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Cytoskeleton and plant salt stress tolerance

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The plant cytoskeleton is a highly dynamic component of plant cells and mainly based on microtubules (MTs) and actin filaments (AFs). The important functions of dynamic cytoskeletal networks have been indicated for almost every intracellular activity, from cell division to cell movement, cell morphogenesis and cell signal transduction. Recent studies have also indicated a close relationship between the plant cytoskeleton and plant salt stress tolerance. Salt stress is a significant factor that adversely affects crop productivity and quality of agricultural fields worldwide. The complicated regulatory mechanisms of plant salt tolerance have been the subject of intense research for decades. It is well accepted that cellular changes are very important in plant responses to salt stress. Because the organization and dynamics of cytoskeleton may play an important role in enhancing plant tolerance through various cell activities, study on salt stress-induced cytoskeletal network has been a vital topic in the subject of plant salt stress tolerance mechanisms. In this article, we introduce our recent work and review some current information on the dynamic changes and functions of cytoskeletal organization in response to salt stress. The accumulated data point to the existence of highly dynamic cytoskeletal arrays and the activation of complex cytoskeletal regulatory networks in response to salt stresses. The important role played by cytoskeleton in mediating the plant cell's response to salt stresses is particularly emphasized.

Cytoskeletal Dynamic Changes Under Salt Stress

Salt stress-induced cytoskeletal dynamic changes are often observed. A long-term observational study of AF and MT array response to salt stress has been finished in Arabidopsis.[1,2] The results show that salt stress can induce AF assembly and bundle formation; however, in seedlings exposed to long-term, high salt stress, polymerized MFs are depolymerized.[1] On the other hand, MTs depolymerize then repolymerize when Arabidopsis seedlings are stressed by salt. The initially depolymerization of MTs appear in both low and high NaCl concentration treatments. But there is a much lower number of cells with MT repolymerization in high salt concentration than in low salt concentration treatments.[2] Remarkably, if the initially disruption of MTs is further induced by oryzalin (a MT disruption drug), a number of cells with MT recovery is obviously increased. It is implied that the initially MT disruption has a close relationship with the following MT reorganization. In addition, in maize roots treated with KCl for several hours, cell elongation and the normal arrangement of MT arrays are disturbed, and that the MTs reorient oblique to the longitudinal axis.[3] It is also found that transverse orientation of MT arrays is remodeled to a more random arrangement in tobacco BY-2 cells after treatment with 150 mM NaCl for 15 min.[4]

Salt stress cause a main harmful aspect of plant intracellular ion imbalance.[5,6] For plant ion imbalance tolerance, a signaling pathway based on the SOS (Salt Overly Sensitive) genes has been established in Arabidopsis, mainly including SOS1, the plasma membrane Na^+/H^+ antiporter, SOS2, a serine/threonine protein kinase and SOS3, a calcineurin B-like calcium-binding protein.[5,6] Under salt stress, the transcription of SOS1, which transports sodium ion (Na^+) into the apoplast to prevent plants from the harm of Na^+ accumulation is phosphorylated and enhanced by SOS2/SOS3 kinase complex mediated through salt-induced calcium ion (Ca^{2+}) signal.[5,6] Because Arabidopsis *sos1* and *sos2* mutants have intracellular Na^+ imbalance, they are hypersensitive to NaCl.[5,6] It has been proved that *sos1* and *sos2* mutants display MT disruption.[7] In 50 mM NaCl treatment, *sos1* mutants' roots display a pattern of right handed growth and MTs are more disordered in their cells than in wild-type Arabidopsis cells.[2]

The Functions of Cytoskeletal Organization in Response to Salt Stress

Pharmacological approach has provided a fairly clear role of cytoskeletal organization under salt stress.[1,2] Wild-type Arabidopsis seedlings are more death by paclitaxel (a MT stabilization drug) and more survival by oryzalin and propyzamide (MT disruption drugs) under salt stress, while almost seedlings in which the MTs are reorganized can withstand salt stress.[2] The results testify that both depolymerization and reorganization of MTs are important for the plant's ability to withstand salt stress. Especially, the salt-induced destruction of MT network is not the result of cell damage, but plays a vital role to response to salt stress. Using AF drugs, the results suggest that disruption of the AF organization reduce the ability of Arabidopsis seedlings to withstand salt stress, whereas AF stabilization increases this ability.[1] Therefore, salt stress-induced AF assembly is a necessary component of salt tolerance in Arabidopsis.

Some cytoskeletal associated proteins involved in plant salt stress tolerance is also found. For example, Phospholipase D (PLD), which is involved in the rearrangement of MFs has been shown to be is involved in ABA- and ROS-mediated processes as part of the plant's responseto abiotic stresses.[4,8] In addition,

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Rodríguez-Milla and Salinas find that Arabidopsis mutations in PFD3 and PFD5 subunits that are implicated in correct folding of tubulin and actin display changes in their developmental patterns and MT arrays.[9] The authors also find that *pfd3* and *pfd5* mutants are hypersensitive to salt stress compared to the wild-type Arabidopsis, while *pfd* mutants reduce levels of α- and β-tubulin in both control and salt-stress treatments, showing PFD3 and PFD5 can be vital cytoskeletal associated proteins involved in the plant salt stress tolerance.[9]

It is well-known that the process of transient calcium ion (Ca^{2+}) influx into the cytoplasm induced by salt stress is an important response mechanism.[5] The results of several studies have shown that MTs may be involved in regulating the activity of Ca^{2+} channels under normal conditions.[10,11] We find notable increases in the free cytosolic Ca^{2+} concentrations ($[Ca^{2+}]_{cyt}$) after salt stress-induced initially depolymerization of the MTs, and that these increases are inhibited when paclitaxel (a MT stabilization drug) is added through using yellow cameleon (YC.3.6) as a calcium reporter. Further, salt-induced recovery of MTs are regulated by the increases in levels of $[Ca^{2+}]_{cyt}$.[2] It is implied that MT depolymerzation triggers the Ca^{2+} influx that has the regulatory effect on MT reassembly under salt stress.

Recently, several studies also provide obvious evidence on cytoskeleton has an important role in the SOS pathway. By using a pharmacological approach, *sos* mutants have abnormal responses to low doses of MT-interacting drugs.[7] Death of *sos1* mutant seedlings grown in MS medium containing 100 mM NaCl is reduced by the addition of paclitaxel, and increased by addition of oryzalin.[1] Disruption of MFs with LatA and CD (AF disruption drugs) results in more *sos2* seedling death, while stabilization of MFs with phalloidin (a AF stabilization drug) with rescues more *sos2* seedlings from death in 150 mM and 200 mM NaCl treatments.[2] Additionally, *sos1* and *sos2* mutants suppress the right-handed root growth phenotype of the Arabidopsis mutations in SPIRAL1 that acts a plant-specific protein that localizes to MTs in vivo.[7,12,13] These results imply that the SOS signaling pathway could contain MTs regulatory mechanisms, while MTs play an active role in the salt tolerance of plants partly by the SOS signaling pathway.

The Factor(s) Induces Cytoskeletal Dynamic Changes Under Salt Stress

Salt stress mainly causes ion imbalance and hyperosmotic stress in plants.[6] Thus, it is a question which factor(s) might play a role in cytoskeleton array reorganization in their response to salt stress. The functions of MTs are associated with SOS signaling pathway, showing that ion imbalance is the major factor responsible for MT dynamic changes in salt-stressed plants. *Pfd* mutants are also hypersensitive to NaCl but not to LiCl or mannitol.[9] MTs in root epidermal cells exhibit abnormalities with 50 mM NaCl treatment and remain normal intact and their orientation after treatment with 100 mM mannitol.[2] Additionally, when grown on medium containing 50 and 100 mM NaCl, seedlings exhibited a pattern of right-skewed root growth induced by MT reorganization. However, seedlings display a normal pattern of root in either 100 or 200 mM mannitol treatments.[2] There are obvious differences in the pattern of root growth and the arrangement of MTs following the treatments with NaCl and mannitol.[2] Taken together, the highly dynamic changes of MT organization are possibly triggered by an ion-specific but not by an osmotic-specific factor.

To determine which factor(s) might play a role in AF assembly and bundle formation in response to salt stress, observational study of MT array response to different mannitol, sorbitol or KCl concentrations stresses in Arabidopsis seedlings are developed. The results show that obvious polymerization of AFs appear in 350 mm mannitol, 350 mM sorbitol or 150 mM KCl treatments, suggesting that both ion imbalance and osmotic stress are major factors in assembly of MFs in salt-stressed plants.[1]

Conclusions

In summary, from the time when they were first discovered in 1963, the known functions of cytoskeleton have expanded from being just static scaffolds to playing critical roles in almost all intracellular activities.[14-17] Although the study on the role of cytoskeleton in the response to abiotic stresses has recently arisen and come into a new subject,[18] the accumulated data emphasize the existence of highly dynamic changes, complex regulatory networks, and the vitally important role of cytoskeleton in the response to salt stresses. It has distinctly proved that the roles of cytoskeleton are involved in SOS signaling pathway, Ca^{2+} influx and some regulatory mechanisms of salt-induced cytoskeletal associated proteins. We believe that accumulating evidence over the next few years will provide further support for the close relationship between cytoskeleton and the adaptation of plants to salt stress. The mechanisms by which cytoskeleton regulates salt stress signalling pathways and the identity of the cytoskeletal associated proteins involved in these mechanisms will be revealed.

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