DE GRUYTER Open Life Sci. 2018; 13: 149–154

Review Article

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Mechanisms of salt tolerance in halophytes: current understanding and recent advances

https://doi.org/10.1515/biol-2018-0020
Received November 22, 2017; accepted January 31, 2018

Abstract: Halophytes are plants that exhibit high salt tolerance, allowing them to survive and thrive under extremely saline conditions. The study of halophytes advances our understanding about the important adaptations that are required for survival in high salinity conditions, including secretion of salt through the salt glands, regulation of cellular ion homeostasis and osmotic pressure, detoxification of reactive oxygen species, and alterations in membrane composition. To explore the mechanisms that contribute to tolerance to salt stress, salt-responsive genes have been isolated from halophytes and expressed in non-salt tolerant plants using targeted transgenic technologies. In this review, we discuss the mechanisms that underpin salt tolerance in different halophytes.

Keywords: halophyte, salt stress, salinity tolerance, salt response gene, transgenic plant

1 Introduction

Plants face many environmental abiotic stresses. These stresses induce a wide variety of survival and tolerance responses, including enhanced accumulation of osmolytes, reduced photosynthesis, closure of stomata, and induction of stress-responsive genes [1-8]. Salinity represents a major abiotic stress that has been associated with significant economic impacts due to loss of arable land and reduced agricultural productivity. More than 950 million hectares of land are affected by elevated salt levels worldwide. Most plants are sensitive to salt stress, and salinity can inhibit plant growth by triggering ionic toxicity and osmotic and oxidative stress [9-13]. Reactive oxygen species (ROS) can also be produced in response to salt exposure, resulting in damage to DNA, proteins, and lipids [14]. In addition, salt stress can negatively affect chloroplast structure, leading to decreases in chlorophyll content and photosynthesis [15, 16].

Plants have developed complex defenses to resist salt stress that rely on a variety of mechanisms, such as osmolyte biosynthesis, alterations in ion homeostasis, intracellular compartmentalization of toxic ions, and ROS scavenging systems [17]. Induction of these pathways through brief exposure to low levels of salt stress, a process called salt acclimation, can improve a plants resistance to salinity [18-20]. However, tolerance to soil salinity levels varies between plant species, and plants can be characterized as halophytes or glycophytes. Halophytes are salt-resistant or salt-tolerant and can complete their life cycles in soil containing more than 200mM NaCl, while glycophytes cannot [17, 21, 22]. Generally, halophytes follow three mechanisms of salt tolerance; reduction of the Na+ influx, compartmentalization, and excretion of sodium ions [17]. Pseudo-halophytes intercept ions in roots and minimize transport to the shoot parts of the plant to protect the main metabolic tissues [23]. Euhalophytes can dilute salt within their succulent leaves or stems and thus have high salt tolerance [17]. Recretohalophytes can actively excrete absorbed salt to theoutside via a typical salt excretory structure in the epidermis [24].

Growth of some obligate halophytes requires high salt concentrations, so salinity may restrict the distributions of some halophyte populations to saline environments [25-28]. Halophytes have developed distinct morphological, structural, and physiological strategies to survive in these high salt environments. To investigate the molecular mechanisms underlying tolerance to salt stress, salt-responsive genes have been isolated from certain halophytes and expressed in glycophytes to validate their function in salt tolerance [29,30]. Halophytes represent promising models to characterize salt tolerance mechanisms. *Suaeda salsa* is a euhalophytic herb that

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occurs both on inland saline soils and in intertidal zones [31]. *S. salsa* has succulent leaves and is highly salt tolerant. Halophytes, such as *Aeluropus, Mesembryanthemum, Suaeda, Atriplex, Thellungiella, Cakile*, and *Salicornia*, serve as model plants for the identification of potential candidates for salt-responsive genes and promoters [32]. In this review, we will focus on recent advances in our understanding of salinity tolerance mechanisms used by halophytes to resist salt stress.

2 Salt secretion through specialized salt glands

A small group of halophytes have evolved specific salt excretory structures, termed salt glands, which can excrete excess salt from plant tissues to enhance salinity tolerance [33]. Halophytes with salt glands are collectively termed recretohalophytes. Salt glands have originated from the epidermis of these plant species, however the structure and mechanism of salt exclusion differs between recretohalophytic species. According to the structural similarities, salt glands can be categorized into 4 groups: salt bladders, multicellular salt glands, bicellular salt glands and unicellular vacuolated secretory hairs [34]. Salt bladders consisting of a large vacuolated cell with or without 1 or 2 stalk cells are only found in *Aizoaceae* and *Amaranthaceae*, in which salt is sequestered in the bladder cell vacuole upon salt stress [35]. A mutant *M. crystallinum* plant deficient in bladder cells was highly sensitive to salt under salt stress compared to the wild type *M. crystallinum*, which indicates the critical importance of salt bladders for salt compartmentalization and ion homeostasis [36]. Most salt glands consist of multiple cells (varying from 4-40 cells) which have cell types differentiated into basal collecting cells and distal secretory cells. The secretory cells have numerous plasmodesmata connections with surrounding mesophyll cells. Thus it appears that salt is actively transported through the collecting cells into the secretory cells [34]. The outer surface of the secretory cells is covered with cuticle. Research by Feng *et al.* [37] in *Limonium bicolar* showed that each of the secretory cells has a pore in the center of the cuticle and observed salt crystals located above the pores. In addition to secretion from the pore, extra salt also could be stored in the cuticular chamber on top of the secretory cells as observed in *Aeluropus littoralis* [38]. The bicellular salt gland with a basal cell and a cap cell is found in *Chloridoid* grasses. The continuous cuticle on the epidermis in some species thickens on top of the cap cell and forms a cuticular chamber that stores secreted salts [39]. The unicellular hairs are found in the wild rice species *Porteresia coarctata*, and appear to lack specific organelles and be completely filled with vacuoles [34].

Molecular genetic studies of salt glands have been limited in the past. However, new methods are increasing our ability to study the detailed function of salt glands at the cellular and molecular level. For instance, scanning electron microscopy has identified a potentially important feature of *L. bicolor* salt glands showing that salt glands in these plants emit fluorescence under UV excitation (330–380 nm) [33]. This autofluorescence arises from ferulic acid localized in the cuticle, which plays an crucial role in salt secretion [40]. Salt secretion is an energy-intensive process that is associated with high levels of water efflux. To recover from water loss, aquaporins play an critical role in re-uptake of water into cells [33, 41]. Inorganic elements extruded through the salt glands include a variety of cations and anions, but high selectivity for Na^+ and Cl^- compared to other ions has been observed [42]. Additionally, recent transcriptomic [24, 43-45], proteomic [46, 47], and metabolomic [48] analyses have reported many candidate genes, proteins and metabolites expressed specifically in salt glands; these candidate genes, proteins and metabolites may play key roles in salt gland development and salt secretion. For example, genes related to ion transport, vesicles, reactive oxygen species scavenging, the abscisic acid-dependent signaling pathway and transcription factors were found to be highly expressed under NaCl treatment in *Limonium bicolor* [43]. In salt bladders cells of *M. crystallinum*, active metabolic changes related to energy generation, UV protection, organic osmolyte accumulation and stress signaling have been identified to be regulated by a number of genes of unknown function in response to salt stress [46-48]. In addition, recretohalophyte *L. bicolor* mutants exhibiting altered salt secretion can be obtained by physical and chemical methods and used to identify potentially critical genes that contribute to salt secretion pathways [49, 50]. The functions of these genes can then be validated by combining established transformation protocols with the leaf disk secretion model [51].

3 Alterations in ion homeostasis and osmotic pressure contribute to salt tolerance

Intracellular compartmentalization of toxic ions using specific transporters represents another key pattern used by halophytes to maintain a moderate cytosolic

K^+/Na^+ ratio in the cytosol. Thus, membrane ATPases and ion transporters play essential roles in salinity tolerance in some halophytes. Expression and activity of plasma membrane and vacuolar membrane H^+-ATPases significantly increased in *Suaeda salsa* in response to NaCl treatment [52, 53]. ATPase activity is required to establish the proton gradient that maintains electrochemical and pH differences across the membrane. Membrane transporters can couple this electrochemical gradient to movement of substrates against their concentration gradients [54]. Thus, the activities of ion transporters or antiporters localized in the plasma membrane and vacuolar membrane are tightly regulated and essential for plant growth and development [55, 56]. Many such ion transporters, including the vacuolar Ca^{2+}/H^+ antiporter [57], the vacuolar H^+/Ca^{2+} transporter [58], the K^+ transporter [59], and others [32, 60] have been cloned and shown to reduce concentrations of Na^+ and Cl^- in the cytosol. Over expression of these transporters can improve salt tolerance by maintaining cytosolic ion homeostasis during salt stress [61, 62].

Under salt stress conditions the osmotic pressure is also severely compromised due to the influx of high concentrations of salt ions. Halophytes have evolved a defense mechanism involving accumulation of osmoprotectants, such as proline, glycine betaine, polyphenols, and soluble sugars, in the cytosol to reduce and balance the osmotic pressure. Overexpression of halophyte genes for enzymes involved in the synthesis of glycine betaine or raffinose, such as choline monooxygenase (CMO) [63], betaine aldehyde dehydrogenase (BADH) [64] and galactinol synthase (GOLS) [65], have been shown to enhance salt stress tolerance in glycophytic plants. Furthermore, expression of these genes is also induced in response to cold, drought, and heat, in addition to salinity, resulting in a concomitant increase in galactinol, raffinose, and α-ketoglutaric acid in transgenic plants [65].

4 Detoxification of ROS and alterations in membrane composition

ROS detoxification pathways play a protective role in the response to salt stress by scavenging toxic radicals generated from the electron transport chains of mitochondria and chloroplasts. Antioxidative defense systems include both non-enzymatic and enzymatic components. One such system is termed theascorbate-glutathione pathway and acts in chloroplasts. A series of enzymes belonging to this system, including monodehydroascorbate reductase (Am-MDAR) [66], glutathione transferases (SbGST, SsGST) [67, 68], ascorbate peroxidases (SssAPX and PtcAPX) [69, 70] and superoxide dismutases (TaSOD) [71], have been identified in several kinds of halophytes and have been shown to play important roles in protecting against salt-induced oxidative stress in higher plants. Overexpression of these genes leads to enhanced NaCl tolerance under salt stress. Overexpression of the *SssAPX* gene,that normally encodes the stromal APX in *S. salsa,* can increase the germination rate, cotyledon growth, survival rate, and salt tolerance of transgenic *Arabidopsis* [72].

In addition to enzymes that scavenge ROS directly certain other types of proteins/enzymes have also been shown to improve a plants antioxidative capacity. Metallothioneins (MTs) can bind to heavy metals and are involved in the homeostasis of essential metals (Cu and Zn),as well as cellular detoxification of nonessential metals (Cd and Hg). For example, cloning of the *Salicornia brachiata* metallothionein gene *sbMT-2* and expression in tobacco resulted in significantly enhanced salt tolerance, a higher membrane stability index, and decreased levels of H_2O_2 and lipid peroxidation (MDA), implicating sbMT-2 in H_2O_2 detoxification. Furthermore, mechanistic analysis revealed elevated expression of key antioxidant enzymes, specifically SOD, POD, and APX, in *sbMT-2*-expressing transgenic plants, further confirming the role of the *SbMT-2* gene and its protein product in ROS scavenging/detoxification [73]. In addition to metallothioneins, S-adenosylmethionine synthetase [74], glycosyltransferase [75], At Fes1A [76] and CCCH-type zinc finger protein have also been shown to participate in salt tolerance by limiting oxidative stress and, additionally, helping to maintain the ionic and osmotic balance [77].

Membrane structure and fluidity regulated by varying the composition and degree of fatty acid saturation of membrane lipids affects membrane permeability and contributes to plant resistance to environmental stressors [78, 79]. Comparative analysis of the membrane lipid and fatty acid composition in the halophyte *Thellungiella halophila* and the glycophyte *Arabidopsis thaliana* under high salinity conditions revealed higher levels of phosphatidylglycerol (PG) and unsaturated fatty acids, as well as a higher double-bond index for monogalactosyldiacylglycerols and PGs in *T. halophila* [80]. Consistent with these observations, transgenic *Arabidopsis* plants expressing the *S. salsa* gene that encodes glycerol-3-phosphate acyltransferase (GPAT), anacyl-esterifying enzyme required for PG synthesis expressed under high-salt conditions, exhibit tolerance to NaCl [81]. Additional studies have revealed that increased levels of unsaturated fatty acids in membrane lipids can protect photosystem II (PSII) and photosystem I (PSI) and enhance photosystem tolerance to salt stress [23, 82]. Furthermore, a nonspecific lipid transfer protein TsnsLTP4 has been shown to be involved in stress tolerance [83].

5 Conclusion

Different types of halophytes have different strategies to cope with high ionic concentrations. For example, small molecules, such as nitric oxide (NO) and hydrogen sulfide (H_2S), have been identified as endogenous gasotransmitters involved in alleviating salt or other kind of stress [84-86]. Genome-wide identification of microRNAs has also revealed putative roles for microRNAs in the salt stress response [87]. Based on results showing that genes cloned from halophytes promote stress tolerance when expressed in glycophytes, expression of these genes could be used to produce transgenic crops with higher levels of salt tolerance suitable for sustainable agriculture in saline-affected areas. Identification of additional salinity-responsive genes from these and other halophytes could help us to better understand salt-tolerance mechanisms and these advances may be applied to the development of hardier transgenic crops.

Conflict of interest: Authors state no conflict of interest.

Acknowledgments: This work was supported by grants from the National Natural Science Foundation of China (31101034) and Natural Science Foundation of Shandong Province (ZR2016CM28).

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