



Molecular Basis of Salinity Stress Tolerance in Plants: Functional Integration of the SOS Signalling Pathway and Ion Homeostasis

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Salinity stress represents one of the most persistent abiotic constraints to agricultural productivity, particularly in irrigated and coastal agroecosystems. Excess sodium accumulation perturbs cellular ion balance, disrupts metabolic homeostasis, and adversely affects plant growth and yield. Plants counter salinity stress through tightly regulated signaling networks and ion transport mechanisms that collectively maintain cytosolic ion equilibrium. Central to these adaptive responses is the Salt Overly Sensitive (SOS) signalling pathway, which mediates calcium-dependent regulation of sodium transport and long-distance ion distribution. This review synthesizes current knowledge on the molecular mechanisms governing salinity tolerance, with emphasis on the coordinated interaction between the SOS pathway and key ion transport systems. Recent advances in functional genomics and molecular physiology are discussed in the context of crop improvement under saline environments.

Keywords: Salinity stress; SOS signalling; Ion transport; Sodium toxicity; Potassium homeostasis; Abiotic stress tolerance

Introduction

Soil salinity is a growing threat to sustainable crop production worldwide and poses a particularly serious challenge to Indian agriculture, where large areas of irrigated land are affected by salt accumulation. Salinity stress primarily arises from the excessive presence of sodium chloride in the rhizosphere, resulting in reduced soil water potential and progressive ionic imbalance within plant tissues (Munns & Tester, 2008). These constraints ultimately manifest as inhibited growth, premature senescence, and substantial yield penalties. At the cellular scale, salinity stress disrupts ion homeostasis by favoring Na^+ influx while impairing K^+ acquisition and retention. Since potassium is indispensable for enzyme activation, membrane potential maintenance, and stomatal regulation, preservation of a high cytosolic K^+/Na^+ ratio is a defining feature of salt-tolerant genotypes. This balance is achieved through the coordinated action of membrane transporters regulated by stress-responsive signaling pathways, among which the SOS pathway occupies a central position.

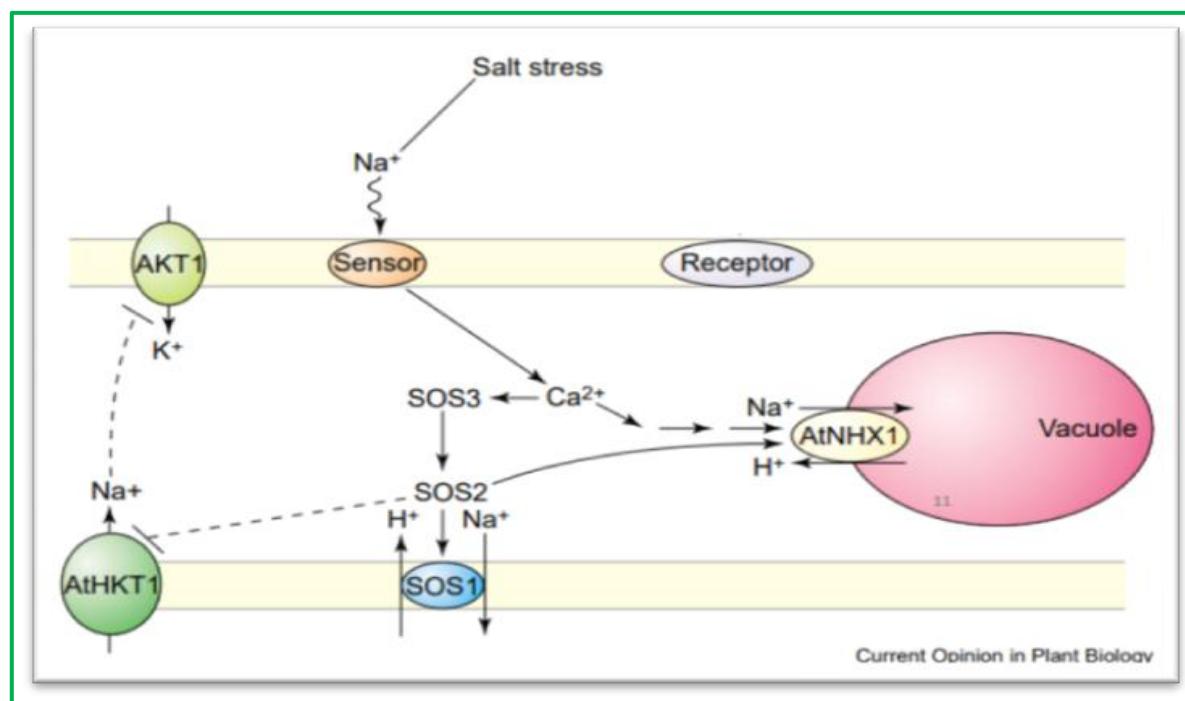
Early Events in Salinity Stress Perception and Signal Transduction

Plant responses to salinity stress are initiated rapidly upon exposure to high external salt concentrations. The immediate phase is dominated by osmotic stress, characterized by reduced water uptake and turgor loss, followed by the accumulation of Na^+ ions in the cytosol, which gives rise to ionic toxicity (Ismail & Horie, 2017). Salt-induced alterations in membrane potential elicit transient increases in cytosolic Ca^{2+} levels. These calcium signatures act as informational signals that are decoded by calcium sensor proteins, including calcineurin B-like proteins (CBLs), calmodulins, and calcium-dependent protein kinases. In addition, secondary messengers such as reactive oxygen species and phospholipid-derived

signals contribute to the activation of transcriptional and post-transcriptional regulatory networks that fine-tune plant adaptive responses.

The SOS Signalling Pathway: Molecular Architecture and Control

The Salt Overly Sensitive pathway constitutes a calcium-regulated signaling module that plays a pivotal role in sodium detoxification under saline conditions. The core components of this pathway include SOS3 (CBL4), SOS2 (CIPK24), and the plasma membrane Na^+/H^+ antiporter SOS1. Upon salt-induced Ca^{2+} elevation, SOS3 binds calcium and undergoes conformational changes that facilitate its interaction with SOS2. The activated SOS2 kinase subsequently phosphorylates SOS1, thereby enhancing its Na^+/H^+ exchange activity and promoting the extrusion of excess Na^+ from the cytosol (Zhu, 2016). Recent evidence indicates that SOS pathway activity is further modulated through protein–protein interactions, phosphorylation dynamics, and transcriptional regulation, highlighting its flexible and context-dependent nature (Ji et al., 2022; Zhang et al., 2023).



Maintenance of Ion Homeostasis under Saline Conditions

Effective salinity tolerance requires the integrated regulation of Na^+ uptake, transport, sequestration, and exclusion, alongside sustained potassium nutrition. High-affinity potassium transporters of the HKT family play a critical role in retrieving Na^+ from the xylem stream, thereby limiting its accumulation in photosynthetic tissues and protecting leaf metabolic functions. At the subcellular level, vacuolar Na^+/H^+ antiporters such as NHX1 and NHX2 facilitate the compartmentalization of excess sodium into vacuoles. This process not only reduces cytosolic toxicity but also contributes to osmotic adjustment. Concurrently, inward-rectifying K^+ channels and high-affinity K^+ transporters ensure adequate potassium supply, reinforcing cellular resilience under salt stress.

Functional Integration of the SOS Pathway with Ion Transport Systems

Rather than operating as an isolated module, the SOS pathway functions as part of a broader regulatory network governing ion homeostasis. SOS2 has been shown to interact with multiple transport proteins beyond SOS1, including vacuolar antiporters and potassium channels, thereby coordinating Na^+ exclusion with intracellular ion compartmentalization. Furthermore, SOS-mediated signaling interfaces with hormonal pathways, particularly abscisic acid, which modulates root system architecture, transpiration rates, and stress-responsive gene expression. Such crosstalk enhances the plasticity of plant responses under

prolonged salinity stress and contributes to tissue-specific ion distribution patterns (Ryu & Cho, 2020; Kumar et al., 2024).

Implications for Crop Improvement

Insights into SOS signaling and ion homeostasis have significant implications for the development of salt-tolerant crop varieties. Transgenic and genome-editing studies have demonstrated that targeted manipulation of SOS pathway components and associated transporters can improve salinity tolerance in major cereals and horticultural crops. However, effective crop improvement requires balanced regulation of ion transport processes, as excessive sodium exclusion may compromise osmotic adjustment. Future efforts should therefore emphasize genotype-specific optimization of SOS signaling and validation under field conditions representative of saline agroecosystems.

Conclusion

Salinity tolerance in plants emerges from the coordinated action of signaling pathways and ion transport mechanisms that collectively preserve cellular homeostasis. The SOS signalling pathway plays a central role in decoding salt-induced calcium signals and regulating sodium extrusion, while its integration with potassium transport and vacuolar sequestration systems ensures metabolic stability. Continued integration of molecular insights with breeding and biotechnological approaches will be essential for enhancing crop performance in salt-affected soils.

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