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Assessing physiological responses of plants to salinity stress

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Abstract
This review deals with the adaptive mechanisms that plants can implement to cope with the challenge of salt stress. Plants tolerant to NaCl implement a series of adaptations to acclimate to salinity, including morphological, physiological and biochemical changes. These changes include increases in the root/canopy ratio and in the chlorophyll content in addition to changes in the leaf anatomy that ultimately lead to preventing leaf ion toxicity, thus maintaining the water status in order to limit water loss and protect the photosynthesis process. Furthermore, we deal with the effect of salt stress on photosynthesis and chlorophyll fluorescence and some of the mechanisms thought to protect the photosynthetic machinery, including the xanthophyll cycle, photorespiration pathway, and water-water cycle. Finally, we also provide an updated discussion on salt-induced oxidative stress at the subcellular level and its effect on the antioxidant machinery in both salt-tolerant and salt-sensitive plants. The aim is to extend our understanding of how salinity may affect the physiological characteristics of plants.

Keywords: Adaptive mechanisms, anti oxidative metabolism, chloroplast, osmotic regulation, oxidative stress, photosynthesis

Introduction

Salinity is one of the most significant environmental challenges limiting plant productivity, particularly in arid and semi-arid climates. Salinity in irrigation water and in soils is one of the major abiotic constraints on agriculture worldwide, and the situation has worsened over the last 20 years due to the increase in irrigation requirements in arid and semi-arid regions such as those found in the Mediterranean area. Soil salinity affects about 800 million hectares of arable lands worldwide. A soil is considered to be saline when the electric conductivity (EC) of the soil solution reaches 4dS m^{-1} (equivalent to 40mMNaCl), generating an osmotic pressure of about 0.2MPa and significantly reducing the yields of most crops. As a consequence, ion toxicity, lead to chlorosis and necrosis, mainly due to Na^+ accumulation that interferes with many physiological processes in plants. The harmful effect of salinity can vary depending on climatic conditions, light intensity, plant species or soil conditions. Depending on the ability of plants to grow in saline environments, they are classified as either glycophytes or halophytes, and their response to salt stress differs in terms of toxic ion uptake, ion compartmentation and/or exclusion, osmotic regulation, CO_2 assimilation, photosynthetic electron transport, chlorophyll content and fluorescence, reactive oxygen species (ROS) generation, and antioxidant defences. Most salinity adaptive mechanisms in plants are accompanied by certain morphological and anatomical changes. Glycophytes, which includes most crop plants, cannot grow in the presence of high salt levels; their growth is inhibited or even completely prevented by NaCl concentrations of 100–200mM, resulting in plant death. Such growth inhibition can even occur in the short term. In contrast, halophytes can survive in the presence of high NaCl concentrations (300- 500mM) because they have developed better salt resistance mechanisms, described above, characteristic of these plants. Halophytes can cope with the effects of salt stress by developing different resistance mechanisms.
These plants can regulate their salt content in the following ways

Salt exclusion: prevents the entry of salts into the vascular system.

Salt elimination: Salt-secreting glands and hairs actively eliminate salts, thus keeping the salt concentration in the leaves beneath a certain threshold.

Salt succulence: If the storage volume of the cells increases progressively with the uptake of salt, the salt concentration can be kept reasonably constant for extended periods.

Salt redistribution: Na^+ and $Cl^–$ can be readily translocated in the phloem so that the high concentrations arising in actively transpiring leaves can be redistributed throughout the plant. Halophytes can also accumulate salt in their cell sap up to a level at which their osmotic potentials are lower than in the soil solution. In addition to salts, the accumulation of soluble carbohydrates plays an important role in maintaining allow osmotic cell sap potential. The ability of the protoplasm to tolerate high concentrations of salt also depends on the selective compartmentalisation of ions entering the cell. The majority of the salt ions are accumulated in the vacuoles. Salt stress is first perceived by the root system and impairs plant growth both in the short term, by inducing osmotic stress caused by reduced water availability, and in the long term, by salt-induced ion toxicity due to nutrient imbalance in the cytosol. Therefore, the two main threats imposed by salinity are induced by osmotic stress and ionic toxicity associated with excessive $Cl^–$ and Na^+ uptake, leading to $Ca2^+$ and K^+ deficiency and too their nutrient imbalances. In addition, s alt stress is also manifested as oxidative stress mediated by R OS. All these responses to salinity contribute to the deleterious effects on plants. Under saline conditions, plants have to activate different physiological and biochemical mechanisms in order to cope with the resulting stress. Such mechanisms include changes in morphology, anatomy, water relations, photosynthesis, the hormonal profile, toxic ion distribution and biochemical adaptation.

Table 1: Different classes of Salinity

Salinity class	ECe range (dS/m)
Non-saline	0-2
Low salinity	2-4
Moderate salinity	4-8
High salinity	8-16
Severe salinity	16-32
Extreme salinity	>32

Quantifying the effects of salinity on plant water relations, transpiration and transpiration use efficiency: Two components of a plant's water relations are water potential and hydraulic conductivity. Water potential refers to the potential energy of water relative to pure water, and therefore determines the direction of water movement, where water moves from a location with a higher water potential to a location with a lower water potential. Hydraulic conductivity refers to the ease with which water can flow from one location to another and therefore affects the rate of water movement. In the face of high salinity, a plant's ability to control these two components is essential. Two additional components, in combination with other components, are the outputs of water potential and hydraulic conductivity, namely the maintenance of water levels in tissue and the maintenance of transpiration. Under saline conditions, plants usually adjust their osmotic potential to maintain turgor pressure and this can exacerbate difficulties with classically used methods to measure RWC. It has been proposed that the ability of plants to maintain normal rates of transpiration under saline conditions is an important indicator of salt tolerance, particularly because transpiration is related to normal rates of CO_2 uptake for photo- synthesis. However, assessment of a plant's transpiration rate using porometer and infra-red gas analysers can be difficult due to rapid changes in stomatal conductance that can occur in both space and time. The genes Involved in TUE remain largely unknown, and the effects of salinity on TUE remain, to our knowledge, largely unstudied. Carbon isotope discrimination has been used for analysis of TUE, and it has been used successfully to improve the water use efficiency of wheat.

Quantifying the effects of salinity on- ion relations

Maintaining ion homeostasis can be particularly challenging for plants under saline conditions, as the accumulation of toxic ions (i.e. Na^+) can perturb the plant's ability to control accumulation of other ions. In most species, Na^+ appears to accumulate to toxic levels before Cl^- does; thus, we focus here on Na^+, because reducing Na^+ in the shoot, while maintaining K^+ homeostasis, is a key component of salinity tolerance in many cereals and other crops.

Accumulation of compatible solutes, such as glycine betaine, proline and polyols, in the cytoplasm is required to balance the decrease in water potential occurring in the vacuole due to ion accumulation in that compartment.

Quantifying the effects of salinity on photosynthesis

The intercellular CO_2 concentration (Ci) is another parameter that has been used to estimate the effects of salinity on photosynthesis. Under salinity, the CO_2 assimilation rate was shown to be better maintained by a salt tolerant species, Eutrema salsugineum (Salt water cress), compared with a sensitive-species, Arabidopsis. However, under salinity stress, leaf expansion, associated with changes in leaf anatomy, is reduced, resulting in higher chloroplast density per unit leaf area, which can lead to a reduction in photosynthesis as measured on a unit chlorophyll basis. It is known that prolonged salt stress may cause changes in leaf anatomy. In general, tolerant species respond by increasing leaf thickness. Anatomical modifications in leaves also include an increase in palisade parenchyma and intercellular spaces and a decrease in spongy parenchyma, serving to facilitate CO_2 diffusion in a situation of reduced stomatal aperture. Damage to the chloroplast is an important aspect of the effect of salinization on leaf cells. The main salt-induced changes in the chloroplast ultrastructure include changes in starch content, disarranged thylakoids and grana and increased numbers of plastoglobuli. In tolerant plants, decreases observed in starch content could suggest that the starch is used for different physiological processes to cope with the salt stress challenge. In salt-tolerant plants, plant growth is less affected. Salt exclusion and salt compartmentalisation in vacuoles and the accumulation of osmolytes are important mechanisms for salt tolerance. Salt stress affects photosynthesis both in the short and long term. In the short term, salinity can affect photosynthesis by stomatal limitations, leading to a decrease in carbon assimilation. In the long term, salt stress can also affect the photosynthetic process due to salt accumulation in young leaves, leading to the loss of photosynthetic pigments and the inhibition of Calvin cycle enzymes.

Quantifying the effects of salinity on plant senescence

Once the plant has accumulated $NaCl^+$ in the shoot and suffers from the toxic effects of $NaCl^+$, the most visible symptom is a yellowing, then browning, of leaves, due to leaf senescence and death. This effect is most visible in older leaves that have had a longer time to accumulate $NaCl^+$ and suffer from the effects of that accumulation. However, it is notable that the leaves of some plants are better able than others to maintain greenness and photosynthetic function for longer in the presence of high levels of $NaCl^+$ in tissues.

Quantifying the effects of salinity on yield-related parameters

The ultimate goal of salinity tolerance research is to increase salinity tolerance in crops for them to maintain yield under ad-verse conditions. Heterogeneity in field salinity is a significant issue in field trials in dry land environments; using irrigated fields can reduce spatial heterogeneity significantly, and irrigation with fresh and brackish water can be effective, at least on sandy soils. The harvest index (HI) has been shown to be affected by salinity. A plant capable of maintaining HI under stress conditions will often have a higher yield. The reason for the maintenance of HI under salinity is not fully understood. Plausible reasons for changes in HI may include a lower shoot biomass reduction, maintenance of tiller number or earlier flowering.

Fig 1: Impact of salt stress on plants

Salt tolerance Mechanisms in plants

Osmotic Adjustment

Osmotic tolerance involves the plant's ability to tolerate the drought aspect of salinity stress and to maintain leaf expansion and stomatal conductance. If the accumulation of salts overcomes the toxic concentrations, the old leaves die and the young leaves, no more supported by the export of photosynthesis, undergo a reduction of growth and new leaves production. The mechanisms involved in osmotic tolerance is 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

Salt (Na+) exclusion

Completely unravelled, it has been demonstrated that the plant's response to the osmotic stress is independent of nutrient levels in the growth medium. In response to osmotic stress, plants produce osmolytes like glycine betaine, trehalose or proline, which protect them from dehydration or protein denaturation. However, oxidative stress-an outcome of ionic stress lead to the production of different enzymatic or non-enzymatic antioxidants, which protect plants from harmful effects of reactive oxygen species.

Tissue tolerance

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 and synthesis and accumulation of compatible solutes within the cytoplasm. 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.

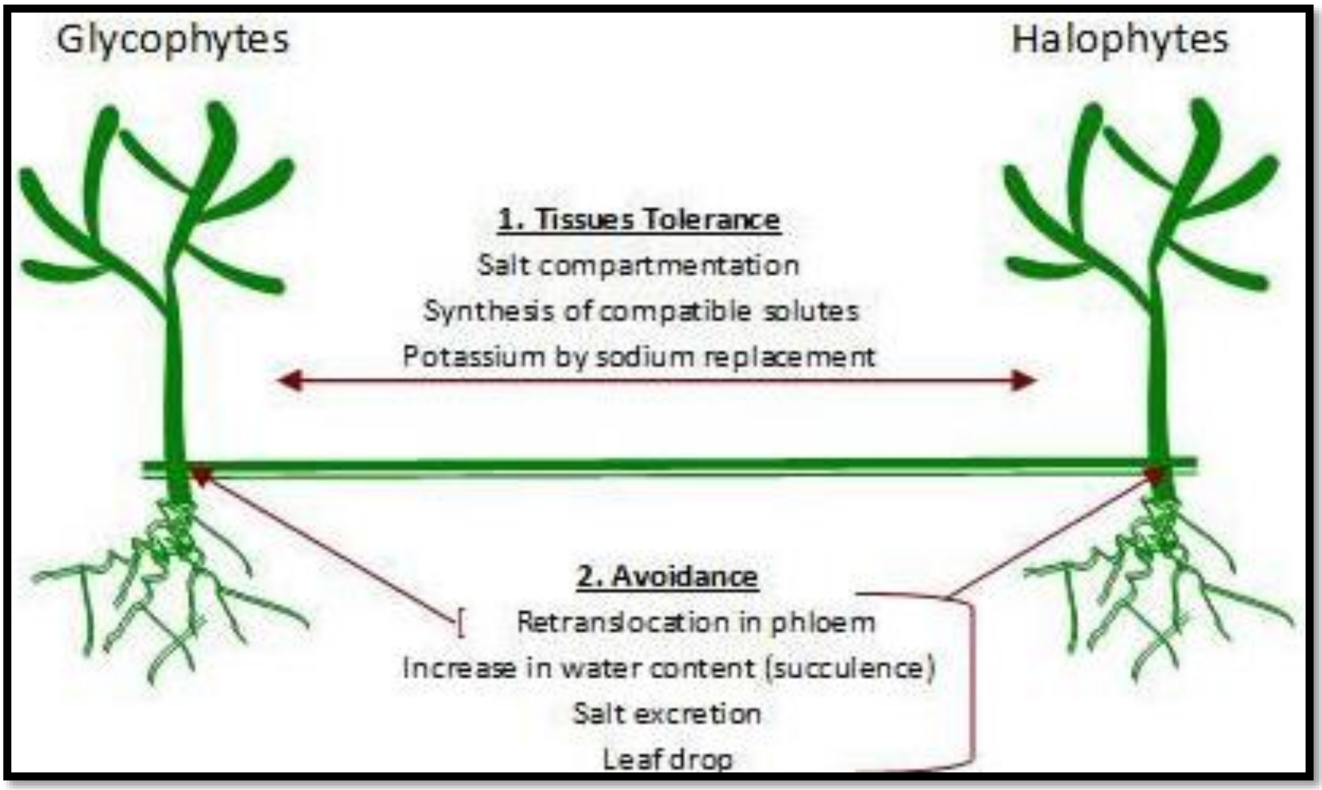

Fig 2: Adaptive strategies for salt tolerance in plants

Conclusions

Salinity is one of the most significant environmental challenges limiting plant productivity. In the short term, salt stress is first perceived by the root system, inducing osmotic stress and causing reduced water availability. In the long term, salt stress induces ion toxicity due to nutrient imbalances in the cytosol. A proper root system can ensure water and nutrient uptake in saline conditions and improve plant resistance to saline conditions. In general, salt stress produces a decrease in the aerial part of the plant partially associated with leaf abscission mediated by ethylene production. This decrease in growth can be considered a mechanism to minimise water loss by transpiration. Moreover, an increased root to shoot ratio has been described under salinity. A bigger root proportion under salt stress can favour the retention of toxic ions, which can be an important mechanism of plant resistance/survival under saline conditions. The accumulation and compartmentalisation of toxic ions and/or compatible solutes is therefore one of the mechanisms involved in salt-tolerance.

Salt tolerance is a complex trait in plants, but molecular and genetic approaches are beginning to characterize the diverse biochemical events that occur in response to salt stress. In the short term, it will remain a challenge to manipulate the essential protective mechanisms in plants and to utilize our biochemical knowledge for optimal molecular engineering of salt tolerance in plants. Research on the physiology of salt tolerance has demonstrated that the overall trait is determined by several sub-traits, any of which can in turn be determined by several genes. With the recognition that the enhanced expression of a number of functionally related genes may be required for optimal improvements in salt tolerance, molecular engineering has been expanded to include proposals for multiple gene transfers to enhance salt tolerance. An equally promising approach to manipulating many genes may emerge as we learn more about the specificity of signalling pathways that turn on transcription of related genes that counteract salt stress at the cellular level. Overall, we are likely to see continued significant progress in our understanding and ability to modify salt tolerance by molecular engineering using both model and crop plants based on knowledge of how salinity affects plant bio-chemistry and physiology through gene expression. However, and depending on the plant species and the severity of the stress, a decrease in both photochemical and non-photochemical quenching parameters can also take place. Constant advances are being made to identify traits that are associated with salinity tolerance, such as measurements of HI and WUE, allowing us to get a better understanding of the complex network of traits that contribute to salinity tolerance.

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