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Salt Stress in Vascular Plants and Its Interaction with Boron Toxicity

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1. Introduction

Among abiotic stresses, high salinity is the most severe environmental stress, impairing crop production on at least 20% of irrigated land worldwide. In addition, the increased salinity of arable land is expected to have devastating global effects, resulting in up to 50% land loss by the middle of the 21st century. Furthermore, there is a deterioration of about 2 million ha (1% of world agricultural lands) because of salinity each year (Mahajan & Tuteja, 2005).
Critically, the problem of salinization is increasing due to the accumulation of tons of salts into the soil as a consequence of bad agricultural practices (e.g., use of fertilizers on a massive scale), draining of aquifers, and a limited regional rainfall. Irrigated land is particularly at risk with approximately one-third being significantly affected by salinity. Despite its relatively small area, irrigated land is estimated to produce one-third of world's food (Munns, 2002), so salinization of this resource is particularly critical.
Water scarcity in arid and semi-arid regions has forced the increased use of recycled waste-water and desalination of salty groundwater resources for agriculture use. Current technologies to desalinate or purify recycled waste-water for agricultural use can effectively reduce the concentrations of most toxic elements with the significant exception of boron (B). Boron in recycled water is often concentrated substantially as a result of the recycling process and as such can significantly impact agricultural soils. Therefore irrigation with saline groundwater containing high B concentration occurs in parts of the world where there is a notable scarcity of water.
The relations between salinity and mineral nutrition of horticultural crops are extremely complex and a complete understanding of the intricate interactions involved would require the input from multidisciplinary team of scientists. Thus, although information about their independent effects is abundant, information about the combined effects of salinity and B is very limited.

2. Resistance to salinity - range of tolerance

Plants, due to their sessile nature, have developed several mechanisms to tolerate the various stresses to which that may be encountered during their life cycles. Most plants are

very sensitive to soil salinity and are known as *glycophytes,* whereas salt-tolerant plants are known as *halophytes.* In general, *glycophytes* cannot grow at 100 mM NaCl, whereas *halophytes* can grow at salinities over 250 mM NaCl.

These adaptations include the synthesis of compatible osmolytes, proper maintenance of ionic balance, the synthesis of detoxifying enzymes of reactive oxygen species (ROS), and other responses. Playing an important role in the proper induction of these responses are: at first, the Ca^{2+} signaling; then, the signaling mediated by abscisic acid (ABA) and, finally, the MAP (Mitogen-Activated Protein) kinases signaling cascade (Tuteja, 2007).

3. Problems caused by salinity

Salinity alters the smooth operation of the plant due to factors ranging from the cellular level to physiological level (Hasegawa et al., 2000; Mahajan & Tuteja, 2005; Munns, 2002), which are outlined as follows:

- Salinity affects the physiology and metabolism of the plant, as it causes both hyperosmotic and hyperionic stresses.
- Due to the high salt concentration, soil water potential (Ψ) becomes more negative, which hinders water uptake by the plant. These salt levels also affect the absorption of nutrients such as K^+, Ca^{2+}, or NO_3^- owing to competition of these ions with Na^+ and Cl^-.
- A physiological damage is observed in leaf transpiration and also a growth inhibition, which increases the toxic effects of the salt within the plant. These alterations might respond, according to recent findings in *Arabidopsis*, to a failure in cortical microtubule organization and helical growth of this plant. A salt buildup also occurs in the old leaves, and the death of them could be a key strategy for plant survival. It has also been observed a decline in photosynthetic activity.
- At cellular level, the presence of Na^+ alters the K^+/Na^+ cytosolic ratio, even though the Na^+ remained extracellular. The alteration in the levels of K^+, due to its importance for plant growth, causes a disruption of osmotic balance, the malfunctioning of the stomata and the inhibition of some enzyme activities.
- Also at cellular level, the entry of Na^+ alters the cell membrane potential, thereby allowing the entry of Cl^- ions. Thus, the Na^+ in concentrations around 100 mM is toxic to cell metabolism and may inhibit some essential enzymes, expansion and cell division, and membrane organization. Associated with this stress, many ROS are produced, with the oxidative damage that this entails (Grattan & Grieve, 1999).

There is therefore a link between the immediate cellular alterations to salt stress and physiological changes taking place in the plant, and which focalize the problems in ionic imbalance and an insurmountable decrease in water potential values for the plant.

4. The response to stress and cross-tolerance

When stress affects any plant a series of responses are triggered at both cellular and systemic level (Tuteja, 2007; Zhu, 2002). According to these authors, synthetically the stress response goes as follows:

- Different receptors (ion channels, receptors serine/threonine kinase or histidine kinase, or G-protein-coupled receptors) located in the plasma membrane perceived stress at that localization.

- These receptors trigger different signal transduction cascades, among which are found as secondary signals Ca^{2+}, inositol phosphate (IP), ABA and ROS.
- These signaling cascades are at the core of the induction of the expression of certain genes that are directly or indirectly involved in protection against this stress. According to the response time we distinguish between early and late response genes. The first, induced in minutes, are transcription factors that determine the expression of late genes, which themselves are involved in stress tolerance and detoxifying enzymes. They comprise ion channels, enzymes, metabolites synthesizing protective chaperone, among others.
- Some of the induced genes are involved in the synthesis of diffusible signals (e.g., ABA, ethylene, salicylic acid) acting in a second wave of signaling, which now affects to the whole organism and determines a global adaptation.

When we analyze the response of plants to stresses of different nature, there is a redundancy in the mechanisms deployed. Thus, plants show cross-tolerance, which means that a plant resistant to a particular condition can develop tolerance to other forms of stress. Although the mechanisms by which develops cross-tolerance occurs remain unknown, it is suspected that cross-tolerance between salinity, drought and cold stress are due to the common consequences (osmotic and oxidative stresses) (Mahajan & Tuteja, 2005; Tester & Davenport, 2003).

5. The case of salt stress

Salt stress is a complex problem, in which experiments show induction of 194 genes in *Arabidopsis*. It requires a perfect orchestration between genetic, epigenetic modifications, pre- and post-transcriptional regulation and also post-translational control. Below we expose the main signaling pathways and safeguard mechanisms induced by salinity (Tuteja, 2007).

5.1 Signaling of salt stress

Signaling is an area of greatest potential for plant research, either in relation to how to detect nutrients, abiotic factors or other organisms (symbionts, harmless or pathogenic). It also is of major interest to optimize the production in agricultural systems. In the case of salt stress we know that the Ca^{2+}-mediated signaling plays a crucial role, followed by ABA-mediated signaling, and with the participation of other routes, such as the MAP kinases (Mahajan & Tuteja, 2005).

5.1.1 Ca^{2+} signaling

Calcium levels in the cytoplasm are maintained below 1 μM by a delicate balance held by carriers that are present in the endoplasmic reticulum (ER), chloroplast and in the vacuole. This homeostasis is a prerequisite for the action of this cation as a second messenger.

In the presence of high salt concentration, at first place there is an increase in cytosolic Ca^{2+} level coming from the apoplast. Then, the entry of Ca^{2+} derived from cellular organelles takes place, which is determined by the action of inositol triphosphate (IP3) formed by the enzyme phospholipase C. This will generate several waves of Ca^{2+} to form a signaling pathway (so called "Ca signature"), which is decoded by several calcium-binding proteins. In *Arabidopsis*, three genes involved in this decoding activity have been described, known as

SOS1, *SOS2* and *SOS3* (Salt Sensitive Overlay), although only *SOS3* encodes a calcineurin B-like protein (CBL), that is, a calcium sensor. The pathway follows with the interaction of SOS3 with SOS2, a serine/threonine kinase that catalyzes the phosphorylation of SOS1 (an antiporter Na^+/H^+) and this determines its activation state. This antiporter is involved in maintaining ionic balance, as we will detail later. In addition of SOS1, other channels and transporters as HKT, NHX and CAX1 are regulated by the SOS2-SOS3 pathway. This pathway is the most important in salinity tolerance, as it seeks to restore the ion balance (Mahajan et al., 2008; Zhu, 2002).

Calcium levels also induce genes responsible for enzymes of ABA synthesis pathway, such as zeaxanthin oxidase, 9-*cis*-epoxycaotenoid dioxygenase, ABA-aldehyde oxidase and molybdenum cofactor sulfurase (Tuteja, 2007). The induction of these genes leads to increased levels of ABA, which acts as a second messenger, as explained later.

Maintenance and restoration of calcium homeostasis is determined by the channel CAX1, an H^+/Ca^{2+} antiporter present in the membrane of the vacuole. The main role of this network is the restoration of basal levels of Ca^{2+} in the cytoplasm, but is also important in order to maintain the osmotic balance during stress.

5.1.2 ABA signaling

The genes responsible for ABA synthesis are induced by salt stress. Once accumulated, this hormone mediates the induction of genes involved in both its own synthesis and its degradation. But when it comes from salt stress responses, genes such as *RD29A* or *RD22* (Responsive to Dehydration), *COR15A* or *COR47* (COld Responsive), the pea DNA helicase 45 (*PDH45*), or pyrroline-5 carboxylate synthetase (*P5CS*, involved in the synthesis of proline), among others, are regulated by ABA (Tuteja, 2007). However, there are activation pathways of those genes independently of ABA.

At the molecular level, there have been described several transcription factors regulated by ABA as well the *cis*-regulatory elements that they recognize. Genes involved in tolerance to salinity are under the control of these promoters and their transcription factors. There are several examples, such as the AREB transcription factor (a leucine zipper transcription factor) that recognizes the ABRE region; or as the DREB2A and DREB2B transcription factors that recognize the region known as DRE/CRT. Other regulatory elements are MYCRS and MYBRS regions recognized by RD22 and MYC/MYB factors that help in the activation of the response, and could be the bridge between different stresses, and an explanation for cross-tolerance (Mahajan & Tuteja, 2005).

5.1.3 Signalling by MAP kinases

The pathway of MAP kinases is well known as a signal transduction system, both intracellular and extracellular. Increases have been detected in the expression of different MAPK, MAPKK and MAPKKK in *Arabidopsis*, alfalfa, tobacco and others, suggesting that this signaling pathway is working on an appropriate response to salt stress (Zhang et al., 2006).

6. Response to salt stress

As already stated, the major damages of salinity resulting from the alterations of Na^+ occur at the ion balance and osmotic levels, which then lead to problems of toxicity and enzyme

inhibition, among others. The main mechanisms involved in resistance to high salt concentrations, namely, restoration of ionic balance, synthesis of compatible osmolytes (also called osmoprotectants, i.e., compatible solutes) such as proline or glycine betaine, expression of detoxifying enzymes of ROS, and helicases are shown in Figure 1.

6.1 Ionic balance

Excess of Na^+ ions produce an imbalance in the ionic equilibrium, which is maintained through the joint action of pumps, together with other ions, and mediated largely by Ca^{2+} signaling. Thus, during salt stress, the expression of numerous channels is modified by the calcium-dependent partner SOS2-SOS3, as already discussed.

There are channels of many different types of channels, which perform different functions for the maintenance of ionic and osmotic homeostasis. On one hand, we have those with greater selectivity for the ion K^+ than for Na^+, such as the KIRC channel (K^+ Inward-Rectifying Channel) that mediates the entry of K^+ after hyperpolarization of the membrane and accumulates this ion over ion Na^+; another example of this type of channel is the HKT channel (Histidine Kinase Transporter), a low affinity transporter for Na^+, which prevents the entry of Na^+ into the cytosol. On the other hand, the entry of Na^+ in plant cells is determined by the NSCC channel (NonSpecific Cation Channel). Another type of channel is provided by the KORC channel (K^+ Outward-Rectifying Channel), which is activated after depolarization of the membrane, mediates the efflux of K^+ and Na^+ entry, which thus is accumulated in the cytosol. To place this movement requires a number of carriers that generate the H^+ gradient needed for channel maintenance. In that sense, transporters as NHX (Na^+/H^+ exchanger) that allows the accumulation of Na^+ in vacuoles are necessary, alleviating the effects of stress; or as channel CAX1 (H^+/Ca^{2+} antiporter) responsible for the maintenance of Ca^{2+} homeostasis (Tuteja, 2007).

6.2 Proline and glycine betaine

Both are osmoprotectants synthesized by many plants in response to various stresses, including salt, and whose main function is to relieve the effects of this stress (Chen & Murata, 2008; Delauney & Verma, 1993). They are not the only ones; there are other osmolytes as polyols and alcohol sugars, whose functions are centered in the maintenance of the osmotic balance, the cell pressure and the protein folding.

Glycine betaine (GB) is synthesized naturally from the choline by the action of the choline monooxygenase and betaine aldehyde dehydrogenase enzymes. In plants where GB is not produced, the overexpression of GB synthesizing genes in transgenic plants resulted in the production of enough amount of GB. With the inclusion of these genes in various plants and other organisms, it has been shown greater tolerance to salinity. Likewise, direct foliar application of the compound also improves the plant response to a saline environment (Tuteja, 2007).

The synthesis of proline is a frequent response in salt stress. This osmolyte is accumulated in the cytosol and allows proper osmotic adjustment. Furthermore, this amino acid also stabilizes subcellular structures, buffers the redox potential and blocks free radicals. It is synthesized from glutamic acid by the action of enzymes pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR). Again, the inclusion of these genes in various plants has improved the tolerance of these transgenic plants to high salt concentrations. The induction of P5CS gene seems be mediated by ABA, as its mRNA

accumulates quickly in response to the treatment with this plant hormone (Chinnusamy et al., 2005; Vinocur & Altman, 2005).

6.3 ROS detoxifying enzymes

Salt stress, like many other stresses, involves the development of ROS such as singlet oxygen (O_2^1), the superoxide radical ($O_2^{-\bullet}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($HO^\bullet$). These species are capable of producing lipid peroxidation, as well as DNA, RNA, and protein oxidative damages that compromise cell and plant viability. For detoxification of these ROS, plants have a battery of enzymes such as superoxide dismutase, ascorbate peroxidase, catalase, and GSH reductase, all induced under salt stress. Furthermore, enzymes such as aldehyde dehydrogenase are also induced, allowing more tolerance to salt stress by eliminating aldehydes produced in reactions between ROS and lipids or proteins (Vinocur & Altman, 2005).

6.4 Helicases

Various stresses, including salinity, induce the expression of genes involved in gene expression machinery, such as several helicases with DEAD box. The answer is given in the presence of Na^+ ions and mediated by ABA. Furthermore, phosphorylation sites in these proteins have been described, which may be a contact point for Ca^{2+} signaling. These helicases have the function of the opening of duplex DNA or RNA, and in this second case we speak of an RNA chaperone function, to avoid unfavorable folds (Owttrim, 2006).
Although the actual mechanism by which helicases increase tolerance to salinity remains unknown, there are two prevailing hypotheses:

- They would stabilize the mRNA transcriptional or translational level. In response to various stresses, secondary structures in the 5' end of mRNA can be performed, and this which could be preventing the proper processing of the RNA.
- They would alter gene expression in association with protein complexes of DNA processing.

6.5 LEA proteins

LEA proteins were first discovered in seed embryogenesis and germination, because they are accumulated in the first phase, and constitute over the 4% of cytoplasmic proteins in some seeds. They constitute a diverse family, but their sequences are enriched in polar amino acid, charged or uncharged, as glicines, glutamic acid or lysines. This hydrophilic character can explain their diverse functions, which include water retention as the protein D-19 from cotton; stabilization of other proteins by hydrophilic and hydrophobic interactions as RAB proteins; formation of a solvation surface around proteins, similar to the sugar solvation surface induced by salinity too; and ion sequestering as HVA1 protein in barley. ABA is inducing LEA protein synthesis in embryogenesis, as has been revealed in some mutants in the ABA signaling, and the same procedure will be controlling the expression of these proteins under salinity (Chourey et al., 2003).

6.6 Other responses

As other stresses, salt stress induces more responses that mentioned above. A brief comment about chaperones and sugar metabolism follows.

Chaperones are involved in the folding of protein, under both normal and abnormal situations. Although it is depending of the kind of chaperones, the ability to isolate the nascent protein or unfolded protein from the high saline cytoplasm can help to achieve the folded state of essential proteins (Choi et al., 2004).

Sugar metabolism is the source of carbon backbones for the whole cell metabolism. Under salt stress a series of cell changes occurs, which include synthesis of osmoprotectants and induction of gene transcription and protein synthesis involved in stress tolerance. Interestingly, genes encoding gliceraldehyde-3-phosphate dehydrogenase, sucrose-phosphate synthase and sucrose synthase are upregulated in response to drought (Ingram & Bartells, 1996), and increased levels of these enzymes are also associated with other environmental stresses in plants. Therefore, given the cross-tolerance between drought and salt stress (Munns, 2002), a similar gene response is very likely that also occurs against salt stress, which would reflect increased energy and carbon backbone requirements.

Finally, careful genetic and biochemical analyses have demonstrated that maturation of *N*-glycans is necessary for plants stress tolerance, and that *N*-glycans are essential not only for protein folding but also for in vivo functions of plant glycoproteins (Kang et al., 2008).

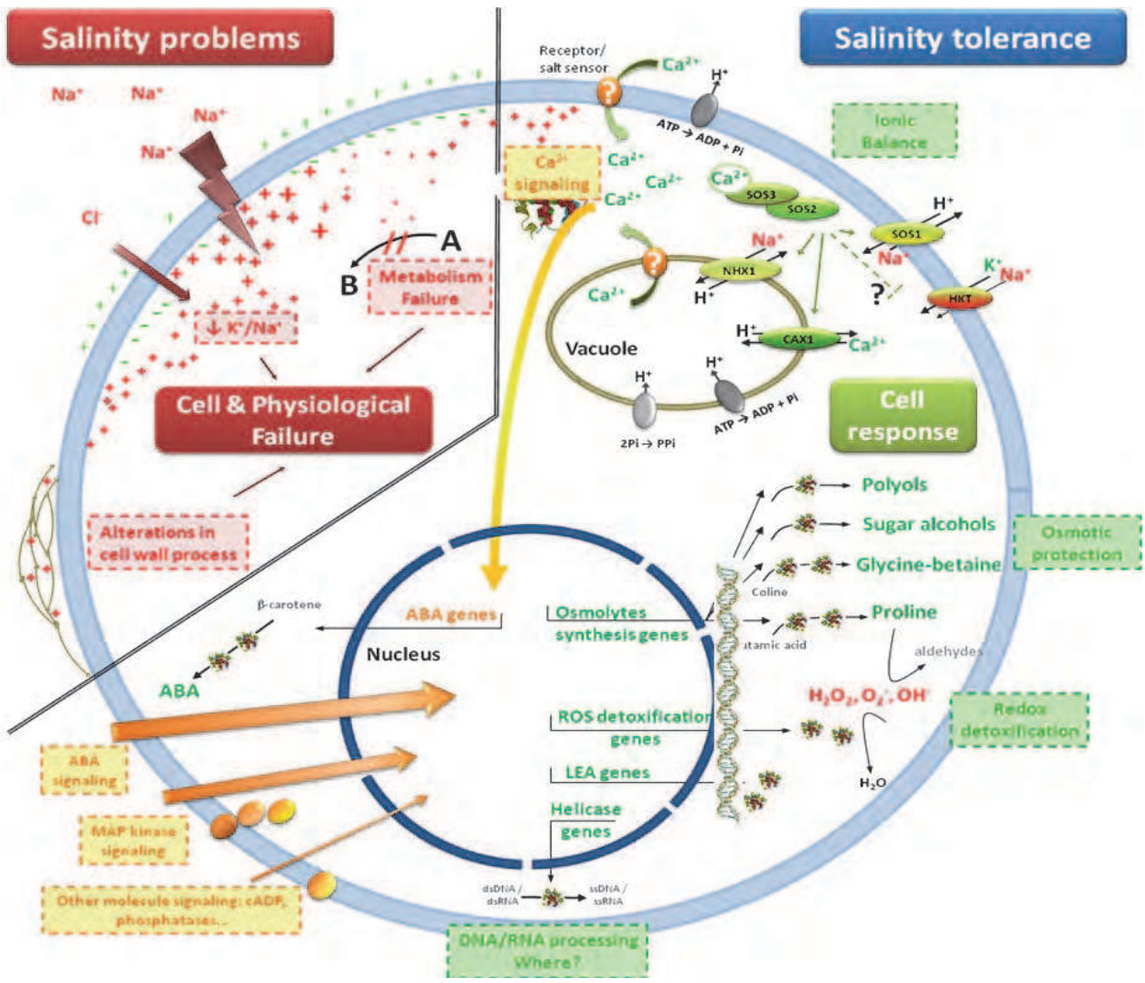


Fig. 1. Regulation of ion homeostasis by SOS pathway and other related pathways in relation to mechanisms of stress tolerance.

7. Boron toxicity

Boron (B) is likely the micronutrient whose concentration inside vascular plants must be kept within the narrowest range for achievement optimal growth and, for this purpose, excess B in soils is more difficult to manage than its deficiency, which can be prevented by fertilization (Herrera-Rodríguez et al., 2010). Although B is found in all cellular compartments (Dannel et al., 2002), its presence is particularly notable in the cell wall where most B is located forming complexes with pectic and galacturonic derivatives with a specific *cis*-diol configuration (Bonilla et al., 2010; Camacho-Cristóbal et al., 2008; O'Neill et al., 1996). Once B is inside the roots, it moves passively with the transpiration stream and it is accumulated in mature leaves, where it can be translocated depending on the presence or not of sugar alcohols capable of forming mobile B-polyol complexes through phloem (Brown et al., 1999). Overall increased B content in mature leaves indicates B immobility, whereas higher B content in young meristematic tissues suggests B mobility. In most plants, B mobility is restricted to the xylem, as they do not biosynthesize significant amounts of polyols (Brown et al., 1999; Brown & Shelp, 1997).

B toxicity is an agricultural problem that reduces crop yield worldwide. Toxicity takes place in vascular plants as B accumulates in shoots, generally following a pattern from leaf base to tip, that leads to chlorosis and necrosis (Marschner, 1995; Reid et al., 2004). As B toxicity alters metabolism and cell division, its symptoms are also manifested as a slowing-down and inhibition of growth, especially in roots, and reductions in yield, along with loss of fruit quality (Grieve et al., 2010; Nable et al., 1997).

Furthermore, high irradiance appears to increase the harmful effects of B toxicity, probably because elevated B contents may impair plant mechanisms to cope with photooxidation stress (Reid et al., 2004).

According to Reid et al. (2004), excess B would overbind compounds with hydroxyl groups in the *cis*-configuration that could explain how this mineral stress exerts its harmful effect. Thus, extra B may bind with pectic polysaccharides and thereby altering cell wall structure; also excess B could alter the structure of primary metabolic compounds through binding to the ribose moieties of ATP (adenosine triphosphate), NADH (nicotinamide adenine dinucleotide, reduced form), NADPH (nicotinamide adenine dinucleotide phosphate, reduced form); finally, high internal B concentrations may negatively affect plant development by binding to ribose of RNA.

Recent reports show changes in gene expressions as a consequence of high internal B concentration (Kasajima & Fujiwara, 2007; Öz et al., 2009; Pang et al., 2010). Although the mechanism by which excess B promotes these changes remains unknown despite many efforts are being made to elucidate it (Kasai et al., 2011), the involvement of a signaling cascade is likely.

8. Boron toxicity tolerance

Boron tolerance appears to be associated with the ability to limit B accumulation in both roots and shoots. Thus, *Bot1* expression, a gene providing tolerance to excess B, was localized in barley roots and youngest leaf blades (Sutton et al., 2007). Other genes encoding B efflux transporters and conferring tolerance to B toxicity in cultivars of wheat (cv. India) and barley (cv. Sahara), namely *TaBOR2* and *HvBOR2*, respectively, have also been reported (Reid, 2007). Therefore, boric acid/borate efflux transporters appear to be key determinants of plant B tolerance, and provide a molecular basis for the generation of highly B-tolerant crops (Takano et al., 2008).

9. Salinity and excess boron

As above mentioned, plant growth and yield are severely affected by salt stress in many regions of the world as a result of osmotic effects, ion toxicities, and mineral disorders (Hasegawa et al., 2000). The response of plants to salinity depends not only on the total ion concentration in the external medium, but also on the chemical nature of the involved ions (Curtin et al., 1993). Nevertheless, most experimental works for salinity studies in plants have been performed with NaCl as a salinizing chemical.

NaCl toxicity is apparent by ion toxicity and osmotic stress. Ion toxicity is due to specific damages by the high levels of Na^+ and Cl^-, reduction of K^+ uptake being a main consequence, among others. Moreover NaCl treatment can increase the electrolyte leakage in tomato roots, indicating that the integrity of their plasma membranes is altered with salt stress (Bastías et al., 2010).

Boron-rich soils with high contents of naturally occurring salinity, and irrigation with groundwater containing high concentrations of salts and B are two common ways by which plants can be subjected to a double stress: salinity and excess B (Nable et al., 1997). For instance, soils with salt and B accumulation occur in South Australia (Marcar et al., 1999) and Jordan River Valley in Israel and Jordan (Yermiyahu et al., 2008); irrigation water with high levels of salts and B has been well documented in San Joaquin Valley in California (Grieve al., 2010), and the Lluta Valley in Chile (Bastías et al., 2004b), among other places.

At first glance, one might think that between salt stress and B toxicity there would be an additive or synergistic relationship. In other words, either the outcome of the two stresses, when occur simultaneously, is equivalent to the sum of the effects of both stresses when applied separately (additive response), or the outcome of the both combined stresses is greater than the sum of them acting separately (synergistic response). However, interactions between salinity and B toxicity are rather complex and it has been reported that an antagonistic response can also exist when both stresses appear simultaneously (Bastías et al., 2004a; Yermiyahu et al., 2008). As summarized by Yermiyahu et al. (2008), there is no agreement regarding mutual relations between salt stress and B toxicity (Grieve et al., 2010).

Apparently, antagonism between salt stress and B toxicity can be a consequence of lower toxicity of NaCl in the presence of high B, lower toxicity of B in the presence of high NaCl, or both. Several reports support that diminution of Cl^- uptake owing to high B could reduce the salt toxicity, since the increased addition of B to the soil did not affect leaf Na^+ content in pepper plants (Yermiyahu et al., 2008), or even decreased it in wheat (Holloway & Alston, 1992). Therefore, B would positively affect to salt stress through decreased Cl^- accumulation in the leaves as a consequence of the reduced Cl^- uptake. Nevertheless, this amelioration is through an as-yet-unknown mechanism.

In turn, reduced leaf B contents with the increase of NaCl concentration in the irrigation water have been widely reported. As an explanation it has been proposed that reduced rates of transpiration would limit the leaf accumulation of B that is transported through the xylem (Yermiyahu et al., 2008).

Another alternative proposal is that the interaction between salinity and B toxicity could be related to aquaporin functionality (Bastías et al., 2004a; Martínez-Ballesta et al., 2008a, 2008b). Under excess external B, significant B transport takes place through the plasma membrane aquaporins (Dordas et al., 2000). The lower aquaporin functionality found in NaCl-treated plants could be related to the reduction of B contents in plants subjected to combined B and NaCl, in comparison with plants treated only with B, which could explain the beneficial effect of salinity against B toxicity (Bastías et al., 2004a). In turn, under salt

stress, the activity of specific membrane components can be influenced by B regulating the functions of certain aquaporin isoforms as possible components of the salinity tolerance mechanism (Martínez-Ballesta et al., 2008b).
In addition, it has been proposed that salt-tolerant plants may be more resistant to toxic B levels because their salt-exclusion mechanisms also contribute to reduce internal B concentrations (Alpaslan & Gunes, 2001).

10. Calcium and boron ameliorate salt tolerance

It is well known that salt stress leads to a Ca^{2+} and K^{+} deficiency and to other nutrient disorders (Cramer et al., 1987; Marschner, 1995). The external supply of Ca^{2+} to the soil ameliorates the damage caused by salinity (La Haye & Epstein, 1971), likely because the integrity of the membrane and its selective capacity is maintained by an adequate supply of Ca^{2+} (Cramer & Läuchli, 1996).
Interestingly, a balanced addition of B and Ca^{2+} together increased tolerance to salt stress in nodulated nitrogen-fixing pea plants, as extra Ca^{2+} can recover nodulation inhibited by salinity and extra B also contributes to nodule development and functionality (El-Hamdaoui et al., 2003a, 2003b). Furthermore, a proper B and Ca^{2+} supplement restores iron content in salt-stressed pea nodules (Bolaños et al., 2006), as well as the germination in salt-stressed pea seeds (Figure 2).
In addition, it has been proposed that interactions among NaCl, B and Ca^{2+} appear to be involved in the stability of the cell wall in plants (Cassab, 1998) and nodules (Bolaños et al., 2003).
It is widely known that both Ca^{2+} and B are needed for cell wall structure. Ca^{2+} stabilizes pectic polysaccharides in cell walls by ionic and coordinate bonding in the polygalacturonic

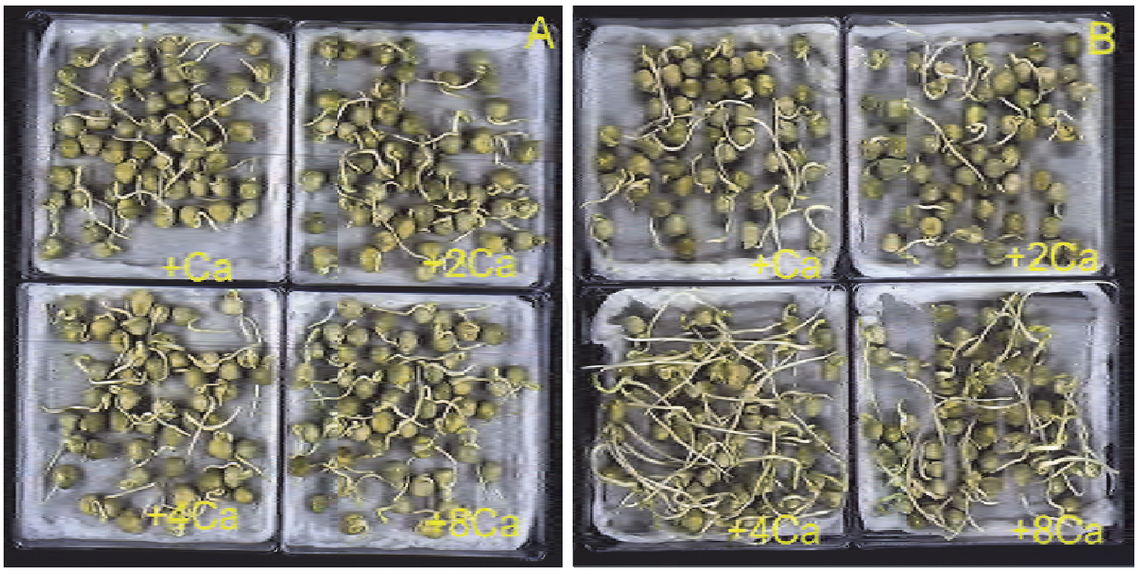


Fig. 2. Effects of supplement with combined boron (**A,** control: 9.3 μM*;* **B,** +6B: 55.8 μM) and calcium (+Ca: 0.68 mM; +2Ca: 1.36 mM; +4Ca: 2.72 mM; +8Ca: 5.44 mM) on germination of *Pisum sativum* cv. Argona seeds after 6 days under salt stress (75 mM NaCl). Boron was added as H_3BO_3 and Ca as $CaCl_2$. Seeds treated with combined +6B and +4Ca had a germination similar to that of those treated without NaCl (control seeds).

acid region (Kobayashi et al., 1999), and B is also essential to the structure and function of the cell forming borate ester cross-linked rhamnogalacturonan II dimer (O'Neill et al., 1996). Besides this structural feature, it has been highlighted that both nutrients share other characteristics, namely, preferential distribution to apoplast, scarce mobility, very low cytosolic concentration, and signaling functions (Bonilla et al., 2004; Camacho-Cristóbal et al., 2008; González-Fontes et al., 2008). Thus, it would not be surprising that Ca^{2+} and B within the cell could contribute co-ordinately to some physiological role, and that the combined addition of both nutrients can palliate the harmful effects caused by salinity.

11. Conclusion

Tolerance to salinity involves processes in many different parts of the plant and can occur at a wide range of organizational levels, from the molecular level to the whole plant. Consequently improvements in salinity tolerance result from close interactions among molecular biologists, geneticists, biotechnologists, and physiologists and benefit from feedback from plant breeders and agronomists. The mechanism of high salt tolerance is just beginning to be understood. However, much effort is still required to understand in detail each product of genes induced by salinity stress and their interacting partners to elucidate the complexity of the signal transduction pathways involved in high salinity stress.

On the other hand, the mechanism of the relationship between B and salinity is not yet elucidated. Nevertheless, the palliative effect of B under saline conditions may be due to an improvement of the functionality of aquaporins, to prevention of salt-induced nutrient imbalance, interactions between B and Ca with respect to cell wall stability, or to a lower Cl-uptake.

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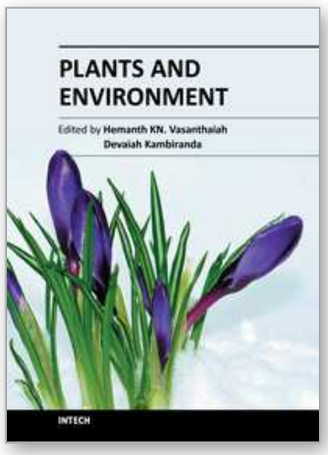
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Changing environmental condition and global population demands understanding the plant responses to hostile environment. Significant progress has been made over the past few decades through amalgamation of molecular breeding with non-conventional breeding. Understanding the cellular and molecular mechanisms to stress tolerance has received considerable scientific scrutiny because of the uniqueness of such processes to plant biology, and also its importance in the campaign â€œFreedom From Hungerâ€. The main intention of this publication is to provide a state-of-the-art and up-to-date knowledge of recent developments in understanding of plant responses to major abiotic stresses, limitations and the current status of crop improvement. A better insight will help in taking a multidisciplinary approach to address the issues affecting plant development and performance under adverse conditions. I trust this book will act as a platform to excel in the field of stress biology.

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