Commentary

Living with Salt

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INTRODUCTION

To grow or not to grow is a simplified decision plants make following a complex assessment when challenged by salt stress. The need to understand how plants determine this under salt stress has pressing importance as we are left with less arable land and diminishing freshwater resources available for conventional agriculture compounded by climate change. Studies done over decadal scales converge on salt tolerance being a complex trait that involves a coordinated response of transcriptional to physiological responses. Primarily using *Arabidopsis*, we have deciphered some of the key aspects that govern salt-stress responses. Now, we are at new frontiers to expand our knowledge base using naturally stress-adapted plants as primary targets of study to understand salt-stress adaptation at unprecedented levels empowered by new molecular tools and resources. In this commentary, we highlight the major mechanisms described by Zhao et al.[1] in the first issue of *The Innovation* on plant salt-stress responses, in relation to new breakthrough research and emerging frontiers toward building salt-tolerant crops designed to fit the needs of a changing world.

SALT SENSING AND SIGNALING

Salt stress is known to elicit osmotic stress, oxidative stress, and ionic imbalance. Therefore, plants are known to use each of these specific stresses to signal excess salt. Zhao et al.[1] reviewed how rapid sensing of osmotic stress from root to shoot can be transmitted using hydraulic pressure differences in the xylem, and Takahashi and Shinozaki[2] have reviewed how mobile small peptides play a role in long-distance salt signaling. Until recently, it was unclear whether plants could distinguish general osmotic stress from ionic stress by sensing Na^+ in the apoplast. The recent breakthrough discovery of plasma membrane sphingolipids identified as the *Arabidopsis* mutant *moca1* showed plants could distinguish Na^+ from osmotic sensors such as OSCA1. Additionally, recent discoveries of HPCA1 (Hydrogen-Peroxide-Induced Ca^{2+} Increases 1) and RAFs (Rapidly Accelerated Fibrosarcomas) demonstrated how salt-stress responses were activated by H_2O_2-induced Ca^{2+} channels and early abscisic acid (ABA)-pathway signaling.[3,4]

Figure 1 presents a brief overview of how the initial salt signal is relayed to multiple tissues that activate ABA signaling pathways and minimizes the outcomes of osmotic and oxidative stress. In our goal toward engineering salt-adapted crops, it is imperative to explore how specific membrane lipids interact with plasma membrane channels and identify microdomain structures that may facilitate physical proximity of sensors, Ca^{2+} channels, and Na^+ exclusion pathway components. The search for sensors at the organellar level and cell-type-specific receptors together with their use of existing or novel signaling intermediates will lead to a more comprehensive understanding of salt sensing.

A COORDINATED RESPONSE TO SALT STRESS

A salt-stress-adapted plant should be able to respond to the stress immediately upon the stress signal and be able to minimize its effects or have a response toolkit ready prior to the signal, to prevent irreversible tissue damage. Studies on *Arabidopsis* have demonstrated how a salt-sensitive plant fails to sustain growth under stress and allows uncurbed accumulation of intracellular Na^+ that, in turn, results in substantial ionic imbalances, oxidative stress, and eventually premature death. Therefore, the response to salt stress is tightly coupled to cell growth and integrity regulated by cell-wall modifications and cell-cycle processes.[1]

A number of ion transporters are coordinately activated to extrude Na^+ from the plant either at the soil-root interface or via salt glands, compartmentalize Na^+ into vacuoles, or exclude Na^+ from actively growing tissue while maintaining uptake of essential ions such as K^+ and avoiding ionic imbalance.[1] The salt-exclusion mechanism driven by the Na^+ transporter SOS1, and its regulatory partners SOS2 and SOS3, are dominant components in acclimating plants to salt stress (Figure 1). Recent studies showed how this well-established system is further regulated by the endosomal sorting complex to enhance SOS2-SOS3 interactions and facilitate appropriate distribution of SOS2 under salt stress.[5]

The accumulation of excess Na^+ in the cytoplasm triggers an array of osmotic adjustments driven by enzymatic as well as non-enzymatic components to maintain cellular homeostasis under osmotic stress (Figure 1). Concurrently, oxidative stress is induced as a derived stress, further escalating cellular damage that requires the coordinated action of multiple hormones for recovery from stress.[1] However, our understanding of how gene-regulatory networks respond to salt stress based on the intensity and duration of the stress, in combination with other biotic and abiotic stresses at different cell and tissue types and at distinct developmental stages, is far from complete.

Unlike *Arabidopsis*, halophytes illustrate evolutionarily successful strategies that allow growth during salt stress. However, the exploration of underlying genetic mechanisms for salt tolerance learned from halophytes has been lagging. This is mainly due to the lack of halophytic models that could effectively use the *Arabidopsis* knowledge base as a functional genomic resource while being amenable to genetic manipulation using convenient methods of transformation that facilitate independent genetic analyses without having to rely on heterologous systems.[6] A handful of halophyte models and crop relatives have been developed with new genomic and molecular tools that make them powerful genetic model systems.[6] Recent improvements in molecular resources made available for several halophyte models are likely to provide substantial headway in bridging the gap of salt-adaptation mechanisms between stress-adapted and sensitive plants.[6]

EMERGING FRONTIERS IN PLANT SALT ADAPTATION

The molecular resources available to synthesize successful adaptive strategies for salt tolerance based on established salt transporters, transcription factors, and signaling molecules identified in salt-sensitive model plants have reached an asymptote. This is more apparent when studies on halophytes only validate what is already known from *Arabidopsis*-based studies and are unable to decipher new functional components that are absent in *Arabidopsis*. Therefore, we highlight predominant emerging frontiers that may lead to breakthrough innovations toward our comprehensive understanding of salt-stress adaptation (Figure 1).

The recent development of model systems closely related to *Arabidopsis* offers powerful tools when designing comparative genetic studies within an evolutionary context to deduce divergent gene-regulatory networks that are influential in adapting to salt stress.[6] Similar strengths could be envisioned for wild relatives of crops used in comparative analyses. Plants are known to form integral partnerships with the microbiome, although most genetic experiments study target plants in isolation. The

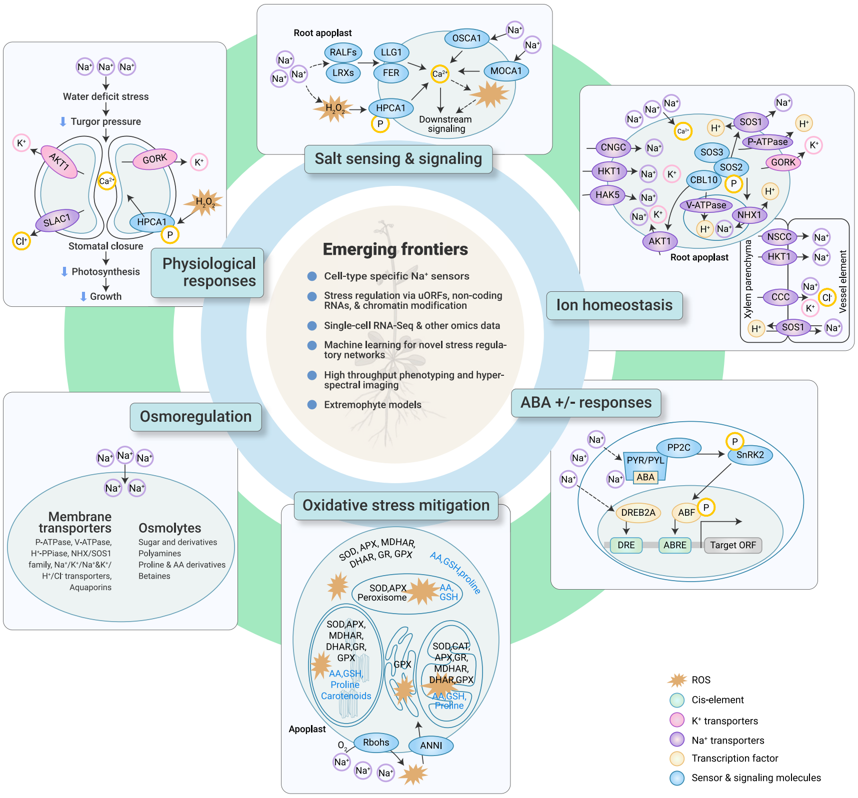

Figure 1. A Brief Overview of Plant Responses to Salt Stress

expanding resources generated for metagenomics present a vast unexplored frontier in studying salt adaptations. Studies on endophytes providing salt tolerance to plants otherwise sensitive to the stress add substantial support for future research exploring the co-evolutionary mechanisms of such traits that require more than one species. Our current understanding of salt-stress responses is largely dominated by genetic regulation implemented by a limited number of canonical protein-coding genes. However, discoveries suggesting the importance of non-coding RNAs and chromatin modifications[7] strongly justify the expansion of experimental designs integrating non-coding genes and epigenetic modifications in search of comprehensive salt-stress responses. Additionally, an array of emerging molecular tools such as single-molecule imaging, single-cell genomics, and synthetic cellular sensors combined with hyperspectral imaging offer an unprecedented level of resources to investigate spatiotemporally diverse salt-stress responses at single-cell-level precision in diverse species.[8–10] Finally, "big data" analytics associated with long-range and high-throughput sequencing, large-scale -omics data, remote sensing, and other high-throughput phenotyping data analyzed using machine-learning algorithms are expected to revolutionize the field of plant stress biology as envisioned for many other frontiers in science.

CONCLUSION AND FUTURE PERSPECTIVES

Despite decades of foundational discoveries, our contemporary knowledge about the mechanisms of Na^+ and Cl^- entry into the cell, the Na^+-sensing mechanisms, and the downstream stress-regulatory networks have significant gaps. Molecular studies performed in controlled environments followed by field experiments will be critical in bridging basic and applied sciences to effectively develop novel cultivars of salt-adapted crops. The use of high-throughput phenotyping techniques, large-scale genomics data including metagenomics associated with plant performance, novel extremophyte models in the search for evolutionary selected strategies for salt-stress adaptation, improved molecular toolboxes equipped with new gene-editing and transformation techniques, and the expanding computational resources including machine-learning algorithms to analyze, integrate, and visualize complex data hold unprecedented potential that can reform future crop development to cope with climate-threatened food security.

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