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Lessons from crop plants struggling with salinity

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ABSTRACT

Salinity is a persistent problem, causing important losses in irrigated agriculture. According to global climate change prediction models, salinity is expected to expand in the near future. Although intensive studies have been conducted on the mechanisms by which plants cope with saline conditions, the multi-component nature of salt stress tolerance has rendered most plant breeding efforts to improve the plant's response to salinity unsuccessful. This occurs despite the extensive genetic diversity shown by higher plants for salt tolerance and the similar mechanisms found in salt-sensitive and salt-tolerant genotypes in response to the presence of excess of salts in the growth media. On the other hand, there is an urge to increase crop yield to the maximum to cope with the growing world population demands for food and fuel. Here, we examine some major elements and signaling mechanisms involved in the plant's response to salinity following the pathway of salt-footprints from the soil environment to leaf. Some of the possible contrasting determinants for a better-balanced resource allocation between salt tolerance and plant growth and yield are considered. Q3

Introduction

In arid and semi-arid regions, salinization of croplands, principally when NaCl is the predominant salt, is one of the most persistent and damaging problems in agriculture. This is because in addition to the instant loss of crop yield, there are the threats of irreversible soil degradation and desertification and the long-lasting contamination of downstream waters and soils.

Soils are considered saline when their electric conductivity reaches $4\,\mathrm{dS\,m^{-1}}$ or more, which is equivalent to 40 mM NaCl [1], although some crops, such as beans, are sensitive to much lower salt concentrations.

Although it is difficult to estimate, about one third of total croplands are considered to suffer from some type of salinization process [2] with the consequent impact on agricultural production. Unfortunately, the amount of land affected by salinity alone or combined with other stresses, is expected to increase in the near future according to the estimations for global climate change [3]. At the same time, the current world population of 7.2 billion is expected to reach 9.6 billion by 2050 [4]. In contrast, the amount of cultivated land is at a premium, while the extension of degraded and barren wasteland used for agricultural activities under the pressure of food and fuel demands is increasing [5]. As a result, there is a need to increase crop yield to fill the gap between current and maximum achievable yields in order to ensure world food security [6], which obviously constitutes a greater challenge in salinized agricultural areas.

Salinity negatively affects all plant developmental stages and induces premature leaf senescence with corresponding deleterious effects on plant yield [7]. Salt-stressed plants face at least three major constraints: water deficit, ion toxicity and ion imbalance [1]. Reduced water availability due to the decrease in the soil osmotic potential affects the most sensitive species unable to regulate their water potential with respect to the soil resulting in the loss of cell turgor. Additionally, anion excess, principally Na^+ and Cl^-, is extremely toxic for most crop plants; compromising plant metabolism and growth, amongst others, by negatively affecting enzyme activity and membrane stability and by enhancing ROS production [1].

Plants have evolved mechanisms to grow in most of the different combinations of salt that can be found in the soil solutions. Although, Angiosperms have been classified into non salt tolerant or glycophytes, and salt tolerant, halophytes, which can even grow at higher salinities than seawater, there is a continuum of tolerance exhibited by different genotypes connecting both ends [5].

Abbreviations: Lpr, root hydraulic conductivity; VDP, vapor pressure deficit.

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Unfortunately, most crop plants are on the glycophyte side of the salt tolerance spectrum and main cereal crops such as wheat, corn and rice as well as leguminous species are quite sensitive to saline conditions. On the other hand, the strategies to acclimate to salinity are similar throughout the plant's responses to the excess of salts, from the most sensitive to the most tolerant genotypes [8]. These mechanisms involve the control of cell water and ion homeostasis in the different plant tissues and the triggering the scavenging mechanisms of toxic compounds [9].

Contrasting results on plant response to salinity have been explained by the hypothesis of a two-phase response model [10]. This model proposes that after short time exposure to salt, the rapid decrease in water availability, due to the continuous osmotic component of salinity, is limiting to plant growth. At longer salt exposure times, a slower ionic phase builds up as Na^+/Cl^- accumulates in the plant tissues leading to ion toxicity or/and ion imbalance [11].

Salt tolerance has been proposed to be principally related to the ability of plant genotypes to regulate Na^+ and Cl^- concentrations in compartments such as the cytoplasm where ion homeostasis needs to be finely controlled in order to avoid inhibitory effects on cell metabolism [11–14].

High Na^+ is toxic and its uptake has to be restricted in tolerant plants, and therefore most of the research conducted to improve crop salt tolerance has been focused on Na^+ exclusion [15]. The findings of Na^+ transporters have given rise to questions about the possible role of Na^+ uptake, and it is still unknown what Na^+ concentrations are toxic for each cell compartment [16,17]. Na^+ toxicity has been related to low Ca^{2+} concentrations [1]. In wheat roots, apart from osmotic effects, high Na^+ concentrations were not toxic unless Ca^{2+} was deficient, which could have favored an increase in cytosolic Na^+ [18]. Bean plants treated with 50 mM Na^+ or K^+ concentrations showed similar decrease in leaf expansion, transpiration rate and increase in leaf ABA [19]. Moreover, also in beans, high Na^+ enhanced leaf K^+ concentrations ameliorating the inhibition in stomatal conductance and CO_2 assimilation caused by high Ca^{2+} supply [20].

Although Cl^- frequently is the most predominant anion in saline soils, the relative importance of high Cl^- concentrations in the plant's response to salinity have attract less attention than its Na^+ counterpart [14]. High Cl^- tissue concentrations have been assumed responsible to cause an ion-specific toxicity in salt-treated plants, principally in those species with a capacity to exclude Na^+ from their shoots [1]. High Cl^- concentrations have been reported to cause membrane damage or enzyme inhibition negatively affecting photosynthetic processes [21].

Salinity also disrupts the cellular homeostasis by inducing increased production of reactive oxygen species (ROS), which can cause oxidative damage if the ROS are not promptly detoxified. The role of ROS homeostasis and signaling in salt-stressed plants has been recently reviewed [22,23]. The cell's antioxidants and ROS-scavenging enzymes are essential for plant survival in saline conditions [24]. Along this line of thought, transgenic Arabidopsis plants overexpressing cytosolic ascorbate peroxidase and transgenic tobacco overexpressing monodehydroascorbate reductase had higher tolerance to salinity compared to wild plants [25,26].

Nonetheless, salinity, as a muticomponent stress, involves many mechanisms of cellular adaptation and metabolic pathways, which has made breeding for salt tolerance largely slow and mostly unsuccessful [15,27,28]. In addition, the higher tolerance and yield of plants reported under laboratory conditions have been found to greatly diminish when they are tested in the field [15,27,28]. In part this is due to the multiple stress situations plants face in natural environments and the fact that plants respond to multiple stresses differently from how they perform under individual stress situations (reviewed by Atkinson and Urwin [5]). Therefore some traits that can be advantageous for coping with one particularly unfavorable situation can become limiting when plants have to face combined stresses. For example, increased transpiration caused by heat stress could enhance the uptake of salts with a consequent increase in plant damage caused by the salinity factor [27]. Nonetheless, some promising pioneering advances have recently been reported. Higher salt tolerance and yield has been found in durum wheat transformed with a Na^+ transporter gene (*TmHKT1;5-A*) from *Triticum monococcum* under field conditions [29]. However, in natural environments, salinity is only just one amongst the continuously changing habitat-specific abiotic and biotic constraints that plants have to resolve, and a solution that fits all situations cannot be expected [15]. In the following section we will consider some of the factors, mechanisms and interactions that are positively and negatively involved in the constant trade-off between salt tolerance and plant growth in saline agricultural lands.

Soil properties reveal some key factors for the plant's response to salinity

Although most of the studies to select genotypes for salinity tolerance are performed in laboratories, final confirmation trials have to be conducted under field conditions. The complexity of factors and heterogeneity of soils and agronomical practices greatly differs from the homogeneity and simplicity of a nutrient solution culture. This obvious fact by sure has hampered the advance in plant breeding for saline conditions [15]. The use of field-based screening procedures would contribute to modify this situation and is expected to provide plant breeders with better tools to identify salt tolerant genotypes [30]. Moreover, the use of local soils can be advantageous and sometimes even essential, as in the case of saline alkaline soils. Most of the research conducted in plant salt tolerance has been done using culture conditions and mineral elements supply characteristic of slightly acidic or neutral soils; for instance, much research has been conducted using modified Hoagland nutrient solution at pH from 5.5 to 6.0 [31]. However, in arid and semi-arid areas, which are most prone to suffer from salinization, alkaline soils are commonly found. Saline-alkaline soils are characterized by high pH and HCO_3^- concentrations, which impose additional constraints for plant growth, amongst others HCO_3^- and CO_3^- toxicity, boron toxicity, and deficiency of essential microelements like Fe and Zn [32]. In saline-alkaline conditions, alkaline toxicity has been reported to reduce growth of plants, including halophytes, even more than salinity [33]. Nonetheless, few studies focused on the plant response to saline-alkaline soils [34,35]. The combined effect of soil salinity and alkalinity on plant growth has recently been considered as a possible reason for the failure of laboratory-bred NaCl-tolerant cultivars when are grown under field conditions [36].

Water logging is another stress factor in expansion due to global climate change that frequently accompanies salinized soils in coastal areas causing important losses in crop production [37]. To grow in salinized flooded soils, plants have to cope with anaerobic conditions and with differing levels of mineral element toxicity and deficiency associated with individual soils [37–40]. For obtaining genotypes able to both maintain growth under saline conditions and to respond to punctual fluctuations in mineral elements availability, it is necessary to identify the possible common elements in the signaling pathways involved in these complex multiple stress responses. Such cross points will be essential drivers for successful future research [38]. Moreover, it must be taken into account that certain soil factors not commonly reproduced under laboratory conditions can largely improve plant growth responses to salinity. Soil heterogeneity in soil texture and of salt and nutrient distribution are examples (discussed in following sections). The

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