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Salinity Stress and Salt Tolerance

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1. Introduction

Salinity is one of the most serious factors limiting the productivity of agricultural crops, with adverse effects on germination, plant vigour and crop yield (R Munns & Tester, 2008). Salinization affects many irrigated areas mainly due to the use of brackish water. Worldwide, more than 45 million hectares of irrigated land have been damaged by salt, and 1.5 million hectares are taken out of production each year as a result of high salinity levels in the soil (R Munns & Tester, 2008). High salinity affects plants in several ways: water stress, ion toxicity, nutritional disorders, oxidative stress, alteration of metabolic processes, membrane disorganization, reduction of cell division and expansion, genotoxicity (Hasegawa, Bressan, Zhu, & Bohnert, 2000; R. Munns, 2002; Zhu, 2007). Together, these effects reduce plant growth, development and survival.

During the onset and development of salt stress within a plant, all the major processes such as photosynthesis, protein synthesis and energy and lipid metabolism are affected (Parida & Das, 2005). During initial exposure to salinity, plants experience water stress, which in turn reduces leaf expansion. The osmotic effects of salinity stress can be observed immediately after salt application and are believed to continue for the duration of exposure, resulting in inhibited cell expansion and cell division, as well as stomatal closure (T. J. Flowers, 2004; R. Munns, 2002). During long-term exposure to salinity, plants experience ionic stress, which can lead to premature senescence of adult leaves, and thus a reduction in the photosynthetic area available to support continued growth (Cramer & Nowak, 1992). In fact, excess sodium and more importantly chloride has the potential to affect plant enzymes and cause cell swelling, resulting in reduced energy production and other physiological changes (Larcher 1980). Ionic stress results in premature senescence of older leaves and in toxicity symptoms (chlorosis, necrosis) in mature leaves due to high Na^+ which affects plants by disrupting protein synthesis and interfering with enzyme activity (Hasegawa, Bressan, Zhu, & Bohnert, 2000; R. Munns, 2002; R Munns & Termaat, 1986). Many plants have evolved several mechanisms either to exclude salt from their cells or to tolerate its presence within the cells.

In this chapter, we mainly discuss about soil salinity, its effects on plants and tolerance mechanisms which permit the plants to withstand stress, with particular emphasis on ion homeostasis, Na^+ exclusion and tissue tolerance. Moreover we give a synthetic overview of the two major approaches that have been used to improve stress tolerance: exploitation of natural genetic variations and generation of transgenic plants with novel genes or altered expression levels of the existing genes. A fundamental biological understanding and knowledge of the effects of salt stress on plants is necessary to provide additional

information for the dissection of the plant response to salinity and try to find future applications for ameliorating the impact of salinity on plants, improving the performance of species important to human health and agricultural sustainability.

2. Soil salinity

The earliest written account of salt lands dates back to 2400 BC and was recorded in the Tigris-Euphrates alluvial plains of Iraq (Russel, Kadry, & Hanna, 1965). Salt-affected lands occur in practically all climatic regions, from the humid tropics to the polar regions. Saline soils can be found at different altitudes, from below sea level (e.g. around the Dead Sea) to mountains rising above 5000 meters, such as the Tibetan Plateau or the Rocky Mountains. Furthermore, the occurrence of saline soils is not limited to desert conditions (Singh & Chatrath, 2001). All soils contain salts, and all irrigation waters, whether from canals or underground pumping, including those considered of very good quality, contain some dissolved salts. In fact, salts are a common and necessary component of soil, and many salts (e.g. nitrates and potassium) are essential plant nutrients. Salts originate from mineral weathering, inorganic fertilizers, soil amendments (e.g. gypsum, composts and manures), and irrigation waters (Kotuby-Amacher, Koenig, & Kitchen, 2000). In particular, the process of soil salinization is dramatically exacerbated and accelerated by crop irrigation. The overall effect of irrigation in the context of salinity is that it “imports” large quantities of new salts to the soil that were not there before (R Munns, Goyal, & Passioura, 2004). Actually, about 2% of the lands farmed by dry-land agriculture, and more than 45 million hectares of irrigated land (at least 20% of total irrigated acreage) have been already damaged by salt (Lauchli, James, Huang, McCully, & Munns, 2008) (Fig. 1).

Mediterranean regions are currently experiencing increasing salt stress problems resulting from seawater intrusion into aquifers and irrigation with brackish water (Rana & Katerji, 2000). While an important cause of salinity in Australian continent is the deposition of oceanic salts carried in wind and rain (R Munns & Tester, 2008). An additional, important source of

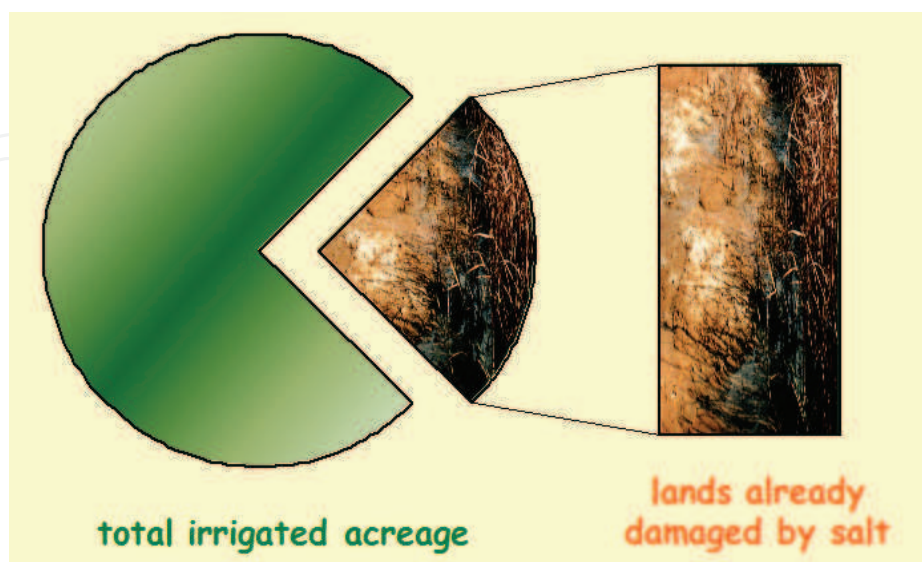


Fig. 1. Percentage of irrigated lands damaged by salinity

salts in many landscape soils comes from ice melters used on roads and sidewalks. The addition of virtually any soluble material will increase soil salinity (Singh & Chatrath, 2001).

Among the various sources of soil salinity, irrigation combined with poor drainage is the most serious, because it represents losses of once productive agricultural land (Zhu, 2007). The irrigation water contains calcium (Ca^{2+}), magnesium (Mg^{2+}), and sodium (Na^+). When the water evaporates, Ca^{2+} and Mg^{2+} often precipitate into carbonates, leaving Na^+ dominant in the soil (Serrano, Culianz-Macia, & Moreno, 1999). As a result Na^+ concentrations often exceed those of most macronutrients by one or two orders of magnitude, and by even more in the case of micronutrients. High concentrations of Na^+ in the soil solution may depress nutrient-ion activities and produce extreme ratios of $\text{Na}^+/\text{Ca}^{2+}$ or Na^+/K^+ (Grattana & Grieveb, 1999). Increases in cations and their salts, NaCl in particular, in the soil generates external osmotic potential that can prevent or reduce the influx of water into the root. The resulting water deficit is similar to drought conditions and additionally compounded by the presence of Na^+ ions (Bohnert, 2007).

Improper management of salinity may lead to soil sodicity, damaging soil structure. In particular, the action of Na^+ ions, when they occupy the cation exchange complex of clay particles, cause soil aggregates to break down, increase bulk density, make the soil more compact and decrease total porosity, thereby hampering soil aeration. As a result, plants in saline soils not only suffer from high Na^+ levels, but are also affected by some degree of hypoxia (Singh & Chatrath, 2001; Tisdale, Nelson, & Beaton, 1993).

According to the USDA salinity laboratory, saline soil can be defined as soil having an electrical conductivity of solution extracted from the water-saturated soil paste ECe (Electrical Conductivity of the extract) of 4 dS m^{-1} (decisiemens per meter), where $4 \text{ dS m}^{-1} \approx 40 \text{ mM NaCl}$ or more (Chinnusamy, Jagendorf, & Zhu, 2005; Kotuby-Amacher, Koenig, & Kitchen, 2000).

Soil type and environmental factors, such as vapour, pressure deficit, radiation and temperature may further alter salt tolerance (Chinnusamy, Jagendorf, & Zhu, 2005). In fields, in fact, the salt levels fluctuate seasonally and spatially, and variation will occur due to the circumstances influencing each particular plant (Estes, 2002). In addition, the continuous use of same soil for growing vegetables results in an increase of salinization.

3. Effects of salinity on plants

Soil salinity is a major factor that limits the yield of agricultural crops, jeopardizing the capacity of agriculture to sustain the burgeoning human population increase (T. J. Flowers, 2004; R Munns & Tester, 2008; Parida & Das, 2005).

At low salt concentrations, yields are mildly affected or not affected at all (Maggio, Hasegawa, Bressan, Consiglio, & Joly, 2001). As the concentrations increase, the yields move towards zero, since most plants, glycophytes, including most crop plants, will not grow in high concentrations of salt and are severely inhibited or even killed by 100-200 mM NaCl. The reason is that they have evolved under conditions of low soil salinity and do not display salt tolerance (R Munns & Termaat, 1986). On the contrary halophytes can survive salinity in excess of 300-400 mM. Halophytes are known to have a capability of growth on salinized soils of coastal and arid regions due to specific mechanisms of salt tolerance developed during their phylogenetic adaptation. Depending on their salt-tolerating capacity, these plants can be either obligate and characterized by low morphological and taxonomical diversity with relative growth rates increasing up to 50% sea water or facultative and found

in less saline habitats along the border between saline and non-saline upland and characterized by broader physiological diversity which enables them to cope with saline and non-saline conditions (Parida & Das, 2005). Measurements of ion contents in plants under salt stress revealed that halophytes accumulate salts whereas glycophytes tend to exclude the salts (Zhu, 2007).

High salinity affects plants in two main ways: high concentrations of salts in the soil disturb the capacity of roots to extract water, and high concentrations of salts within the plant itself can be toxic, resulting in an inhibition of many physiological and biochemical processes such as nutrient uptake and assimilation (Hasegawa, Bressan, Zhu, & Bohnert, 2000; R. Munns, 2002; R Munns, Schachtman, & Condon, 1995; R Munns & Tester, 2008). Together, these effects reduce plant growth, development and survival. A two-phase model describing the osmotic and ionic effects of salt stress was proposed by Munns (1995) (Fig. 2).

Plants sensitive or tolerant to salinity differ in the rate at which salt reaches toxic levels in leaves. Timescale is days or weeks or months, depending on the species and the salinity level. During Phase 1, growth of both type of plants is reduced because of the osmotic effect of the saline solution outside the roots. During Phase 2, old leaves in the sensitive plant die and reduce the photosynthetic capacity of the plant. This exerts an additional effect on growth.

In the first, osmotic phase, which starts immediately after the salt concentration around the roots increases to a threshold level making it harder for the roots to extract water, the rate of shoot growth falls significantly. An immediate response to this effect, which also mitigates ion flux to the shoot, is stomatal closure. However, because of the water potential difference between the atmosphere and leaf cells and the need for carbon fixation, this is an untenable long-term strategy of tolerance (Hasegawa et al., 2000). Shoot growth is more sensitive than root growth to salt-induced osmotic stress probably because a reduction in the leaf area development relative to root growth would decrease the water use by the plant, thus allowing it to conserve soil moisture and prevent salt concentration in the soil (R Munns & Tester, 2008). Reduction in shoot growth due to salinity is commonly expressed by a reduced leaf area and stunted shoots (A. Läuchli & Epstein, 1990). The growth inhibition of leaves sensitive to salt stress appears to be also a consequence of inhibition by salt of symplastic xylem loading of Ca^{2+} in the root (A. Läuchli & Grattan, 2007). Final leaf size depends on both cell division and cell elongation. Leaf initiation, which is governed by cell



Fig. 2. Scheme of the two-phase growth response to salinity. Adapted from Munns (1995).

division, was shown to be unaffected by salt stress in sugar beet, but leaf extension was found to be a salt-sensitive process (Papp, Ball, & Terry, 1983), depending on Ca^{2+} status. Moreover the salt-induced inhibition of the uptake of important mineral nutrients, such as K^+ and Ca^{2+} , further reduces root cell growth (Larcher, 1980) and, in particular, compromises root tips expansion (Fig. 3). Apical region of roots grown under salinity (Fig. 3 C, D) show extensive vacuolization and lack of typical organization of apical tissue. A slight plasmolysis due to a lack of continuity and adherence between cells is present with a tendency to the arrest of growth and differentiation. Otherwise, control plants root tips (Fig. 3 A, B) are characterized by densely packed tissues with only small intercellular spaces.

The second phase, ion specific, corresponds to the accumulation of ions, in particular Na^+ , in the leaf blade, where Na^+ accumulates after being deposited in the transpiration stream, rather than in the roots (R. Munns, 2002). Na^+ accumulation turns out to be toxic especially in old leaves, which are no longer expanding and so no longer diluting the salt arriving in them as young growing leaves do. If the rate at which they die is greater than the rate at which new leaves are produced, the photosynthetic capacity of the plant will no longer be able to supply the carbohydrate requirement of the young leaves, which further reduces their growth rate (R. Munns & Tester, 2008). In photosynthetic tissues, in fact, Na^+ accumulation affects photosynthetic components such as enzymes, chlorophylls, and carotenoids (Davenport, James, Zakrisson-Plogander, Tester, & Munns, 2005). The derived reduction in photosynthetic rate in the salt sensitive plants can increase also the production of reactive oxygen species (ROS). Normally, ROS are rapidly removed by antioxidative mechanisms, but this removal can be impaired by salt stress (Allan & Fluhr, 1997; Foyer & Noctor, 2003). ROS signalling has been shown to be an integral part of acclimation response to salinity. ROS play, in fact, a dual

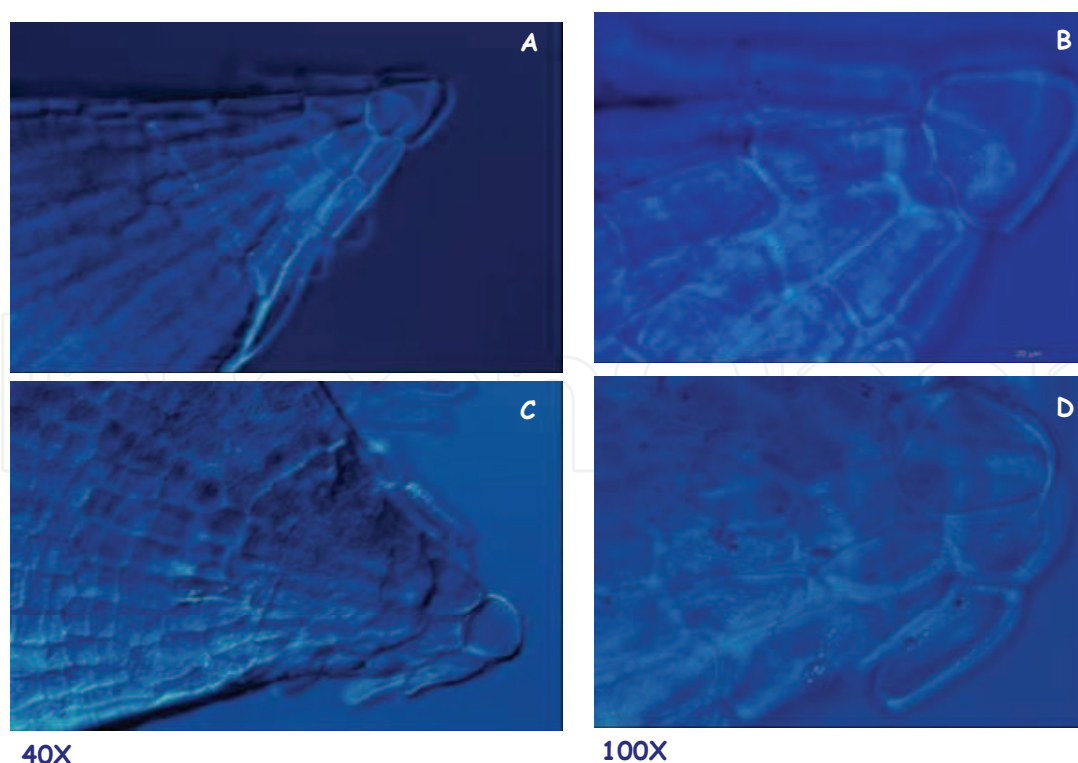


Fig. 3. Root tips of durum wheat grown in absence (A, B) or presence of 100 mM NaCl (C, D) observed by DIC microscopy (P. Carillo, D. Parisi, E. Maximova, unpublished data).

role in the response of plants to abiotic stresses functioning as toxic by-products of stress metabolism, as well as important signal transduction molecules integrated in the networks of stress response pathway mediated by calcium, hormone and protein phosphorylation (Miller, Suzuki, Ciftci-Yilmaz, & Mittler, 2010).

ABA plays an important role in the response of plants to salinity and ABA-deficient mutants perform poorly under salinity stress (Xiong, Gong, Rock, Subramanian, Guo, Xu, et al., 2001). Salt stress signalling through Ca^{2+} and ABA mediate the expression of the late embryogenesis-abundant (LEA)-type genes including the dehydration-responsive element (DRE)/C-repeat (CRT) class of stress-responsive genes. The activation of LEA-type genes may actually represent damage repair pathways (Xiong, Schumaker, & Zhu, 2002).

Salt and osmotic stress regulation of *Lea* gene expression is mediated by both ABA dependent and independent signalling pathways. Both the pathways use Ca^{2+} signalling to induce *Lea* gene expression during salinity. It has been shown that ABA-dependent and -independent transcription factors may also cross talk to each other in a synergistic way to amplify the response and improve stress tolerance (Shinozaki & Yamaguchi-Shinozaki, 2000).

4. Salt tolerance

The mechanisms of genetic control of salt tolerance in plants have not yet fully understood because of its complexity. There are in fact several genes controlling salinity tolerance in the different species whose effect interacts strongly with environmental conditions. Thus, genetic variation can only be demonstrated indirectly, by measuring the responses of different genotypes. Probably the most suitable response to measure is growth or yield, especially at moderate salinities (Allen, Chambers, & Stine, 1994). Salt tolerance, in fact, can be usually assessed as the percent biomass production in saline versus control conditions over a prolonged period of time (this usually correlates with yield) or in terms of survival, which is quite appropriate for perennial species (R. Munns, 2002).

Salt tolerance may vary considerably with genetic traits. A plant species' tolerance for salinity will be overridden by a sudden exposure to salinity, even if the species is a halophyte (Albert, 1975). Different adaptive mechanisms may be involved in gradual acclimation to salinity in contrast to adjustment to a sudden shock. The sensitivity to salinity of a given species may change during ontogeny. Salinity tolerances may increase or decrease depending on the plant species and/or environmental factors. For some species, salt sensitivity may be greatest at germination, whereas for other species, sensitivity may increase during reproduction (Howat, 2000; Marschner, 1986).

Plants have evolved several mechanisms to acclimatize to salinity. It is possible to distinguish three types of plant response or tolerance: a) the tolerance to osmotic stress, b) the Na^+ exclusion from leaf blades and c) tissue tolerance (R Munns & Tester, 2008).

4.1 Osmotic tolerance

The growth of salt-stressed plants is mostly limited by the osmotic effect of salinity, irrespective of their capacity to exclude salt, that results in reduced growth rates and stomatal conductance (Fricke *et al.* 2004; James *et al.* 2008). In fact, osmotic tolerance involves the plant's ability to tolerate the drought aspect of salinity stress and to maintain leaf expansion and stomatal conductance (Rajendran, Tester, & Roy, 2009). It was demonstrated in a study of genetic variation in tolerance to osmotic stress on 50 international durum

varieties and landraces that there is a positive relationship between stomatal conductance and relative growth rate in salt treated plants and that higher stomatal conductance is related to higher CO₂ assimilation rate (R.A. James, von Caemmerer, Condon, Zwart, & Munns, 2008). But if the accumulation of salts overcomes the toxic concentrations, the old leaves die (usually old expanded leaves) and the young leaves, no more supported by the export of photosynthates, undergo a reduction of growth and new leaves production. For this reason increased osmotic tolerance involves an increased ability to continue production and growth of new and greater leaves, and higher stomatal conductance. The resulting increased leaf area would benefit only plants that have sufficient soil water, such as in irrigated food production systems where a supply of water is ensured, but could be undesirable in water-limited systems (R Munns & Tester, 2008). At the end, while the mechanisms involved in osmotic tolerance related to stomatal conductance, water availability and therefore to photosynthetic capacity to sustain carbon skeletons production to meet the cell's energy demands for growth have not been completely unraveled, it has been demonstrated that the plant's response to the osmotic stress is independent of nutrient levels in the growth medium (Hu, Burucs, von Tucher, & Schmidhalter, 2007).

4.2 Na⁺ exclusion

In the majority of plant species grown under salinity, Na⁺ appears to reach a toxic concentration before Cl⁻ does, and so most studies have concentrated on Na⁺ exclusion and the control of Na⁺ transport within the plant (R Munns & Tester, 2008). Therefore, another essential mechanism of tolerance involves the ability to reduce the ionic stress on the plant by minimizing the amount of Na⁺ that accumulates in the cytosol of cells, particularly those in the transpiring leaves. This process, as well as tissue tolerance, involves up- and down-regulation of the expression of specific ion channels and transporters, allowing the control of Na⁺ transport throughout the plant (R Munns & Tester, 2008; Rajendran, Tester, & Roy, 2009). Na⁺ exclusion from leaves is associated with salt tolerance in cereal crops including rice, durum wheat, bread wheat and barley (Richard A. James, Blake, Byrt, & Munns, 2011). Exclusion of Na⁺ from the leaves is due to low net Na⁺ uptake by cells in the root cortex and the tight control of net loading of the xylem by parenchyma cells in the stele (Davenport, James, Zakrisson-Plogander, Tester, & Munns, 2005). Na⁺ exclusion by roots ensures that Na⁺ does not accumulate to toxic concentrations within leaf blades. A failure in Na⁺ exclusion manifests its toxic effect after days or weeks, depending on the species, and causes premature death of older leaves (R Munns & Tester, 2008).

An efficient cytosolic Na⁺ exclusion is also got through operation of vacuolar Na⁺/H⁺ antiports that move potentially harmful ions from cytosol into large, internally acidic, tonoplast-bound vacuoles. These ions, in turn, act as an osmoticum within the vacuole, which then maintain water flow into the cell, thus allowing plants to grow in soils containing high salinity. Antiports use the proton-motive force generated by vacuolar H⁺-translocating enzymes, H⁺-adenosine triphosphatase (ATPase) and H⁺-inorganic pyrophosphatase (PPiase), to couple downhill movement of H⁺ (down its electrochemical potential) with uphill movement of Na⁺ (against its electrochemical potential) ". AtNHX1 is the Na⁺/H⁺ antiporter, localized to the tonoplast, predicted to be involved in the control of vacuolar osmotic potential in Arabidopsis (Apse, Aharon, Snedden, & Blumwald, 1999).

Durum wheat is a salt-sensitive species and germination and seedling stages are the most critical phases for plant growth under salinity (Flagella, Trono, Pompa, Di Fonzo, & Pastore, 2006). Its sensitivity to salt stress is higher than bread wheat, due to a poor ability to exclude

Na⁺ from the leaf blades, and a lack of the K⁺/Na⁺ discrimination character displayed by bread wheat (Gorham, Hardy, Jones, Joppa, & Law, 1987; Lauchli, James, Huang, McCully, & Munns, 2008). However, a novel source of Na⁺ exclusion has been found in an unusual durum wheat genotype named Line 149. Genetic analysis has shown that line 149 contains two major genes for Na⁺ exclusion, named Nax1 and Nax2 (Rana Munns, Rebetzke, Husain, James, & Hare, 2003). The proteins encoded by the Nax1 and Nax2 genes are shown to increase retrieval of Na⁺ from the xylem in roots, thereby reducing shoot Na⁺ accumulation. In particular the Nax1 gene confers a reduced rate of transport of Na⁺ from root to shoot and retention of Na⁺ in the leaf sheath, thus giving a higher sheath-to-blade Na⁺ concentration ratio. The second gene, Nax2, also confers a lower rate of transport of Na⁺ from root to shoot and has a higher rate of K⁺ transport, resulting in enhanced K⁺ versus Na⁺ discrimination in the leaf (R. James, Davenport, & Munns, 2006). The mechanism of Na⁺ exclusion allows the plant to avoid or postpone the problem related to ion toxicity, but if Na⁺ exclusion is not compensated for by the uptake of K⁺, it determines a greater demand for organic solutes for osmotic adjustment. The synthesis of organic solutes jeopardizes the energy balance of the plant. Thus, the plant must cope ion toxicity on the one hand, and turgor loss on the other (R Munns & Tester, 2008).

The knowledge on how Na⁺ is sensed is still very limited in most cellular systems. Theoretically, Na⁺ can be sensed either before or after entering the cell, or both. Extracellular Na⁺ may be sensed by a membrane receptor, whereas intracellular Na⁺ may be sensed either by membrane proteins or by any of the many Na⁺-sensitive enzymes in the cytoplasm. In spite of the molecular identity of Na⁺ sensor(s) remaining elusive, the plasma-membrane Na⁺/H⁺ antiporter SALT OVERLY SENSITIVE1 (SOS1) is a possible candidate (Silva & Gerós, 2009). In fact, in Arabidopsis, ion homeostasis is mediated mainly by the SOS signal pathway (Yang et al. 2009). SOS proteins are sensor for calcium signal that turn on the machinery for Na⁺ export and K⁺/Na⁺ discrimination (Zhu, 2007). In particular, SOS1, encoding a plasma membrane Na⁺/H⁺ antiporter, plays a critical role in Na⁺ extrusion and in controlling long-distance Na⁺ transport from the root to shoot (Shi, Ishitani, Kim, & Zhu, 2000; Shi, Quintero, Pardo, & Zhu, 2002). This antiporter forms one component in a mechanism based on sensing of the salt stress that involves an increase of cytosolic [Ca²⁺], protein interactions and reversible phosphorylation with SOS1 acting in concert with other two proteins known as SOS2 and SOS3 (Oh, Lee, Bressan, Yun, & Bohnert, 2010) (Fig. 4).

Both the protein kinase SOS2 and its associated calcium-sensor subunit SOS3 are required for the posttranslational activation of SOS1 Na⁺/H⁺ exchange activity in Arabidopsis (Qiu, Guo, Dietrich, Schumaker, & Zhu, 2002; Quintero, Martinez-Atienza, Villalta, Jiang, Kim, Ali, et al., 2011), and in rice (Martínez-Atienza, Jiang, Garcíadeblas, Mendoza, Zhu, Pardo, et al., 2007). In yeast, co-expression of SOS1, SOS2, and SOS3 increases the salt tolerance of transformed yeast cells much more than expression of one or two SOS proteins (Quintero, Ohta, Shi, Zhu, & Pardo, 2002), suggesting that the full activity of SOS1 depends on the SOS2/SOS3 complex. Recently, SOS4 and SOS5 have also been characterized. SOS4 encodes a pyridoxal (PL) kinase that is involved in the biosynthesis of pyridoxal-5-phosphate (PLP), an active form of vitamin B6. SOS5 has been shown to be a putative cell surface adhesion protein that is required for normal cell expansion. Under salt stress, the normal growth and expansion of a plant cell becomes even more important and SOS5 helps in the maintenance of cell wall integrity and architecture (Mahajan, Pandey, & Tuteja, 2008).

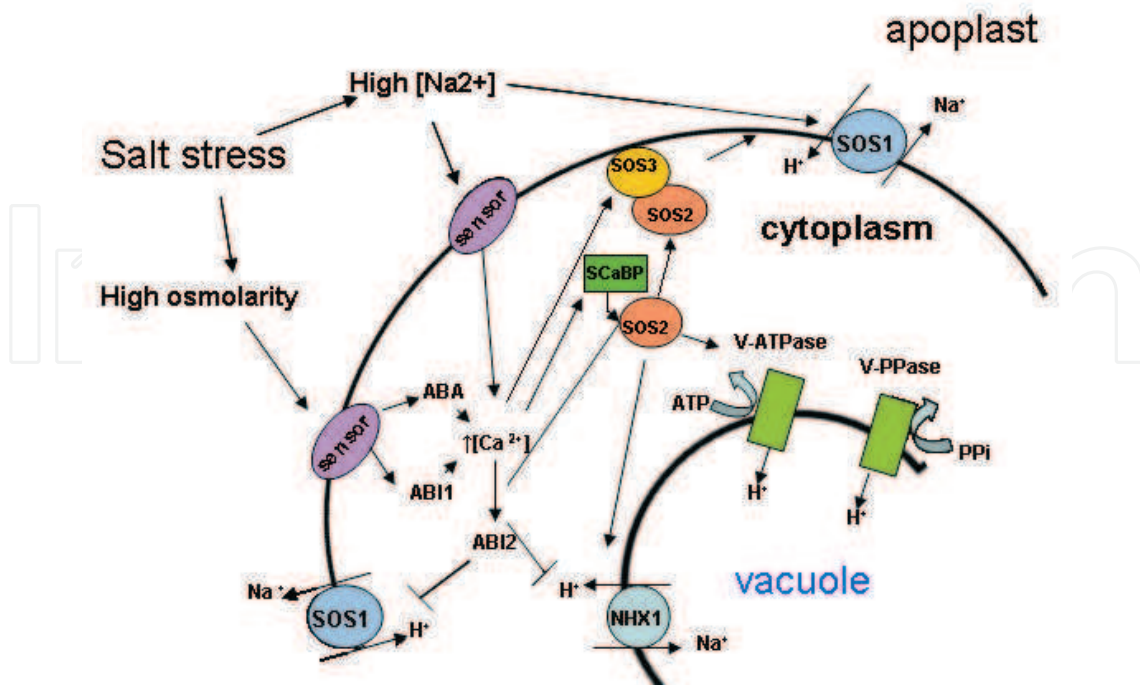


Fig. 4. Signalling pathways responsible for Na^+ extrusion in *Arabidopsis* under salt stress. Excess Na^+ and high osmolarity are separately sensed by unknown sensors at the plasma membrane level, which then induce an increase in cytosolic $[\text{Ca}^{2+}]$. This increase is sensed by SOS3 which activates SOS2. The activated SOS3-SOS2 protein complex phosphorylates SOS1, the plasma membrane Na^+/H^+ antiporter, resulting in the efflux of Na^+ ions. SOS2 can regulate NHX1 antiporter activity and V- H^+ -ATPase activity independently of SOS3, possibly by SOS3-like Ca^{2+} -binding proteins (SCaBP) that target it to the tonoplast. Salt stress can also induce the accumulation of ABA, which, by means of ABI1 and ABI2, can negatively regulate SOS2 or SOS1 and NHX1. Adapted from Silva & Gerós (2009).

4.3 Tissue tolerance

The third mechanism, tissue tolerance entails an increase of survival of old leaves. It requires compartmentalization of Na^+ and Cl^- at the cellular and intracellular level to avoid toxic concentrations within the cytoplasm, especially in mesophyll cells in the leaf (R Munns & Tester, 2008) and synthesis and accumulation of compatible solutes within the cytoplasm. Compatible solutes play a role in plant osmotolerance by various ways, protecting enzymes from denaturation, stabilising membrane or macromolecules or playing adaptive roles in mediating osmotic adjustment (Ashraf & Foolad, 2007). The function of the compatible solutes is not limited to osmotic balance. Compatible solutes are typically hydrophilic, and may be able to replace water at the surface of proteins or membranes, thus acting as low molecular weight chaperones (Hasegawa, Bressan, Zhu, & Bohnert, 2000). These solutes also function to protect cellular structures through scavenging ROS (Hasegawa et al., 2000; Zhu, 2001). Compatible solutes are small molecules, water soluble and uniformly neutral with respect to the perturbation of cellular functions, even when present at high concentrations (Sakamoto & Murata, 2002; Yancey, Clark, Hand, Bowlus, & Somero, 1982). They comprise nitrogen containing compounds such as amino acids, amines and betaines, but also organic acids, sugars and polyols (Mansour, 2000) (Fig. 5).

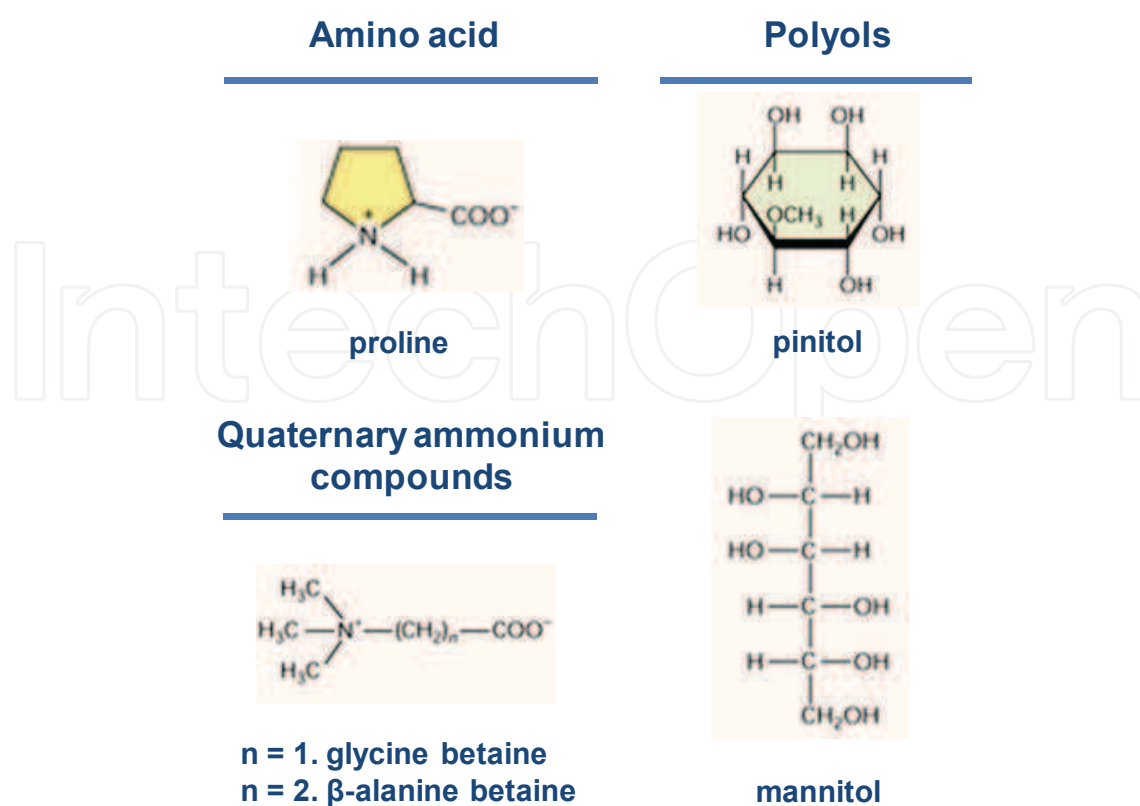


Fig. 5. Chemical structures of some important compatible compounds.

Among the best known compatible solutes, proline and glycine betaine (GB) have been reported to increase greatly under salt and drought stresses (R. Munns, 2002; Sakamoto & Murata, 2002) and constitute the major metabolites found in durum wheat under salt stress, as in other Poaceae (Ashraf & Foolad, 2007; Carillo, Mastrolonardo, Nacca, & Fuggi, 2005; Sairam & Tyagi, 2004). In many halophytes, proline and/or glycine betaine concentrations in leaves contribute to the osmotic pressure in the cell as a whole (T. J. Flowers, Troke, & Yeo, 1977). In glycophytes, their concentrations are much lower but if partitioned exclusively to the cytoplasm, they could generate a significant osmotic pressure and then balance the vacuolar osmotic potential. In durum wheat seedlings, proline can contribute for more than 39% of the osmotic adjustment in the cytoplasmic compartments of old leaves, while the contribution of GB can account for up to 16% of the osmotic balance in younger tissues, independently of nitrogen nutrition, unlike proline (Carillo et al. 2008).

Proline (Fig. 5) is a proteinogenic amino acid with an exceptional conformational rigidity, essential for primary metabolism, which normally accumulates in large quantities in response to drought or salinity stress (Ashraf & Foolad, 2007; Carillo, Mastrolonardo, Nacca, Parisi, Verlotta, & Fuggi, 2008; Hasegawa, Bressan, Zhu, & Bohnert, 2000; Szabados & Savouré, 2010). Its accumulation normally occurs in the cytosol where it contributes substantially to the cytoplasmic osmotic adjustment (Ketchum, Warren, Klima, Lopezgutierrez, & Nabors, 1991).

Proline accumulation is due primarily to de novo synthesis associated with decreased oxidation and utilization, but increased transport processes are also likely involved (Aubert, Hennion, Bouchereau, Gout, Bligny, & Dorne, 1999; Flagella, Trono, Pompa, Di Fonzo, & Pastore, 2006; Kishor, Hong, Miao, Hu, & Verma, 1995). Proline accumulation occurs rapidly after the onset of stress and this supports the hypothesis that this accumulation is initially a

reaction to salt stress and not a plant response associated with tolerance (Carillo, Mastrolonardo, Nacca, Parisi, Verlotta, & Fuggi, 2008; de Lacerda, Cambraia, Oliva, Ruiz, & Prisco, 2003). In addition to its role as an osmolyte for osmotic adjustment, proline contributes to stabilizing sub-cellular structures (e.g. membranes and proteins), scavenging free radicals, and buffering cellular redox potential under stress conditions. It may also function as a protein compatible hydrotrope (Srinivas & Balasubramanian, 1995), alleviating cytoplasmic acidosis, and maintaining appropriate NADP⁺/NADPH ratios compatible with metabolism (Hare & Cress, 1997). Also, rapid breakdown of proline upon relief of stress may provide sufficient reducing agents that support mitochondrial oxidative phosphorylation and generation of ATP for recovery from stress and repairing of stress-induced damages (Carillo, Mastrolonardo, Nacca, Parisi, Verlotta, & Fuggi, 2008; Hare & Cress, 1997). Furthermore, proline is known to induce expression of salt stress responsive genes, which possess proline responsive elements (e.g. PRE, ACTCAT) in their promoters (Ashraf & Foolad, 2007; Chinnusamy, Jagendorf, & Zhu, 2005).

GB (Fig. 5) is an amphoteric compound that is electrically neutral over a wide range of physiological pH values and is extremely soluble in water despite a non-polar hydrocarbon moiety that consists of three methyl groups. The molecular features of GB allow it to not only act as an osmoregulator but also to interact with both hydrophilic and hydrophobic domains of macromolecules, such as protein complexes (Sakamoto and Murata 2002; Chen and Murata 2008) and enzymes, stabilising their structures and activities, and maintaining the integrity of membranes against the damaging effects of excessive salt, cold, heat and freezing (Rhodes and Hanson 1993; Gorham 1995; Sulpice *et al.* 1998; Sakamoto and Murata 2002). It has also been suggested that GB plays a role as a scavenger of ROS generated during these various stresses (Papageorgiou and Murata 1995; Ashraf and Foolad 2007). A comparison of near-isogenic maize lines with contrasting GB accumulation showed that lines that were homozygous for the *Bet1* (GB accumulation) gene had a 10–20% higher biomass under saline conditions (Saneoka *et al.* 1995; Munns and Tester 2008). However, while proline is probably the most widely distributed osmolyte accumulated in plants (Delauney and Verma 1993; Szabados and Savoure 2010), the occurrence of GB seems to be restricted to several halophytes and a few crop plants (Weretilnyk *et al.* 1989). Metabolic engineering of GB biosynthesis by the insertion of foreign genes from plants or microbes in plants not naturally accumulating it improved their tolerance to salt, drought and extreme temperature stresses, despite the very low amounts of GB accumulated by these plants (Sakamoto and Murata 2002; Sulpice *et al.* 2003; Quan *et al.* 2004; Chen and Murata 2008; Ashraf and Akram 2009).

4.4 Engineering salt tolerance in plants

Several efforts have been undertaken to enhance the salt tolerance of economically important plants by traditional plant breeding as well as by biotechnological approaches. Traditional breeding programs trying to improve abiotic stress tolerance have had some success, but are progressing relatively slow being limited by the polygenic inheritance (Silva & Gerós, 2009). In fact, the susceptibility or tolerance to salinity in plants is a coordinated action of multiple stress responsive genes, which also cross talk with other components of stress signal transduction pathways. Therefore, the inconsistent results obtained employing traditional approaches may be ascribed to the difficulty to identify genomic regions controlling resistance in “Perennial” quantitative trait locus (QTL) end to the long time (also twenty years) required for their introgression by breeding.

Molecular marker technology has developed rapidly over the last decade, with the development of high-throughput genotyping methods that have made it possible to analyze the QTL's responsible for tolerance. The identification of these regions is fundamental for helping the selection efficiency in breeding programs and mapping the major genes controlling salt tolerance in order to operate genetic manipulations using the real candidate genes rather than non-specific abiotic responsive genes. Many studies have focused on mapping QTLs for salt tolerance-related traits in rice because of its requirement for irrigation for maximum yield, its sensitivity to salinity and its relatively small genome (T.J. Flowers, Koyama, Flowers, Sudhakar, Singh, & Yeo, 2000). Better results have been obtained at the seedling stage, while the expression and relationship of QTLs detected in different developmental stages are more difficult to study and fully understand at tillering and reproductive stages (Alam, Sazzadur Rahman, Seraj, Thomson, Ismail, Tumimbang-Raiz, et al., 2011; Prasad, Bagali, Hittalmani, & Shaahidhar, 2000). Recently, QTLs related to antioxidant content and the response of tomato antioxidants to salt-stress have also been identified. Although these QTLs may be useful for the development of higher antioxidant tomato cultivars, whether or not a direct correlation between antioxidant levels and salinity tolerance exists is more difficult to prove (Frary, Gol, Keles, Okmen, Pinar, Sigva, et al., 2010). Contrary to the notion that multiple traits introduced by breeding into crop plants are needed to implement salt-tolerant plants, one of the main strategies for improving plant salt tolerance has been through the overexpression of single genes that are either induced by stress and/or have been shown to be required for normal levels of tolerance. Transgenic plants overexpressing the genes participating in the synthesis or accumulation of osmoprotectants that function for osmotic adjustment, such as proline (Kishor, Hong, Miao, Hu, & Verma, 1995), glycinebetaine (Holmström, Somersalo, Mandal, Palva, & Welin, 2000) or other osmolytes show increased salt tolerance. Other genes that encode enzymes that are involved in oxidative protection, such as glutathione S-transferase, peroxidase, superoxide dismutase, ascorbate peroxidases, and glutathione reductases, can also be modified to improve plant salt tolerance (Yang, Chen, Zhou, Yin, Li, Xin, et al., 2009). Overexpression of regulatory genes in signalling pathways, such as transcription factors (DREB/CBF) and protein kinases (MAPK, CDPK) also increases plant salt tolerance (Chen, Ren, Zhong, Jiang, & Li, 2010). The overexpression of the vacuolar Na^+/H^+ antiporter has shown to improve salinity tolerance in several plants (Silva & Gerós, 2009). The first evidence showed that the overexpression of AtNHX1 in Arabidopsis plants promoted sustained growth and development in soil watered with up to 200 mM NaCl (Apse, Aharon, Snedden, & Blumwald, 1999), although recent evidences report that transgenic Arabidopsis do not show a significantly improved salt tolerance as compared to that of control plants (Yang, et al., 2009). In addition, transgenic tomato plants overexpressing AtNHX1 were able to grow, flower and produce fruit in the presence of 200 mM NaCl (H.-X. Zhang, Hodson, Williams, & Blumwald, 2001; H. Zhang & Blumwald, 2001). Also, transgenic tobacco plants overexpressing GhNHX1 from cotton and transgenic rice overexpressing the Na^+/H^+ antiporter gene clone from OsNHX1 exhibited higher salt tolerance (Fukuda, Nakamura, Tagiri, Tanaka, Miyao, Hirochika, et al., 2004; Wu, Yang, Meng, & Zheng, 2004). Overexpression of AtNHX1 in *Petunia hybrida* enhanced salt and drought tolerance in this plant, which accumulated more Na^+ , K^+ , and proline in their leaf tissue than that of the WT *Petunia* plants, maintaining high water contents and high ratio of K^+/Na^+ (Xu, Hong, Luo, & Xia, 2009). By introgressing Nax genes from *Triticum monococcum* into hexaploid bread wheat (*Triticum aestivum*), the leaf blade Na^+ concentration was reduced by 60% and the

proportion of Na⁺ stored in leaf sheaths was increased. The results indicate that Nax genes have the potential to improve the salt tolerance of bread wheat (Richard A. James, Blake, Byrt, & Munns, 2011). The increased expression in tomato and rice of Arabidopsis Arginine Vasopressin 1 (AVP1), encoding a vacuolar pyrophosphatase acting as a proton pump on the vacuolar membrane, enhanced sequestering of ions and sugars into the vacuole, reducing water potential and resulting in increased salt tolerance when compared to wild-type plants (Pasapula, Shen, Kuppu, Paez-Valencia, Mendoza, Hou, et al., 2011). Furthermore, overexpression of genes encoding Late Embryogenesis Abundant (LEA) proteins, which accumulate to high levels during seed development, such as the barley HVA1 (Xu et al., 1996) and wheat dehydrin DHN-5 (Brini et al., 2007), can enhance plant salt tolerance, although their function is obscure.

5. Conclusions

Salinity is a significant problem affecting agriculture worldwide and is predicted to become a larger problem in the coming decades (<http://www.fao.org/ag/agl/agll/spush/>). The detrimental effects of high salinity on plants can be observed at the whole-plant level in terms of plant death and/or decrease in productivity (Parida & Das, 2005). Some plant species are clearly more flexible than others in their requirements for survival in salty environments. An understanding of how single cell responses to salt are coordinated with organismal and whole-plant responses to maintain an optimal balance between salt uptake and compartmentation is fundamental to our knowledge of how plants successfully adapt to salt stress. (Volkmar, Hu, & Steppuhn, 1998). Use of both genetic manipulation and traditional breeding approaches will be required to unravel the mechanisms involved in salinity tolerance and to develop salt-tolerant cultivars better able to cope with the increasing soil salinity constraints (Rajendran, Tester, & Roy, 2009). It is important to underline that transgenic technology is certainly useful for aiding the search for the cellular mechanisms that increase tolerance, but the complexity of the traits is likely to mean that the road to engineering such tolerance into sensitive species will be long (T. J. Flowers, 2004). Anyway, there are a number of reasons for optimism. These include recent developments in the area of plant molecular biology, among which in particular the complete sequencing of model plant genomes, the production of T-DNA insertional lines of Arabidopsis for gene tagging and the availability of microarray analysis tools which offer advantages and solutions to the complex intriguing questions of salt resistance and tolerance (Hussain, Chandrasekhar, Hazara, & Sultan, 2008).

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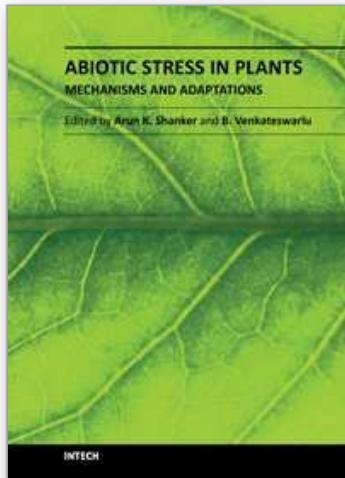
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World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly divided into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

How to reference

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