Plant Salinity Tolerance

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Article Contents

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Soil salinity is one of the major abiotic stresses limiting plant growth and resulting in crop yield reductions. The adverse effects of salinity stress on plant growth happens in two phases: the osmotic phase, which occurs immediately after salt stress and results in a rapid inhibition in plant growth; and the ionic phase, which occurs after several days or weeks of salt stress, when ions accumulate to high toxic concentrations in the shoot and affects shoot function. Plants have evolved several mechanisms to deal with salt stress, which can be divided into three mechanisms: osmotic tolerance, ion exclusion and tissue tolerance.

Introduction

Soil salinity is a serious abiotic stress affecting plant growth, reproduction and yield. According to the Food and Agriculture Organization of the United Nations (FAO) report in 2008, more than 800 million hectares of the world's lands are salt affected (FAO, 2008). Global warming, water deficiency and many irrigation practices are contributing to the increase in soil salinisation, and thus strongly impact global crop yields (Yamaguchi and Blumwald, 2005). Soil salinisation can be classified into primary and secondary salinisation (Carrow and Duncan, 2011). Primary salinisation refers to naturally salt-affected soils (due to its geographical and historical origin), predominantly found in the Middle East, North Africa, Australia and regions of the former Soviet Union (Wicke *et al*., 2011). Secondary salinisation is due to human intervention and is a result of several processes such as deforestation, which increases groundwater salinity as a result of salt migration (Salama *et al*., 1999); improper irrigation practices such as irrigation with low quality water; or excessive irrigation that causes a rise of groundwater levels that then reach sub-soil mineral stocks (Rengasamy, 2006). About 20–50% of irrigated lands are affected by secondary salinisation (Pitman and Läuchli, 2002). Climate change is also contributing to secondary salinisation, because the increase of temperatures increases irrigation requirements, resulting in higher salinisation of certain areas. This secondary salinisation is expected to cause the loss of 16 000 km^2 of arable land annually (Ghassemi *et al*., 1995). Saline soil is characterised by high concentrations of soluble salts, where there is an electrical conductivity (EC) of 4 $dS\ m^{-1}$ or higher (approximately equivalent to 40 mM NaCl), which generates an osmotic pressure of approximately 0.2 MPa (USDA-ARS, 2008).

Plants vary greatly in their responses to salinity. Generally, plants can be classified into two broad classes: halophytes (salt-tolerant plants) and glycophytes (salt-sensitive plants). Halophytes are native to saline environments and have, therefore, developed several mechanisms to tolerate high salt concentrations (Flowers *et al*., 1977; Flowers *et al*., 1986). Halophytes have a wide range of salinity tolerance, some of them are able to maintain their best growth rate only at high salt concentrations – for example *Atriplex vesicaria* can produce high yields under 700 mM NaCl (Flowers *et al*., 1977), and *Salicornia europaea* can tolerate up to 1000 mM NaCl (Flowers *et al*., 1977; Flowers and Colmer, 2008). Most plants are glycophytes (Greenway and Munns, 1980), and they are relatively sensitive to salt stress; however, there is variation among them. For example, maize, onion, rice, citrus, pecan, lettuce and beans are highly sensitive to salinity (Greenway and Munns, 1980). Bread wheat (*Triticum aestivum*) is moderately tolerant to salt stress (requiring 100–200 mM NaCl for optimum growth) and barley is most salt tolerant among cereals (Flowers *et al*., 1977). The model plant *Arabidopsis* is considered as a salt sensitive species when compared with other species. Although plants species are traditionally grouped as halophytes and glycophytes, there is often significant genetic variations in the salinity tolerance within each group (and even within one species), and there is, in reality, a continuum of tolerance across the range of plants.

Studying salinity tolerance of salt tolerant species, such as halophytes, provides more information on salinity tolerance traits than studying salt sensitive species. *Thellungiella salsuginea* (originally known as *Thellungiella halophila*) can be considered to be a model halophyte. It is tolerant to a wide range of abiotic stresses, such as low humidity, freezing and high salinity (Bressan *et al*., 2001; Inan *et al*., 2004; Amtmann, 2009). Its genome has been sequenced and it shares 92% sequence homology with

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the genome of *Arabidopsis thaliana* (Wu *et al*., 2012). These features (the high similarity between the genomes of *A. thaliana* and *T. salsuginea*, and the great difference in salinity stress tolerance between them) make *T. salsuginea* a good model to conduct comparative salinity tolerance studies with *Arabidopsis* to characterise salinity tolerance traits (Taji *et al*., 2004).

Salinity affects plant growth through two different mechanisms: the osmotic effect and the ionic effect, and so plants have several mechanisms to tolerate salt stress (Munns and Tester, 2008). In this article, the effects of soil salinity on plant growth and survival as well as the molecular mechanisms that plants develop to tolerate soil salinity will be discussed.

Sodium Sensing

Knowledge about sodium sensing is still very limited. Theoretically, the increase in Na^+ concentrations can be sensed extracellularly, intracellularly or both. Extracellular Na^+ is probably sensed by a membrane receptor, whereas the intracellular Na^+ is probably sensed by membrane proteins or Na^+-sensitive enzymes. The best-characterised signalling pathway is the SOS (SALT OVERLY SENSITIVE) pathway, activated by Ca^{2+} signalling (Zhu, 2007). In this pathway, high Na^+ concentration causes an increase in the cytosolic free Ca^{2+} concentration, which is sensed by the calcineurin B-like protein CBL4 (previously known as SOS3). The activated SOS3 interacts with CBL-interacting protein kinase (CIPK24, previously known as SOS2) (Halfter *et al*., 2000). The CBL4/CIPK24 (SOS3/SOS2) complex phosphorylates and activates the plasma membrane SOS1 which mediates Na^+ efflux from root cells (Qiu *et al*., 2002; Quintero *et al*., 2002; Shi *et al*., 2002).

The Effect of Salt Stress on Plants

Salinity stress adversely affects plant growth. The effect of salinity stress happens in two distinct phases which can be separated by their time of initiation: the osmotic phase, which occurs immediately, within minutes to days of salt exposure and results in a rapid decrease in plant growth and a decrease in the rate of elongation of young leaves and initiation of new leaves. The second phase is the ionic phase, which occurs when the salt builds up in the shoot after several days of salt exposure. It results in high sodium accumulation in old leaves and premature senescence (Munns and Tester, 2008). Each phase has different mechanisms to cope with the effects of salt on plant growth; here we will discuss about these two phases in more detail.

The Osmotic Phase of Salt Stress

The first effect of salt stress on plants occurs when the salt concentrations start to build up in the soil around the root zone area. These high concentrations of salt in the soil decrease the osmotic potential of the soil water, which decrease the ability of plant roots to take up water. As a result, plants reduce the expansion of their growing leaves and close their stomata to reduce the amount of water loss by transpiration (**Figure 1**). This effect is known as the osmotic effect of salinity stress, which is similar to the effect of drought stress (Munns and Tester, 2008). Stomatal closure is thought to be mediated by a local synthesis of ABA rather than long-distance transport from roots (Fricke *et al*., 2004). The overall effect of the salt-induced osmotic stress is an immediate decrease in plant growth with the rate of leaf expansion and new leaf emergence reduced. At a cellular level, osmotic stress reduces cell elongation and division and thus leaves become smaller and thicker. The effect of osmotic stress continues throughout plant growth so, over time, shoot development is reduced, so fewer branches or fewer lateral shoots are formed. There will also be an effect on plant reproductive development, such as earlier flowering or a reduced number of florets. Root growth is less affected by salt than shoot growth, but, recently, detailed studies on the effects of salinity on root architecture are emerging (Julkowska *et al*., 2017) the formation of new seminal or lateral roots is reduced, but little is known about this (Munns and Tester, 2008).

The negative effects of osmotic stress on plant growth happens mainly, but not solely, due to the osmotic effect of salinity. The effect of high salt concentration around the root is not the only reasons of plant growth reduction - there is also a Na^+ specific effect associated with the growth reduction (Sümer *et al*., 2004; Munns and Tester, 2008). The mechanism by which leaf growth is inhibited is still unknown; however, it is thought that the reduction of leaf growth must be regulated by a long-distance signalling from root that reduces shoot growth (Munns and Tester, 2008; Roy *et al*., 2014), such as from long-distance Ca^{2+} waves (Choi *et al*., 2014).

The Ionic Phase of Salt Stress

The second phase of plant response to salinity is the response to ionic stress. This phase starts when the Na^+ starts to build up in the shoot to high toxic concentrations. Sodium accumulation in the leaves inhibits photosynthesis and induces premature leaf senescence of older leaves (**Figure 1**) (Seemann and Critchley, 1985; Tsugane *et al*., 1999). In addition, Na^+ can displace the essential potassium ion (K^+) in proteins, and thus interferes with ribosome function and protein production. Moreover, it interferes with the function of numerous enzymes and transcription factors and other proteins that require K^+ (Tester and Davenport, 2003).

The effect of the ionic phase dominates plant responses in the case of high salt concentrations, in sensitive plants and/or in the plants that have an insufficient ability to control Na^+ transport. Most salinity studies focus on transport and control of Na^+ rather than Cl^-, perhaps because in most of the major cereals, Na^+ appears to reach toxic concentrations before Cl^- (Munns and Tester, 2008).

Mechanisms of Salinity Tolerance

As salt stress has several different effects on plants, plants have evolved several mechanisms to tolerate salt stress. These

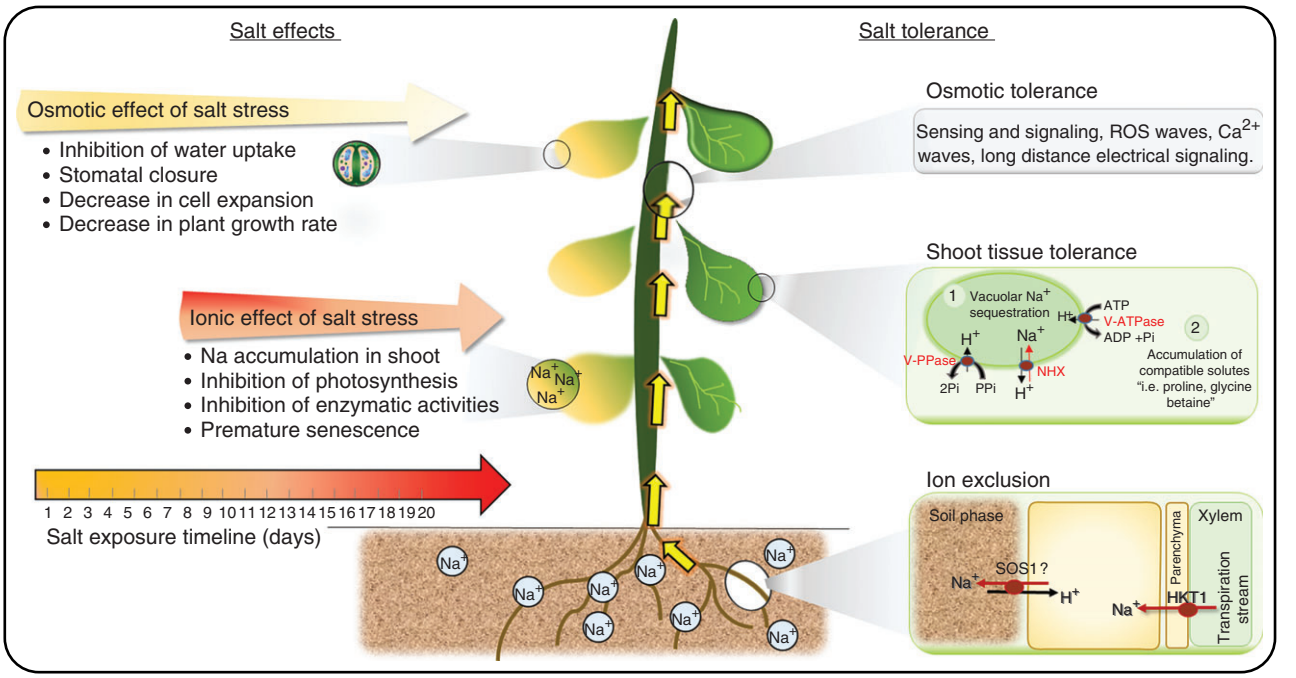

Figure 1 The effects of salt stress on plants and salinity tolerance mechanisms. Left side: the effect of salt stress on plants, which is thought to occur in two phases: the osmotic phase, which starts immediately after first exposure to high salt concentrations and may continue throughout exposure to salt; and the ionic phase, which occurs after several days of salt exposure, once ion concentrations have built up to high levels in the shoot and started to affect shoot function. The right side of the figure summarises the three main mechanisms of salinity tolerance in plants: osmotic tolerance, where long-distance signals are transmitted from root to shoot to minimise the effect of salt stress on the reduction of shoot growth; tissue tolerance, which involves salt compartmentalisation in the vacuole (mediated by ion transporters and proton pumps) and accumulation of compatible solutes; and ion exclusion which involves several mechanisms that prevent the accumulation of toxic concentrations of Na^+ and Cl^- within leaves, which involves, in particular, Na^+ retrieval from xylem and Na^+ efflux back to the soil.

mechanisms can be classified into three main categories: osmotic tolerance, ion exclusion and tissue tolerance.

Osmotic tolerance: It refers to the ability of plants to maintain growth immediately after salt exposure. So far, little is known about osmotic tolerance, and most of the hypotheses are related to long-distance signalling that controls shoot growth reduction. These signalling mechanisms are thought to be mediated by ROS waves, Ca^{2+} waves or long distance electrical signalling (**Figure 1**). Differences in osmotic tolerance is perhaps due to differences in the initial signal perception of salt stress or differences in the long-distance signalling.

Shoot ion exclusion: It is sodium exclusion by roots to prevent Na^+ accumulation to toxic concentration in photosynthetically active tissues. This occurs by controlling the net Na^+ influx into the shoot which depends on the influx of Na^+ from soil into root cells; the efflux of Na^+ from these cells back into the soil; the efflux of Na^+ from root cells in the inner half of the root to the xylem; and Na^+ retrieval from the xylem back into these cells (Munns and Tester, 2008). So far, two transporters have been identified to be involved in Na^+ exclusion: SOS1 (salt overly sensitive, also known as NHX7) and HKT (high-affinity potassium transporter family) as shown in **Figure 1**. SOS1 is a plasma membrane-localised Na^+/H^+ antiporter and may be involved in Na^+ exclusion back to the soil (Wu *et al*., 1996; Shi *et al*., 2000; Qiu *et al*., 2002; Shi *et al*., 2002). The Na^+ transport activity of SOS1 depends on the proton gradient generated by the plasma membrane-localised ATPase (Conde *et al*., 2011). The role of *SOS1* in salinity stress tolerance is suggested because the overexpression of *SOS1* in *Arabidopsis* has been reported to increase salinity tolerance in transgenic plants (Yang *et al*., 2009) and *Arabidopsis* mutants lacking *SOS1* are salt sensitive (Wu *et al*., 1996).

HKT is another ion transporting family of proteins that is also involved in controlling Na^+ distribution in plants. The HKT family is divided into two classes based on their protein sequence and transport activity (Platten *et al*., 2006). Class I HKT proteins mediate Na^+-selective transport (Uozumi *et al*., 2000; Mäser *et al*., 2002b) and class II proteins mediate Na^+/K^+ co-transport (Rubio *et al*., 1995). *Arabidopsis* has only one HKT protein (AtHKT1;1), which belongs to class I. AtHKT1;1 is proposed to be localised in the root stele and retrieves Na^+ from the xylem, thus preventing it from reaching the shoot via the transpiration stream (Davenport *et al*., 2007). Reduction in activity of *AtHKT1;1* results in hypersensitivity to salinity, associated with high concentrations of Na^+ in the leaves and reduced Na^+ concentrations in the roots (Mäser *et al*., 2002a; Berthomieu *et al*., 2003). Moreover, cell-type-specific overexpression of *AtHKT1;1* in the root stele decreases Na^+ transport to the shoot and enhances plants salinity tolerance (Møller *et al*., 2009).

As mentioned earlier, one way to improve salinity tolerance is by preventing Na^+ from reaching the shoot. However, when Na^+ does reach the shoot, tissue tolerance is the second effective mechanism to tolerate ionic phase of salt stress.

Shoot tissue tolerance: If a plant fails to exclude Na^+ from the shoot, such as when growing in very high salinity, Na^+ starts to accumulate in the shoot at high, toxic concentrations that would have a detrimental effect on many biological processes. It is suggested that Na^+ accumulation in the cytosol is particularly problematic. Therefore, plants have evolved several mechanisms to remove Na^+ from the cytosol to increase their ability to tolerate high concentrations of salt accumulation in the shoot. One of the most common tissue tolerance mechanisms is Na^+ compartmentalisation in the vacuole. Several channels and transporters in the vacuole appear to be involved in regulating Na^+ sequestration from cytosol to vacuole, such as members of the vacuolar NHX (Na^+/H^+) transporter family, which appears to be involved in transporting Na^+ from the cytosol into the vacuole (**Figure 1**). NHX activity is energised by an electrochemical potential difference in H^+ generated by the tonoplast membrane-localised H^+-ATPase and/or H^+-PPase (Conde *et al*., 2011). Overexpression of vacuolar *AtNHX1* or *AVP1* was correlated with higher salinity tolerance (Apse *et al*., 1999; Gaxiola *et al*., 2001).

Accumulation of Na^+ in the vacuole needs osmotic adjustment, which can be achieved by increasing the concentration of cytosolic K^+ to sub-toxic levels and by synthesising organic solutes that are compatible with metabolism, even at high concentrations (and thus are called 'compatible solutes') (Munns and Tester, 2008). There are four types of compatible solutes that accumulate by different plant species: nitrogen-containing solutes such as proline and glycine betaine; sugars such as sucrose and raffinose; straight-chain polyhydric alcohols (polyols) such as mannitol and sorbitol; and cyclic polyhydric alcohols (cyclic polyols) (Chen and Murata, 2002; Munns, 2005). Another role of compatible solutes is to stabilise the tertiary structure of proteins (Rhodes *et al*., 2002). Several enzymes controlling the rate of compatible solutes synthesis have been involved in enhancing salinity tolerance. For example, enhancing the expression of *Δ-pyrroline-5-carboxylate synthetase* (*P5CS*)gene, the rate-limiting enzyme in proline biosynthesis in plants, increases salinity tolerance of the model plant *Arabidopsis thaliana* (Chen *et al*., 2013). However, the synthesis of compatible solute comes with an energy cost which occurs at the expense of plant growth. Nevertheless, this process allows the plant to survive and gives it a chance to recover from high salinity (Raven, 1985; Munns and Tester, 2008).

Na^+ sequestration into the vacuole is a common strategy used by both halophytes and glycophytes, indicated by the observation that the enzymes of halophytes are not more tolerant than the enzymes of glycophytes. *In vitro* assays of enzymes from halophytes and glycophytes showed that both have a similar sensitivity to salt, suggesting that Na^+ sequestration is an important tissue tolerance mechanism for both halophytes and glycophytes (Tester and Davenport, 2003; Munns and Tester, 2008). Another mechanism of tissue tolerance, which is mostly developed by halophytes, is Na^+ excretion by salt glands (modified trichome) or salt bladders – salt is transported to these glands or bladders, which will then be removed later on by rain or winds (Flowers *et al*., 1977; Flowers *et al*., 1986).

It is important to note that the mechanisms of salinity tolerance are not exclusive, which means that the presence of one mechanism (e.g. shoot-ion exclusion) does not prevent other mechanisms of salt tolerance (e.g. tissue tolerance) to take place. There is no evidence that one plant is committed to only one strategy; it is expected that some tolerance mechanisms are effective at one stage of salt stress but may become less efficient at other stages. For instance, osmotic tolerance may be effective in moderate salinity; however, Na^+ exclusion from shoots may be more effective in higher salt concentrations. It is possible that all of these mechanisms occur in all plants (to some extent), but their effectiveness depends on species and external conditions (Roy *et al*., 2014).

Glossary

Compatible solutes Low molecular weight compounds, electrically neutral, highly soluble and nontoxic when accumulated to high concentrations. They reduce the osmotic potential inside the cell and help to stabilise proteins and membranes structures.

Glycophytes Salt-sensitive plant species.

Halophytes Salt-tolerant plant species.

Ion exclusion The process of preventing Na^+ accumulation in the shoot by root. It involves up- and downregulation of specific ion transporters to control the amount of Na^+ being transported to the shoot.

Ionic stress A condition where Na^+ accumulation in the shoot to high toxic concentrations interferes with many cellular processes including photosynthesis and other metabolic processes.

Na^+ sequestration The process of transporting Na^+ from cytosol into vacuole to minimise Na^+ accumulation in the cytosol.

Osmotic stress A condition due to high concentrations of salt in soil which decrease the ability of plant roots to take up water. It causes a rapid inhibition of plant growth, smaller leaves, fewer branches or tillers.

Salt stress A condition where high salt concentration in soil causes an inhibition of plant growth or plant death.

Salt tolerance The ability of a plant to maintain growth at moderate or high concentrations of salt.

Soil salinity Soil that is characterised by high concentrations of soluble salts. Saline soil is defined as having an electrical conductivity (EC) of 4 dS m^{-1} or higher (approximately equivalent to 40 mM NaCl).

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