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Minireview

Calcium- and salt-stress signaling in plants: Shedding light on SOS pathway

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Abstract

As salt stress imposes a major environmental threat to agriculture, understanding the basic physiology and genetics of cell under salt stress is crucial for developing any transgenic strategy. Salt Overly Sensitive (*SOS*) genes (*SOS1–SOS3*) were isolated through positional cloning. Since *sos* mutants are hypersensitive to salt, their characterization resulted in the discovery of a novel pathway, which has helped in our understanding the mechanism of salt-stress tolerance in plants. Genetic analysis confirmed that SOS1–SOS3 function in a common pathway of salt tolerance. This pathway also emphasizes the significance of Ca^{2+} signal in reinstating cellular ion homeostasis. SOS3, a Ca^{2+} sensor, transduces the signal downstream after activating and interacting with SOS2 protein kinase. This SOS3–SOS2 complex activates the Na^+/H^+ antiporter activity of SOS1 thereby reestablish cellular ion homeostasis. Recently, SOS4 and SOS5 have also been characterized. SOS4 encodes a pyridoxal (PL) kinase that is involved in the biosynthesis of pyridoxal-5-phosphate (PLP), an active form of vitamin B6. SOS5 has been shown to be a putative cell surface adhesion protein that is required for normal cell expansion. Under salt stress, the normal growth and expansion of a plant cell becomes even more important and SOS5 helps in the maintenance of cell wall integrity and architecture. In this review we focus on the recent advances in salt stress and SOS signaling pathway. A broad coverage of the discovery of SOS mutants, structural aspect of these genes and the latest developments in the field of SOS1–SOS5 has been described.

Keywords: Abiotic stress; Antiporters; Calcium-binding proteins; Calcium signaling; CBL; CIPK; Salt stress; Signal transduction; SOS pathway

The maintenance of intracellular ionic homeostasis is fundamental to the physiology of a living cell. It is vital for the cell to keep the concentration of toxic ions below a threshold level and accumulate essential ions. Intracellular K^+ and Na^+ homeostasis is important for the functioning of many cytosolic enzymes and excess of Na^+ ions are toxic for cell metabolism. The maintenance of K^+ and Na^+ homeostasis becomes even more crucial under a salt stress, which also imposes an oxidative stress on cellular machinery. Disequilibration of Na^+ ions due to salt stress often leads to catastrophic pathologies, which affect cell survival, growth and division. Therefore, soil salinity has become a serious environmental stress limiting plant growth and productivity worldwide. Saline soil is abundant in Na^+ ions, which are cytotoxic to cells when they accumulate in higher concentrations (above 100 mM). This can inhibit the activity of many essential enzymes, cell division and expansion, membrane disorganization and osmotic imbalance, which finally lead to growth inhibition [1]. Higher concentrations of Na^+ ions can also lead to reduction in photosynthesis and production of reactive oxygen species. Potassium plays vital role in various processes such as metabolism, growth, and stress adaptation. Potassium functions in the cell by directly interacting with proteins resulting in enzyme activation, stabilization of protein synthesis, and neutralization of negative charges on proteins. At the same time, alteration in K^+ ions (due to impact of high salinity stress) can disturb the osmotic balance, function of stomata and

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function of several enzymes [2–6]. To circumvent Na^+ build up in the cytoplasm, plant cells employ various transporters, which include Na^+/H^+ transporters both at the plasma membrane and tonoplast to efflux Na^+ ions out of the cell in the apoplastic space or to sequester them in the vacuole, respectively [7,8]. The deposition of high salt concentration, Na^+ in particular can alter the basic texture of the soil resulting in decreased soil porosity and consequently reduced soil aeration and water conductance. High salt deposition in the soil generates a zone of low water potential in the soil making it increasingly difficult for the roots to acquire both water as well as nutrients from the soil. Salt stress therefore results in a water-deficit conditions in the plants and takes the form of a physiological drought [6]. The basic understanding of a signaling cascade, which ranges from perceiving of a stress signal, signal transduction, gene regulation affecting the ion transport network within the cell are crucial for the amelioration of plants under salt stress. Salt tolerance is a complex multigenic trait and involves ionic and osmotic re-equilibrium to maintain a state of homeostasis in the cell. It is a coordinated interplay of a battery of genes, which are upregulated as a consequence of salt-stress perception, whose products finally lead to a state of homeostasis and salt tolerance. This review presents a brief description of calcium and salt-stress signaling in general and the recent advances in the field of SOS signaling pathway in plants.

Calcium and salt stress signaling

The crop production is decreasing rapidly due to the negative impact of various environmental stresses whereas word population is increasing dramatically and may reach from 6 billions to ~9.3 billions by the year 2050 (httl://www.unfpa.org/swp/200/), therefore, it is very important to develop the stress tolerant varieties to cope up with this upcoming problem of food security. Among stresses, salt stress is one of the principal factors resulting in the decrease of the average yield of major crops causing losses worth hundreds of million dollars each year [6]. The area of salt affected land is already more than 9000×10^6 ha, which is a massive threat to agriculture [9]. Furthermore, there is a deterioration of about 2×10^6 ha (~1%) of world agricultural lands due to salinity each year. The soil salinity may be due to poor water management, high evaporation, and heavy irrigation and also due to previous exposure to sea water. The sea water contains ~3% NaCl, where Na^+ is ~460 mM, Mg^{2+} is 50 mM and Cl^- is ~540 mM and many other ions in small quantities [6]. Tolerance or susceptibility to salt stress in plants is a coordinated action of various genes including those encoding calcium-binding proteins and other components of stress-signaling pathways. These components may cross talk with each other, however little information is available on this aspect.

Various aspects of plant growth and development and stress physiology are mediated by chemical signaling through many chemicals such as calcium ions (Ca^{2+}), which function as a major secondary-messenger signaling molecule and plays a fundamental role in plant growth and development under normal as well as stress conditions. The extracellular stress signal is first perceived by the membrane receptors, which then activate large and complex signaling cascade intracellularly including the generation of second messengers such as Ca^{2+}. This increased cytosolic Ca^{2+} initiates the stress signaling pathways for stress tolerance (Fig. 1) [1,6,10].

The Ca^{2+} release can be primarily from extracellular source (apoplastic space) as addition of EGTA or BAPTA blocked calcineurin (a calcium-binding protein phosphatase-2B protein in yeast and animal cells)-mediated activity, (Fig. 1). Ca^{2+} release may also result from activation of PLC[1] (phospholipase C), leading to hydrolysis of PIP2 to IP3 and subsequent release of Ca^{2+} from intracellular Ca^{2+} stores. Furthermore, calcium-binding proteins (calcium sensors) can provide an additional level of regulation in the calcium signaling. These sensor proteins recognize and decode the information provided in the calcium signatures, relay the information downstream to initiate a phosphorylation/dephosphorylation cascade leading to regulation of gene expression (Fig. 1). The signal cascade results in the expression of multiple stress-responsive genes, the products of which can provide the phenotypic response of stress tolerance directly or indirectly. The stress response could also be a growth inhibition or programmed cell death (apoptosis), which will depend upon how many and which kind of genes gets up- or down-regulated (Fig. 1).

In general, stress signals results in cytosolic Ca^{2+} perturbations, which are unique and precisely decoded by Ca^{2+}-sensing proteins to relay the signaling cascade. The relatively recently discovered calcium sensor, calcineurin B-like proteins (CBLs), and their interacting partners CBL-interacting protein kinases (CIPKs), have emerged as key networks which play an important role in plants in response to calcium and stress signaling. CIPK initiates a phosphorylation cascade, which further regulate down-stream components for stress tolerance [10–13]. In *Arabidopsis*, AtCBL4 is a SOS3 and CIPK24 is a SOS2.

SOS mutants

The work leading to the discovery of SOS genes was initiated in 1996 by Zhu and coworkers [14]. There was some incongruity over selecting *Arabidopsis* as a system for isolating salt-sensitive mutants as this plant is salt-sensitive to begin with, which is characteristic of most glycophytic plants. However, *Arabidopsis* is capable enough of tolerat-

[1] *Abbreviations used:* PLC, phospholipase C; CBL, calcineurin B-like protein; CIPK, CBL-interacting protein kinase; ABA, absicisic acid; ROS, reative oxygen species; RCD, radical-induced cell death; EGFP, enhanced green fluorescent protein; ABI2 abscisic acid-insensitive 2; PPI, protein phosphatase interaction; CNB, calcineurin B; SSLP, simple sequence length polymorphism; PL, pyridoxal; PLP, pyridoxal-5-phosphate, PN, pyridoxine; PM, pyridoxamine.