



Review

Physiological and biochemical perspectives of non-salt tolerant plants during bacterial interaction against soil salinity

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ABSTRACT

Climatic changes on earth affect the soil quality of agricultural lands, especially by increasing salt deposition in soil, which results in soil salinity. Soil salinity is a major challenge to growth and reproduction among glycophytes (including all crop plants). Soil bacteria present in the rhizosphere and/or roots naturally protect plants from the adverse effects of soil salinity by reprogramming the stress-induced physiological changes in plants. Bacteria can enrich the soil with major nutrients (nitrogen, phosphorus, and potassium) in a form easily available to plants and prevent the transport of excess sodium to roots (exopolysaccharides secreted by bacteria bind with sodium ions) for maintaining ionic balance and water potential in cells. Salinity also affects plant growth regulators and suppresses seed germination and root and shoot growth. Bacterial secretion of indole-3-acetic acid and gibberellins compensates for the salt-induced hormonal decrease in plants, and bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase synthesis decreases ethylene production to stimulate plant growth. Furthermore, bacteria modulate the redox state of salinity-affected plants by enhancing antioxidants and polyamines, which leads to increased photosynthetic efficiency. Bacteria-induced accumulation of compatible solutes in stressed plants regulates plant cellular activities and prevents salt stress damage. Plant-bacterial interaction reprograms the expression of salt stress-responsive genes and proteins in salinity-affected plants, resulting in a precise stress mitigation metabolism as a defense mechanism. Soil bacteria increase the fertility of soil and regulate the plant functions to prevent the salinity effects in glycophytes. This review explains the current understanding about the physiological changes induced in glycophytes during bacterial interaction to alleviate the adverse effects of soil salinity stress.

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1. Introduction

Glyphophytes are plants that can grow optimally in soil containing low sodium concentrations and their survival is adversely affected by the accumulation of salt in soil (Horie et al., 2012). Several crop plants are glycophytes and their growth and yields are considerably reduced by global climatic changes, including low precipitation, high rate of evaporation, and irrigation using hard water (Shrivastava and Kumar, 2015). The rate of salinized arable land is increasing annually by 10% and it has been assessed that ~50% of agricultural land would be salinized by 2050 (Jamil et al., 2011). Crop productivity is declining yearly owing to the adverse effects of soil salinity. To prevent food scarcity for the increasing human population, several studies from different perspectives are being conducted to enhance the stress tolerance of crop plants grown in saline soils using diverse strategies. Although traditional crop breeding has been practiced to develop tolerance to salt stress, only limited success has been achieved owing to the complex genetic nature of this trait (Flowers, 2004). Further, transgenic plant technology and molecular breeding applications to develop salt-tolerant agricultural plants have also achieved limited success (Bhatnagar-Mathur et al., 2008; James et al., 2008; Wang et al., 2003). Alternately, substances that mitigate salt stress and promote plant growth, such as phytohormones (Khadri et al., 2006), triacontanol (Radhakrishnan and Ranjitha-Kumari, 2008), and polyamines (Radhakrishnan and Lee, 2013) have been considered beneficial in increasing the salt stress tolerance in crop plants. Some of the physical factors (gamma irradiation and magnetic field) pre-treatment could mitigate the toxic effects of salt stress in crop plants (Baek et al., 2005; Radhakrishnan et al., 2012).

There is some evidence that some microorganisms have the potential to help alleviate salinity stress. Generally, plants are anchored in soil to absorb water and nutrients and for physical support. Soil contains nutrients as well as biologically important macro and microorganisms (Barber, 1995; Edwards and Fletcher, 1988). The beneficial effects of microorganisms (such as bacteria and fungi) on plant growth are well documented (Kang et al., 2014a,b; Radhakrishnan and Lee, 2015). The chloroplast and mitochondria in the plant cell are evolutionarily considered as endophytic symbionts that have evolved from free-living bacteria (Margulis, 1970). This understanding has strongly indicated that soil microbes and plants have mutually interacted for their growth and survival. Microorganisms beneficial to plants secrete metabolites that solubilize the complex organic substances into simpler forms making them easily available to plants, enhance plant growth, and protect plants from diseases and other abiotic stresses (Bianco and Defez, 2009; Karlidag et al., 2013; Lopez-Gomez et al., 2014a,b; Kang et al., 2015a). In particular, bacterial synthesis of aminocyclopropane-1-carboxylate (ACC) deaminase, exopolysaccharides, indole-3-acetic acid (IAA), gibberellins (GAs), hydrogen cyanide (HCN), proline, nodulation factors, 5-aminolevulinic acid, and siderophores, as well as the ability for phosphate solubilization, potassium solubilization, nitrogen fixation, and ammonia production in bacteria can increase the salt stress tolerance in plants (Qurashi and Sabri, 2011; Mohamed and Gomaa, 2012; Kang et al., 2014b; Nunkaew et al., 2014; Munoz et al., 2014; Palaniyandi et al., 2014). The identification of salt-tolerant and plant growth-promoting bacteria could be beneficial

in increasing crop yields under conditions of soil salinity (Zahir et al., 2009; Ahmad et al., 2012; Martinez et al., 2015a). Bacterial isolates of *Bacillus* and *Pseudomonas* have been widely reported as plant growth-promoting bacteria under salt stress conditions (Table 1). In addition, other bacterial isolates of *Achromobacter*, *Acinetobacter*, *Aeromonas*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Brachybacterium*, *Brevibacterium*, *Burkholderia*, *Clostridium*, *Curtobacterium*, *Ensifer*, *Enterobacter*, *Exiguobacterium*, *Geobacillus*, *Haererohalobacter*, *Halobacillus*, *Halomonas*, *Klebsiella*, *Kocuria*, *Methylobacterium*, *Micrococcus*, *Nitrincola*, *Oceanobacillus*, *Ochrobactrum*, *Paenibacillus*, *Planococcus*, *Promicromonospora*, *Raoultella*, *Rhizobium*, *Rhodopseudomonas*, *Serratia*, *Sinorhizobium*, *Sphingomonas*, *Staphylococcus*, *Streptomyces*, and *Variovorax* genera have been identified and documented as having the capacity to mitigate the toxic effects of salinity stress in plants (Table 1).

Bacteria can survive in unfavorable environmental conditions, including drought, increased salinity, and extreme temperatures by synthesizing specific metabolites to adapt to the harsh environments (Sandhya and Ali, 2015). The inoculation and enrichment of salt-tolerant bacteria populations in salt-affected agricultural lands would be beneficial in enhancing the yields of crop plants. Although, several studies have reported that salt-tolerant bacteria enhance plant growth and yield, only a few studies have focused on the bacteria-induced functional changes in plant physiology and metabolism against salt stress. To understand the mechanism by which bacterial fertilizers mitigate the adverse effects of salinity stress in plants, this review assesses the biochemical and physiological changes induced in salt-stressed plants on interaction with beneficial soil bacteria.

2. Bacterial metabolites promoting salt tolerance in plants

Bacteria synthesize and secrete various substances that are helpful in conferring tolerance against salt stress in plants. Several salt-tolerant bacteria and their metabolites (listed in Table 1) can mitigate the adverse effects of salinity stress in plants by regulating plant cell physiological conditions. The predominant metabolite, ACC deaminase, is synthesized by *Achromobacter*, *Aeromonas*, *Alcaligenes*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Ochrobactrum*, *Planococcus*, *Pseudomonas*, *Raoultella*, *Rhizobium*, *Serratia*, *Streptomyces*, and *Variovorax* and inoculation of these bacteria in saline soil is an accepted method for increasing salt tolerance in plants (Ashraf et al., 2004; Mayak et al., 2004; Zahir et al., 2009; Mohamed and Gomaa, 2012; Wu et al., 2012; Bal et al., 2013; Liu et al., 2013; Nadeem et al., 2013; Nautiyal et al., 2013; Rajput et al., 2013; Palaniyandi et al., 2014; Akhtar et al., 2015; Koc, 2015; Paulucci et al., 2015; Upadhyay and Singh, 2015; Wang et al., 2016).

In addition, *Acinetobacter* and *Pseudomonas* produce GAs and *Alcaligenes*, *Arthrobacter*, *Azotobacter*, *Bacillus*, *Curtobacterium*, *Ensifer*, *Enterobacter*, *Halobacillus*, *Klebsiella*, *Micrococcus*, *Nitrincola*, *Ochrobactrum*, *Paenibacillus*, *Planococcus*, *Pseudomonas*, *Sinorhizobium*, and *Streptomyces* produce IAA, which also support plant growth under salt stress (Bianco and Defez, 2009; Tiwari et al., 2011; Mohamed and Gomaa, 2012; Qurashi and Sabri, 2012; Rojas-Tapias et al., 2012; Bal et al., 2013; Desale et al., 2014; Kang et al., 2014a,b; Kim et al., 2014; Palaniyandi et al., 2014; Ali et al., 2015; Cardinale et al., 2015; Paulucci et al., 2015; Singh et al., 2015;

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