Biochemical and Biophysical Research Communications xxx (2017) 1–6

Contents lists available at ScienceDirect

Biochemical and Biophysical Research Communications

journal homepage: www.elsevier.com/locate/ybbrc

Plant salt-tolerance mechanism: A review

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ARTICLE INFO

Article history:
Received 5 November 2017
Accepted 7 November 2017
Available online xxx

Keywords:
Salt tolerance
Plant
Osmotic stress
Ion toxicity
Oxidative stress
Salt tolerance genes

ABSTRACT

Almost all crops that are important to humans are sensitive to high salt concentration in the soil. The presence of salt in soil is one of the most significant abiotic stresses in farming. Therefore, improving plant salt tolerance and increasing the yield and quality of crops in salty land is vital. Transgenic technology is a fast and effective method to obtain salt-tolerant varieties. At present, many scholars have studied salt damage to plant and plant salt-tolerance mechanism. These scholars have cloned a number of salt-related genes and achieved high salt tolerance for transgenic plants, thereby showing attractive prospects.

In this paper, the salt-tolerance mechanism of plants is described from four aspects: plant osmotic stress, ion toxicity, oxidative stress, and salt tolerance genes. This review may help in studies to reveal the mechanism of plant salt tolerance, screen high efficiency and quality salt tolerance crops.

1. Introduction

Soil salinity is a major abiotic stress in agricultural crop productivity worldwide. Salt stress has a significant effect on plant growth and development. Under salt treatment, the seed germination, root length, plant height, and fructification of plant are significantly inhibited [1]. Osmotic stress is the first stress experienced when a plant is exposed to saline soil and it instantly affects plant growth [2]. Ion toxicity occurs later when salt levels reach a threshold, beyond which the plant cannot maintain ion homeostasis and growth [3]. Ion toxicity and osmotic stress are primary stresses that can cause oxidative stress and a series of secondary stresses. Salt stress also leads to a decrease in photosynthesis [4] and results in a substantial decrease of crop yield worldwide [5]. This phenomenon has led to research into salt tolerance with the aim of improving crop plants [6].

Plants develop a large number of physiological and biochemical strategies to cope with stresses [7]. After stress signals are transmitted to the cells, multiple secondary signals are activated and intracellular Ca^{2+} level increases instantaneously, which can trigger a phosphorylation cascade reaction and act on proteins involved in cell defense or transcription factors. Then, transcription factors regulate the expression of stress response genes, so that plants gradually adapt to stress. Stromal closing, osmolyte accumulation, and increased Na^+/H^+ antiporter or activity all occur under salt treatment.

Attempts to improve the salt tolerance of crops through conventional breeding programs have achieved limited success because salt tolerance is genetically and physiologically complex [8]. At present, the two main techniques used to salinize soil are: transforming the soil with chemical or physical methods, and cultivating salt-tolerant crop varieties through biotechnology [9]. The former is costly and increases the secondary salinization of the soil and adds a large number of chemical substances. Therefore, the cultivation of salt-tolerant crop varieties is highly important. The salt-tolerance mechanism of the plant is the theoretical basis for cultivating transgenic resistant varieties.

In this review, we summarize salt-induced osmotic stress, ion toxicity, and oxidative stress to plants. Considerable research data on the physiological, biochemical, and molecular mechanisms of salt tolerance have also been collected.

2. Plant salt-tolerance mechanism

2.1. Accumulation of osmotic adjustment substances

Salinity stress adversely impacts plant metabolism through ion

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https://doi.org/10.1016/j.bbrc.2017.11.043
0006-291X/

toxicity, osmotic stress, and oxidative stress [10]. The response to osmotic stress primarily involves osmotic adjustments. Osmotic adjustment is critical for maintaining cell turgor, which enables the maintenance of plant metabolic activity and in turn plant growth and productivity [11]. Plants synthesize proline, soluble sugars, glycine, betaine, and other osmolytes to promote osmotic balance at the cellular level [12–14].

Proline, as an important osmotic adjustment substance, exists in plant cells in the free state and possesses low molecular weight, high water solubility, and no net charge in the physiological pH range. Plant cells tend to accumulate soluble osmotic adjustment substances to alleviate osmotic stress caused by salt stress, especially the biosynthesis of proline is clearly activated [15]. Proline content can be used as a physiological index of plant resistance to stress tolerance [16]. Wheat *Ta-UnP*, which was amplified by our laboratory for the first time, can significantly improve the salt tolerance of transgenic *Arabidopsis* and rice. After salt stress, the content of proline in transgenic *Arabidopsis thaliana* was significantly increased, thereby maintaining the osmotic potential and protecting plant cells from stress (Fig. 1a).

The Δ1-pyrroline-5-carboxylate synthetase (P5CS) is the rate-limiting enzyme in proline biosynthesis in plants and is controlled by the transcriptional level of P5CS [17]. The gene encoding P5CS is the key to ABA biosynthesis in plants. Under salt treatment, the proline content in Ta-UnP-over-expressing *Arabidopsis* plants increased remarkably. Moreover, the expression level of *P5CS* in *Ta-UnP* transgenic plants became highly induced. *Ta-UnP* could affect the expression of *P5CS* gene through the ABA signaling pathway to improve the content of proline in transgenic plants to resist osmotic stress and improve the salt tolerance of plants (Fig. 1b).

Soluble sugars mainly include glucose, sucrose, trehalose, and so on. They can stabilize the cell membrane and protoplast [18]. Moreover, they protect soluble enzymes from high intracellular concentrations of inorganic ions [19]. Carbon and the energy of the other organic syntheses are derived from soluble sugars. Under salt

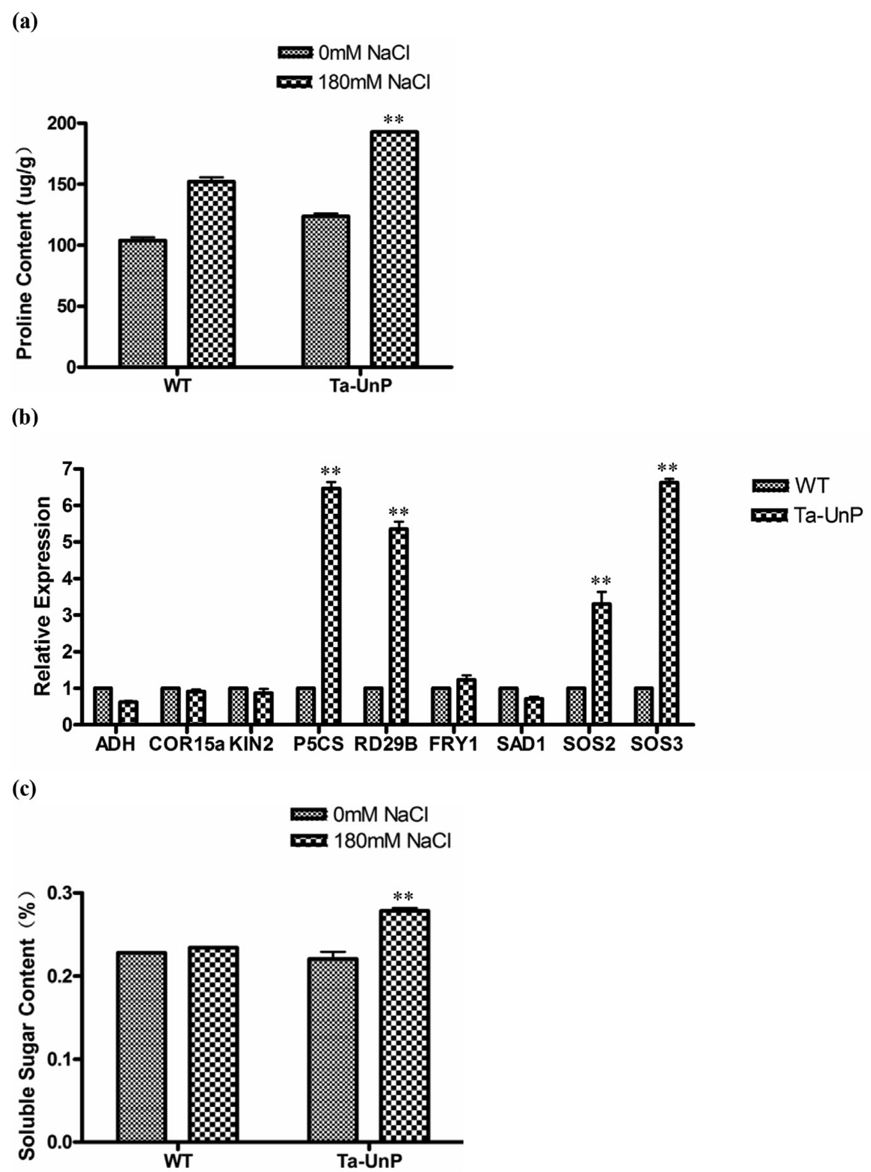

Fig. 1. Content of proline, content of soluble sugar and relative expression of nine stress-related genes in *Ta-UnP* transgenic *Arabidopsis* plants (from Liang et al., 2014). (a) Content of proline; (b) Content of soluble sugar; (c) Relative expression of nine stress-related genes in *Ta-UnP* transgenic *Arabidopsis* plants.

Please cite this article in press as: W. Liang, et al., Plant salt-tolerance mechanism: A review, Biochemical and Biophysical Research Communications (2017), https://doi.org/10.1016/j.bbrc.2017.11.043