that half of all people on earth will face difficulties associated with insufficient supplies of fresh water.

3. As a result of changes in the global climate, countries in the Mediterranean region might anticipate seeing significant setbacks by the end of this century, while other regions of the world can anticipate experiencing increasing rainfall.
4. Irrigation uses up approximately 70% of the world's available water. Since 1966, when there were just 1.5 million km² of irrigated land, that number has more than doubled to reach 2.70 million km² now. This suggests that approximately 20% of arable areas were being irrigated at the end of the previous century. Forty percent of all crops have been produced on this territory.
5. The expansion of the irrigated area leads to an increase in the amount of water that is used by irrigation systems, and this increase is progressive. This demand for additional irrigation water is a result of an expansion in arable land, in an area where blue water is already scarce or is no longer available at all. The lack of available water and the spread of desertification pose new dangers to human health, natural ecosystems, and the economies of a number of nations, significantly undermining the viability of sustainable development initiatives. As a result, an integrated strategy to problem solving is necessary, one that incorporates prospects for economically, socially, and eco-friendly growth (Duda and El-Ashry 2000).

18.3 Salinity and Freshwater Scarcity

In light of the steadily decreasing availability of freshwater resources and the salinization of the soil, one important goal is to assess the capacity of indigenous halophytes for widespread commercial usage in arid regions. One of the main goals of the research is to find and choose plant species that can handle salt stress. This is achieved by selecting and employing biomarkers to characterize halophytes, figuring out how to use water that isn't typical, like seawater, and choosing halophytes and salt-tolerant glycophytes that might be important for human or animal nutrition. There are a variety of natural salty habitats, some of which are located directly next to saltwater bodies (like a coastal salt marsh) and others that are located further inland (saline lakes, lowlands of dryland and desert terrain, and high evaporation basins). One major drawback of this idea is that even at low quantities in soil water, Na⁺ (a cation) and Cl⁻ (an anion) are harmful to humans, plants, and most animals. That is why most estimates for managing water supply ignore it. Although we are resistant to using seawater, we must immediately find a way to the salinization. Salinization of the soil surface is increased by irrigation water use in both dry and semi-dry zones. Solutes from irrigation water can collect in soils in arid places of the world and eventually reach levels that are harmful to plant growth.

18.4 Sustainable Use of Salt-Affected Soils

Many crop species have lost systems for dealing with salt stress and other abiotic stresses as a result of being domesticated (Munns 1993; Serrano 1996). As saline levels rise, the majority of crop plants are unable to completely express their genetic potential for growth, development, and production, and their economic worth decreases (Maas 1990; Läuchli and Epstein 1990). Therefore, increasing crop plant's salt tolerance is crucial for agricultural research. Wild populations of halophytes are a powerful genetic source for crop plant improvements in salt tolerance (Glenn et al. 1999; Serrano et al. 1999; Khan et al. 2009).

Advanced salt-tolerant crop species can be developed domestically, or genetic resources can be kept in gene bank for usage in crop species development program through traditional or modern molecular breeding techniques. Alternating your crop rotation might help you save water in dry areas. In contrast to established crops like maize, soybeans, rice, etc., some of these plants now produce less. They are not acceptable in regions, where crops with good yields can be cultivated. However, some cases of halophytes being used in industry, ecology, or agriculture are well documented. In agronomic studies, halophytes have been evaluated for their potential as a vegetable, fodder, and oilseed crops due to their adaptability. Growing halophytes in seawater necessitate the use of a leaching percent to maintain optimal salinity in soil, although, at less salinity, these plants outmatch their non-halophyte counterparts in terms of both yield and water efficiency. Different plant species are employed for wastewater treatment in various nations. Different plants have been shown to have varying degrees of success at either detoxifying themselves or precipitating contaminants. Under addition, there are several coastal plants (see halophytes or xerohalophytes) that have been exploited as crops or bred to increase output thanks to their ability to thrive in saltwater irrigation. The medicinal properties of the products of several halophytes and their potential use in the bioremediation of salt-contaminated soils are discussed. It has been proven that ruminants can benefit from eating silage made from these plants.

18.5 Classification of Halophytes

Typical environments for halophytes include saline semideserts, mangrove swamps, marshes, sloughs, and seashores, where the soil and water are salty and the plant cannot develop or sustain itself without human intervention. A halophyte's adaptation to a salty environment might involve either salt tolerance (see halotolerant) or salt aversion. Plants that are not obligate halophytes but still thrive in a salty environment (by, for example, completing their reproductive life cycle during the rainy season) are sometimes called facultative halophytes (e.g., *Aster tripolium*, *Atriplex* sp., *Plantago* sp., *Chenopodium quinoa*). Plants called "obligate halophytes" (halophytes found in arid environments are known as xerohalophytes.) require saltier than 0.5% NaCl water to thrive (*Arthrocnemum* sp., *Frenkenia* sp., *Kochia* sp., *Prosopis* sp.) (Koyro and Lieth 1998) (Fig. 18.2). There are lot of closely

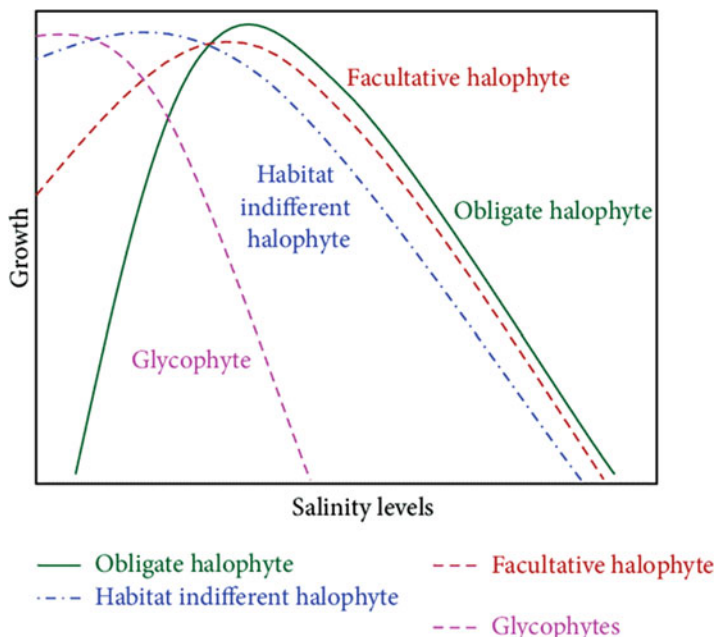


Fig. 18.2 Growth pattern of halophyte under saline condition (Hasanuzzaman et al. 2014)

related plant families, but only a handful of them have independently evolved the structural, phenological, physiological, and biochemical processes for salt tolerance. Almost all plant species are glycophytes, and thus are extremely sensitive to high salinity (e.g., most agricultural crops). Habitat-indifferent are defined as growth preferentially on salt-free soils, but in salt soils has better growth compared to glycophytes (*Sasola* sp., *Festuca rubra*, *Agrostis stolonifera*, *Juncus bufonius*).

18.6 Methods for Enhancing Generalized Salt Resistance

Why does an organism react when it is exposed to salt? The level of salt resistance is proportional to the amount of stress applied. Both salt tolerance and salt aversion are forms of resistance. There are a few common ways to categorize halophytes, including secretor vs. succulents and excluders vs. includers. Physiological and biochemical modifications are required for salt tolerance, as electrolyte accumulation threatens the survival of protoplasm. It is possible for plants to avoid salt by making structural and physiological adjustments to either reduce intracellular salt concentrations or to physically exclude salt from the roots. In theory, salt exclusion or salt inclusion both can lead to salt tolerance (Fig. 18.3).

Research into the physiology and biochemistry of halophytes has revealed a wide variety of adaptations involved in salt resistance. These include salt excretion, genetic regulation, ion compartmentalization, osmolyte synthesis, germination

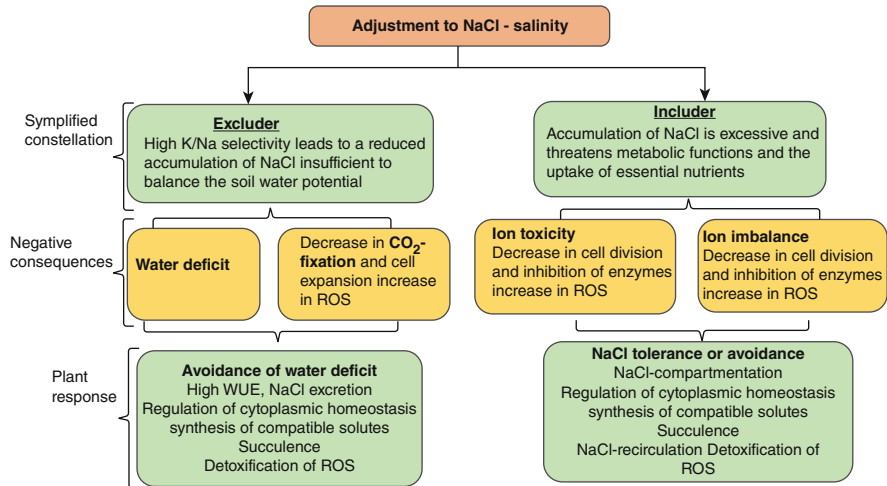


Fig. 18.3 Flow chart depicting the potential methods by which vascular halophytes respond to high external NaCl salt. (Modified after Marschner 1995)

responses, osmotic adaptation, succulence, selective ion transport, and absorption. There are a number of significant plant responses to excessive NaCl salinity that have been described in the literature that help plants escape salt harm and safeguard the symplast (Koyro and Huchzermeyer 2004; Marschner 1995; Mengel and Kirkby 2001; Munns 2002)

1. A modification in the water potential, a reduction in the matric and osmotic potentials, and an increase in the rate of organic solute synthesis are all included. To prevent protein aggregation, often known as “salting out,” the majority of halophilic species and all halotolerant organisms expend energy to keep salt out of their cytoplasm. In order to be able to live in environments with high salinities, halophiles have evolved two distinct mechanisms that stop the osmotic transport of water out of their cytoplasm and keep them from drying out. Both approaches are successful because they raise the osmolarity levels found on the inside of the cell. The first step involves the accumulation of certain organic compounds with low molecular weight in cytoplasm; these substances are referred to as suitable solutes. These can either be synthesized once more or gathered from the surrounding environment. Some of the common forms of compatible (suitable) solutes are amino acids, sugars, polyols, and betaines as well as derivatives of some of these compounds. These solutes can be classified as neutral or zwitterions.
2. Controlling the ratio of water lost to carbon dioxide taken up during photosynthesis; increasing the efficiency with which water is used, or switching to a CAM photosynthesis system.
3. Ion selectivity is used to keep homeostasis, especially in the cytoplasm of important organs like salt glands. This is done through selective uptake or

exclusion, compartmentation of Na^+ and Cl^- in the vacuole, translocation in the phloem, growing parts, storage organs, selective ion transport in the shoot and flowering parts of plants.

4. High capacity for the storage of NaCl in the vacuoles of a whole plant organ, typically in older and wilting sections (for example, in leaves that are intended to be shed later) or in specialized structures like hairs. Excessive NaCl concentration can be diluted by increasing the water content in tissue. This is accomplished by expanding the volume of the tissue.

18.7 Morphological Adaptment to Salinity

In many situations, halophytes benefit from different processes and specific morphological traits that help reduce the amount of salt in their tissues and seeds, especially those that are used for photosynthesis, storage, or reproduction. Changes in halophytes' shapes include a way for them to get rid of salt and a more sticky texture. According to Marschner 1995, excreting halophytes have glands that can secrete extra salts from plant parts. Salt glands can be found in a wide variety of plant families that are not related to each other, as well as in some grasses. Alkali grass (*Puccinellia phryganodes*), saltgrass (*Distichlis spicata*), cordgrass (*Spartina alterniflora*, *S. patens*), and shoregrass have all evolved a basic structure that comprises two-celled trichomes that act as salt-collecting chambers (*Monanthochloe littoralis*). Additionally, *Tamarix* (Tamaricaceae), *Frankenia* (Frankeniaceae), and several common mangroves have complex salt glands. The leaf surfaces of *Atriplex* (saltbush) have vesiculated trichomes (hairs). Extra electrolytes are stored in the bladder cells, which, in the event of a bladder cell rupture, return the salt back to the environment. Additionally, the presence of trichome layer gives the leaves of *Atriplex* a silvery reflectivity, which was found to reduce the production of ROS by preventing some UV radiation from reaching the leaf tissues (ROS). Succulence is seen in many halophyte taxa that live in saline settings. To reduce salt toxicity, succulents employ increased water content within big vacuoles. By storing salt ions in vacuoles, toxins are separated from the cytoplasm and organelles of the cell. When the leaf on a stem segment sheds, salts are expelled from the plant. *Chenopodium*, *Arthrocnemum*, *Batis*, *Allenrolfea*, *Suaeda*, *Nitrophila*, *Halimione*, *Zygophyllum*, and *Salicornia* all exhibit succulence.

18.8 Cash Crop Halophyte Screening

It is not necessary for halophytic organisms to exhibit any specialized morphological adaptations in order to endure the high salt of seawater. It is necessary for plants, whether or not they have salt glands, to focus on three interrelated components of their activity in order to develop salt tolerance. Damage must be avoided at all costs, homeostatic conditions must be restored, and growth must pick up where it left off. The capacity of vascular plants to adapt to conditions of high sodium concentrations

and low water potential is essential to their growth and survival in settings with high levels of salinity. This is because too much salt in the outside solution of plant cells can hurt them in many ways. It is very rare for a single trait to make a big difference in how well someone can live in an environment with a lot of NaCl. In order to obtain a survey about the processes constitution ultimately results to the salinity tolerance of specific species, it is necessary to conduct an exhaustive investigation using a QCS, with the examination of at least one or more of multiple factors (Koyro 2003). These mechanisms are associated to the primary limitations that are placed on plant development when it occurs on salty substrates. Some of these problems are a lack of water, a limit on how much CO₂ can be absorbed, nutritional imbalance and ion toxicity. Salt extrusion reduces ion toxicity while hastening the plant's loss of water and thereby lowering its capacity to take in carbon dioxide. The uptake of salt (inclusion) makes osmotic correction easier, but it also increases the risk of toxicity and nutritional imbalance (Fig. 18.2). According to Mengel and Kirkby (2001), the presence of soluble salts can influence development in a number of different ways. To begin, plants may be subjected to a stressful level of water deficit. Second, it is possible that certain ions, in high enough quantities, could be toxic and cause disorders of the body's physiological systems. Finally, high salt concentrations might lead to intracellular abnormalities.

18.9 CO₂ vs. Water Loss

In saline environments, the soil solution and atmosphere typically have low water potentials, which can make it difficult for terrestrial plants to thrive. It is essential under these conditions to reduce water loss (due to transpiration) that is greater than the rate at which water is being taken in. This is only conceivable if the plant has a lower water potential than the soil it is growing in. It was realized how important the time period was, which give rise to the concept of a "two-phase growth response" to salinity (Munns 1993, 2002; Mengel and Kirkby 2001). Initial stage of the growth reduction process can be thought of as an osmotic or water-stress phase. Even when subjected to high salinity treatment, the plants *Spartina townsendii*, *Aster tripolium*, *Sesuvium portulacastrum*, and *Beta vulgaris* sp. *maritima* have an appropriate adjustment mechanism. The entire turgescence of the leaves can be attributed to the fact that the osmotic potentials of all four halophytes, as well as many others, were sufficiently low at all salinity levels. Plants capacity to maintain high photosynthesis rate despite low water loss rates is the primary factor that determines the amount of biomass produced, it is imperative that plant water loss be kept to a minimum on soils with low water potentials. In this state of tension, the generation of biomass by a plant is dependent on both its rate of energy consumption and its rate of carbon buildup (CO₂ net photosynthesis). If the plant's rate of CO₂ fixation goes below its rate of CO₂ production (the compensation point), the plant will have reached a critical point. Because of this, the analysis of growth decrease and net photosynthesis is an essential component of the screening technique. This is especially important near the limit of salt tolerance. Koyro and Huchzermeyer state that

many plants exhibit a combination of low (but positive) net photosynthesis, low transpiration, high stomatal resistance, and low internal CO₂ concentration at their threshold salinity tolerance (e.g., *Aster tripolium*, *Spartina townsendii*) (Koyro and Huchzermeyer 2004). Nevertheless, there is a broad spectrum of diversity among halophytes. Two extremely succulent halophytes, *Sesuvium portulacastrum* and *Avicennia marina*, can endure if the water balance is still positive and does not interfere with photosynthesis. Net photosynthesis and water usage efficiency (WUE) both increase in *Sesuvium*, but stomatal resistance decreases. These results highlight the critical need of studying the control of gas-exchange mechanisms at high salinity in connection to other factors (such as water relations). At high salinity, a water shortage is one of the most significant constraints, and it can lead to a reduction in CO₂ uptake. One such basis for evaluating their capability for use is the balance between the amount of water lost and the amount of CO₂ that is taken in.

18.10 Ion Imbalance vs. Ion Toxicity

It is important for halophytes' salt tolerance that they overcome ion toxicity and nutritional imbalance, two of the most significant growth inhibitors in saline environments. The rate at which salt-tolerant plants transfer Na⁺ and Cl⁻ to their leaves is often slower than that of salt-sensitive plants (Munns 2002). However, for maximal growth and to reach low solute potentials, some halophytes even require an overabundance of salts (Flowers et al. 1977; Greenway and Munns 1980). Alternately, by filtering away the majority of the salt, excessive concentrations can be avoided. These halophytes, which are also known as salt excluders, adapt to salinity by excluding ions, which requires the endogenous synthesis of osmotically active solutes in order to satisfy turgor pressure requirements (Mengel and Kirkby 2001). Even animals with salt bladders may benefit from this adaptive trait. However, the literature mostly discusses NaCl salinity as though a shared reaction between Na⁺ and Cl⁻ (both ions) is what causes a salt damage. Salt tolerance was not linked to Na⁺ exclusion in maize by Schubert and Lauchli (1986). Separating the two ions is essential for comprehending the various tolerance to salt mechanisms. As opposed to that, an example of a Na-excluder that has high levels of Cl in its leaves is the *Laguncularia racemosa* plant, which contains salt glands (Koyro et al. 1997). Leaves of plants such as *Atriplex papula*, *Atriplex vesicaria*, *Atriplex nummularia*, *Suaeda occidentalis*, *Suaeda brevifolia*, *Salicornia utahensis*, and amongst others, are able to store sodium and chloride despite the presence of a salty environment (salt-includers). In this case, the leaves are sticky, which is a typical adaptation for halophytes (Kinzel 1982; Mengel and Kirkby 2001). This is done to lower the concentration of toxic ions. Producing sugar alcohols (*Laguncularia racemosa*, Mannitol present in leaves) or soluble carbohydrates (*Beta vulgaris* ssp. *Maritima*, Sucrose present in tap roots) or organic acids (like amino acids) or lowering the matric potential allows these species to maintain the water potential low and the charge balanced. Creating organic solutes, on the other hand, takes a lot of energy the creation of these solutes results in a reduction in the energy condition of the plant.

The result is, a compromise in Na and Cl-excluding species is required for plant survival, and this is a slowdown in plant growth. That has nothing to do with toxicity or a lack of necessary nutrients.

18.11 Salinity Tolerance Mechanism

One common way to figure out how plants deal with salt stress at the molecular level is to look how salt stress changes the activity or expression of cellular processes and genes (Hasegawa et al. 2000a, b), which has helped us learn more about how complicated it is for plants to handle salt. Studies have provided a better understanding of how the tolerance mechanism work in halophytes (Flowers and Colmer 2008; Colmer and Flowers 2008) as well as their possible use in farming and environmental services (Rozema et al. 2013). There are three ways that halophytes work that need to be studied.

- Vacuolar compartmentalization.
- Sodium extrusion and the SOS mechanism, which permits cytoplasmic ion homeostasis.
- A process of taking and recycling sodium.

1. Since Na toxicity is the primary stressor in saline soils, much effort has been put into identifying the ion transporters and regulatory mechanisms responsible for Na⁺ homeostasis and the maintenance of a high cytoplasmic Na⁺/K⁺ ratio. Overexpressing the vacuolar-type sodium and proton antiporter (Na⁺/H⁺ antiporter) gene from the halophytic plant *Atriplex gmelini* (Ag NHX1 = vacuolar Na⁺/H⁺ exchanger) resulted in a salt-sensitive rice cultivar with significantly greater salt tolerance than the wild type rice (Ohta et al. 2002). If large-scale genetic transfer can improve crop plants' salt tolerance, then more work like this could be beneficial in the near future. It has become clear that the Salt Overly Sensitive (SOS) signaling pathway, which is made up of the SOS1, SOS2, and SOS3 proteins, is important for both the recognition of and resistance to salt stress. A calcium signal induced by salt stress is thought to activate a protein kinase complex consisting of SOS2 and SOS3 (Zhu 2003). The Na⁺/H⁺ antiporter SOS1, located in the plasma membrane, is responsible for Na⁺ excretion into the apoplast and is phosphorylated and activated by this protein kinase complex.
2. To a lesser extent, SOS3-like calcium-binding proteins may potentially control Na⁺ transport in tonoplast. Excretion across the plasmalemma (SOS1) is an efficient route for keeping the cytosolic Na⁺ content low, but vacuolar compartmentalization of sodium (Na⁺) ions is also important. A Na⁺/H⁺ antiporter mediates the uptake of Na⁺ into the vacuole. In order to generate the proton-motive force necessary for this transport, an ATPase and an H⁺-pyrophosphatase work together. Na⁺ sequestration into vacuoles was improved and salt tolerance

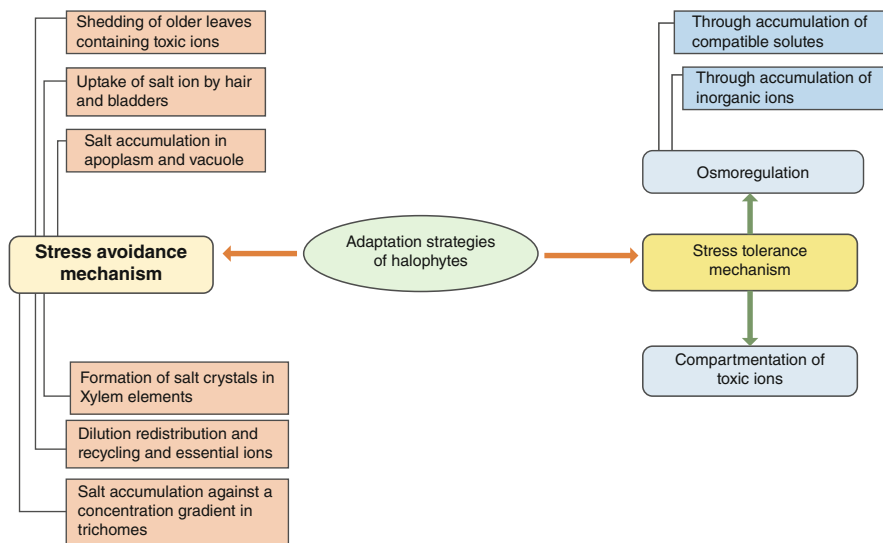


Fig. 18.4 The physiological basis for halophytes salt tolerance and resistance. (Adapted from Devi et al. 2019)

was increased when the tonoplast Na^+/H^+ antiporter and vacuolar H^+ -pyrophosphatase (AVP1) both were overexpressed (Gaxiola et al. 2001).

3. It is believed that a calcium signal brought on by salt stress activates a protein kinase complex made up of SOS3 and SOS2. Phloem tissue is the only organ in which the HKT1 gene is expressed, and it plays a crucial role in regulating sodium concentration in phloem sap (Fig. 18.4).

HKT1 probably helps Na^+ ion transport from the leaves to the stem and roots by letting Na^+ ions get into the phloem sap in the leaves and get out of it in the roots. Uozumi et al. 2000 observed that keeping K^+ uptake sustained, under salt stress requires the Na^+/K^+ symporter HKT1, a high-affinity carrier. Na^+ overload suppressed HKT1-mediated K^+ inflow and decreased HKT1 expression in transgenic wheat increased salt tolerance and decreased Na^+ absorption (Laurie et al. 2002). According to Katiyar-Agarwal et al. (2005), HKT1 being a crucial factor in tolerance of salt. Although, conventional breeding programs have had relatively little success in increasing crop salt tolerance because the trait is so complicated, both genetically and physiologically. These molecular investigations, in conjunction with rapid salt resistance testing techniques, could lead to new insights into how to boost crop yields in salty environments.

18.12 Conclusion and Future Prospective

Rising soil salinity is the main danger to agricultural production. Different plants behave differently to salinity. However, halophytes are able to survive under salinity due to ion selectivity and vacuolar compartmentalization. Various biotechnological techniques are used to create tolerant and high-yield crop types in order to address these problems. Transgenic food crops have been developed to deal with food scarcity, but much work need to be done in this field. Instead, of waiting for conventional salt-tolerant crops, we can use cash crop halophytes to take advantage of saline land. A new concept called “Biosaline Agriculture” has been developing over the last few decades. In this, several halophytes are grown to employ irrigation of saline or brackish water in place of normal crop plants. Three significant problems can be resolved in this way: First, saline or brackish water will be used for biosaline agriculture, and high-yielding glycophytic crops might be irrigated with good quality water that would otherwise be diverted for human use (Nikalje et al. 2019). The halophyte can also be utilized as attractive plants, biofuel, food (vegetables and edible oils), forage and fodder, medicinal, biofuel, and landscaping. Thirdly, the non-edible halophytes have been used in ecological balancing, phytoremediation of hazardous metals, textile dyes, etc., phytodesalination of soils impacted by salt, and other environmental clean-up projects. Halophytes can thrive in challenging circumstances without suffering a yield penalty because they have a built-in tolerance to various biotic and abiotic stresses. These multifunctional plants must be examined for their output and possible application in environmental remediation. It may be prioritized to domesticate these plants with many applications so they can replace traditional crops. Biosaline agriculture will undoubtedly offer a lot of potential as a complement to sustainable agricultural practices in the years to come (Fig. 18.5).

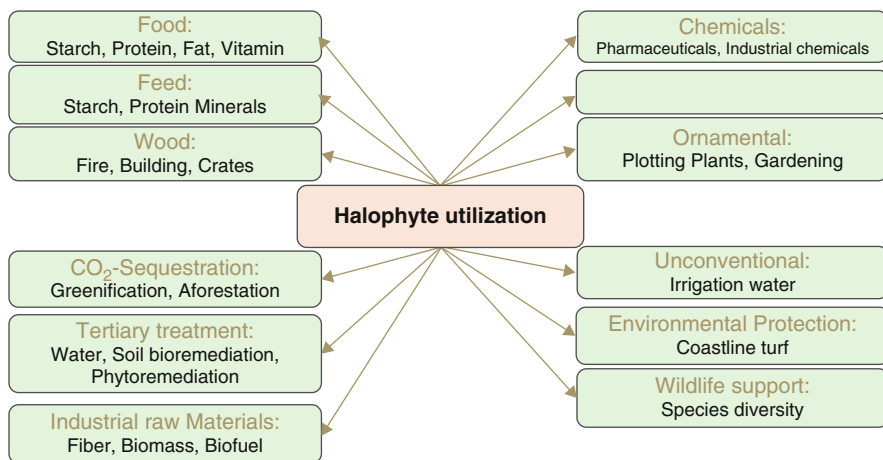


Fig. 18.5 Utilization of halophytes for the purpose of achieving economic benefits and cleaning up the environment. (Adapted from Nikalje et al. 2019)

References

- Bates DC (2002) Environmental refugees? Classifying human migrations caused by environmental change. *Popul Environ* 23(5):465–477
- Bilsborrow R, Delargy P (1990) Land use, migration and natural resource deterioration: the experience of Guatemala and the Sudan. *Pop Dev Rev* 16:125–147
- Colmer TD, Flowers TJ (2008) Flooding tolerance in halophytes. *New Phytol* 179:964–974
- Darkoh MBK (1982) Population expansion and desertification in Tanzania. *Desertif Contr* 6:26–33
- Devi S, Kumar A, Mann A, Arya SS, Chand G, Kumar N, Kumari A, Pooja RB, Kumar A (2019) Intra-habitat variability of halophytic flora of north-West India. In: Hasanuzzaman M, Shabala S, Fujita M (eds) *Halophytes and climate change: adaptive mechanisms and potential uses*. CABI, Oxfordshire, pp 38–54
- Duda AM, El-Ashry MT (2000) Addressing the global water and environment crises through integrated approaches to the management of land, water and ecological resources. *Water Int* 25(1):115–126
- Ericson JA, Freudenberger MS, Boege E (2001) Population dynamics, migration, and the future of the Calakmul Biosphere Reserve. In: *Biological diversity*. CRC Press, Boca Raton, FL, pp 261–292
- FAO (2000) Global network on integrated soil management for sustain-able use of salt- affected soils. FAO, Rome. <http://www.fao.org/ag/agl/agll/spush>
- Findlay AM (1996) Population and environment in arid regions, policy and research paper No. 10. IUSSP Scientific Committee on Population and Environment, Aubervilliers
- Flowers TJ, Colmer TD (2008) *Salinity tolerance in halophytes*. Wiley, New York, NY
- Flowers TJ, Troke PF, Yeo AR (1977) The mechanism of salt tolerance in halophytes. *Annu Rev Plant Physiol* 28(1):89–121
- Gaxiola RA, Li J, Undurraga S, Dang LM, Allen GJ, Alper SL, Fink GR (2001) Drought-and salt-tolerant plants result from overexpression of the AVP1 H+ pump. *Proc Natl Acad Sci* 98(20): 11444–11449
- Gleick PH (1994) Reducing the risks of conflict over fresh water resources in the Middle East. In: *Studies in environmental science*, vol 58. Elsevier, Amsterdam, pp 41–54
- Gleick PH (2000) *The world's water 2000-2001. The Biennial Report on Freshwater Resources*. Island Press, Washington, DC
- Glenn EP, Brown JJ, Blumwald E (1999) Salt tolerance and crop potential of halophytes. *Crit Rev in Plant Sci* 18(2):227–255
- Greenway H, Munns R (1980) Mechanisms of salt tolerance in nonhalophytes. *Annu Rev Plant Physiol* 31(1):149–190
- Hasanuzzaman M, Hossain MA, Teixeira da Silva JA, Fujita M (2012) Plant responses and tolerance to abiotic oxidative stress: antioxidant defense is a key factor. In: Bandi V, Shanker AK, Shanker C, Mandapaka M (eds) *Crop stress and its management: perspectives and strategies*. Springer, Berlin, pp 261–316
- Hasanuzzaman M, Nahar K, Fujita M (2013a) Plant response to salt stress and role of exogenous protectants to mitigate salt-induced damages. In: Ahmad P, Azooz MM, Prasad MNV (eds) *Ecophysiology and responses of plants under salt stress*. Springer, New York, NY, pp 25–87
- Hasanuzzaman M, Nahar K, Fujita M et al (2013b) Enhancing plant productivity under salt stress—relevance of poly-omics. In: Ahmad P, Azooz M, Prasad MNV (eds) *Salt stress in plants: omics, signaling and responses*. Springer, Berlin, pp 113–156
- Hasanuzzaman M, Nahar K, Mahabub Alam M, Bhowmik PC, Hossain MA, Rahman MM, Vara Prasad MN, Qzturk M, Fujita M (2014) Potential use of halophytes to remediate saline soils. *Biomed Res Int* 2014:589341
- Hasegawa M, Bressan R, Pardo JM (2000a) The dawn of plant salt tolerance genetics. *Trends Plant Sci* 5(8):317–319
- Hasegawa PM, Bressan RA, Zhu JK, Bohnert HJ (2000b) Plant cellular and molecular responses to high salinity. *Annu Rev Plant Biol* 51(1):463–499

- Katiyar-Agarwal S, Verslues P, Zhu J (2005) Mechanisms of salt tolerance in plants. *Plant Nutr Food Secur Hum Health Environ Protect* 23:44–45
- Khan MA, Ansari R, Ali H, Gul B, Nielsen BL (2009) *Panicum turgidum*, a potentially sustainable cattle feed alternative to maize for saline areas. *Agric Ecosyst Environ* 129:542–546
- Kinzel H (1982) *Pflanzenökologie und Mineralstoffwechsel*. Verlag Eugen Ulmer, Stuttgart, p 534
- Koyro HW (2003) Study of potential cash crop halophytes by a quick check system: determination of the threshold of salinity tolerance and the ecophysiological demands. In: Lieth H et al (eds) *Cash crop halophytes: recent studies*. Springer, Dordrecht, pp 5–17
- Koyro HW, Huchzermeyer B (2004) Ecophysiological needs of the potential biomass crop *Spartina townsendii* Grov. *Trop Ecol* 45(1):123–139
- Koyro HW, Lieth H (1998) Salinity conversion table. 2 enlarged ed.
- Koyro H-W, Wegmann L, Lehmann H, Lieth H (1997) Physiological mechanisms and morphological adaptation of *Laguncularia racemosa* to high salinity. In: Lieth H, Hamdy A, Koyro H-W (eds) *Water management, salinity and pollution control towards sustainable irrigation in the Mediterranean region: salinity problems and halophyte use*. Technomack Publication, Bari, pp 51–78
- Läuchli A, Epstein E (1990) Plant responses to saline and sodic conditions. *Agric Salin Assess Manag* 71:113–137
- Laurie S, Feeney KA, Maathuis FJ, Heard PJ, Brown SJ, Leigh RA (2002) A role for HKT1 in sodium uptake by wheat roots. *Plant J* 32(2):139–149
- Lokhande VH, Suprasanna P (2012) Prospects of halophytes in understanding and managing abiotic stress tolerance. In: Ahmad P, Prasad MNV (eds) *Environmental adaptations and stress tolerance of plants in the era of climate change*. Springer, New York, NY, pp 29–56
- Maas EV (1990) Crop salt tolerance. In: *Agricultural salinity assessment and management*. ASCE, New York, NY, pp 262–304
- Mahajan S, Tuteja N (2005) Cold, salinity and drought stresses: an overview. *Arch Biochem Biophys* 444(2):139–158
- Manchanda G, Garg N (2008) Salinity and its effects on the functional biology of legumes. *Acta Physiol Plant* 30(5):595–618
- Marschner H (1995) *Mineral nutrition of higher plants*, 2nd edn. Institute of Plant Nutrition University of Hohenheim, Stuttgart
- Mengel K, Kirkby EA (2001) *Principles of plant nutrition*. Kluwer Academic Publishers, Dordrecht; Boston, MA; London
- Moench M (2002) Water and the potential for social instability: livelihoods, migration and the building of society. *Nat Res Forum* 26(3):195–204
- Munns R (1993) Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. *Plant Cell Environ* 16(1):15–24
- Munns R (2002) Comparative physiology of salt and water stress. *Plant Cell Environ* 25(2): 239–250
- Munns R (2005) Genes and salt tolerance: bringing them together. *New Phytol* 167(3):645–663
- Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annu Rev Plant Biol* 59:651–681
- Nikalje GC, Bhaskar SD, Yadav K, Penna S (2019) Halophytes: prospective plants for future. *New Phytol* 179:945–963
- Ohta M, Hayashi Y, Nakashima A, Hamada A, Tanaka A, Nakamura T, Hayakawa T (2002) Introduction of a Na⁺/H⁺ antiporter gene from *Atriplex gmelini* confers salt tolerance to rice. *FEBS Lett* 532(3):279–282
- Pitman MG, Läuchli A (2002) Global impact of salinity and agricultural ecosystem. In: Läuchli A, Lüttge U (eds) *Salinity: environment—plants—molecules*. Kluwer Academic, Dordrecht, pp 3–20
- Rozema J, Muscolo A, Flowers T (2013) Sustainable cultivation and exploitation of halophyte crops in a salinising world. *Environ Exp Bot* 92:1–3
- Schubert S, Läuchli A (1986) Na⁺ exclusion, H⁺ release, and growth of two different maize cultivars under NaCl salinity. *J Plant Physiol* 126(2–3):145–154

- Serrano R (1996) Salt tolerance in plants and microorganisms: toxicity targets and defense responses. *Int Rev Cytol* 165:1–52
- Serrano R, Mulet JM, Rios G, Marquez JA, de Larrinoa IF, Leube MP, Mendizabal I et al (1999) A glimpse of the mechanisms of ion homeostasis during salt stress. *J Exp Bot* 50:1023–1036
- Stuart JR, Tester M, Gaxiola RA, Flowers TJ (2012) Plants of saline environments. Access Sci. <http://www.accessscience.com>
- Uozumi N, Kim EJ, Rubio F, Yamaguchi T, Muto S, Tsuboi A, Bakker EP, Nakamura T, Schroeder JI (2000) *Plant Physiol* 122:1249–1259
- White C (2014) 28. Understanding water scarcity: definitions and measurements. In: *Global water: issues and insights*, p 161
- World Bank (1999) *World development report*. World Bank, Washington, DC
- Zhu JK (2003) Regulation of ion homeostasis under salt stress. *Curr Opin Plant Biol* 6(5):441–445