Review Article

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Spatial and time course pattern of salt stress-induced changes in higher plants.

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Salt excess in the rhizosphere induces osmotic, nutritional and metabolic disturbances that bring about crop growth reduction and yield losses. While largely documented in the literature, these disturbances are separately analyzed in term of anatomy and time course that are usually limited by experiment conditions. It is of necessity to establish a chronology of changes involved during salt stress at different anatomical levels of plant. In the present review, we attempted to dissect and locate physiological and molecular events that occurred upon exposure of higher plants to salt stress. This analysis integrated various experimental approaches to give further understanding on salt stress response and to highlight valuable traits of salt sensitivity/tolerance of plants.

Key words: salt stress, tolerance, sensitivity, plant, cell, molecule.

Plant tolerance to salt is defined as the ability to withstand effects of salt excess in the medium (Maas, 1993). Referring to this definition, considerable research is undertaken to evaluate plants material response to salinity using multiple experimental models. Generally, studying salt stress effects on higher plants revolves around three main research areas (i) Mechanisms of salt ions transport across cell membranes (Apse and Blumwald, 2007). It includes a physiological and molecular study of ion transporters involved in the collection, extrusion, compartmentalization and mobility control of salt ions in plants (Diédhiou and Golldack, 2006; Takahashi *et al.,* 2009). (ii) Metabolic pathways involved to conquer salt toxicity (see Hasegawa *et al.,* 2000). (iii) Regulation of genes expression under salt stress (Xiong and Zhu, 2002; Silva-Ortega *et al.,* 2008). This kind of research is improved by advances in molecular biology, including the use of genomics that allows rapid analysis of large numbers of genes (Seki *et al.,* 2001; Sun *et al.,* 2010). Eventually, these works aimed to select biomarkers that have physiological significance and enable to predict plant tolerance to salt stress (Zhu, 2000; Xiong and Zhu, 2001).

Actually, new features of tolerance or sensitivity to salt are being identified in order to improve or to select cultivars for agriculture. Moreover, these new data allow a revision of the traditional classification of plants to halophytes and glycophytes, based on the ability to grow on saline medium (Flowers *et al.,* 1977) without taking in account experiment duration and specific tissue or subcellular responses. In the present review, we go over the sequential occurrence of main events upon exposure to salt stress at different plant scales.

SPATIAL PATTERN OF SALT STRESS-INDUCED CHANGES

Changes at the whole plant scale: Plant tolerance to salt excess at the whole plant level is determined by its ability (a) to prevent the absorption of salt ions, which depends to

the root system selectivity (Amtmann and Sanders, 1999); (b) to control the loading of salt ions into xylem; (c) to the desalinization of xylem sap: salt ions are retained in the roots, stems, petioles and leaf sheaths, involving exchange of Na^+/ K^+ ions between the sap and the root cells or conducting vessels of the stem-petioles system; (d) to re-export salt ions into phloem, thereby avoiding the accumulation of Na^+ and Cl^- in the developing tissues at the aerial part (Figure 1), (e) to sustain ion homeostasis; (f) to excrete salt ions through special glands on the leaf surface of some halophytes plants (Figure 1, see Barhoumi *et al.,* 2007).

Changes at the cell scale: Salt tolerance at the cell level is determined by sustaining adequate metabolic activity despite the accumulation of salt ions. This is ensured by sufficient osmotic adjustment, salt ions sequestration to maintain integrity of enzyme systems within different cellular compartments and keeping hormonal balance that regulates growth activity.

Osmotic adjustment and safety of cell machinery: Sequestration of Na^+ and Cl^- into vacuole is balanced by concomitant accumulation of K^+ and organic osmolytes in the cytoplasm (Lee *et al.,* 2008). Generally, organic osmolytes are present as simple sugars (fructose, glucose), sugar with alcohol function (glycerol, sorbitol, inositol methyl), and complex carbohydrates (theralose, raffinose). Likewise, osmolytes may be compatible polyamine compounds (proline, glycine betaine, alanine betaine, proline betaine, tetrahydro-2-methyl-4-carboxy pyrimidine), or sulfated compounds (choline sulfate, dimethyl sulfonium propironate) (Nuccio *et al.,* 1999). These compounds can be accumulated to high levels without disrupting cellular metabolism, with negligible effect on pH and charge balance in the cytosol or inside organelles.

However, the signal transduction pathways leading to the formation of these osmolytes are not yet elucidated (Hare *et al.,* 1999). For example, genes involved in biosynthesis of proline are partly induced by salt or water stress (Xiong *et al.,* 2001; Ortega *et al.,* 2008). On the other hand, expression of genes encoding enzymes of proline catabolism is often repressed by the same type of stress (Reymond *et al.,* 2000). In addition, the biosynthesis of osmolytes may be subject to negative feedback. Thus the production of proline in plants is regulated by levels of P5CS enzyme (Δ1-pyrroline-5-carboxylate synthetase) (Hong *et al.,* 2000).

Besides their osmotic functions, these compounds have a protective role on cytoplasmic proteins (Hong *et al.,* 2000; Munns, 2002; Hoque *et al.,* 2007). Particularly, they enable to alleviate effects of reactive oxygen species (ROS) on enzyme activities (Holmstrom *et al.,* 2000). For instance, glycine betaine ensures the integrity of the plasma membrane and thylakoids under salt or heat stress conditions (Rhodes and Hanson, 1993). However, detoxification of ROS generated by salt stress involves antioxidant enzymatic pathways that are more efficient than accumulation of osmolytes (Tsai *et al.,* 2004), such as superoxide dismutase, catalase and ascorbate peroxidase (Wang *et al.,* 2009). The increased activity of these enzymes is often correlated with improved plant tolerance to salt stress (Tsugane *et al.,* 1999).

Maintain of hormonal Balance: Inhibition of plant growth by salt stress at cellular scale occurs through a decrease in cell expansion and division. Disruption of these processes is linked to hormonal imbalance induced by salinity (Wang *et al.,* 1998). Plant hormones (abscisic acid, gibberellic acid, cytokinins) are growth regulators and their exogenous application can increase tolerance to salt (Xiong and Zhu, 2002). In particular, abscisic acid (ABA) was found to be involved in gene expression in response to salt stress (Rock, 2000, Zhu *et al.,* 1997). Induction of ABA synthesis by salt stress or drought in the roots is an endogenous signal conveyed through the transpiration stream to regulate organ growth of the aerial part and the opening of the stomata (Davies and Zhang, 1991). Also, the induced accumulation of ABA maintains root elongation despite the drop in water potential under salt stress (Saab *et al.,* 1990). Several authors consider that the beneficial effects of ABA result from its inhibitory action on the synthesis or the signaling pathways of ethylene (Spollen *et al.,* 2000; Sharp, 2002). Indeed, stimulation of root elongation was obtained when applying an inhibitor of ethylene biosynthesis (Spollen *et al.,* 2000). In

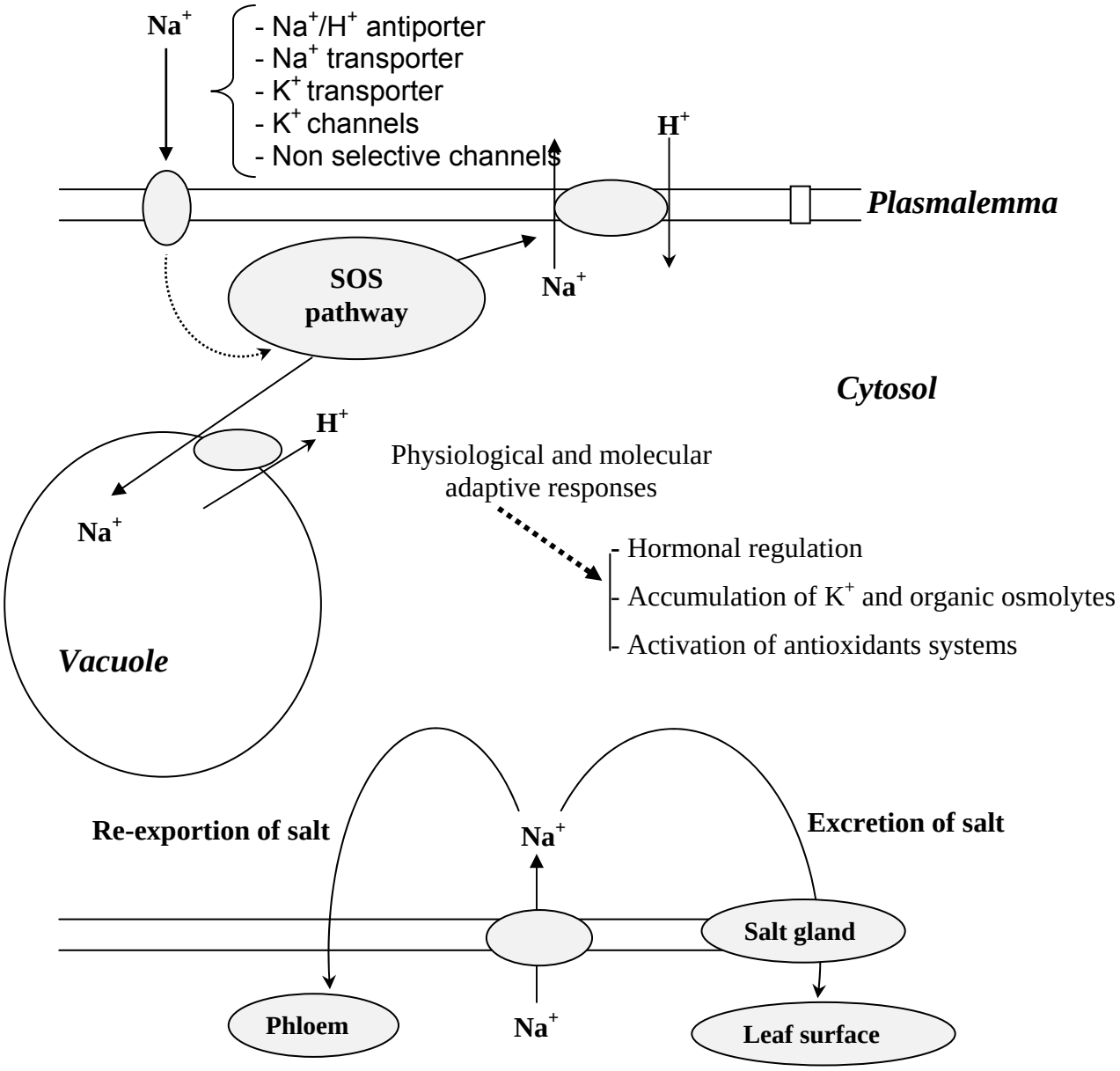

Figure: 1. Schematic representation of major adaptive strategies and events occurring upon exposure of higher plants to salt stress: sequestration, re-exportation and excretion of Na^+; osmotic adjustment (accumulation of osmolytes); hormonal regulation; activation of antioxidant systems; involvement of SOS pathway (see Xiong and Zhu, 2002).

the shoots, ABA stimulates leaf expansion by decreasing ethylene production (Sharp *et al.,* 2000). It seems that ABA to ethylene ratio in the cell plays a determinant role in the regulation of plant growth under salt stress.

Changes at molecular scale: Membrane transporters are molecules of great importance; they are involved in the forefront of regulating salt ions movement (Amtmann and Sanders, 1999, Blumwald *et al.,* 2000, Schachtman and Liu, 1999; Tyerman and Skerritt, 1999). In fact, the salt ions including Na^+ have no specific transporters, but they can have access to nonselective cation channels or to low and high affinity transporters systems of K^+ (Amtmann and Sanders, 1999). Conversely, Na^+ can be excreted from the cytoplasm to the external environment through Na^+/H^+ exchange

maintained by pH gradient between both sides of the plasma membrane (Blumwald *et al.,* 2000). These processes cooperate to control the absorption and compartmentalization of salt into vacuoles through Na^+/H^+ plasmic and tonoplastic antiporters (Blumwald *et al.,* 2000).

It has been shown that Arabidopsis cells have a plasma membrane Na^+/H^+ carrier specific to Na^+ (Xiong and Zhu, 2002). This transporter is encoded by SOS1 gene (Salt Overly Sensitive 1) (Figure 1). The over-expression of SOS1 in Arabidopsis increases tolerance to salt stress of transformed plants. The catalytic activity of SOS1 type (Na^+/H^+) was demonstrated in vitro in various species including tomato. The activity of SOS1 in Arabidopsis is regulated by a complex of two proteins known as SOS2 and SOS3. Firstly, high concentrations of Na^+ in the medium induce a rapid increase in the concentration of Ca^{2+} in the cytoplasm. Protein SOS3, termed Ca^{2+}-sensor is activated by calcium flux. In turn, SOS3 interacts with and activates protein kinase SOS2. Protein SOS2 in the active state regulates the Na^+ efflux against the influx of H^+ at the transporter SOS1. Also, SOS2 is involved in the induction of genes involved in ion homeostasis. At the tonoplast, SOS2 activates the Na^+/H^+ ATPase and pyrophosphatase (Figure 1). Several authors suggest that plants grown in the absence of salt stress have probably lost the SOS mechanism for regulating Na^+ homeostasis.

CHRONOLOGICAL PATTERN OF SALT STRESS-INDUCED CHANGES

New approaches towards salt stress studies emphasized the importance of treatment duration (Munns, 2002; Debouba *et al.,* 2007; Pinheiro *et al.,* 2008). It was stated that when exposure duration to salt is not enough long, differences in growth between tolerant and sensitive species are not significant (Munns *et al.,* 1995; Pinheiro *et al.,* 2008).

Responses to short term salt stress: Sudden addition of salt in the culture medium is instantly associated with changes in growth rate in leaves. A rapid and transient decline in the rate of leaf expansion has been reported in maize (Cramer and Bowman, 1991, Neumann, 1993), rice (Yeo *et al.,* 1991), wheat and barley (Passioura and Munns, 2000). Similar effects were found in the presence of KCl, mannitol or polyethylene glycol (PEG) (Yeo *et al.,* 1991; Chazen *et al.,* 1995). This finding indicates that the abrupt decrease in growth is not specific to salt stress, it is rather associated to a rapid change of cells water status. Passioura and Munns (2000), showed that this phase of rapid decline in growth can be prevented if we maintain a fairly high water status in leaf cells. Likewise, roots growth rate is rapidly and temporarily reduced upon exposure to NaCl (Rodriguez *et al.,* 1997). Similar effects were also obtained in the presence of KCl and mannitol, confirming that this response is related to a sudden change of water status in root cells (Frensch and Hsiao, 1995).

After several minutes, the rate of leaf growth recovered gradually to stabilize at a low level of activity (Passioura and Munns, 2000). It should be noted that the resumption of low growth activity observed in the presence of NaCl, is also obtained with equivalent doses of mannitol or KCl, indicating that this phase of low activity is not necessarily due to the presence of Na^+ and Cl^- (Yeo *et al.,* 1991; Passioura and Munns, 2000).

Growth recovery is tightly dependent on plant tissue and severity of stress (Frensch and Hsiao, 1997; Lacerda *et al.,* 2005). Hsiao and Xu, (2000) showed that recovery of growth in salt stressed maize was faster in roots than in leaves. Frensch and Hsiao, (1997) found that growth recovery in the roots occurs 01 hour after application of a moderate osmotic stress (0.1 to 0.4 MPa), whereas Rodriguez et al. (1997) reported that it takes 24 hours after treatment if we apply higher doses of osmoticum (0.7 MPa or 150 mM NaCl).

Response to long term salt stress

After at least 24 hours of salt treatment, growth rate reached a low level of activity, particularly in leaves (Munns and Sharp, 1993). This is related to osmotic effects of salinity, since at this stage salt ions have not reached toxic levels in cells (Hu and Schmidhalter, 1998).

Beyond 24 hours of salt treatment, data on water status are no longer sufficient to explain the variations in growth rate activity. Indeed, at this stage of treatment, improving water status of leaf cells did not prevent the salt-induced decrease in plant growth and leaf expansion (Gowing *et al.,* 1990; Munns *et al.,*

2000; Taleisnik *et al.,* 2009). These results support the involvement of plant hormones, rather than water status or ion toxicity in growth regulation.

After several days, salt ions accumulate to toxic levels, and the effects become visible especially in older leaves (Munns, 1988). Salt toxicity is usually due to the inability of cells to effectively compartmentalize salt ions into vacuoles. During treatment, concentration of salt ions increases more rapidly in the cytoplasm than in vacuole (Rawson *et al.,* 1988). Consequently, apoplastic and symplasmic accumulation of salt ions can cause enzymes inactivation and cell dehydration (Nomura *et al.,* 1998).

Obviously, effects of salt stress are more perceptible after weeks of treatment, particularly in sensitive species (Pinheiro *et al.,* 2008). These effects manifested by yellowing leaf and fall of older leaves. The rate of loosing leaves will determine the length of plant survival period on saline medium. Although, plant can survive if the appearance of new leaves rate exceeds that of the loss of old leaves.

The survival of perennial plants in saline environment depends on their ability to prevent the accumulation of salt ions at levels toxic in old leaves and maintain an adequate rate of emerging new leaves. In addition, at this developing stage, plant should save the reproductive organs from salt ions toxicity. In cereals, salinity reduced the number of flower buds, disrupts and delays flowering and maturity of plants (Munns and Rawson, 1999). However, the salt ions are usually accumulated at low levels in reproductive organs (Na^+ = 50 mM and Cl^- = 5-15 mM).

It appears that reproductive development is more sensitive to osmotic effects of salt. In salt sensitive plants, accumulation of salt ions during growth may also cause death of young leaves, and these plants could not reach the fruiting stage. While tolerant plants maintain good vegetative and reproductive activity, despite a large accumulation of salt ions in their organs (Debez *et al.,* 2004).

CONCLUSION

Data available in literature show that plant response to salt is closely related to the duration of treatment, analyzed tissue and stage of development. Hence, it seems imperative to consider experiment duration, especially in comparative studies among species. In fact, we should bear in mind that response to salt involves physiological and molecular events occurring during stress and at several anatomical levels. These events should be integrated and interpreted at the whole plant level to evaluate sensitivity/tolerance of species.

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