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MECHANISMS OF PLANT RESPONSE TO SALINITY STRESS: CURRENT UNDERSTANDING AND RECENT PROGRESS

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Abstract

Salinity is considered as a major abiotic stress for plants as it challenges plant growth and productivity severely. Plants have developed plenty of biochemical, physiological and metabolic strategies to deal with salt stress at multiple levels. A better understanding of these contrivances is an important step towards achieving the goal of sustainable development of agriculture. This review aims to provide a brief overview of our current understanding of plant salt-tolerance mechanisms from five aspects: specialized salt glands, ion homeostasis and osmotic adjustment, antioxidant defense system, hormonal regulation and modifications in membrane composition. Finally, we highlight unsolved issues that remain to be addressed in future studies.

Key words: Salinity stress, Mechanisms, Abiotic stress

Introduction

Plants may be subjected to diverse abiotic stresses, such as cold, drought, flooding and salinity during their life cycle due to their sessile nature. These abiotic stresses adversely affect plant growth and development, leading to substantial crop losses worldwide. Among these conditions, salinity stress has emerged as a serious and major one as it affects about 70% of the farm soils around the world (Zhang *et al.*, 2017).

High salt concentration impairs the ability of plants to absorb water and could generate various stresses, such as ionic, osmotic and oxidative stress to plants which may exert negative effects on various important physiological, biochemical and metabolic processes, including photosynthesis, respiration and protein synthesis, ultimately leading to inhibited growth and development or death (Feng *et al.*, 2014; Farooq *et al.*, 2017; Gao *et al.*, 2019; Yan *et al.*, 2020).

Plants have evolved various contrivances for responding and adapting to salt stress at multiple levels including molecular, cellular, tissue, morphological and physiological level (Deng *et al.*, 2016; Zhao *et al.*, 2018; Xiao *et al.*, 2019; Zhang *et al.*, 2019). Generally, they achieve this goal either by expelling excess salt out of the cells or through rapid and harmonized changes to tolerate the presence of salts within the cells.

It becomes more and more urgent and important to cultivate salt-tolerant crop varieties to feed the ever-increasing human population nowadays; while exploring and investigating plant salt-stress response mechanisms will provide valuable information for it. Here, we will present recent advances in our understanding of major strategies by plant to cope with salt threats.

Strategies of salt tolerance by plants

Specialized salt glands: Specialized epidermal structures, terms salt glands, have been developed by some halophytes, called recretohalophytes, to resist salinity (Deng *et al.*, 2015; Dassanayake & Larkin, 2017). Salt glands could be categorized into four structural types: salt bladders, multicellular glands, bicellular hairs and unicellular hairs. Bladders, the simplest form of salt glands which are composed of a large vacuolated cell with or without 1 or 2 stalk cells are only found in Aizoaceae and Amaranthaceae. These plants could sequester salt in the bladder cell vacuole to avoid damage to their growth. Multicellular glands are the widely distributed type of salt glands, consisting of cells differentiated into basal collecting cells and distal secretory cells. Upon salt stress, salt could be collected by collecting cells from mesophyll cells around and transported to secretory cells (Dassanayake & Larkin, 2017). The third type of salt glands, bicellular hairs, consisting of a basal cell and a cap cell, are mainly found in chloridoid grasses. For these plants, the cuticle around the salt gland could form a chamber to store secreted salts. Unicellular hairs exist in the wild rice species *Porteresia coarctata* and are highly vacuolated. The number of salt hairs can be regulated by *P.coarctata* to adapt to external salt concentration (Sengupta & Majumder, 2010).

Mechanisms underlying salt secretion from the salt glands are of great interest to researchers in recent years (Feng *et al.*, 2015; Yuan *et al.*, 2016; Garcia *et al.*, 2017). A proteomic approach was applied to compare the proteome of salt gland-rich tissues and salt gland-deprived tissues of the mangrove tress species *Avicennia officinalis* in order to identify proteins present in the former, which shed light on future research designed to demonstrate salt secretion mechanisms of salt glands (Tan *et al.*, 2015). Besides, using *Limonium bicolor* as an optimal model, Yuan *et al.*, screened the transcriptome of *Limonium bicolor* leaves in response to salt treatment, identifying the candidate genes in the salt gland involved in salt secretion, and proposed a model for salt secretion pathway of the salt gland (Yuan *et al.*, 2016).

Salt glands are nature's desalination devices that harbor potentially valuable information about salinity stress adaption. It is believed that the combination of various advanced molecular and cellular technologies will bring better understanding of how salt glands contribute to salinity tolerance.

Ion homeostasis and osmotic adjustment: One deleterious effect imposed by salinity stress is ion toxicity or imbalance, which could give rise to decreased enzymatic activities and photosynthetic rate. Na^+/K^+ ratio plays an important role in plant salinity tolerance, and therefore plants need to maintain a low Na^+/K^+ ratio in the cytosol for survival, that is, to keep the concentration of toxic ions such as Na^+ low and accumulate essential ions such as K^+ (Shao *et al.*, 2014; Almeida *et al.*, 2017).

Ion compartmentalization is a vital strategy for plants to achieve ion homeostasis. Na^+ is pumped into vacuoles, leading to reduced detrimental effects of excess Na^+ in the cytosol and the vacuolar Na^+/H^+ antiporters are thought to contribute to the sequestration of Na^+ (Kumar *et al.*, 2017). On the other hand, Ca^{2+} plays important roles in maintaining Na^+/K^+ balance, which can activate high-affinity K^+ uptake, as well as ameliorate Na^+ toxicity by decreasing Na^+ influx (Han *et al.*, 2012; Lu *et al.*, 2016). Recently, Zheng *et al.*, identified the glycosyltransferase QUA1 as an important regulator of cytoplasmic Ca^{2+} level under salinity conditions through screening Arabidopsis mutants which are defective in stress-induced Ca^{2+} increase (Zheng *et al.*, 2017).

Osmotic pressure can also be greatly compromised by salinity stress when salt concentration exceeds a threshold level. Plants have evolved osmotic adjustments to meet this challenge (Zhao *et al.*, 2010; Ilangumaran & Smith, 2017). A variety of organic solutes of low molecular weight, known as osmotica or osmolytes, including amino acids, such as proline, glycine, betaine, soluble sugar or its derivative compound, are synthesized to compromise osmotic stress at the cellular level. These compatible osmoprotectants are present in cytosol and can be accumulated in considerable amounts but do not interfere with cellular central metabolism (Slama *et al.*, 2015; Wang *et al.*, 2017).

Proline is present widely in higher plants and increases under salinity stress. It is considered to be involved in cytomembrane stabilization and intracellular enzyme structure maintenance (Wang *et al.*, 2017). To unravel the protective roles of proline upon salinity stress, researchers investigated the metabolic regulation responses of proline-added *T. halophilus* by using the metabolomic approach. The study revealed proline as an effective protective molecule for *T. halophilus* in enhancing the salt resistance of cells by means of the regulation of related metabolic pathways (He *et al.*, 2017).

Antioxidant defense system: Salt stress can bring about the overproduction of various reactive oxygen species (ROS), such as superoxide (O_2^-), hydroxyl radical (OH), hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$), which could severely impair cellular structures and components via peroxidation of lipids and oxidation of proteins (Kumar *et al.*, 2017). An antioxidant defense system, including a range of antioxidative enzymes like catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), glutathione peroxidases (GPX), glutathione S-transferases (GST), and glutathione reductase (GR); as well as low molecular weight non-enzymatic antioxidants like nitric oxide (NO), ascorbic acid (ASH), glutathione, carotenoids, flavones, and flavonoids, has been equipped with plants to scavenge ROS (Song and Wang, 2015; Chen *et al.*, 2016; Chokshi *et al.*, 2017; Siddiqui *et al.*, 2017).

One of the crucial ROS-scavenging enzymes, Ascorbate peroxidase (APX), contributes to H_2O_2 detoxification by catalyzing the conversion of H_2O_2 into H_2O, and thus it could be directly involved in safeguarding plants from detrimental conditions, such as salinity stress (Gerszberg & Hnatuszko-Konka, 2017; Pandey *et al.*, 2017). Cao *et al.*, compared wild-type tobacco plants with transgenic ones overexpressing PcAPX (a cytosolic APX gene from *Populus tomentosa*), and revealed that under unfavorable conditions, such as salt, drought and oxidative stress, the transgenic plants showed more stress tolerance ability. The study identified APX as a key antioxidant enzyme in abiotic stress tolerance in plants (Cao *et al.*, 2017).

Besides antioxidative enzymes which can remove ROS directly, a number of non-enzymatic antioxidant molecules have also been shown to enhance the antioxidant capacity of plants. Nitric oxide (NO), a small non-charged, water and lipid soluble gaseous free radical, is an essential redox-signaling molecule in plant biology. It acts as a versatile messenger in multiple physiological processes and mediates abiotic stress tolerance in plants (Hasanuzzaman *et al.*, 2018). There has been increasing interest in the roles of NO in plant tolerance against salinity stress in recent years. By altering the enzymatic activity of several SOD isoforms, exogenously applied nitric oxide reduces salinity-induced oxidative damage in maize (Klein *et al.*, 2018). It has been reported that under salt stress, NO treatment at 100 μM could alleviate the salt-induced decrease in photosynthetic performance of Indian Mustard (Fatma & Khan, 2014). Furthermore, when Mustard grown under salinity stress received sulfur (S), NO enhanced photosynthetic capacity of them more effectively by regulating oxidative stress, S-assimilation pathway and NO generation (Fatma *et al.*, 2016).

Plant hormonal regulations: Plant hormones act as essential endogenous cues that contribute to plant resistance to adverse environmental stressors. Advances in the field of plant stress signaling and adaptive response, mainly using model organisms such as *Arabidopsis thaliana* and *Oryza sativa*, have shown the mechanisms of how plant hormones are concerted to signaling networks for salinity resistance (Li *et al.*, 2016; Pandey *et al.*, 2017).

The phytohormone abscisic acid (ABA) is known to play crucial roles in plant responses to various non-optimal environmental conditions like drought, salinity and pathogen infection. Synthesis of ABA increased greatly when plants are exposed to salinity or drought stress (Zhu, 2002). It has been well established that the expression of ABA biosynthesis-related genes such as ABA aldehyde oxidase, ABA3, and 9-cis-epoxycarotenoid dioxygenase are induced rapidly in stress conditions (Xiong & Zhu, 2003).

ABA initiates stomatal closure and a loss of guard cell turgor through a signaling cascade to prevent water loss. Substantial progress has been made in revealing the molecular mechanisms of ABA-mediated modulating of stomatal aperture in guard cells (Bauer *et al.*, 2013; Eisenach *et al.*, 2017; Ha *et al.*, 2018). Briefly, ABA triggers activation of two types anion channels, S-type (slow-sustained) and R-type (rapid-transient) in the guard cell membrane, leading to plasma membrane depolarization and a flow of ions. There are also studies showing reactive oxygen species (ROS) or cytosolic Ca^{2+} as the key second messenger in this process (Wang *et al.*, 2013; Brandt *et al.*, 2015). Recently, a small peptide CLE25 was identified as a mobile signaling cue that could modulate stomatal closure via ABA in long-distance signaling in dehydration stress response (Takahashi *et al.*, 2018).

In addition to ABA, many other hormones, such as gibberellin (GA), cytokinins (CK), jasmonate, ethylene, have been established as vital molecules involved in alleviation of salinity stress in plants. Various investigations have unraveled the presence of crosstalk network among different hormonal pathways (Song *et al.*, 2014; Jiroutova *et al.*, 2018). Elucidating more specific mechanisms of elaborate web of hormonal crosstalk will be an important theme in the realm of stress response research.

Modifications in membrane composition: Membrane structure modifications through changes of fatty acid saturation of membrane lipids contribute to the maintenance of homeostasis of membrane permeability and have beneficial effect on plant tolerance to environmental stress (Mikami & Murata, 2003; Lopalco *et al.*, 2013).

Increased levels of unsaturated fatty acid in membrane lipids enhanced salt tolerance of photosystem II in the halophyte Thellungiella compared to that in the glycophyte Arabidopsis (Sui & Han, 2014). Consistent with the above investigations, overexpression of *SsGPAT* (glycerol-3-phosphate acyltransferase gene from *Suaeda salsa*) gene confers enhanced salt stress resistance in Arabidopsis by increasing the content of *cis*-unsaturated fatty acid in phosphatidylglycerol (PG), and further retarding the photoinhibition of PSII and PSI (Sui *et al.*, 2017). Interestingly, a recent report demonstrated the role of lipid droplets (LDs) in defense against salinity stress in *Parachlorella kessleri*, which could supply enzymes and substances in the process of membrane reconstruction (You *et al.*, 2019).

Concluding remarks: Abiotic stresses like cold, drought, flooding, salinity have detrimental influence on crop growth and yield; while plants have developed powerful strategies to counteract these stresses to complete the life cycle and survive safely. Understanding the salt stress-mediated adaptive responses and associated resistance mechanisms might help in improving the performance of crop plants under saline conditions or design crop plants that could better adapt to salt stress. This review highlights several aspects of salinity stress tolerance mechanisms, including the development of special salt secretory structures, ion homeostasis and osmotic adjustment, antioxidant defense system, plant hormonal regulations as well as alterations in membrane compositions. However, salt stress tolerance is a complicated trait involving multiple physiological, biochemical and metabolic pathways, while many puzzles in this field remain to be solved. The relationship of different resistance strategies and their crosstalks should be studied to tackle the problem of salinity in a more effective way.

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