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MECHANISMS OF SALT TOLERANCE IN RICE

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India would need to produce about 311 million tonnes of food grains by 2030, to feed about 1.43 billion people, and by 2050, when the country's population is projected to reach 1.8 billion, this amount might rise to 350 million tonnes. Rice is a major cereal crop for more than 3 billion people globally and its demand is expected to increase by 38% by 2050. However, abiotic stresses critically limit the rice production, resulting in significant yield losses. Salt is a two edged sword and salinity is next major threat to rice production after drought. About 50% of world's arable land is predicted to be salt-affected and in India, salt-affected land covers 6.73 Mha, with the number anticipated to rise to 16.2 million by 2050. Rice is sensitive to salinity at seedling and reproductive stages. The first component of this stress is osmotic, and arises from NaCl induced reduction of the solute potential of the soil solution, which in turn reduces the water uptake by plants. The second component is ionic (ion toxicity), which arises from accumulation of noxious quantities of Na^+ in the cells and tissues of the plants which adversely affect its growth and development. Rice yield tend to decline when EC is more than 3 dSm^{-1} with 12% yield decrement per unit increase in EC (Munns and Tester, 2008). Hence, there is an urgent need to develop salt-tolerant rice cultivars to sustain rice production. Advancement in our understanding of abiotic stress tolerance mechanisms of crop plants and application of modern biotechnological techniques, marker-assisted selection (MAS) and genetic engineering are important to develop stress tolerant varieties.

Different Salt Tolerance Mechanisms in Rice

1. Sodium Homeostasis

Uptake of Na^+ at the root-soil boundary is believed to occur mainly through non-selective cation channels (NSCC), including the cyclic nucleotide-gated channels (CNGCs) and glutamate receptors (GLRs), as well as through some high affinity K^+ transporters (HKTs), K^+ channels including the Arabidopsis K^+ transporter (AKT1) and high-affinity K^+ uptake transporter (HAK). The Na^+ absorbed by the root then moves to the xylem with the aid of other transporters and channels which is delivered to the shoot, especially to the leaf blade, where its effects are most felt (Hanin *et al.*, 2016). In glycophytes, regulating this transport of Na^+ to the leaf is crucial and will be a determinant in their adaptation to salt stress. Therefore, transporters that operate to reverse the processes involved in Na^+uptake and translocation would be relevant, although Na^+ uptake, translocation and accumulation in the leaf is not always correlated with salt stress sensitivity (Munns and Tester, 2008). For example barley plants tolerate salt stress by accumulating salt in the leaves for osmotic adjustment.

2. Resistance to radial transport and xylem loading of Na^+

When Na^+ is taken up at the level of the root and moves radially to the stele, it is loaded into the xylem and taken up to the shoot in the transpiration stream. Restricting the radial movement of Na^+ across the root will greatly reduce the amount loaded into the xylem for delivery to the shoot. In addition to this observation, the SOS1 antiporter localized to the root epidermis offers the first line of resistance to Na^+ uptake, by extruding Na^+ to the external soil environment. At the cortical level, OsHKT2;1 has been shown to prevent radial transport of Na^+ at the root.

Maintaining minimal shoot Na^+/ K^+ ratios is an important stress tolerance trait in some halophytes and tolerant glycophytes (Katschnig *et al.*, 2015). To achieve this, the regulation of xylem loading at the root is crucial. SOS1 localized to the stele is believed to mediate xylem loading of Na^+ in both glycophytes and halophytes, especially under high salinity.

3. Restriction of Na^+ transport to the leaf

Once Na^+ is loaded into the xylem, it is transported via transpiration to the leaf. HKT and SOS1 found in the stem, mainly of dicots, and HKT (HKT1;4) in the sheath of monocots, participate in reducing the amount of Na^+ reaching the leaf, by retrieving Na^+ from the xylem into xylem parenchyma cells, thereby regulating Na^+ delivery to the leaf blade (Assaha *et al.*, 2017).

Class I HKT transporters are located at the xylem/symplast boundary and show high specificity for Na^+, thus mediating Na^+ unloading from xylem into xylem parenchyma cells of the shoot and root.

4. Regulation of toxic Na^+ accumulation in the leaf blade

The leaf blade is the central hub of most metabolic processes in plants and so needs to be protected from Na^+-induced damage. Therefore, under salt stress, Na^+ reaching the leaf needs to be rapidly redistributed in a way that will not hamper any metabolic processes. One such action was shown involving AtHKT1;1mediated Na^+ recirculation from the leaf to the root via the phloem (Fujimaki *et al.*, 2015).

5. Potassium homeostasis

The maintenance of constant intracellular concentration is crucial because K^+ is involved in a myriad of growth, developmental, reproductive and physiological processes, including germination, osmoregulation, stomatal regulation, nyctinastic movement of leaves, enzyme activation, loading and unloading of sugars in phloem, as a counter-ion for nitrate translocation, cytosolic pH regulation, stabilization of membrane potential and protein trafficking to protein-storage vacuoles.

Since salt stress often induces perturbations in the cellular K^+ homeostatic balance, with a consequential alteration in all these physiological processes, it has become increasingly certain that maintaining a high cytosolic K^+ / Na^+ ratio would constitute a stress tolerance strategy. This optimal K^+ / Na^+ ratio, especially under stress, can only be achieved if the root K^+ uptake, xylem loading for translocation to the shoot and cellular influx are enhanced, while detrimental cytosolic K+ efflux is restricted at the same time (Himabindu *et al.*, 2016).

6. Mechanisms favouring root K^+ uptake

The membrane potential is largely negative in order to maintain high intracellular K^+ concentrations. Maintaining more negative (inside) membrane potential is a key factor in salt stress tolerance.In fact, HAK is the only K^+ uptake transporter that is known to operate in this range of external K^+ concentrations, and this characteristic activity for high-affinity K^+ transport renders plants expressing the HAK transporter genes very tolerant to low K^+ conditions (Himabindu *et al.*, 2016).

7. Intracellular Na^+/ K^+ and pH homeostasis

Maintaining high cytosolic K^+/ Na^+ is a prerequisite for salt stress tolerance as this ensures optimal cellular metabolic functions. Under salt stress, the competitive inhibition of K^+ uptake by Na^+ often leads to the Na^+ interfering in many K^+dependent processes, thereby inhibiting them. For example Na^+ replaces K^+ in binding sites on enzymes resulting in enzyme deactivation and consequent interruption of the metabolic processes concerned. Also, the influx of Na^+ in cells depolarizes the membranes, leading to K^+ efflux through depolarization activated KOR, such as GORK. To counter this excessive Na^+ influx, SOS1 offers the first line of defense, by actively extruding the absorbed Na^+ back to the extracellular spaces (Anschutz *et al.*, 2014).

In xylem parenchyma cells, this extrusion will lead to the xylem Na^+ loading depending on external Na^+ concentration. Vacuolar sequestration of Na^+ is another very important strategy in the regulation of cytosolic Na^+ accumulation. However retention of the sequestered Na^+ has been proposed as a key stress tolerance mechanism, as Na^+ leakage back to the cytoplasm via the fast vacuolar (FV), and slow vacuolar (SV) channels, has been associated with salt sensitivity. Therefore, mechanisms that will favour the uptake and transport of K^+ and the maintenance of high cytosolic K^+/ Na^+ ratios should be relevant to the growth and tolerance of glycophytes

Rice plants mainly employ three mechanisms, ion exclusion, osmotic tolerance, and tissue tolerance to adapt in salt stress. These mechanisms are brought in to play during the various stages of Na+ uptake from soil and its translocation to shoot.

Conclusion

Understanding partly why halophytes are more salt-tolerant than glycophytes could constitute useful targets for engineering salt stress tolerance. In addition, novel regulatory pathways have been uncovered which, although augmenting the complexity of salinity, could also serve as important targets for improving salt stress tolerance.

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