



Review

Evaluation of proline functions in saline conditions

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ABSTRACT

More than one third of the world's irrigated lands are affected by salinity, which has great impact on plant growth and yield worldwide. Proline accumulation under salt stress has been indicated to correlate with salt tolerance. Exogenous application as well as genetic engineering of metabolic pathways involved in the metabolism of proline has been successful in improving tolerance to salinity. Correlation between proline accumulation as well as its proposed roles and salt adaptation, however, has not been clearly confirmed in several plant species. In addition, the studies relating proline functions and plant salt tolerance are always carried out in growth chambers, and are not successfully verified in field conditions. Further, plant salt tolerance is a complex trait, and studies based solely on proline accumulation do not adequately explain its functions in salinity tolerance, and thus it is difficult to interpret the discrepancies among different data. Moreover, several reports indicate that Pro role in salt tolerance is a matter of debates, as whether Pro accumulation has adaptive significance or is a consequence of alterations in cellular metabolism induced by salinity. As no consensus is obtained on the exact roles of proline production, proline exact roles in the adaptation to saline environments is therefore still lacking and is even a matter of debates. It is obvious that comprehensive future research is needed to establish the proline exact mechanism by which it enhances plant salt tolerance. We propose, however, that proline might be essential for improving salinity tolerance in some species/cultivars, but may not be relevant in others. Evidence supporting both arguments has been presented in order to reassess the feasibility of the proposed roles of Pro in plant salt tolerance mechanism.

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1. Introduction

Salt stress is one of the major environmental stresses drastically affecting plant growth and productivity, and it is estimated that more than one third of the world's irrigated lands is affected by salinity (Munns and Tester, 2008). The deleterious effects of salinity on plants are ascribed to osmotic, ionic and oxidative stresses (Mansour and Ali, 2017). High salt concentrations in the soil lower soil water potential, which imposes water deficit or osmotic stress of salinity. Salt stress builds up toxic Na⁺ and Cl⁻ and decreases beneficial K⁺ and Ca²⁺ levels, which causes ionic stress. It is reported that osmotic stress shows its effects at short term salinity exposure (phase 1) whereas ionic component effects prevail at salinity long exposure (phase 2) (Munns and Tester, 2008).

Oxidative stress is a secondary stress induced by salinity, in which reactive oxygen species (ROS) are produced and attack membrane lipids, proteins and nucleic acids (Das et al., 2016). It is worth mentioning that reactive oxygen species may act as protective agents, not always damaging, as they play a role in signaling pathways and thus stress tolerance under saline conditions, which depending upon ROS concentration and time (Sah et al., 2016). Furthermore, the negative impact of salt stress on the world comes from the fact that salinity-induced reduction of farmable land is in conflict with the elevated demand for food all over the world. Global food production needs to be increased by 38% and 57% by 2025 and 2050, respectively (Rengasamy, 2006) if food supply to the growing world population is to be maintained at current levels. As most of the suitable land has been cultivated and exploring new areas to increase food production is rarely possible, our goal should be therefore to increase the yield per unit of land rather than increasing the cultivated area. Increasing the yield of crop species in optimal soils and in less productive lands is hence a must. In order to achieve this goal, a close cooperation among scientists of several

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disciplines: plant physiology, molecular biology and plant breeding should be present to develop tolerant crop plants (Mansour, 2014). Additionally, to unmask the puzzle of salt tolerance mechanisms, plant physiologists should first carry out an intensive and comprehensive research to identify the master traits for salt tolerance. Simultaneous engineering of these traits by transgenic technologies must be then considered as a promising feasible strategy to improve salt tolerance in crop plants. It is crucial after that to carry out field tests of the transgenic plants in order to verify the correlation between such traits, Pro proposed functions and salt tolerance as well as productivity in natural field saline conditions.

One of the cellular responses to saline conditions is the alteration of metabolism and production of compatible solutes, which are distributed among different organisms. Compatible compounds can be highly accumulated in different species without disturbing their intracellular metabolism (Hasegawa et al., 2000). Preferential occurrence of these solutes has been however reported in specific organisms, which may indicate their function diversity. Further, different species accumulate exclusively or preferentially one type and/or several types of osmolytes for osmotic homeostasis. In support to that, five species of halophytes showed great variation in osmolyte accumulation under salinity (Maimaiti et al., 2016), supportive of species-specific osmotic adjustment mechanisms. Among different compounds functioning as compatible solutes, quaternary amino acid derivatives such as proline (Pro), glycinebetaine, β -alaninebetaine, and prolinebetaine are found in various plants under stress conditions (Mansour, 2000; Slama et al., 2015; Nahar et al., 2016). Among quaternary amino acid derivatives, glycinebetaine and Pro are the most common solutes produced in plants under various stress conditions (Nahar et al., 2016; Mansour and Ali, 2017). Glycinebetaine responses and functions under high salinity have been recently reassessed in a review by Mansour and Ali (2017), and hence the current review focuses on the data drawn from the responses of Pro to salt stress in plant species/cultivars contrasting in their response to salinity. In addition, the role of different amino acids in plant adaptation to salt imposition is given below.

It has been reported that amino acids, such as Pro, alanine, valine, isoleucine, glutamic acid, arginine, serine, glycine, aspartic acid, amides such as glutamine and asparagine, and non-protein amino acids such as γ -aminobutyric acid, pipercolic acid, citrulline and ornithine are accumulated in higher plants under different conditions of abiotic stress (Mansour, 2000; Hayat et al., 2012), and thus may play role in stress tolerance. The cellular source of these amino acids is the primary metabolic pathways (Slama et al., 2015). NaCl-treated wheat seedlings showed 1.6-fold increase in total free amino acids compared with nontreated seedlings (Parida and Das, 2005), suggestive of amino acid possible role in saline conditions. In addition, total free amino acid of peanut leaf increased up to 5.5-fold at 150 mM NaCl, but did not change significantly at 50 mM or 100 mM comparing with their controls (Parida and Jha, 2013), which was proposed to play a role in osmotic adjustment and protection of cellular macromolecules. Moreover, modulation in amino acid pool in flax has been found relatively early at 6 h of osmotic stress, indicative of a signaling role for these compounds (Quero et al., 2014). The work of Choudhury et al. (2007) however reveals that Pro always increases more markedly than the other amino acids in tobacco plants under salinity and drought stresses. Binzel et al. (1987) have also shown that Pro represents about 80% of the total amino acid pool in tobacco cells under NaCl stress, and thus highly contributed to cell solute potential. In accordance, other evidence report that Pro is one of the most abundantly occurring amino acids in plants exposed to salinity (Simon-Sarkadi et al., 2005; Slama et al., 2015). These studies also demonstrate that Pro content manipulation affects the stress-induced changes in the

concentration of several other amino acids, suggestive of coordinated regulation of amino acid metabolic pathways. Furthermore, *YHem1* transformation has been shown to increase the concentrations of free amino acids in the transgenic leaves of canola (Sun et al., 2015). Recently, Bertrand et al. (2016) reported that accumulation of amino acids was greater in the salt tolerant rhizobial strain as well as salt tolerant alfalfa, which contributed to plant protection and enhancement of alfalfa salt tolerance. The free amino acids of spinach leaves remarkably increased when submitted to mild salt stress, but was declined after longer salt treatment giving only a minor contribution as osmolyte (Martino et al., 2003). It seems that after longer salt imposition the free amino acids were directed to protein biosynthesis for maintenance purposes under stress condition. Conversely, free amino acid concentration was decreased by 34% in NaCl-treated halophyte *Atriplex portulacoides* (Benzarti et al., 2015), suggesting that amino acids contribution to salt tolerance may vary among glycophytes and halophytes.

Pro accumulation is one of the most prominent changes in plant metabolism in response to salt stress. Reports have demonstrated that Pro is significantly elevated in response to saline environments, and this accumulation has been thus suggested to correlate with plant salt tolerance (Mansour, 2000; Hasegawa et al., 2000; Chen et al., 2007; Pardo-Domenech et al., 2016; Ahmad et al., 2016; Nahar et al., 2016). These works indicate that Pro play a key role in osmotic adjustment and as a protectant. Recent study, however, illustrates that Pro cannot scavenge singlet oxygen, superoxide, nitrogen dioxide, nitric oxide, or peroxyxynitrite, but only scavenge hydroxyl radical (Signorelli et al., 2014), which puts Pro role as ROS scavenger under stress in question. Supporting to the notion that the proposed Pro functions cannot be always confirmed and need further evaluation, Signorelli (2016) considers “Pro accumulation as a consequence of the benefits produced by its metabolism activation more so than the molecule itself”, similarly as it occurs during fermentation. Briefly, cells during fermentation accumulate lactate and ethanol to produce NAD^+ necessary for glycolysis continuation, while lactate and ethanol (analogous to Pro) have no relevant role in the cells. Furthermore, in spite of the putative roles of Pro in acclimation of plants to saline environment, there is still much to be learned about the specific mechanisms beyond phenomenon for the following reasons: i) several inconsistencies exist in the published data regarding Pro accumulation and functions under salt stress, ii) effects of Pro on plants vary with its concentrations, duration and developmental stage, iii) Pro elevation does not guarantee that a plant will survive the salt stress and even can induce damage, and iv) not all plant species, even transgenes, are able to adapt their metabolism to enhance synthesis and accumulation of Pro under stress conditions. These apparent contradictions therefore lead us to reevaluate the Pro functions under saline conditions. Pro will hence be reviewed and discussed in detail in the next sections, in terms of biosynthesis, functions, exogenous application, and engineering. Data supporting the idea that Pro could be considered a reliable stress marker participating in plant adaption to salt stress, and those contradict with this assumption will be addressed, in order to reevaluate the biological relevance and contribution of Pro in plant salt tolerance. (see Table 1).

2. Proline biosynthesis

Biosynthesis of Pro in plants is by either the glutamate pathway or the ornithine pathway. The glutamate pathway accounts for major Pro accumulation during stress. Pro is synthesized from glutamic acid via pyrroline-5-carboxylate (P5C) by two successive reductions catalyzed by P5C synthase (P5CS) and P5C reductase

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