Plant Salt Stress

Advanced article

Jian-Kang Zhu, *University of California, Riverside, California, USA*

Plant salt stress is a condition where excessive salts in soil solution cause inhibition of plant growth or plant death. On a world scale, no toxic substance restricts plant growth more than does salt. Salt stress presents an increasing threat to plant agriculture. 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.

Article Contents

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Introduction

Ubiquitously, no toxic substance restricts plant growth more than does salt. Salt stress presents an increasing threat to plant agriculture. 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. The reason for this so-called 'secondary salinization' (as opposed to primary salinization of seashore salty marshes) is simple: water will evaporate but salts remain and accumulate in the soil. The stresses created by a high salt concentration in the soil solution are 2-fold. First, many of the salt ions are toxic to plant cells when present at high concentrations externally or internally. Typically, sodium chloride constitutes the majority of the salts. Sodium ions are toxic to most plants, and some plants are also inhibited by high concentrations of chloride ions. Second, high salt represents a water deficit or osmotic stress because of decreased osmotic potential in the soil solution. The mechanism of plant salt tolerance is a topic of intense research in plant biology. The objectives are to understand the control of ion homeostasis and osmotic regulation, and to use the knowledge to engineer crop plants with enhanced salt tolerance.

Salt Stress Damage to Plants

General symptoms of damage by salt stress are growth inhibition, accelerated development and senescence and death during prolonged exposure. Growth inhibition is the primary injury that leads to other symptoms although programmed cell death may also occur under severe salinity shock. Salt stress induces the synthesis of abscisic acid which closes stomata when transported to guard cells. As a result of stomatal closure, photosynthesis declines and photoinhibition and oxidative stress occur. An immediate effect of osmotic stress on plant growth is its inhibition of cell expansion either directly or indirectly through abscisic acid.

Excessive sodium ions at the root surface disrupt plant potassium nutrition. Because of the similar chemical nature of sodium and potassium ions, sodium has a strong inhibitory effect on potassium uptake by the root. Plants use both low- and high-affinity systems for potassium uptake. Sodium ions have a more damaging effect on the low-affinity system which has a low potassium/sodium selectivity. Under sodium stress, it is necessary for plants to operate the more selective high-affinity potassium uptake system in order to maintain adequate potassium nutrition. Potassium deficiency inevitably leads to growth inhibition because potassium, as the most abundant cellular cation, plays a critical role in maintaining cell turgor, membrane potential and enzyme activities. **See also**: Nitrate, Potassium and Phosphate in Plants

Once sodium gets into the cytoplasm, it inhibits the activities of many enzymes. This inhibition is also dependent on how much potassium is present: a high sodium/potassium ratio is the most damaging. Even in the case of halophytes that accumulate large quantities of sodium inside the cell, their cytosolic enzymes are just as sensitive to sodium as enzymes of glycophytes. This implies that halophytes have to compartmentalize the sodium into the vacuole, away from cytosolic enzymes.

An important factor in the battle between sodium and potassium ions is calcium. Increased calcium supply has a protective effect on plants under sodium stress. Calcium sustains potassium transport and potassium/sodium selectivity in sodium-challenged plants. This beneficial effect of calcium is mediated through an intracellular signalling pathway that regulates the expression and activity of potassium and sodium transporters. Calcium may also directly suppress sodium import mediated by nonselective cation channels.

Glycophytes and Halophytes

Most plants are glycophytes that cannot tolerate salt stress. Halophytes are plants that naturally grow under high salinity and are therefore tolerant of salt stress. A survey of halophytes showed that they are widespread among the various orders of higher plants (Flowers *et al*., 1977). This widespread occurrence among higher plants is indicative of a polyphyletic origin of halophytes.

Whereas glycophytes are severely inhibited or even killed by 100–200 mmol L^{-1} NaCl, halophytes can survive salinity in excess of 300 mmol L^{-1}. Some halophytes can tolerate extremely high levels of salts. For example, *Atriplex vesicaria* can produce high yields in the presence of 700 mmol L^{-1} NaCl, while *Salicornia europaea* plants would remain alive in 1020 mmol L^{-1} NaCl. On the other extreme are very salt-sensitive glycophytes, for example fruit trees such as citrus and avocado, which are sensitive to a few millimoles per litre of NaCl.

Measurements of ion contents in plants treated with salt stress revealed that halophytes accumulate salts whereas glycophytes tend to exclude the salts. Considering that halophytes often grow under very high salinity, it is not surprising that they have evolved mechanisms to accumulate ions in order to lower cell osmotic potential. This osmotic adjustment is necessary because the plants have to continue to extract water from the salty solution to meet transpirational demands of their leaves. More than 80% of the accumulated ions in halophytes are carried in the transpirational stream of the xylem to the leaves. Some halophytes have also evolved specialized cells in the leaves and stems to remove the salts out of the plants. These specialized cells, termed salt glands, can take up salt from neighbouring cells, and excrete it on the leaf surface, where it is removed by rain or wind. **See also**: Plant Ion Transport

Because developing extremely salt-tolerant crops through conventional breeding or genetic engineering is still a daunting task, some attempts have been made to domesticate halophytes for use as food, forage or oilseed crops. Such attempts have identified *Salicornia bigelovii* as a promising crop. It is a leafless, succulent, annual salt-marsh plant that flourishes in saltwater. The plant can be grown with seawater irrigation and yield oil that is comparable in quantity and quality to soybean and other oilseed crops. However, seawater irrigation is currently costly and its application is eventually restricted to coastal desert land.

Sodium Tolerance Mechanisms

Genetic analysis has shown that maintenance of a low concentration of cytoplasmic sodium is the key to sodium tolerance (Zhu, 2002). Mutant plants that cannot do so have significantly decreased sodium tolerance. First, sodium stress has to be sensed by an as yet unknown receptor(s). Presently, it is also not known whether extracellular or intracellular sodium is sensed. It has been speculated that the plasma membrane sodium/proton antiporter might function as a sensor for sodium ions. The first detectable response to sodium stress is a rise in the cytosolic-free calcium concentration. This calcium signal serves as a second messenger that turns on the machinery for sodium export and potassium/sodium discrimination. In plant cells, the sensor protein for this calcium signal is termed SOS3. It is so designated because a loss-of-function mutation in this protein renders the *Arabidopsis thaliana* plant overly sensitive to salt. SOS3 is in a complex with the serine/threonine protein kinase SOS2. Upon receiving the calcium signal, the kinase complex is activated to phosphorylate target proteins such SOS1. SOS1 encodes a plasma membrane sodium/proton antiporter that is responsible for removing sodium from the cells (Zhu, 2002). The sodium extrusion activity of SOS1 depends on SOS3 and SOS2.

An important mechanism for dealing with cytosolic sodium is to store it in the vacuolar compartment where it is not in contact with cytosolic enzymes. Vacuolar compartmentation of sodium is achieved by the action of sodium/proton antiporters on the tonoplast, the vacuolar membrane. The proton gradient that drives the antiport is generated by the tonoplast proton-ATPase and pyrophosphatase. Compartmentation of sodium into the vacuole not only separates sodium from cytosolic enzymes, it also helps offset the low extracellular osmotic potential created by salt stress. The protein kinase SOS2 responsible for activating the plasma membrane sodium/proton antiporter, is also important for the activation of vacuolar sodium/proton antiporters.

Vacuolar compartmentation of sodium is perhaps more important for halophytes that actively accumulate large amounts of sodium. Because the cytosolic enzymes are not tolerant to sodium inhibition in those halophytes, most of the accumulated sodium needs to be stored in the vacuole. Indeed, it is not uncommon to find sodium at concentrations that approximate 0.5 mol L^{-1} or more in the vacuoles of halophytes. The counter ions are typically chloride and malate.

Changes in Metabolism During Salt Stress

Perhaps, the most dramatic change in metabolism occurs in the ice plant (*Mesembryanthemum crystallinum*) under salt stress. Within days, salt stress can elicit a change from C3 to the CAM (crassulacean acid metabolism) mode of photosynthesis in this succulent plant. Some of the enzymatic machinery for CAM metabolism, e.g. phosphoenolpyruvate (PEP) carboxylase, is induced by a few hours of salt stress. The main advantage of the CAM metabolism is an increased water use efficiency because the stomata only open at night when evaporative water loss is at a minimum. **See also**: C_3 Carbon Reduction Cycle; Crassulacean Acid Metabolism

A metabolic change common to most if not all plants is the accumulation of low molecular weight organic solutes under salt stress. These solutes include linear polyols (glycerol, mannitol or sorbitol), cyclic polyols (inositol or pinitol and other mono- and dimethylated inositol derivatives), amino acids (glutamate or proline) and betaines (glycine betaine or alanine betaine). Plants that often experience nitrogen limitation may accumulate sulfonium compounds, e.g. dimethylsulfonium propionate, which are equivalent to the nitrogen-containing betaines. Unlike the inorganic solutes such as sodium and chloride ions, these organic solutes even at high concentrations are not harmful to enzymes and other cellular structures. For this reason, these organic compounds are often referred to as compatible osmolytes. At high concentrations, compatible solutes certainly function in osmotic adjustment. This is especially true in halophytes, which often accumulate between 0.5 and 4.0 mol L^{-1} of compatible osmolytes in the cells. The high concentration of compatible osmolytes reside primarily in the cytosol, to balance the high concentration of salt outside the cell on one side, and on the other, to counter the high concentrations of sodium and chloride ions in the vacuole.

Not only are the organic solutes not harmful, they may also have a protective effect against damage by toxic ions or dehydration. Genes encoding rate-limiting enzymes for polyol, proline and glycine betaine biosynthesis have been overexpressed in transgenic tobacco and *A. thaliana*. The transgenic plants constitutively producing compatible osmolytes perform better than control plants under salt stress. The protective effect cannot be fully explained by the osmotic adjustment theory because in most cases the transgenic plants only produce several millimoles per litre more of the engineered osmolytes, concentrations too low to contribute significantly to osmotic adjustment. Data suggest that the low amount of compatible osmolytes may protect plants by scavenging oxygen-free radicals caused by salt stress. The importance of antioxidants in salt stress tolerance is also supported by experiments showing a positive effect of genetically engineered production of oxygen-free radical scavenging enzymes on plant performance under salinity. **See also**: Transgenic Plants

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