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Review

Salt-tolerant genes from halophytes are potential key players of salt tolerance in glycophytes

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ABSTRACT

Crop productivity strongly depends on several biotic and abiotic factors. Salinity is one of the most important abiotic factors, besides drought, extreme temperatures, light and metal stress. The enhanced burden of secondary salinization induced through anthropogenic activities increases pressure on glycophytic crop plants. The recent isolation and characterization of salt tolerance genes encoding signaling components from halophytes, which naturally grow in high salinity, has provided tools for the development of transgenic crop plants with improved salt tolerance and economically beneficial traits. In addition understanding of the differences between glycophytes and halophytes with respect to levels of salinity tolerance is also one of the prerequisite to achieve this goal. Based on the recent developments in mechanisms of salt tolerance in halophytes, we will explore the potential of introducing salt tolerance by choosing the available genes from both dicotyledonous and monocotyledonous halophytes, including the salt overly sensitive system (*SOS*)-related cation/proton antiporters of plasma (*NHX/SOS1*) and vacuolar membranes (*NHX*), energy-related pumps, such as plasma membrane and vacuolar H^+ adenosine triphosphatase (*PM* & *V-H^+ATPase*), vacuolar H^+ pyrophosphatases (*V-H^+PPase*) and potassium transporter genes. Various halophyte genes responsible for other processes, such as crosstalk signaling, osmotic solutes production and reactive oxygen species (ROS) suppression, which also enhance salt tolerance will be described. In addition, the transgenic overexpression of halophytic genes in crops (rice, peanut, finger millet, soybean, tomato, alfalfa, jatropha, etc.) will be discussed as a successful mechanism for the induction of salt tolerance. Moreover, the advances in genetic engineering technology for the production of genetically modified crops to achieve the improved salinity tolerance under field conditions will also be discussed.

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1. Introduction

Plants have been divided into salt-tolerant ‘halophytes’ and salt-sensitive ‘glycophytes’, depending on growth performance of these organisms in saline habitats. Glycophytes display severely subdued growth and even death in the presence of 100–200 mM of salt, whereas halophytes specifically belonging to the dicotyledonous halophyte group can survive in more than 200 mM (Flowers and Colmer, 2008; Shabala, 2013). High salinity is one of the most severe abiotic environmental factors, and at a global scale, no other substance is as deleterious as salt in restricting plant growth and development. Thus, salt tolerance in glycophytic crop species has become a major issue in the last several years (Zhu, 2000; Slama et al., 2015). The primary salinization of water occurs through natural processes leading to increased salt input, decreased freshwater input, or increased freshwater extraction. However, secondary salinization through human activities poses a much greater and ever-increasing problem. As soil salinity increases, the extraction of water from the soil becomes increasingly difficult for plants. In addition, salinity has often been associated with the decreased yield and stability of some crop species (Hasegawa et al., 2000; Rengasamy, 2006). Surprisingly, an estimated one to two percent reduction in the world’s irrigated area is observed yearly as an effect of salinization, indicating the severity and importance of secondary salinization. This obstacle must be addressed for sustainable agriculture development (Tuteja, 2007). A promising approach involves the introduction of halophytic genes via genetic engineering methods to produce salt-tolerant glycophytic crop varieties (Munns and Tester, 2008; Bose et al., 2015).

The priority on fascinating halophytes and their salt tolerance genes primarily reflects the mechanisms by which these plants tolerate waters and soils that have a high content of salt. Generally, most halophytic cells contain more than 500 mM Na^+ and Cl^-, except for extreme halophytes, such as *Tecticornia*, which contains approximately 2000 mM intracellular Na^+, to maintain positive turgor pressure for osmotic adjustments (Flowers et al., 2015). To survive in high salinity conditions, the osmotic movement of water in and out of the cytoplasm of the cells of halophytes occurs to prevent desiccation. In addition to the adjustment of the water potentials, the enhanced exclusion and sequestration of excess salts, formation of salt glands and bladders to accumulate additional salts, maintenance of net K^+ to Na^+ selectivity, synthesis of organic solutes, scavenging of ROS and maintenance of water use efficiency (H_2O loss per net CO_2 uptake) also contribute to effective salt tolerance in these plants (Ozgur et al., 2013; Shabala et al., 2014; Shabala and Pottosin, 2014). Hence, gene homologs from halophytes would be particularly interesting, as these genes might be functionally more efficient than those from glycophytes (Tables 1–3).

In contrast, there is evidence that the glycophytic genes also confer salt tolerance when expressed in different model species, including crop species (Zhang and Blumwald, 2001; He et al., 2005; Hou and Bartels, 2015). However, the origin of the salt tolerance of halophytes has evolved through the accumulation of adaptive mutations leading to physiological and biochemical modifications required to thrive in high salinity (Rozema and Flowers, 2005; Bromham, 2014). In certain cases, orthologs from halophytes might be functionally more superior for growth in saline-rich areas than their counterparts in glycophytes, exhibiting tolerance level up to 500 mM (Song and Wang, 2014). In addition, halophytes also maintain bioenergetic processes (photosynthesis and respiration) with less utilization of produced energy for stress adjustment and saving higher energy, while glycophytes do not (Kosova et al., 2013a,b; Bose et al., 2014a,b; Srivastava et al., 2015). The modified lipid composition of the tonoplast layer of halophytes contributes to low sodium ion leakage back into the cytosol as a valid contribution to the salt tolerance observed in these plants (Leach et al., 1990; Glenn et al., 1999). Recently, Aquino et al. (2011) argued that the accumulation of sulfated polysaccharides (SP) in salt-tolerant species is associated with salt tolerance, and glycophytes do not contain these polysaccharides. In addition these authors suggested that negatively charged cell wall polysaccharides might play a role in high salt stress tolerance, and therefore halophytic plants exhibit adaptation to high salt environments, a trait likely conserved during plant evolution. Differences in metal uptake between glycophytes and halophytes are also important concerns for variations in tolerance (Jordan et al., 2002; Anschutz et al., 2014). Progress in the isolation and characterization of halophytic orthologs and the identification of the roles for these genes in salinity tolerance has been achieved; few transgenic glycophytic crop plants have been produced through the introduction of halophyte genes (see below). Overall, the proper selection of candidate genes requires thorough knowledge of the molecular mechanisms of halophytes. Although the current understanding of these mechanisms recently developed, herein we summarized what is a known, identifying gaps in the knowledge, and proposed potential halophytic genes for the introduction of increased salt tolerance.

2. Unique salt tolerance mechanisms in halophytes

The widespread occurrence of halophytes among higher plants of different phylogenetic clades indicates the polyphyletic origin of salt tolerance and explains the diversity in growth patterns compared with glycophytes. Thus, it is likely that there is no single salt tolerance mechanism in these organisms. In most studies, salt tolerance genes from halophytes showed homology with those of glycophytes, but the salt tolerance mechanisms in halophytes might differ in various qualitative and quantitative respects (Rozema and Schat, 2013; Cabot et al., 2014; Bose et al., 2015). Most of the information concerning salt tolerance mechanisms in halophytes gathered recently, indicating that they might involve a range of adaptations, such as osmotic tolerance, ion exclusion or inclusion and tissue tolerance, proved their dominance in exhibiting salt tolerance when compared to glycophytes (Radyukina et al., 2007; Ellouzi et al., 2011; Bose et al., 2014a,b; Shabala and Pottosin, 2014).

Full genome, transcriptome and proteome comparisons between related glycophytes and halophytes might be adequate strategies to test this hypothesis. Based on recent expression studies, including transcriptome and proteome analyses of the responses of various glycophytic and halophytic plant species to salinity, revealed differences between these plants (Jithesh et al., 2006a,b; Wang et al., 2008; Barkla et al., 2012; Dinakar and Bartels, 2013; Yang et al., 2013; Very et al., 2014). It is likely that