Chapter 10
Mangroves: An Underutilized Gene Pool to Combat Salinity

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Abstract Salinity is a global problem, being aggravated by climate change, scanty rainfall, poor irrigation systems, salt ingression, water contamination, and other environmental factors. The salinity stress tolerance mechanism is a very complex phenomenon, and stress pathways are co-ordinately linked to impart salt tolerance. Although a number of salt-responsive genes have been reported from the halophytes, there is always a quest for promising stress-responsive genes that can modulate plant physiology according to salt stress. Several known genes, like antiporters, antioxidant encoding genes, and some novel genes, were isolated from halophytes and explored for developing stress tolerance in the crop plants (glycophytes). We provide here a comprehensive update on salinity-induced adverse effects on soils and plants. In this chapter, the physiological and biochemical adaptation strategies that help mangroves and crop plants grow and survive in salinity-affected areas are reviewed. In this review, mangroves are discussed as an underutilized gene pool of salt-responsive genes that can be utilized for developing salinity tolerance in crop plants using strategies, like genetic engineering and molecular breeding by marker-assisted breeding phenotyping technologies, GWAS, etc.

Keywords Salt stress · Mangroves · Mechanisms of tolerance · Salinity tolerance genes · Physiology · Molecular breeding methods · QTLs · Phenotyping · GWAS

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10.1 Introduction

Salt stress is a grave concern limiting crop production and causing damage amounting to 27.3 billion dollars annually (Qadir et al. 2014), forcing to look for expansion of irrigated agriculture to saline water. A 50% increase in the demand for food and fresh water is predicted by 2050 to sustain the expected 10–13 billion people (Gleeson et al. 2012; UN Water and Energy 2014; FAO 2017). The scarcity of food is bound to increase more than ever before, especially in sub-Saharan Africa, the Middle East, and South Asia, where population growth far exceeds agricultural productivity (FAO 2017). If we achieve the attainable productivity in these regions in rice, maize, and wheat, the productivity can be increased by 230%, 135%, and 224%, respectively, in these crops in the sub-Saharan region and by 129%, 83%, and 61% in South Asia (Mueller et al. 2012). The situation requires us to expand the irrigated agriculture to saline water which forms 98% of global water resources (Morton et al. 2019). Morton et al. (2019) define salt tolerance as the ability to maintain desirable plant performance traits under salt stress relative to control conditions.

Salt tolerance is the ability of the plant to reverse the deleterious effects of high salt concentration and grow to complete its lifecycle. Halophytes or salt-loving plants are further classified as obligate and facultative based on their dependence on salt for optimal growth. Studies on selected halophytes to investigate the salt requirement for growth and development showed that salts are not compulsorily required for the development of halophytic species, but the availability of water and nutrients is the key limiting factor for growth in natural saline habitats (Grigore et al. 2012). It is also hypothesized that halophytes got distributed to saline areas to avoid competition with glycophytic species (Mishra and Tanna 2017).

Mangroves are facultative halophytes tolerant to fluctuating salinity levels. Downton (1982) and Clough (1984) have included mangroves under obligate halophytes. Mangroves grow optimally at a salt concentration ranging from 5 to 25% (Downton 1982; Clough 1984; Ball 1988; Burchett et al. 1989; Ball and Pidsley 1995). Species-specific variations in the range of tolerance to salinity are reported (Ball 1988). Total absence and excessive NaCl are found to inhibit the growth of several mangrove species (Downton 1982; Clough 1984; Burchett et al. 1989; Pezeshki et al. 1990; Ball and Pidsley 1995). Mangroves being adapted to high salinity serve as models for studies on plant responses to salinity

Studies on salt tolerance mechanisms of model systems, like *Arabidopsis thaliana* and the facultative halophyte *Mesembryanthemum crystallinum* (Apse et al. 1999; Nanjo et al. 1999; Liu et al. 2000; Quesada et al. 2000; Shi et al. 2000; Zhu 2000; Elphick et al. 2001; Ratajczak et al. 1994; Low et al. 1996; Golldack and Dietz 2001; Su et al. 2001; Agarie et al. 2007), are many. Downton (1982) and Clough (1984) stressed the need to study mangroves as salt stress adaptors. The use of mangroves for breeding salt-tolerant crops has been reinstated by several authors (Meera et al. 2013).

Soil salinization is the accumulation of soluble salts in the soils (Bockheim and Gennadiyev 2000). Arid and semi-arid climates particularly favor this, with evapotranspiration volumes being greater than precipitation volumes throughout the year. Saline soils are defined as those with an electrical conductivity (EC) of the saturation soil paste extract of more than 4 dS/m at 25 °C, which corresponds to approximately 40 mM NaCl, producing an osmotic pressure of approximately 0.2 MPa (Munns and Tester 2008; USDA-ARS 2008). Salts may include chlorides, sulfates, carbonates, and bicarbonates of sodium, potassium, magnesium, and calcium. The diverse ionic composition of salt-affected soils results in a wide range of physiochemical properties. A significant reduction in yield is observed in crops grown on soils with an EC value above 4.

Saline-sodic soils are those with a combination of high alkalinity, high Na+, and high salt concentration (Eynard et al. 2005), whereas sodicity refers to the amount of Na+ retained in the soil. High sodicity (more than 5% of Na+ of the overall cation content) causes the clay to swell excessively when wet, causing limited air and water movements and poor drainage. Salts may arise naturally in subsoil (primary salinization) or maybe be introduced (secondary salinization) by soil amendments, inorganic fertilizers, and irrigation with brackish water (Carillo et al. 2011). These have led to the salinization of more than 6% of the world's total land area (800 million hectares). Of the current 230 million ha of irrigated land, 45 million ha (19.5%) has already been damaged by salt (FAO 2017). Among the salinity-affected soils, saline, sodic, and saline-sodic account for 60, 26, and 14%, respectively. Approximately 736 (65%), 227 (20%), 53 (5%), and 114 (10%) Mha of all salinity-affected soils are further categorized as slightly, moderately, highly, and extremely salinity-affected soils, respectively; the severity, varying across the world. Middle East, Australia, North Africa, and the former Soviet Union account for 176, 169, 161, and 126 Mha of land, respectively (Rahman et al. 2021). NaCl is the most soluble and widespread salt; plants have evolved mechanisms to tolerate/exclude it while allowing the acquisition of other nutrients available at low concentrations, such as phosphate, potassium, and nitrate (Hanin et al. 2016)

In glycophytes (most crop plants), growth is inhibited or even completely prevented by NaCl concentrations of 100–200 mM, resulting in plant death (Munns and Termaat 1986), even by short-term exposure (Hernández and Almansa 2002). On the other hand, halophytes survive in high NaCl concentrations (300–500 mM) as they are better equipped with characteristic salt resistance mechanisms (Hernández and Almansa 2002; Parida and Das 2005). Euhalophythes (plants growing in saline habitats) regulate their salt content by salt exclusion by preventing the entry of salts into the vascular system, salt elimination via. salt-secreting glands and hairs that eliminate salts, salt succulence i.e. increasing the storage volume cells progressively with the uptake of salt by uptake of water and thereby maintaining salt concentration constant and salt redistribution, by Na+ and Cl− being readily translocated through phloem so as to redistribute the increase in concentration caused by actively transpiring leaves (Acosta-Motos et al. 2017)

Based on their capacity to tolerate salt concentrations, halophytes are named obligate halophytes exhibiting low morphological and taxonomical diversity with optimal growth rates in highly saline habitats. Facultative halophytes are found inhabiting less saline habitats along the border between saline and non-saline upland and are characterized by broader physiological diversity enabling them to thrive under saline and non-saline conditions. Mangroves are generally considered facultative halophytes, though some authors include them under the obligate category, such as Downton 1982 and Clough 1984 (Meera et al. 2013).

Santos et al. (2016) developed a database of halophytes, namely, eHALOPH (http://www.sussex.ac.uk/affiliates/halophytes/), to accumulate the information on plant species that survive under 80 mM or higher salt concentrations. They classified the halophytes into seven groups, typically growing in aquatic conditions or on wet soil (hydrohalophytes); clifftops, rocky and sandy seashores, and saltmarshes (chasmophytes); deep-rooted plants obtaining water from a deep underground source that may or may not be saline (phreatophytes); sandy soils (psammophiles); adapted to extreme drought-prone areas (xerophytes); species predominantly invading and colonizing highly disturbed sites or regions (weedy halophyte); and adapted to inland salt desert and saline habitats (Xerohalophytes). In addition, based on the physiological basis of salt tolerance as well as the accumulation and transportation of ions, Breckle (1995) classified halophytes into three major categories, including recretohalophytes (with salt-secreting structures), euhalophytes (dilute absorbed salts, succulents), and salt-exclusion halophytes (also referred to as salt excluders—shed leaves with toxic levels of salt) (Rahman et al. 2021).

Mangroves represent a group of plants (woody halophytes) adapted to withstand harsh coastal conditions, like high salinity, extreme temperatures, and anaerobic soils. The molecular mechanism behind the origin, diversification, and adaptation of these stress-tolerant trees are ever so relevant with respect to climate change. The mangroves comprise around 80 species derived from 20 plant families with genetic, physiological, and anatomical adaptations to withstand extreme environmental conditions (Duke et al. 1998; Duke 2013). Mangroves serve as models for stress tolerance and as reservoirs for novel genes and proteins involved in salt tolerance. With the onset and development of salt/ drought stress within a plant, major processes, such as photosynthesis, protein synthesis, and lipid metabolisms, are affected. Biochemical and physiological mechanisms involving water relations, photosynthesis, and accumulation of various inorganic ions and organic metabolites contribute to salt tolerance. The ability of the plant to react to high salinity depends on the genes that are expressed during stress (Sreeshan et al. 2014)

Rajalakshmi and Parida (2012) reported mangroves as a resource for abiotic stress genes, like high lactate dehydrogenase activity in the roots of mangrove *Suaeda maritima* (Weston et al. 2012). Mangroves being unique grow equally well under extreme saline conditions and under freshwater conditions and can be used as source material for isolation of stress-tolerant genes (Tomlinson 1986). *Avicennia marina*, *Bruguiera cylindrica*, *Bruguiera gymnorhiza*, *Aegiceras corniculatum*, *Rhizophora stylosa*, and *Rhizophora mucronata* have been used to source genes concerned with stress tolerance. EST sequencing of a salt-stressed *Avicennia marina* leaf library revealed that 30% novel cDNAs with no homology to previously characterized genes in public databases (Mehta et al. 2005), of which 26 clones were highly upregulated and five clones were downregulated during salt stress. The suppression subtractive hybridization (SSH) approach led to the isolation of a number of salt-tolerant genes from the root of mangrove *Bruguiera cylindrica*; 81 salt-induced cDNAs were identified, of which 42 did not have homology to previously reported cDNAs (Wong et al. 2007). *Bruguiera gymnorhiza*, cDNA libraries constructed from the leaves and roots revealed 44 putative salt tolerance genes, including Bg70 and cyc02 homologs (Miyama et al. 2006). Transgenic Arabidopsis plants overexpressing these two genes and lipid transfer and ankyrin genes exhibited increased tolerance to NaCl (Ezawa and Tada 2009). SSH analysis of salt-stressed leaves *Aegiceras corniculatum* led to the isolation of 577 ESTs, of which 30 ESTs showed no homology to any previously reported sequence (Fu et al. 2005). Suppressive subtraction was used to isolate salt-responsive genes from the roots of *Rhizophora stylosa* (Mohammad et al. 2011).

It is suggested that the majority of mangrove plants are angiosperms which first appeared in the fossil record as sparse montane shrubs during the Early Cretaceous (Takhtajan 1980). Fossils of mangroves have been found since the end of the Palaeozoic, as coastal vegetation, before the origin of angiosperms (Tomlinson 1986). True mangroves consisting of three genera of mangroves are found to have originated during the Palaeocene Eocene thermal maximum (PETM), ~55-5 Myr ago, when the sea level rose due to the melting of ice. Some of the land plants developed specialized structures and characters to combat the salty environment, prior to whole-genome duplication (WGD). Mangroves are found to strongly prefer 4 AAS and avoid five others across the genomes as in Convergent evolution (He et al. 2020).

Geological and fossil records based on pollen, fruits, and wood of Nypa, Avicennia, Sonneratia, Rhizophoraceae, and mangrove associates have led Srivastava and Prasad (2019) to trace the origin of mangroves to Late Cretaceous till Miocene. The oldest geological record of Nypa palm (late Cretaceous) exemplifies the broad ecological tolerance and pantropical distribution of mangroves. Sea-level rise and humid climate led to the development of 12 genera of mangroves in nine families and their expansion and multiplication in newer regions during early to middle Eocene (~50–40 Ma). Neogene latitudinal contraction, extinction, and migration, the Himalayan uplift, and the establishment of the Asian summer monsoon caused the mangrove distribution of the Indian subcontinent. Three genera, Avicennia, Nypa, and Rhizophora, found along the Tethys Sea coasts may be the ancestors of Old World mangroves, and four genera adding Pelliciera to the above three flourishing along America's coasts may have descended to form the New World mangroves.

10.2 Salt Stress Tolerance

Salt-resistant plants show several adaptations in their morphological, physiological, and biochemical characteristics, which help them adapt to the deleterious effects caused by salinity. Plants inhabiting saline environments confront challenges, like water loss, decrease in photosynthetic activity, leaf ion toxicity, etc. These plants show adaptations, like changes in leaf anatomy, increase in chlorophyll content, and root/canopy ratio, and evolve certain mechanisms to protect photosynthetic machineries, like photorespiration pathway, water–water cycle, and xanthophyll cycle. Studies have revealed the interaction of salt-induced oxidative stress at the subcellular level and its impact on antioxidant systems in salt-tolerant and salt-sensitive plants, thereby revealing the effect of salinity on physiological processes (Acosta-Motos et al. 2017).

An elevation in soil salinity adversely affects plant growth and development in several ways. A highly saline soil creates water paucity and this, in turn, lowers the osmotic potential of soil water, which interrupts imbibition in plant seeds and severely affects seed germination (Ashraf and Harris 2013; Acosta-Motos et al. 2015a, b). As a consequence of disruption in seed imbibition, plant shows alteration in enzymatic activities, protein metabolism, hormonal imbalance, a decline in the seed reserve utilization, and eventually damage to the ultrastructure of cells, tissues, and organs (Acosta-Motos et al. 2015a, b; Mazher et al. 2007). The elevated soil salinity primarily has a negative impact on plant growth and biomass after seed germination, which varies with salinity levels, duration of salt exposure, and the type of plant species (Ashraf and Harris 2013). When a plant cell is exposed to salinity, within seconds, the cell gets shrunk by dehydration (Passioura 1988). A shrunken cell can regain its size over hours, but the cell elongation rates remain reduced (Vamerali et al. 2003). Cell division rates are also hindered, leading to an overall decrease in plant growth (Franco et al.) Salinity can also produce obvious damage to the older leaves, as well as the mortality of older and younger leaves, leading to plant death before seed maturity (Passioura 1988; Vamerali et al. 2003). The roots are the most exposed to saline soils and serve as a primary conduit for mineral translocation to aerial portions of the plant. Root responses are primarily responsible for the lower growth rate of plants under salinity (Franco et al. 2011a, b). Salt stress reduces the water potential of the soil solution, interfering with root water conductivity, thereby reducing water and mineral influx to the plant body (Ma et al. 2010). High concentrations of Na+ and Cl in soil solution limit micronutrient uptake and accumulation, causing signal transduction, membrane stability, chlorophyll production, and stomatal opening to be disrupted (Franco et al. 2011a, b; Steudle 2000). Furthermore, the detrimental effects of salinity on photosynthesis also lead to the breakdown of photosynthetic pigments. Plants exposed to salt stress had lower stomatal density, stomatal conductance, photosynthetic activity, and carbon assimilation, but higher mesophyll resistance, lowering photosystem (PS)-I, and PS-II light absorption efficiency (Ranathunge et al. 2010). Salt stress also reduces the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), a crucial enzyme involved in the assimilation of carbon dioxide (CO2) during photosynthesis' dark phase (Miteva et al. 1992). Salinity also stimulates the generation of reactive oxygen species (ROS), such as the hydroxyl radical (OH·), superoxide (O_2·), hydrogen peroxide (H_2O_2), and singlet oxygen ($^1O_2$), in cellular organelles, such as chloroplasts, mitochondria, peroxisomes, and the endoplasmic reticulum (Munns 2005; Koyro 2006). Increased ROS levels can harm plant growth and development by reducing protein synthesis, destroying cell membranes, generating genomic instability, and damaging the photosynthetic system (Mostofa et al. 2021). Despite the fact that Cl^- is the most prevalent anion in salt soils, it has received less attention than Na+ in terms of its effects on plant performance, as well as its uptake and transport processes inside plants (Whiley et al. 2002). Cl^- is an important micronutrient, thought to have functions in enzyme activation in the cytoplasm, oxygen evolution during photosynthesis, membrane potential stability, and plant cell turgor pressure, and pH maintenance (Whiley et al. 2002). Cl^-, on the other hand, has far more harmful effects than Na^+ in disturbing the normal activities of cells once it has accumulated excessively (Whiley et al. 2002). All of the abovementioned salinity-induced negative impacts on plants result in a reduction in crop production; however, the severity and extent of the damage vary between plant species (Whiley et al. 2002).

To summarize, salt stress produces a considerable decrease in plant growth in salt-sensitive plants, especially in the aerial part. The accumulation of phytotoxic ions in leaves results in a nutrient imbalance, causing decreased K+ and Ca2+ levels. Salinity also topples over the plant's water relations, leading to lower leaf relative water content (RWC) and leaf water potential (ψl). When photosynthesis rate (PN) decreases, chlorophyll content and chlorophyll fluorescence parameters decrease in parallel. Oxidative stress at the subcellular level takes place, the synthesis of ethylene and abscisic acid (ABA) increases, and a decrease occurs in indol-3-acetic acid (IAA) and cytokinin (CK) synthesis, causing senescence in salinized leaves. Due to the stress, chloroplast gets damaged, and starch accumulates. The accumulation of salts in the root zone causes a decrease in osmotic potential, root water potential (ψr), and the root hydraulic conductivity (Lp), diminishing the water available to the root zone and causing a nutrient imbalance in roots (Acosta-Motos et al. 2017).

Euhalophytes (salt-loving plants) may also store salt in their cell sap to the point that their osmotic potentials are lower than the soil solution. Aside from salts, soluble carbohydrates play a crucial function in maintaining a low osmotic cell sap potential. The protoplasm's capacity to tolerate high salt concentrations is dependent on the compartmentalization of ions entering the cell. The vacuoles gather the majority of the salt ions (includer mechanisms). Salt stress affects plant development in the short term by producing osmotic stress owing to decreased water availability and in the long term by salt-induced ion toxicity due to nutritional imbalance in the cytosol (Munns 2005; Koyro 2006). Salinity leads to the excessive uptake of salts, like sodium and chloride as well as deficiency of calcium and potassium, also the production of ROS. All of these salinity responses contribute to the negative impacts of salt stress on plants (Hernandez et al. 1993, 1995; Hernández et al. 2003; Mittova et al. 2003). To deal with the stress caused by saline environments, plants should activate several physiological and biochemical systems. Morphology, anatomy, water relations, photosynthesis, the hormonal profile, toxic ion distribution, and biochemical adaptability (such as the antioxidative metabolism response) are examples of such systems (Rahman et al. 2021).

Among glycophytes and halophytes and between different species of the same family and genus, differences in response to saline water irrigation are found. Plant responses also depend upon the salt concentration in irrigation water and the time of exposure. Munns 1992 found that while salts do not directly affect development, they do alter turgor, photosynthesis, and/or the activity of certain enzymes. Vacuoles serve as the storage unit of incoming salt. With the increase in the concentration of and the subsequent rise of salt in the cell walls or cytoplasm, vacuoles may no longer sequester incoming salt (ionic phase), resulting in a drop-in soil water potential (osmotic phase), followed by salt damage in leaves, eventually leading to decline in growth. Munns 1992 discovered that salt accumulation in old leaves causes them to die, thereby reducing the availability of carbohydrates and/or growth hormones in the meristematic areas causing restricted growth. The development of particular metabolites that directly impede growth is influenced by the fact that plant growth is limited by the drop-in photosynthetic rate and excessive uptake of salts (Mazher et al. 2007; Rahman et al. 2021)

10.3 Morphology of Roots and Aerial Parts

Root performance is determined by the anatomy of the root system (length, root diameter, and so on), which allows plants to collect water and nutrients and hence enhance the replacement of water lost from the plant (Passioura 1988). Roots act as an interface between the plant and soil, and optimal root systems can enhance shoot growth and improve plant yield (Vamerali et al. 2003). Plants with a more extensive root system appear to be healthier since it helps them reach deeper layers of soil for water and nutrients (Franco et al. 2011a, b). Recent studies have found that alternative root characteristics, such as tiny roots, can be more beneficial for shoot development (Ma et al. 2010). Even a few roots in moist soil can supply significant amounts of water, regardless of the number of roots. The permeability of roots to water is also determined by other root features, such as the number and diameter of xylem vessels, the breadth of the root cortex, the number of root hairs, and the suberin deposition in both the root exodermis and endodermis (Steudle 2000; Ranathunge et al. 2010). Furthermore, changes in soil environmental conditions (such as temperature, lack of oxygen, mechanical impedance, and salt) can have a significant impact on root structure. The cell walls of salinized plants' root cells are frequently thickened and twisted unevenly (Shannon et al. 1994). Salts encourage the suberization of the hypodermis and endodermis in woody tree roots, resulting in the development of a well-developed Casparian strip closer to the root apex (Walker et al. 1984). Furthermore, certain plants' morphology reveals their salinity sensitivity. Avocado trees, for example, have a shallow root structure with little ramification, which reduces their water and nutrient absorption capacity (Schaffer et al. 2013) and makes them more sensitive to soil salt (Bernstein et al. 2004). These physical characteristics limit the crop's distribution to places with good irrigation water. The root system morphology of *Callistemon citrinus* plants has also been observed to be altered by saline water irrigation (Álvarez and Sanchez-Blanco 2014). Furthermore, Álvarez et al. (2011) and Álvarez and Sánchez-Blanco (2013) reported similar reactions in *C. citrinus* under deficit irrigation, implying that the effect of water stress on root system morphology in *C. citrinus* is very similar to that caused by irrigation with salty water. The same behavior was found in *Euonymus japonica* plants irrigated with a NaCl solution and reclaimed water having various salt concentrations, which resulted in a reduction in total root length, particularly in thin (0.5 mm) and medium thickness (0.5–2.0 mm) roots (Gómez-Bellot et al. 2013a, b). Franco et al. and Croser et al. showed an increase in root diameter (hypertrophy) in response to salt in various plant species (*Picea sp., Pinus banksiana*, *Portulaca oleracea*). The higher root density observed in these plants suggests greater robustness and, presumably, a higher accumulation of reserves (Franco et al. 2011a, b; Gómez-Bellot et al. 2013a, b; Croser et al. 2001), which would improve plant resistance to saline environments and speed up the establishment of plants, particularly ornamental plants for gardening and landscaping. High sodium uptake ratio values cause sodicity, which increases soil resistance, reduces root growth, and reduces water movement through the root with a decrease in hydraulic conductivity (Rengasamy and Olsson 1993). In general, when plants are irrigated with low-quality water, their root hydraulic conductivity decreases. In reality, one of the most important criteria influencing the long-term viability of a recycled water irrigation system is root hydraulic conductivity. Root hydraulic conductance is usually stated in terms of the dry weight (DW) of the entire root, ignoring the effect of root design on water uptake capacity. However, the number of fine roots, which determine the root length and surface area, can vary substantially for any given root dry weight value, altering the water absorption level (Fitz Gerald et al. 2006; Zobel et al. 2007). Furthermore, the rootstock qualities impact the plant response to salinity in assays using grafts. Abiotic stress is mitigated more effectively by salt-tolerant rootstocks than by salt-sensitive rootstocks. It was found that *Clemenules mandarin* trees grafted on Carrizo (salt-sensitive rootstock) had lower fruit output and quality than Cleopatra (salt-tolerant rootstock) when both were irrigated with NaCl solution (30 mM) (Navarro et al. 2010). Salt-tolerant rootstocks were found to boost the output of a commercial pepper cultivar under saline irrigation in trials conducted by Penella et al. (2015, 2016). Different nutritional and physiological responses, such as ionic regulation, optimum photosynthetic performance, and sink strength maintenance, were observed. Inoculating the roots with arbuscular mycorrhizal fungi (AMF), which are important bioameliorators for saline soils, is another way to relieve or protect plants from saline stress. Navarro et al. (2014) investigated the impact of AMF in alleviating the detrimental effects of salt stress in citrus seedlings inoculated with a combination of AMF (*Rhizofagus irregularis* and *Funneliformis mosseae*). This protective effect, or synergic interaction, is enhanced when salt-tolerant rootstocks are used. When the roots develop in a salty environment, good AMF–soil–plant interactions make it viable to utilize reclaimed water. Salt stress causes a general drop-in fresh weight (FW) or DW in all plant tissues, although it is most visible in the aerial section. A drop-in FW or DW has been linked by many writers to a reduction in the number of leaves and leaf abscissions. Some experiments have indicated that a specific Cl build-up in the leaves of salt-stressed plants triggers high-efficiency 1-aminocyclopropane-1-carboxylic acid (ACC) synthesis and conversion to ethylene, releasing enough hormone to trigger leaf abscission as seen in citrus leaves and other plants (Tudela and Primo-Millo 1992). In the halophyte *Allenrolfea occidentalis*, salt and osmotic stress aided the conversion of ACC to ethylene (Chrominski et al. 1988). Early events during the osmotic phase of salt stress induce leaf senescence prior to the huge build-up of harmful ions, according to experiments conducted on tomato. The advancement of senescence in salinized leaves may be aided by an indirect impact associated to early ABA build-up and a reduction in IAA and CK levels. The ethylene precursor ACC, on the other hand, is the key hormonal signal that is temporally linked to the initiation of oxidative damage, chlorophyll fluorescence reductions, and significant Na+ build-up (Albacete et al. 2008; Ghanem et al. 2008). A decrease in total leaf area is another common reaction to salt stress. The earliest response of glycophytes exposed to salt stress is reduced leaf growth (Munns and Termaat 1986). When the stomata are closed, the observed reduction in canopy area could be interpreted as an avoidance mechanism that reduces water loss through transpiration (Savé et al. 1994; Ruiz-Sánchez et al. 2000). This action may favor the preservation of harmful ions in the roots, reducing their build-up in the plant's aerial section (Munns and Tester 2008; Colmer et al. 2005). Cell wall characteristics alter under salinity, and leaf turgor and photosynthetic rates (PN) decrease, resulting in a decrease in total leaf area (Franco et al. 1997; Rodrıguez et al. 2005). Furthermore, excessive salt concentrations inhibit stem development (which is a component of the aerial portion). Reduced leaf and stem diameters result in a reduction in the size of all aerial parts as well as the plant's height. The most frequent response to salt stress is an increase in root to shoot ratio or a decrease in the shoot to root ratio, which is due to characteristics associated with water stress (osmotic impact) rather than a salt-specific effect (Hsiao and Xu 2000). Under salt stress, a higher root percentage may favor the preservation of harmful ions in this organ, limiting their transfer to the aerial portions. This reaction might be a common plant resistance/survival strategy under saline conditions (Cassaniti et al. 2009, 2012). Reduced plant growth (Munns and Tester 2008), restricting leaf expansion (Cramer 2002a, b), and disrupting the interaction between the aerial and root portions (Tattini et al. 1995) are all effects of high salt concentrations in irrigation water. Some plant species have shown a higher dry root mass than shoot dry mass under high salinity, resulting in an increased root to shoot ratio, which is thought to improve the water and nutrient source/sink ratio under such conditions (Zekri and Parsons 1989).

Plants react to salt and drought stress in similar ways, and the processes involved are similar. Salt and drought stress have an impact on every part of plant physiology and metabolism. These are good candidates for genetic modification to increase salt and drought resistance. Ionic and osmotic stress signaling for re-establishing cellular homeostasis under stress conditions, detoxification signaling to control and repair stress damages, and signaling to coordinate cell division and expansion to levels appropriate for the particular stress condition are the three functional categories of salt and drought stress signaling (Zhu 2002). Single-function genes and regulatory genes are two types of genes that are triggered by salt stress. Osmolytes, transporters/channel proteins, antioxidative enzymes, lipid biosynthesis genes, polyamines, and other protective metabolites are all produced by the first group of genes. Regulatory proteins, such as basic leucine zipper (bZIP), drought-responsive element-binding protein (DREB), myelocytomatosis/myeloblastoma (MYC/MYB), and no apical meristem, ATAF 1, 2, and cup-shaped cotyledon (NAC), affect the expression of several downstream salt stress tolerance genes (Shinozaki and Yamaguchi-Shinozaki 2007; Agarwal and Jha 2010). These two types of genes interact in the signaling pathways indicated above to provide abiotic stress tolerance.

Under salt stress, secondary metabolites, such as the products of phenylpropanoid biosynthesis, are among the molecules accumulating in plants to combat it (Korkina et al. 2007). In salt-stressed *Kandelia candel*, the total concentration of phenols showed no significant difference between 0 and 200 mM NaCl treatments, but it increased 17% under 500 mM NaCl stress. Anthocyanins and proanthocyanidins levels also increased significantly when NaCl concentration increased from 200 to 500 mM. The lignin concentration also increased, although it nearly peaked at 200 mM NaCl. The most abundant amino acid under all three conditions was glutamine (Glu) which accounted for >50% of the total free amino acid concentration in the leaves of *K. candel*. Threonine and histidine increased fivefold and 34-fold under 500 mM NaCl stress. Proline did not show an increase in concentration. GABA, a four-carbon non-protein amino acid, also showed an increase. The concentration of free Glu, serine, valine, and lysine also increased significantly in response to salt stress. The GSH (an antioxidant) levels in the leaves of *K. candel* also showed 27% increase at 200 mM and 15% increase at 500 mM NaCl (Wang et al. 2016a, b).

10.4 Chromatin Modifications and Epigenetics in Salt Tolerance

A plant's ability to adapt to varied environmental pressures is thought to be aided by chromatin alteration, also known as epigenetic modifications (Gómez-Bellot et al. 2013a, b; Fernández-García et al. 2014). The role of chromatin remodeling in plant stress physiology has been understood through multiple studies. Plants, when hyper osmotically primed and later grown under control conditions (showing apparently no changes compared to untreated plants), were noticed to have accumulated less Na+ ions when salt was added and thus found much tolerant than untreated ones. Further, it was observed that HKT1expression in pretreated plants was more intense than in control, which may be the reason for variation in Na+ deposition. No conclusive evidence of epigenetic inheritance of salt tolerance from one generation to the next has been found in research on salinity to date. The ploidy status of a plant also has a significant impact. In Arabidopsis, auto polyploidy has been demonstrated to account for enhanced salt resistance, which results in more effective potassium accumulation (Zhen et al. 2010; Deinlein et al. 2014).

Seed priming using phytohormones has emerged as a viable technique of abiotic stress management in plants from stresses by increasing antioxidant enzyme activity, reducing oxidative damage, and improving plant growth. This method enhances abiotic stress tolerance in crop plants and can be used to maintain sustainable crop production in drought, salinity, and flood-prone areas around the world (Rahman et al. 2021).

10.5 Small RNAs

Small RNAs in plants are complex as they are derived through several pathways and play a vital role in abiotic stress regulation. One of the candidates in regulatory RNA, viz., small non-coding RNAs (ncRNAs), regulate distinct biological activities in plants as well as other organisms. MicroRNA (miRNA) and siRNA, which are ncRNAs, participate in the regulation of the expression of vital genes in distinct biological processes by RNA interference (RNAi). Hence, crop improvement utilizes the strategy of siRNA and miRNA interference. Various studies have confirmed the role of miRNA in salinity stress response. Enhanced salt stress tolerance has been shown by the transgenic Arabidopsis and creeping bent grass, which overexpressed miR393, a resistant form of TIR1, and rice miR528, respectively. In Arabidopsis, it was observed that water loss was reduced and germination rate decreased, whereas in the other, tiller number has increased (Chen et al. 2015; Yuan et al. 2015). Pan et al. 2016 has found that miR172a participates in the salt stress tolerance of soybean by downregulating the expression of an AP2/EREBP type transcription factor SSAC1 by acting as a long-distance signal. Microarray studies by Ding et al. (2009) found that miR156, miR164, miR167, and miR396 family members of maize were downregulated and miR162, miR168, miR395, and miR474 were upregulated during salt stress. sRNAs that regulate salt stress and impart salinity tolerance in the plant have been identified. A 24 nt long siRNA was found to regulate the expression of MYB74; an Arabidopsis salinity-induced transcription factor, by RNA-directed DNA methylation (Xu et al. (2015). Silencing of the rice floral meristem-specific cytokinin oxidase (OsCKX2) using siRNA-based approach, provided salinity tolerance without any yield loss (Joshi et al. 2018a, b). RNAi is a promising technology for obtaining crop varieties tolerant to different types of abiotic stresses and with improved yield since they are relatively safer than transgenics. RNAi has great scope since it can engineer the plant by controlling the regulation of vital genes and transcription factors involved in stress responses. Identification of sRNAs and their corresponding targets enhance the scope of engineering plants for stress tolerance. sRNA-based engineering of plants is mainly done through overexpression and short-term tandem mimicry (STTM) for the regulation of sRNAs. STTM approach has been performed for the knockdown of miR166 maize, resulting in abiotic stress tolerance (Li et al. 2020). In RNAi technique, transformed plants that express dsRNA show genetic modification and confer resistance against abiotic stresses. Moreover, deregulation of target genes using artificial miRNA (amiRNA) and ta-siRNA (ata-siRNAs) can also be done (Cisneros and Carbonell 2020). Overexpression of miRNA can be obtained by expressing pre-miRNA in expression vectors. The latest clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein (Cas) technology has high potential in developing abiotic stress-tolerant varieties by editing MIR genes. The utilization of micro peptides, a translational product of pri-miRNA, is yet to be deciphered (Iborra et al. 2001; Prasad et al. 2020; Tiwari and Rajam 2022)

10.6 Nanoparticles

Nanoparticles (NPs) may be described as materials with diameters between 1 and 100 nm in at least one dimension. It has been observed that NPs minimize the uptake of heavy metals by modifying the expression of genes responsible for metal uptake and thereby reduce HM bioaccumulation. Furthermore, NP treatment improves the physiological and biochemical parameters of the plants, such as enhancing the synthesis of defense enzymes (SOD, POX, CAT, APX, etc.); augmenting nutrient uptake; decreasing the loss of electrolytes; improving pigments and soluble proteins; reducing peroxidation; and causing a rise in the levels of proline, glutathione, and phytochelatins. These attributes are primarily responsible for the overall increase in the abiotic stress tolerance of the crops by NP treatment and the effect may vary slightly according to the genotype (Rajput et al. 2021). NPs can be successfully used in plant genetic engineering as a genome editor also. All of these factors make NPs a perfect candidate to boost plant immunity against abiotic stress (Khalil et al. 2021).

Both drought and cadmium stresses were reduced by the application of iron oxide NPs (IONPs) and hydrogel nanoparticles (HGNPs) simultaneously in rice (Ahmed et al. 2021). Levels of both hydrogen peroxide and lipid peroxidation after drought were reduced when γ-Fe_2O_3 NPs were delivered by irrigation in a nutrient solution to *Brassica napus* plants grown in soil (Palmqvist et al. 2017).

10.7 Species and Mechanisms

Many species which are conventionally regarded as halophytes are sensitive to salinity and several species among glycophytes show resistance to salinity and other abiotic stresses. Halophytes are the best models for studying salinity tolerance mechanisms in plants (Shabala 2013; Flowers and Colmer 2015; Himabindu et al. 2016). Several reports suggest that both glycophytes and halophytes possess similar mechanisms to resist salinity stress, but the difference lies in the quantitative aspect, not the qualitative (Anjum et al. 2012; Rai et al. 2012; Bartels and Dinakar 2013; Sreeshan et al. 2014; Joshi et al. 2015; Volkov 2015; Muchate et al. 2016). Functional validation of salinity tolerance in halophytes is done in transgenic systems. Salt tolerance in halophytes is possibly due to the difference in the expression level of important genes that participate in salt tolerance or the production of comparatively active proteins, which are involved in stress tolerance (Anjum et al. 2012; Das and Strasser 2013; Himabindu et al. 2016; Muchate et al. 2016). *Thellungiella salsuginea*, a halophyte closely related to the model plant *Arabidopsis thaliana* is regarded as a model system for studying halophyte genes responsive to salinity (Amtmann 2009; Bartels and Dinakar 2013). Genomic studies in *T. salsuginea* provide insights into the genetic basis of halophyte salinity tolerance mechanisms (Wu et al. 2012). Comparative microarray studies on *T. salsuginea* showed that when compared to Arabidopsis, only a few genes were induced in *Thellungiella* on exposure to salt (Taji et al. 2004). However, Wong et al. (2006) reported that compared to *Arabidopsis*, *Thellungiella* differentially expressed 154 genes under salt stress. A random gene transfer from *Lepidium crassifolium*, a halophyte related to *Arabidopsis*, resulted in increased salinity tolerance in *Arabidopsis* (Rigó et al. 2016). Most of the halophytic genes transferred to crop species belong in the category of antiporters, ROS scavangers, K+ transporters, ion channels, protein candidates in signal transduction, antioxidants, and novel genes from extreme halophytes, like Salicornia *brachiata* (Udawat et al. 2014, 2017; Singh et al. 2016a, b; Mishra and Tanna 2017).

Studies indicate that transformation of salt sensitive plants with halophytic genes can impart salinity tolerance to them. A variety of transporters encoding genes from different halophytic species are transferred to salt sensitive species, showing enhancement in salt tolerance. For example, *N. sibirica* NsNHX1 gene transformed to poplar plant, SbHKT1 gene from *S. bigelovii* to cotton, ZxNRT1.5 of *Zygophyllum xanthoxylum* in Arabidopsis, resulted in increased salt tolerance in transgenic lines (Mwando et al. 2020; Nanjo et al. 1999; Navarro et al. 2010; Rahman et al. 2021). Mangroves accumulate low molecular mass compatible solutes, such as pinitol, mannitol, and proline in the cytoplasm to maintain ionic balance (Hasegawa et al. 2000; Ashihara et al. 2003). Major osmoregulatory compounds are different in different mangrove species. Pinitol is the osmoregulator for *Bruguiera gymnorrhiza*, *Kandelia candel*, and *Rhizophora stylosa* (Hibino et al. 2001), mannitol for *Sonneratia alba* and *Lumnitzera racemosa* (Yasumoto et al. 1999; Ashihara et al. 2003), and carbohydrates for *Acanthus ilicifolius*, *H. littoralis*, and *H. tiliaceus* (Popp et al. 1985). Among these osmoregulators, the amino acid proline is regarded as a good osmoregulator, and its concentration is positively correlated with resistance to abiotic stresses (Matysik et al. 2002). Moreover, it can also act as a reactive oxygen scavenger and provide membrane and protein stability (Alia et al. 1991; Hanson and Burnet 1994). Along with proline, glycine betaine also acts as an osmoregulator, and they are accumulated through betaine/proline transporters AmT1, 2, and 3 (Waditee et al. 2002).

Salicornia is also a functional food since it contains unique oligosaccharides (Mishra et al. 2013), metabolites (Mishra et al. 2015), and sulfur-rich seed storage proteins (Jha et al. 2012). *Porteresia coarctata*, a wild rice relative with great salinity and submergence tolerance, had 152,367 distinct transcript sequences discovered by transcriptomics (Garg et al. 2014). To decipher important metabolic pathways, researchers identified 15,158 genes implicated in salinity and submergence tolerance. Salinity and submergence tolerance in rice are engineered using genes from halophytes (Garg et al. 2014).

10.8 Promoters of Halophytic Genes and Transgene Expression

Crop plants must be engineered with a powerful and well-regulated promoter. According to a comparative transcriptome study, many stress-related genes were constitutively expressed at greater levels in T. halophila than in their A. thaliana homologs (Taji et al. 2004, 2010). This study reveals that halophytes have a well-functioning transcriptional regulatory network for stress-responsive genes. The presence of several stress-inducible motifs was discovered in the cis-regulatory regions of different stress-responsive genes from certain halophytes recently (Tiwari et al. 2014, 2016). Yin et al. (2002) discovered that salt stress substantially induces the promoter of the AcBADH gene in *Atriplex centralasiatica*, which has two salt-responsive enhancer areas (located from 1115 to 890 and 462 to 230) and one silencer region (placed between 890 and 641). Under salt stress (400 mmol/L NaCl), the SlBADH gene promoter segment (300 bp alone) from *Suaeda liaotungensis* displayed roughly 6.3-fold more expression when compared to the control (Zhang et al. 2008). Under salt stress, the TsVP1 gene promoter from the halophyte *T. halophila* featured a 130-bp unique cis-acting region, which resulted in increased GUS expression in transgenic Arabidopsis (Sun et al. 2010). Under NaCl stress (200 mmol/L), an 897-bp promoter region of the SlPEAMT gene (*S. liaotungensis*) showed an 18.6-fold increase in GUS activity (Li et al. 2016). These findings demonstrate that even a short section of promoter might include critical cis-acting elements that influence gene expression in stressful situations. Basic elements were also found in the promoters of CMO genes from *S. liaotungensis* and *Salicornia europaea*, indicating that they were salt inducible (Li et al. 2007; Wu et al. 2011). In the halophyte *M. crystallinum*, Schaeffer et al. (1995) found enhancer and silencer areas involved in the transcriptional activation of salt-responsive expression of CAM (Crassulacean Acid Metabolism) genes. AlSAP is a promoter found in *Aeluropus littoralis* that is age dependent, abiotic stress inducible, organ specific, and tissue specific (Saad et al. 2011). Furthermore, in transgenic rice, gusA expressed at the same level as AlSAP transcript under the control of the AlSAP gene promoter (Ben-Saad et al. 2015). They also discovered that the regulatory domains of two orthologs, AlSAP and OsSAP9 (from rice), regulate and induce stress in distinct ways in rice. Sun et al. (2010) discovered a 130-bp unique cis-acting element in the promoter region of the halophyte *T. halophila* (TsVP1) that promotes GUS production in transgenic Arabidopsis under salt stress. Under abiotic and biotic stress conditions, the CBL1 gene promoter identified from *Ammopiptanthus mongolicus* regulated the production of the reporter gene (Guo et al. 2010). The inclusion of enhancer and repressor binding sites in the cis-regulatory elements, as well as stress-inducible motifs, was shown in a model for transcriptional regulation of the SbpAPX gene (from *S. brachiata*) (Tiwari et al. 2014). Similarly, a variety of abiotic stress sensitive cis-regulatory motifs was found in the SbGSTU promoter, which governs the expression of the GSTU gene in *S. brachiata* (Tiwari et al. 2016). As evident from these studies, the halophytic promoters appear to be a good choice for developing abiotic stress tolerance in crops by high-level transgene expression.

10.9 Salt-Responsive Genes in Halophytes and Salt Tolerance in Transgenics

The most prevalent method of using antiporters, regulated by a multigene family, includes Na+ efflux, compartmentalization of Na+ in vacuoles, and inhibition of Na + input (Rajendran et al. 2009; Kronzucker and Britto 2011). Several antiporters from glycophytes and halophytes have been functionally described (Kronzucker and Britto 2011; Sreeshan et al. 2014). Under the control of the non-specific CaMV35S promoter, overexpression of glycophytic transporters producing genes (NHX, SOS, HKT, ATPase, etc.) exhibited tolerance in the range of 150–250 mM NaCl, although their halophytic homologs offered a tolerance of up to 400 mM NaCl (Kronzucker and Britto 2011; Sreeshan et al. 2014; Volkov 2015). Under salt stress treatments, the effects of overexpression of halophytic genes were commonly observed, but under control (unstressed) conditions, there was negligible difference between wild-type plants and transgenic lines (Jha et al. 2011a, b; Joshi et al. 2012; Volkov 2015; Tiwari et al. 2015; Singh et al. 2016a, b; Udawat et al. 2016). In many crops, including tomato, brassica, maize, and wheat, the glycophytic NHX gene from *A. thaliana* was used to acquire salt tolerance (Zhang et al. 2001; Xue and Loveridge 2004; Yin et al. 2004). Other glycophytic NHX1 genes, such as BnNHX1 (*Brassica napus*), GhNHX1 (*Gossypium hirsutum)*, and HbNHX1 (*Hordeum brevisubulatum*), have also been shown to induce salt tolerance in tobacco (Wang et al. 2004; Wu et al. 2004; Lü et al. 2005). The NHX1 genes from halophytes and glycophytes demonstrated salt tolerance activity, although the salt tolerance intensity differed. In *Oryza sativa*, the antiporter AgNHX1 (from the halophyte *Atriplex gmelini)* has a 75% amino acid sequence similarity to AtNHX1 (from *Arabidopsis thaliana*) and a greater salt tolerance (Hamada et al. 2001; Ohta et al. 2002). Compared to glycophytic counterparts, transgenic plants overexpressing AgNHX1 (*A. gmelini*), SaNHX1 (*Spartina anglica*), or SsNHX1 (*Suaeda salsa*) demonstrated resistance to 300–400 mM NaCl (Ohta et al. 2002; Zhao et al. 2006; Lan et al. 2011). In transgenic tobacco, overexpression of the SbNHX1 gene resulted in 200 mM salt tolerance; however, only 100 mM NaCl tolerance was reported in transgenic jatropha and castor plants (Joshi et al. 2013; Patel et al. 2015). Other halophytic genes, including as SbpAPX, SbUSP, and SbGSTU, were overexpressed in transgenic plants and demonstrated superior salinity tolerance (200–300 mM NaCl) than their glycophytic homologs (Jha et al. 2011a, b; Udawat et al. 2016; Singh et al. 2014a, b). When compared to the identical gene from the glycophyte, *Panax ginseng*, transgenic Arabidopsis plants overexpressing the TIP1 gene from the halophyte *T. salsuginea* showed higher salt tolerance (Peng et al. 2007). In the transgenic plants, APX and GST from rice showed lesser tolerance up to 150–200 mM than the same genes (200–300 mM NaCl) from the *halophyte S. brachiata* (Lu et al. 2007a, b; Jha et al. 2011a, b; Sharma et al. 2014; Singh et al. 2014a). Overexpression of a stress-associated protein gene (AlSAP) from *A. littoralis* has recently been shown to increase abiotic stress tolerance in tobacco, wheat, and rice (Ben-Saad et al. 2015). They also discovered that several abiotic conditions activate AlSAP transcripts, the rice OsSAP9 ortholog gene being predominantly stimulated by cold and heat treatments. Antiporter SOS1 gene expression was found to be greater in *Thellungiella species* than in Arabidopsis, according to a transcript expression study (Oh et al. 2010). Similarly, numerous genes involved in Na+ excretion, compartmentation, and diffusion, including SOS2, NHX1, and HKT1, were expressed at greater levels in Thellungiella than in Arabidopsis (Taji et al. 2010). To examine the Na+ hypersensitive response, Arabidopsis lines overexpressing either AtHKT1 (*A. thaliana*) or TsHKT1 (*T. salsuginea*) were studied, and AtHKT1 lines showed slower root development than TsHKT1 lines (Ali et al. 2012). In transgenic lines expressing AtHKT1, shoot sensitivity was detected. They also discovered that salt stress causes a substantial upregulation of TsHKT1 but a strong inhibition of AtHKT1 expression (Ali et al. 2012). These findings show that halophytes are to be investigated further in order to source novel genes and to produce transgenic crop plants with a better level of salt tolerance than their glycophytic counterpart genes.

10.10 Mangrove Genes for Salt Tolerance

Salt tolerance was induced in various plants in a variety of ways, including transformation and overexpression of genes associated with abiotic stress tolerance (Singla-Pareek et al. 2001; Vinocur and Altman 2005; Bhatnagar-Mathur et al. 2008; Ashraf and Akram 2009). Many reviews on various areas of salt stress tolerance have recently been published (Zhu 2003; Agarwal et al. 2006; Umezawa et al. 2006; Apse and Blumwald 2007; Gaxiola et al. 2007; Shinozaki and

Yamaguchi-Shinozaki 2007; Century et al. 2008; Shao et al. 2008a, b; Rodríguez-Rosales et al. 2009; Agarwal and Jha 2010).

The application of mangrove genes has been found to be effective in elevating the salt tolerance capacity of plants, and individual genes are exploited for the same. Sultana et al. (2012) overexpressed AeMDHAR genes in rice to improve salt tolerance. AeMDHAR is an enzyme that confers salt tolerance by scavenging ROS. A mangrove candidate gene(s) for salt tolerance is MYB. MYB1 gene was isolated from salt-secreting mangrove *Avicennia marina* and constitutively expressed in tobacco for enhanced tolerance to salt (Ganesan et al. 2012).

Salt-tolerant plants overcome environmental stress through antioxidant defense systems. Many enzymes are involved in this strategy of defense, among which superoxide dismutase functions as the first line of defense. Prashanth et al. (2008) studied the superoxide dismutase genes in *Avicennia marina*, and the cDNA was transferred into the rice. The transformed rice showed elevated defense against methyl viologen-mediated oxidative stress as well as salinity stress. *Avicennia marina* CSRG1 gene was seen to elevate the salt defense mechanisms against a plethora of ions in the transformed tobacco plant. Reported to encode 197 amino acids with no homologous sequence found in the gene bank (Hantao et al. 2004). MDAR (Monodehydroascorbate reductase) is another salt-induced gene that induces resistance to salinity in transformed tobacco (Kavita and Alka 2010). Such studies prove that mangroves are a hub of genes that give tolerance against a combination of environmental stresses by activating different types of pathways involved in antioxidant protection, homeostasis, and regulatory pathways (Shinozaki and Yamaguchi-Shinozaki 2007; Agarwal and Jha 2010).

One hundred and seven salinity-tolerant candidate genes were identified and isolated from a mangrove plant, *Acanthus ebracteatus Vahl,* and verified in *E. coli* host (Nguyen et al. 2007). Huang et al. 2003 isolated ten cDNAs from genes of *Kandelia candel* and studied their expression. Of these, two were unknown; three belonged to small heat shock proteins (sHSPs) and ADP ribosylation factor categories, five genes were repressed under NaCI stress, two encoded cyclophilins, and three tonoplast intrinsic proteins, early light-induced protein, and 60S ribosomal protein, respectively.

cDNA library constructed from *A. marina* leaves and screened for betaine aldehyde dehydrogenase genes (BADH) which efficiently catalyze the oxidation of betaine aldehyde, one of which showed higher expression under salinity in *E. coli* expression systems (Hibino et al. 2001). *Rhizophora mucronata* leaves were used to analyze free amino acids and the expression of selected genes. Chromatograms showed the accumulation of free amino acids, like proline, glycine, aspartic acid, valine, leucine, and glutamic acid, in the presence of salt. Among the genes studied (P5CS, BADH, NHX1), BADH gene was found to be expressed more during salt stress (Sreeshan et al. 2018). Several stress-related gene homologs, such as chaperonin-60, clpP protease of the clp/Hsp100 family of chaperones, ubiquitin, eukaryotic elongation factor 1 A (eEF1A), drought-induced AtDi19 gene of *Arabidopsis thaliana*, and secretory peroxidase, were successfully isolated from *A. marina* (Tanaka et al. 2002).

Table 10.1 Over expression of mangrove gene for salt tolerance

Gene	Mangrove source	Transgenic plant	References
AcMDHAR	*Acanthus ebracteatus*	Rice	Sultana et al. (2012)
AmMYB	*Avicennia marina*	Tobacco	Ganesan et al. (2012)
Cu/ZnSOD	*Avicennia marina*	Rice	Prashanth et al. (2008)
CSRG1	*Avicennia marina*	Tobacco	Hantao et al. (2004)
Am MDAR		Tobacco	Kavitha et al. (2010)

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The role of mangrove-specific allene oxide cyclase (mangrin) in salt tolerance was revealed by functional screening for cDNAs in the mangrove *Brugiera sexangula* (Yamada et al. 2002). Meera et al. 2013 reviewed a list of the reported salt-responsive mangrove genes (Table 10.1) and a list for future use (Table 10.2). Some of the genes were reported to induce salt/ drought tolerance to include Na^+ H^+ antiporter (Apse et al. 1999; Apse et al. 2003; Jha et al. 2010), dehydrin (DHN) (Brini et al. 2007), late embryogenesis abundant protein (LEA)-bZip (Qu et al. 2012), phytoene synthase (Han et al. 2008), DREB (Bhatnagar-Mathur et al. 2007), aquaporin (Peng et al. 2007), glutathione S-transferase (Chen et al. 2012), fatty acid desaturase (Zhang et al. 2012), trihelix transcription factor genes GmGT-2A and GmGT-2B (Xie et al. 2009), and mannose-1-phosphate guanyl transferase (Kumar et al. 2012) as reviewed by Meera et al. (2013).

Mangroves form an ideal system to unveil the genetic background of salt tolerance. Genome and transcriptome sequence information form the basis of gene characterization in mangrove species.

Salt stress-induced transcriptome of *Bruguiera gymnorhiza* root tissues was profiled using the oligo microarray (NCBI GEO accession no. GSE10942). The study came out with a vivid observation that emphasizes the importance of tissue-specific transcriptome. The expression profiles were more or less similar in the lateral and main roots. The nucleotide sequence data were also generated for the screening of ESTs (DDBJ accessions AB429341-AB429362) (Yamanaka et al. 2009). The first mangrove de novo transcriptome analyses were carried out in *Rhizophora mangle* (Rhizophoraceae) and *Heritiera littoralis* (Malvaceae) Dassanayake et al. 2009). *Rhizophora mangle* transcriptome is the foundation for MTDB. The transcriptome analysis of another mangrove species, *Sonneratia alba,* was performed in 2011. Also, genes responsible for salt tolerance of *Sonneratia alba* were identified through in silico annotations (Chen et al. 2011). Transcriptome analysis was performed and compared between *Acanthus ilicifoli*us and its terrestrial relative *Acanthus leucostachyus* (Yang et al. 2015a). Little is known about the origin and evolution of species of Ceriops. In a recent study, Illumina-based transcriptome sequence analysis of two Ceriops species (*Ceriops zippeliana* and *Ceriops tagal*) and one of their terrestrial congenator (Pellacalyx yunnanensis) was successfully conducted (Yang et al. 2015b). *Nypa fruticans* is the one and only monocot species among true mangroves. De novo transcriptome profiling of *Nypa fruticans* was conducted so as to compare the simple sequence repeats with other palm trees (He et al. 2015). Leaf tissue-specific transcriptome sequence and de novo assembly

Table 10.2 List of salt responsive mangrove genes suggested to be used in future transgenic works

Gene	Mangrove source	References
Glutathione S- transferase Z1	*Acanthus*	Nguyen et al. (2007)
Glutathione transferase	*ebracteatus*	Nguyen et al. (2007)
Manganese superoxide dismutase	*Acanthus*	Nguyen et al. (2007)
Myo-insitol 1-phosphate synthase	*ebracteatus*	Nguyen et al. (2007)
Homogentisate	*Acanthus*	Nguyen et al. (2007)
phytylprenyltransferase	*ebracteatus*	Nguyen et al. (2007)
Carotenoid cleavage dioxygenase1–1	*Acanthus*	Nguyen et al. (2007)
Glutamate synthase (ferredoxin)	*ebracteatus*	Nguyen et al. (2007)
Glutamine synthetase	*Acanthus*	Nguyen et al. (2007)
Glutamine synthetase GS58	*ebracteatus*	Nguyen et al. (2007)
Glycine dehydrogenase	*Acanthus*	Nguyen et al. (2007)
Putative alanine aminotransferase	*ebracteatus*	Nguyen et al. (2007)
Putative quinone reductase	*Acanthus*	Nguyen et al. (2007)
NAD malate dehydrogenase	*ebracteatus*	Nguyen et al. (2007)
NADP-malic enzyme	*Acanthus*	Nguyen et al. (2007)
Plastidic aldolase	*ebracteatus*	Nguyen et al. (2007)
Plastidic aldolase NPALDP1	*Acanthus*	Nguyen et al. (2007)
Latex plastidic aldolase	*ebracteatus*	Nguyen et al. (2007)
Phospholipid/ glycerol	*Acanthus*	Nguyen et al. (2007)
acyltransferase	*ebracteatus*	Nguyen et al. (2007)
Chloroplast protease	*Acanthus*	Nguyen et al. (2007)
Amino acid permease-like protein	*ebracteatus*	Nguyen et al. (2007)
Plasma membrane intrinsic protein	*Acanthus*	Nguyen et al. (2007)
Ubiquitin-conjugating enzyme fam-	*ebracteatus*	Nguyen et al. (2007)
ily protein	*Acanthus*	Nguyen et al. (2007)
E3 ubiquitin ligase SCF	*ebracteatus*	Nguyen et al. (2007)
33 kDa polypeptide of water oxidiz-	*Acanthus*	Nguyen et al. (2007)
ing	*ebracteatus*	Nguyen et al. (2007)
Germin-like protein	*Acanthus*	Nguyen et al. (2007)
Proline rich protein	*ebracteatus*	Nguyen et al. (2007)
Putative salt tolerance protein	*Acanthus*	Nguyen et al. (2007)
Universal stress protein (USP)	*ebracteatus*	Nguyen et al. (2007)
14-3-3 protein	*Acanthus*	Nguyen et al. (2007)
GTP binding protein	*ebracteatus*	Nguyen et al. (2007)
Small GTP binding protein Sar1BNt	*Acanthus*	Nguyen et al. (2007)
Zinc finger (DNL type) family pro-	*ebracteatus*	Huang et al. (2003)
tein	*Acanthus*	Huang et al. (2003)
Calcium binding EF hand family	*ebracteatus*	Huang et al. (2003)
Cyclic nucleotide and calmodulin	*Acanthus*	Hibino et al. (2001)
regulated	*ebracteatus*	Tanaka et al. (2002)
DNAJ Heat shock protein	*Acanthus*	Tanaka et al. (2002)
cytosolic class I loss molecular mass	*ebracteatus*	Tanaka et al. (2002)
HSP	*Acanthus*	Tanaka et al. (2002)
cytosolic class II low molecular mass	*ebracteatus*	Tanaka et al. (2002)Tanaka et al.
HSP	*Acanthus*	(2002)
ADP-ribosylation factor (ARF)	*ebracteatus*	Fan et al. (2009)
Betaine aldehyde dehydrogenase	*Acanthus*	Yamada et al. (2002)
(BADH)	*ebracteatus*	
Chloroplast chaperonin-60	*Acanthus*	
Clp protease (clpP)	*ebracteatus*	

(continued)

Table 10.2 (continued)

Gene	Mangrove source	References
Ubiquitin Translation elongation factor-1 a Drought-induced 19 (AtDi119) Secretory peroxidase fructose-1,6-bisphosphate aldolase Mangrin(Allene oxide cyclase)	*Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Acanthus ebracteatus* *Kandelia candel* *Kandelia candel* *Kandelia candel* *Avicennia marina* *Avicennia marina* *Avicennia marina* *Avicennia marina* *Avicennia marina* *Avicennia marina* *Avicennia marina* *Sesuvium portulacastrum* *Brugiera sexangula*	

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of datasets of *Asiatic mangrove Rhizophora mucronata* Lam. were performed to develop a reference sequence database to decode gene candidates involved in stress tolerance (Meera et al. 2020).

Plants have a system developed to detoxify this MG consisting of two major enzymes: glyoxalase I (Gly I) and glyoxalase II (Gly II), and hence known as the glyoxalase system. Recently, a novel glyoxalase enzyme, named glyoxalase III (Gly III), has been detected in plants, providing a shorter pathway for MG detoxification. Glyoxalase systems have strong interactions in conferring abiotic stress tolerance in plants through the detoxification of ROS and MG. Upregulation of both Gly I and Gly II, as well as their overexpression in plant species, showed enhanced tolerance to various abiotic stresses, including salinity and drought (Espartero et al. 1995; Veena et al. 1999; Skipsey et al. 2000; Jain et al. 2002; Singla-Pareek et al. 2003, 2008;

Saxena et al. 2005; Yadav et al. 2005; Hossain and Fujita 2009; Lin et al. 2010; Mustafiz et al. 2011; Tuomainen et al. 2011; Wu et al. 2013; Hasanuzzaman et al. 2017a, b).

Meera and Augustine (2020) reported and characterized the GLY I, II, and III in *R. mucronata,* establishing their role in the salinity response of the plant. Glutathione is the key regulator of routine glyoxalase pathway, and relative expression of some glutathione catabolic enzymes and 14 glutathione-dependent transporter proteins under saline conditions was analyzed. Also suggested the feasibility of using mangrove glyoxalases to induce higher salt tolerance in crop plants. Salt-induced changes in gene expression levels of glyoxalase enzymes in the mangrove species were evaluated. The expression status of glutathione synthetic and catalytic enzymes, as well as glutathione regulated transporter protein, was estimated. Rm GLY I was found to be more responsive to salinity stress than the other two glyoxalases. A lead for probable structural stability of mangrove glyoxalases under salinity is also suggested.

10.11 Salinity Tolerance in Crop Species

Barley makes an excellent model for salinity tolerance in cereals as it is the most tolerant among the cultivated cereals (Munns and Tester 2008). A significant QTL on chromosome number 2 was found to be associated with salt tolerance by studies on NILs differing only in the target QTL (Xu et al. 2012) by biochemical and proteomic analyses. Tolerant NILs maintained lower Na+ content in leaves and higher K+ content in the roots when compared to sensitive lines under salt conditions. H2O2, MDA, and proline accumulation was noticed in salinity-sensitive NILs. Proteomic studies using two-dimensional gel electrophoresis and tandem mass spectrometry analyses identified 53 and 51 differentially expressed proteins (associated with photosynthesis, ROS scavenging, and ATP synthase) in the leaves and roots, respectively; Zhu et al. (2020).

Three hundred seventy-seven two-row spring barley cultivars during both the vegetative, in a controlled environment, and the reproductive stages, in the field were used to set up a diversity panel for association mapping for the different components of salinity tolerance. It was observed that the two developmental stages did not share genetic regions associated with the components of salinity tolerance, suggesting that different mechanisms play distinct roles throughout the barley life cycle. Genetically defined regions containing known flowering genes (Vrn-H3, Vrn-H1, and HvNAM-1) were found responsive to salt stress. A salt-responsive locus, such as 7H, 128.35 cM, was associated with grain number per ear, and a gene encoding a vacuolar H+-translocating pyrophosphatase, HVP1, was identified as a candidate. A QTL on chromosome 3H (139.22 cM), significant for ear number per plant, and a locus on chromosome 2H (141.87 cM), which was associated with a yield component, interacted with salinity stress.

HVP1 could be the candidate vacuolar H+-translocating pyrophosphatase underlying the 7H locus. Arabidopsis vacuolar pyrophosphatase AVP1 showed increased shoot biomass production and yield under saline field conditions (Han et al. 2015). Therefore, HVP1 merits further investigation as the causal gene underlying the 7H locus. The means for ear number per plant and grain number per ear for each condition (control or saline) and genotype at these three loci (2H, 141.87 cM; 3H, 139.22 cM; and 7H 128.35 cM). The condition, the genotype, and the condition-by-genotype interaction showed all three as possible candidates for salinity tolerance in barley (Saade et al. 2020).

The genetics of salinity tolerance in barley during germination is reviewed by summarizing reported quantitative trait loci (QTLs) and functional genes by Mwando et al. (2020). Gene candidates for salinity tolerance in Arabidopsis, soybean, maize, wheat, and rice have been blasted and mapped on the barley reference genome. The genetic diversity of three reported functional gene families for salt tolerance during barley germination, namely, dehydration-responsive element-binding (DREB) protein, somatic embryogenesis receptor-like kinase and aquaporin genes, is discussed. The DREB gene family is found to be more diverse in barley than in wheat and rice.

Salinity tolerance in barley is grouped into four classes based on their function (Wu et al. 2011; Walia et al. 2006; Wu et al. 2011; Yin et al. 2018): (1) osmotic protectors, like HvPIP2;5 (Alavilli et al. 2016), HVA1 (Lal et al. 2008), HvDREB1, HvCBF4, HvWRKY38 (Gürel et al. 2016), and ROS scavengers, like trehalose synthesis, mannitol-1-phosphate dehydrogenase (M1PD), and pyrroline-5-carboxylase synthetase (P5CS); (2) Na+ and K+ transporters, like the high affinity potassium transporter (HKT) family (e.g., HvHKT1;5 (Hazzouri et al. 2018; Huang et al. 2019), HvHKT1;1 (Han et al. 2018), HvHKT2;1 (Mian et al. 2011; Assaha et al. 2017), HvHAK1 (Mangano et al. 2008), HvHKT1, HvHKT2 (Qiu et al. 2011), the Na+ /H+ exchanger (NHX) family (HvNax4 (Rivandi et al. 2011), and salt overly sensitive (SOS) engaged Na+/H+ antiporters (HvSOS1 (HvNHX7), HvSOS2 (HvCIPK24), HvSOS3 (HvCBL4), HvNHX1, HVA) (Yousefirad et al. 2018; Wu et al. 2019); (3) Regulatory proteins, like the CBF/ DREB (C-repeat-binding protein/ dehydration-responsive element-binding protein) family (e.g., HvRAF (Jung et al. 2007), HvAP2/ERF (ethylene response factor) (Guo et al. 2016), HvDREB1 (Xu et al. 2009), HvCBF4, HvWRKY38 (Gürel et al. 2016), HvDRF1 (Xue and Loveridge 2004)) in the signaling pathways of long-distance and downstream gene expression. Wu et al. (2011) identified twenty CBF genes have in barley, which enhances tolerance to drought, salinity, and low temperature; and (4) Jasmonate inducers, like (JA) biosynthesis, late embryogenesis abundant (LEA) protein genes (e.g., HVA1 expressed in response to water and salinity stresses, HVA22 expressed in response to dehydration, extreme temperatures, ABA secretion, and salinity stress (al-Yassin and Khademian 2015).

Wheat genes showed the highest sequence similarity to barley (90.93%), followed by maize (83.00%), rice (67.58%), soybean (59.43%), and Arabidopsis (57.94%). The aquaporin-like superfamily protein (HORVU2Hr1G096360.13) had the highest expression levels in the first three development stages of embryo, embryo shoot, and embryo root. PEG treatments showed a high positive correlation has been to salinity stress, indicating that salt stress in germinating seeds is mostly osmotic (Mano et al. 1996). Dehydrogenases (Jörnvall et al. 1984) in embryos catalyze the oxidation of D-glucose to synthesize sugars for osmoprotective functions (Witzel et al. 2010).

Dehydrins, a subfamily of LEA proteins from *Hordeum vulgare* (aba2), enhanced seed germination and water uptake in transgenic lines of Arabidopsis under salinity stress (Calestani et al. 2015; Hara 2010); a role in cellular detoxification also suggested as they contain lipids and has metal-binding capacity preventing lipid peroxidation (Cheng et al. 2002; Krüger et al. 2002; Alsheikh et al. 2003; Koag et al. 2003, 2009)

Somatic embryogenesis receptor-like kinase (SERK) genes (HvSERK1/2/3) isolated from barley were induced in microspore derived embryogenic callus under salt stress (Li et al. 2016), indicating their protective role for developing embryos during salinity stress.

A gene encoding DREB proteins in *H. vulgare* (HvDREB1) induced by exogenous ABA to enhance germination and early root growth in Arabidopsis plants under salinity stress was reported (Xue and Loveridge 2004). TF HvDREB1 is a member of the AP2 group of the DREB subfamily that is vital for regulating responses to various stresses (Agarwal et al. 2006; Xu et al. 2008) and reportedly improves salt, drought, and cold responses in transgenic plants (Oh et al. 2007).

Barley ERF-type TF HvRAF improved seed germination and root growth under salinity stress but was not induced by ABA treatment in transgenic Arabidopsis plants (Jung et al. 2007).

Overexpression of a barley aquaporin gene HvPIP2;5 in yeast enhanced salt and osmotic stress tolerance. In transgenic Ar*abidopsis* the gene showed better seed germination and root growth than the wild type under salinity stress (Alavilli et al. 2016)

Three genes' families—DREB protein, SERKs, and aquaporin gene—were considered for further analysis based on their high numbers of hits. The proteins from the three genes were blasted on the Phytozome (https://phytozome.jgi.doe.gov/pz/portal.html) to download matched homologs (>30%) in 40 different plant species. Gene alignments showed three distinct regions across the sequences of the gene families. The start and end sections of the sequences were more divergent than the middle segments. The phylogenetic tree shows that DREB proteins are no more diverse in barley than in wheat or rice (Mwando et al. 2020).

10.12 Phenotyping Technologies for Comprehensive Salt Stress Phenotyping

Several high throughput (HTP) systems have emerged, the majority of which rely on regular, non-invasive, automated imaging to the phenotype of tens, hundreds, or even thousands of plants in a short period of time (Furbank and Tester 2011; Ghanem et al. 2015; Junker et al. 2015). In both controlled and outdoor situations, these methods make phenotyping large numbers of genotypes easier. Red green blue (RGB), thermal infrared (TIR), chlorophyll fluorescence (ChlF), and, more recently, multispectral and hyperspectral imaging are all used by HTP systems (Humplík et al. 2015; Fahlgren et al. 2015).

10.13 Harnessing the Genetic Diversity of Exotic Germplasm

To supplement the genetic scarcity of modern elite cultivars, several sources of genetic variation are accessible. Because variations can be directly produced in commercial germplasm, genetic diversity generated artificially through mutagenesis has proven to be a beneficial resource for a variety of agricultural species (Caldwell et al. 2004; Mba 2013; Nikam et al. 2015; Gulfishan et al. 2016; Çelik and Atak 2017; Pando and Deza 2017; Wang et al. 2017; Tu Anh et al. 2018). Given that salt tolerance is most likely the result of the combined actions of multiple pathways, the ability to develop salt-tolerant variations intentionally is definitely restricted. On the other hand, as seen in landraces or wild cousins of crops, these are quite likely to evolve through natural selection in plants that are subjected to adverse environmental conditions (Mayes et al. 2012). As a result, it is critical to research the naturally diverse germplasm that is available.

The rapid advancement of DNA sequencing and genome assembly capabilities over the last decade has made genomic characterisation of novel and uncharacterized germplasm—potential salt tolerance allele and gene repositories easier. Over 300 plant species now have reference genome sequences (as of March 2018; http://www.plabipd.de/), with chromosome-level assemblies for several major crops, like rice, maize, and wheat, as well as less well-known species like quinoa; Schnable 2012; Mayer et al. 2014; Jackson 2016; Jarvis et al. 2017.

The capacity of these genomic resources to facilitate the capture and description of genetic diversity is their greatest value. Indeed, from well-established genotyping chips to more modern genotyping-by-sequencing methods, such as various reduced representation sequencing and whole-genome re-sequencing approaches, high-quality genomes breed high-quality genotyping (Bevan et al. 2017; Dwivedi et al. 2017; Scheben et al. 2017). With these methods, large numbers of accessions may now be genotyped fast and cheaply, with the potential for millions of single-nucleotide polymorphisms (SNPs) to be discovered. Genomic resources, such as diversity panels and mapping populations (e.g., bi-parental, nested association), are now available for all sequenced main crop species, a number of wild relatives, and increasingly for the aforementioned orphan crops (Rasheed et al. 2018).

10.14 Single-Step GWAS as New GWAS Technique (ssGWAS)

The most comprehensive information for genetic evaluation comes from the ssGWAS approach. The ssGWAS approach allows researchers to assess all available Table 10.2. Data in one step, including genetic markers, phenotype records, and pedigree information. Much recent research has verified this method and successfully implemented ssGWAS in pigs (Howard et al. 2015; Wu et al. 2018) and other species (Silva et al. 2017), yielding higher power and more exact estimates than other models. Thus, in a single model, genetic markers, repeat measurements of each variable, spatial and design elements, and marker–treatment interaction may all be considered. The statistical power of the conclusions from this procedure is projected to increase because each individual plant is used as input data rather than the genotype means. Because of the inclusion of the interaction model in the ssGWAS, allows finding important loci particularly related to salt stress, which could be advantageous for **complicated quantitative salt tolerance traits** with multiple components that can be successfully deconstructed by a ssGWAS model.

10.15 Conclusions and Future Perspectives

Climate change and global warming necessitate the cultivation of plant species that can survive under ambient salinity and extremes of temperature. Mangroves are extremophiles that have evolved their own mechanisms to cope with extremes of temperature and salinity. They still remain as an untapped and underutilized gene pool for genes providing tolerance to abiotic stress. The emergence of a mangrove species as a model plant for the molecular elucidation of salinity/abiotic stress tolerance can enlighten our understanding of the salt tolerance mechanisms.

Many a time, expressed genes in transgenic systems have proven to be salt resistant. As abiotic stress tolerance is a multigenic trait, researchers aim to pyramid more than one type of gene involved in stress tolerance for enhanced transgenic system efficacies. While every researcher's ambition is to find the elusive “master control” that activates the complete cascade of genes in the abiotic stress pathway, current methodologies have made significant progress in understanding the fundamental mechanism of abiotic stress tolerance in plants. In the future, mangroves, including facultative and obligate halophytes, have the potential to be a rich repository for genes for QTL-based techniques used in abiotic stress tolerance breeding, which includes salinity tolerance. Enormous progress has been made in understanding halophyte abiotic stress response systems with the aid of techniques, like transcriptomic profiling and QTL mapping (Flowers 2004). At the molecular level, however, there are several gaps in the pathways implicated in salt stress responses. For a complete knowledge of plant cell adaptation to salt stress, a far deeper understanding of protein–protein interactions and intracellular alterations is required.

Multiple studies have revealed that both biotic and abiotic stresses influence the expression of several common genes that work together to impart stress tolerance. Stress tolerance cannot be altered by manipulating a single trait as there are many component traits. Also, it is clear that overexpression or suppression of genes has far-reaching consequences. Overexpression of some of the abiotic stress-responsive genes from halophytes in crop systems has been encouraging. Apart from being a Na +/H+ vacuolar antiporter, AtNHX1 mutant plants displayed altered expression of genes related to intravesicular trafficking (Sottosanto et al. 2004). To uncover the genes linked with a QTL area, current methodologies employ DNA arrays in conjunction with QTL mapping. In order to solve the problem of abiotic stress tolerance, QTL mapping and marker-assisted breeding may be the best option. The ability to pyramid or combine QTLs for diverse stress tolerances is a key benefit of this strategy (Takeda and Matsuoka 2008). While overexpression of genes can result in greater stress tolerance, it is critical to test these transgenic systems in open field circumstances, where the crops are exposed to a range of stressors at different phases of plant growth (Rajalakshmi and Parida 2012). As 21 of the 28 crops cultivated are largely glycophytes, it is crucial to emphasize the molecular distinctions between these two plant groups, which is indispensable for glycophyte transformation utilising halophytic candidate genes, opening up a new line of research into how to prepare crops for increased soil salt. Despite their significant implications, knowledge of the discovery, metabolic activities, and isolation of key genes linked with salt tolerance in halophytes is relatively restricted. As a result, identifying and characterization novel salt tolerance-associated genes from halophytes, as well as their subsequent use in genetic engineering, are critical areas of plant research that require more attention in order to sustainably increase crop production and achieve global food security in the face of climate change. Future research should concentrate on identifying halophytic plants that have numerous salt tolerance mechanisms and can generate more biomass in order to remove the greatest amount of salts from polluted soils. Furthermore, after more than a century of research on halophytes, numerous basic physiological, biochemical, and molecular pathways remain unknown. As a result, further research is needed to understand the underlying salt tolerance processes of halophytes in order to improve soil conservation. Furthermore, new genetic and omic research has revealed that salt tolerance is a complex feature that is influenced by whole-plant responses rather than a single gene or protein. Exploration of the salt tolerance capability of diverse halophytes, as well as the production of transgenic plants with improved remediation properties, is therefore critical for sustainable agriculture in salinity-affected areas, as well as for mitigating the effects of global climate change (Rahman et al. 2021). While examining salt tolerance, yield is usually the most significant factor, but biomass, fruit or grain quality, and other factors may also be relevant. Other qualities (e.g., transpiration, photosynthetic activity, metabolite profiles) should be evaluated as possible variables contributing to salt tolerance in terms of these traits of real-world importance rather than as measures of salt tolerance in and of themselves (Mitchell et al. 2019). Correlation studies may be used to acquire insight into the eventual contribution of component qualities to salt tolerance in terms of yield using a suitably detailed phenotyping approach. Despite the fact that each of these components is complicated in and of itself, this disambiguation aids in the dissection of salt tolerance for yield into basic portions that are more genetically traceable than the total. The processes and subcomponents that contribute to salt tolerance for yield can change across and within species, as well as during development and across different environmental circumstances. Genotype, salt stress concentration and distribution (e.g., temporal dynamics, topography), developmental stage at which stress is imposed, weather conditions, cultivation practices, soil type, and water availability are all important factors to consider (Greenway and Munns 1980; Tal and Shannon 1983; Mano and Takeda 1997; Foolad 1999; Yamaguchi and Blumwald 2005). To supplement the genetic scarcity of current elite cultivars, several sources of genetic diversity are accessible. Because variations may be directly created in commercial germplasm, genetic diversity generated artificially by mutagenesis has proved to be a beneficial resource for a variety of agricultural species (Caldwell et al. 2004; Mba 2013; Nikam et al. 2015; Gulfishan et al. 2016; Çelik and Atak 2017; Pando and Deza 2017; Wang et al. 2017; Tu Anh et al. 2018). Given that salt tolerance is most likely the result of the combined actions of many pathways, the ability to develop salt-tolerant variations intentionally is clearly restricted (Mitchell et al. 2019)

Rapidly growing genome-wide association models in plants are promising and extremely valuable tools for finding alleles and markers. In crops like rice, combining genomic selection with information from population structure, GWAS, and the known genetic architecture of certain traits has resulted in greater breeding efficiency (Spindel et al. 2015). Plant species are yet to be bred for salt tolerance through genomic selection. Lower genotyping costs and better genomic models for predicting breeding values will help speed up the delivery of superior breeding lines with salt tolerance. Selection of high-yield stress resistant crops that boost agricultural productivity can be made by identifying the link between genotype and phenotype. Furthermore, the use of genome editing technologies will allow for the confirmation of causative gene activity. CRISPR-Cas9, for example, is predicted to reveal causal links between candidate genes discovered by GWAS and phenotypic features in order to conduct tailored molecular-assisted breeding programs (Yin et al. 2017). Genome editing, on the other hand, will not only aid in the functional validation of loci of interest but will also allow for the simultaneous change of many genetic loci in elite crops, advancing breeding programs, and the translation of discoveries to the field. Novel genetic resources, such as understudied crops, and new imaging techniques, such as HTP, combined with new statistical association models, will speed up the discovery of new stress tolerance pathways leading to the development of enhanced salt tolerance in crop plants.

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