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Review article

Mechanisms of plant growth promoting *rhizobacteria* (PGPR) and *mycorrhizae* fungi to enhancement of plant growth under salinity stress: A review

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ABSTRACT

Salinity is the major environmental factor limiting plant growth and productivity. Under salinity conditions, plant growth is affected by a number of factors such as hormonal and nutritional imbalance, ion toxicity, physiological disorders, susceptibility to diseases, etc. Plant growth under stress conditions may be enhanced by the application of microbial inoculation including plant growth promoting rhizobacteria (PGPR) and mycorrhizal fungi. These microbes can promote plant growth by regulating nutritional and hormonal balance, producing plant growth regulators, solubilizing nutrients and inducing resistance against plant pathogens. The present review comprehensively discusses on the effectiveness of PGPR and mycorrhizal fungi for enhancing plant growth under salinity stress. The mechanisms involved in plant salinity tolerance under stress conditions have been discussed at length in this review. Also the review discusses the role of rhizobacteria and mycorrhizae in combination in enhancing plant growth under stress conditions.

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1. Introduction

The world population, currently ~7 billion, continues to increase so that by 2020 it is estimated to reach ~8 billion. There is a real concern regarding our ability to feed all of these people, an endeavor that requires that agricultural productivity continues to increase. Thus, more than ever, obtaining high yields is the main challenge for agriculture. In addition, in recent years both producers and consumers have increasingly focused on the health and quality of foods, as well as on their organoleptic and nutritional properties (Elisa and Bernard, 2011). Soil microorganisms with beneficial activity on plant growth and health represent an attractive alternative to conventional agricultural (Antoun and Pre´vost, 2005). Although plant growth promoting rhizobacteria (PGPR) occur in soil, usually their numbers are not high enough to compete with other bacteria commonly established in the rhizosphere. Therefore, for agronomic utility, inoculation of plants by target microorganisms at a much higher concentration than those normally found in soil is necessary to take advantage of their beneficial properties for plant yield enhancement. (Igual, 2001). Salinization of soil is a serious problem and is increasing steadily in many parts of the world, in particular in arid and semi-arid areas (Giri et al., 2003; Al-Karaki, 2006). At present, out of 1·5 billion hectares of cultivated land around the world, about 77 million hectares (5 %) is affected by excess salt content (Sheng et al., 2008). The direct effects of salt on plant growth may involve, (a) reduction in the osmotic potential of the soil solution that reduces the amount of water available to the plant causing physiological drought – to counteract this problem plants must maintain lower internal osmotic potentials in order to prevent water movement from roots into the plant soil (Feng et al., 2002; Jahromi et al., 2008); (b) toxicity of excessive Na+ and Cl− ions towards the cell – the toxic effects include disruption to the structure of enzymes and other macromolecules, damage to cell organelles and plasma membrane, disruption of photosynthesis, respiration and protein synthesis (Juniper and Abbott, 1993; Feng et al., 2002); and (c) nutrient imbalance in the plant caused by nutrient uptake and/or transport to the shoot leading to ion deficiencies (Marschner, 1995; Adiku et al., 2001). Plants, in their natural environment are colonized both by external and internal microorganisms. Some microorganisms, particularly beneficial bacteria and fungi can improve plant performance under stress environments and, consequently, enhance yield (Brown, 1974; Levy et al., 1983; Creus et al., 1998). Arbuscular mycorrhizal fungi (AMF) are associated with the roots of over 80 % terrestrial plant species (Smith and Read, 1997) including halophytes, hydrophytes and xerophytes. In this respect, biological processes such as mycorrhizal application to alleviate salt stress would be a better option. AMF have been shown to promote plant growth and salinity tolerance by many researchers. They promote salinity tolerance by employing various mechanisms, such as enhancing nutrient acquisition (Al-Karaki and Al-Raddad, 1997), producing plant growth hormones, improving rhizospheric and soil conditions (Lindermann, 1994), altering the physiological and biochemical properties of the host (Smith and Read, 1995) and defending roots against soil-borne pathogens (Dehne, 1982). Inoculations of wheat seedlings with bacteria that produce exopolysaccharates (EPS) affect the restriction of sodium uptake and stimulation of plant growth under conditions of stress caused by high salinity. Corn, beans and clover inoculated with AM fungi improved their osmoregulation and increased proline accumulation which resulted in salinity resistance (Grover et al., 2010). This review will cover the effect of AMF in saline soils in relating to the alleviation of salt stress and mechanisms used by PGPR to enhancement of growth plants.

2. Plant growth promoting rhizobacteria and plant growth

PGPR promote plant growth by employing certain mechanisms and protect the plant from salinity. These agents can increase plant tolerance against stress conditions. Furthermore, some of these mechanisms may be present in one particular strain of bacteria while absent in others. For example, some Pseudomonas species have the ability to lower stress-induced ethylene concentration by ACC-deaminase enzyme and also decrease the availability of Na+ by producing exopolysaccharides. In saline conditions, elevated level of sodium (Na+) not only disturbs the uptake of other nutrients but also causes specific ion toxicity (Ashraf, 1994). For salinity tolerance and maintenance of osmotic potential in a plant, a high K +/Na+ ratio is very essential (Hamdia et al., 2004). Certain PGPR strains also have the ability to protect the plants from the harmful effects of high Na+concentration in the saline soil environment. They do this by their ability to produce exopolysaccharides. The exopolysaccharides so produced reduce Na+ uptake in the plant by binding it and also by biofilm formation (Geddie and Sutherland, 1993; Khodair et al., 2008; Qurashi and Sabri, 2012). The reduced availability of Na+ results in lowering the uptake of Na+ thereby maintaining high K+/Na+ ratio that enables the plant to survive better in salt stressed conditions (Ashraf et al., 2004; Han and Lee, 2005; Khodair et al., 2008). The exopolysaccharides also play an important role in plants exposed to water deficit conditions. As drought conditions cause a negative influence on plants as well as on microbial population, these exopolysaccharides also protect the bacteria and plants from desiccation, and enable them to continue their growth under water deficit conditions (Sandhya et al., 2009).

3.Phosphate solubilization

The Phosphate solubilization effect seems to be the most important mechanism of plant growth promotion in moderately to fertile soils. Strains from the genera Pseudomonas, Bacillus and Rhizobium are among the most powerful P solubilizers (Rodriguez and Fraga, 1999). A number of theories have been proposed to explain the mechanism of phosphate solubilization. Important among them are, Acid production and Proton and enzyme theory.

4. Acid production theory

According to this theory, the process of phosphate solubilization by Phosphate solubilization microorganisms (PSMs) is due to the production of organic acids which is accompanied by the acidification of the medium (Puente et al., 2004). A decrease in the pH of the filtrate from the initial value of 7.0 to a final value of 2.0 was recorded by many workers (Illmer and Schinner, 1992). The analysis of culture filtrates of PSMs has shown the presence of number of organic acids such as malic, glyoxalic, succinic, fumaric, tartaric, alpha keto butyric, oxalic, citric, 2-ketogluconic and gluconic acid (Fasim et al., 2002; Kim et al., 1997). The amount and type of the organic acid produced varied with the microorganism. The organic acids released in the culture filtrates react with the insoluble phosphate. The amount of soluble phosphate released depends on the strength and type of acid. Aliphatic acids are found to be more effective in P solubilization then phenolic acids and citric acids. Tribasic and dibasic acids are also more effective than monobasic acids. In the presence of tribasic acids and dibasic acids, a secondary effect appears due to the ability of these acids to form unionized association compounds with calcium thereby removing calcium from the solution and increasing soluble phosphate concentration (Gaur and Gaind, 1999). Fasim et al., (2002) have reported bacterial solubilization of insoluble zinc oxide and zinc phosphate, mediated by the production of gluconic and 2-ketogluconic acid. Gluconic acid is the principal organic acid produced by Pseudomonas sp. (Illmer and Schinner, 1992) and Burkholderia cepacia (Rodríguez and Fraga 1999) Rhizobium leguminosarum (Halder et al., 1990) Sinorhizobium meliloti (Halder and Chakrabartty, 1993) and Bacillus firmus (Banik and Dey, 1982) produce noticeable amounts of 2-ketogluconic acid. Besides organic acids, inorganic acids such as nitric and sulphuric acids are also produced by the nitrifying bacteria and thiobacillus during the oxidation of nitrogenous or inorganic compounds of sulphur which react with calcium phosphate and convert them into soluble forms (Gaur and Gaind, 1999). The nature and type of acid production is mainly dependent on the carbon source (Reyes et al., 1999). In general, oxalic, citric, and gluconic acid, are strong solubilizing agents of feldspar, biotite, and phyllosilicates, (Torre et al., 1993).

5. Proton and enzyme theory

Esterase type enzymes are known to be involved in liberating phosphorus from organic phosphatic compounds. PSMs are also known to produce phosphatase enzyme along with acids which cause the solubilization of P in aquatic environment (Alghazali et al., 1986). Solubilization without acid production is due to the release of protons accompanying respiration or ammonium assimilation (Parks et al., 1990). More solubilization occurs with ammonium salts than with nitrate salts as the nitrogen source in the media (Gaur and Gaind, 1999). Solubilization of Ca–P complexes is quite prevalent among PSB, whereas the release of P by Fe–P or Al–P is very rare.

6. Hormones production by PGPR

PGPR produce hormones that are believed to be related to their ability to stimulate plant growth. Indole-3-acetic acid is a phytohormone which is known to be involved in root initiation, cell division, and cell enlargement (Salisbury et al, 1994). This hormone is very commonly produced by PGPR (Barazani and friedman, 1991). Most commonly, IAA-producing PGPR are believed to increase root growth and root length, resulting in greater root surface area which enables the plant to access more nutrients from soil. Cytokinins are a class of phytohormones which are known to promote cell divisions, cell enlargement, and tissue expansion in certain plant parts (Salisbury et al, 1994). Cytokinin is produced by Pseudomonas fluorescens isolating from the rhizosphere of the soybean (salamone et al, 2001). Gibberellins are most commonly associated with modifying plant morphology by the extension of plant tissue, particularly stem tissue (Salisbury et al, 1994). Evidence of Gibberellic Acid production by PGPR is rare; however, Gutierrez-Manero et al. (2000) provide evidence that four different forms of Gibberellic Acid are produced by Bacillus pumilus and B. licheniformis. Ethylene is the only gaseous phytohormone. It is also known as the wounding hormone because its production in the plant can be induced by physical or chemical perturbation of plant tissues (Salisbury et al, 1994). Glick et al (2003) put forward the theory that the mode of action of some PGPR was the production of 1-carboxylate deaminase, an enzyme which could cleave ACC, the immediate precursor to ethylene in the biosynthetic pathway for ethylene in plant. The signaling pathway that is activated in this case depends on ethylene but is independent of SA and JA signaling (Ryu et al, 2004). It would be interesting to investigate the capacity of plant growth promoting Pseudomonas spp. to produce 2, 3-butanediol.

7. Arbuscullar mycorrhizae and salt stress alleviation

Mycorrhizae are mutualistic associations of fungi and roots. The fungus benefits from a steady supply of sugar from the host plant. The host plant benefits because the fungus increases the surface area for water uptake and mineral absorption. Mycorrhizal fungi also secrete growth factors that stimulate root growth and branching. Mycorrhizal associations consist of two major types, Ecto mycorrhizae and Arbuscular mycorrhizae. In ectomycorrhizae, the mycelium of the fungus forms a dense sheath over the surface of the root. These hyphae form a network in the apoplast, but do not penetrate the root cells. Ectomycorrhizae occur in about 10% of plant families including pine, spruce, oak, walnut, birch, willow, and eucalyptus.In arbuscular mycorrhizae(AMF), microscopic fungal hyphae extend into the root. These mycorrhizae penetrate the cell wall but not the plasma membrane to form branched arbuscules within root cells. Hyphae can form arbuscules within cells; these are important sites of nutrient transfer. Arbuscular mycorrhizae occur in about 85% of plant species, including grains and legumes. The mycorrhizae stimulate growth of plants via, Enhancement of water absorption and minimal water stress, Enhancement of nutrients uptake by plants, specially, in high salinity levels, protection of plants against root pathogens via exudates of water soluble compounds such as amino acids, organic acids and phenolic compounds in mycorrhizal roots. AMF have been known to occur naturally in saline environments (Yamato et al., 2008). Aliasgharzadeh et al (2001) observed that the most predominant species of AMF, Glomus intraradices, G. versiform and G. etunicatum, in the severely saline soils of the Tabriz plains (electrical conductivity of soils (ECe) around 16 dS m−1). Rabie et al (2005) reported that the dry wet of lettuce plants inoculated with AM fungi at the salinities of control, 2, 4 and 12 ds/m, increased by 3.4, 8.2, 11.7 and 29.3 % respectively, compared with non inoculated plants, indicating the more effectiveness of AM at the higher levels of salt stress. Arbuscular mycorrhizaes promote salinity tolerance by employing various mechanisms, such as, enhancing nutrient acquisition (Al-Karaki and Al-Raddad, 1997), producing plant growth hormones, improving rhizospheric and soil conditions (Lindermann, 1994), altering the physiological and biochemical properties of the host (Smith and Read, 1995) and defending roots against soil-borne pathogens (Dehne, 1982).

8. Nutrient uptake

8.1. phosphorous

Soil salinity significantly reduces the absorption of mineral nutrients, especially phosphorus (P), because phosphate ions precipitate with Ca^{2+}, Mg^{2+} and Zn^{2+} ions in salt-stressed soils and become unavailable to plants (Azcón-Aguilar et al., 1979). Mycorrhizal inoculation can increase P concentration in plants by enhancing its uptake facilitated by the extensive hyphae of the fungus which allows them to explore more soil volume than the non-mycorrhizal plants (Ruiz-Lozano and Azcón, 2000). It is estimated that external hyphae deliver up to 80 % of a plant's P requirements (Matamoros et al., 1999). Improved P nutrition in AM-inoculated plants may improve their growth rate, antioxidant production and nodulation enhancement and nitrogen fixation in legumes (Garg and Manchanda, 2008).

8.2. Nitrogen

Salinity interferes with nitrogen (N) acquisition and utilization by influencing different stages of N metabolism, such as, NO3− uptake and reduction and protein synthesis (Frechill et al., 2001). Increased N uptake in an AM plant may due to a change in N metabolism brought about by changes in the enzymes associated with N metabolism (Govindarajulu et al., 2005). Studies have reported that improved N nutrition may help to reduce the toxic effects of Na ions by reducing its uptake and this may indirectly help in maintaining the chlorophyll content of the plant (Giri and Mukerji, 2004). However, the exact mechanisms used by AMF to uptake N under salt-stress conditions are not clearly understood. Mardukhi et al (2011) indicated that AM fungi significantly enhanced the concentrations of all nutrients including N, P, K, Ca, Mg, Mn, Cu, Fe and Zn in shoots in different wheat genotypes.

9. Biochemical changes

9.1. Osmoregulation

During stress conditions plants need to maintain internal water potential below that of soil and maintain turgor and water uptake for growth (Tester and Davenport 2003). This requires an increase in osmotica, either by uptake of soil solutes or by synthesis of metabolic (compatible) solutes (Zhifang and Loescher 2003). The solutes that accumulate vary with the organism and even between plant species and a major category of organic osmotic solutes consists of simple sugars (mainly fructose and glucose), sugar alcohols (glycerol and methylated inositols) and complex sugars (trehalose, raffinose andfructans) (Bohnert and Jensen 1996). Others include quaternary amino acidderivatives (proline, glycine betaine, β-alanine betaine, proline betaine, tertiaryamines 1,4,5,6-tetrahydro-2-mehyl-4-carboxyl pyrimidine), and sulfoniumcompounds (choline osulfate, dimethyl sulfonium propironate) (Yokoi et al. 2002). These compounds are generally present in low concentrations when the plant is not under salt stress (Feng et al., 2002). Sharifi et al. (2007) reported a higher proline concentration in AM soybean than the non-AM plants at different salinity levels (0, 50, 100, 150 and 200 mm NaCl). They also observed that in AM plants, a higher level of proline concentration is found in roots than shoots. This may be due to the fact that the roots are the primary sites of water absorption and, therefore, must maintain osmotic balance between water-absorbing root cells and the external media.

10. Physiological changes

Salt stress can affect the plant by disrupting its physiological mechanisms such as, water status, gas exchange, membrane disruption, decreasing photosynthetic efficiency.

10.1. Chlorophyll content

Increasing salinity causes a reduction in chlorophyll content due to suppression of specific enzymes that are responsible for the synthesis of photosynthetic pigments (Sheng et al., 2008). In the presence of mycorrhiza, the antagonistic effect of Na+ on Mg2+ uptake is counter balanced and suppressed (Giri et al., 2003). A higher chlorophyll content in leaves of mycorrhizal plants under saline conditions has been observed by various authors (Giri and Mukerji, 2004; Sannazzaro et al., 2006; Zuccarini, 2007; Colla et al., 2008; Sheng et al., 2008).

10.2. Water status

Plants in saline soils are subjected to physiological drought (Fuzy et al., 2008). Many authors have reported that plants inoculated with AMF maintain relatively higher water content compared with non inoculated plants (Colla et al., 2008; Jahromi et al., 2008; Sheng et al., 2008). This is facilitated by the improved hydraulic conductivity of the root at low water potential (Kapoor et al., 2008). The improved root conductance is associated with a longer root and an altered root system morphology induced by AMF (Kothari et al., 1990).

Another mechanism used by AM fungi to facilitate plant growth under salinity stress is the regulation of plant nutrition. High Na+ concentration under salinity stress is detrimental for normal plant growth and low K+/Na+ ratio has been observed generally in salt sensitive plants (Ashraf et al., 2004). Therefore, improved K+/Na+ ratio is believed to be a potential indicator of salinity tolerance in most plants. The AM fungi also play an important role in maintaining a high K+/Na+ ratio in host plants exposed to saline conditions (Giri et al., 2007; Sannazzaro et al., 2006; Selvakumar and Thamizhiniyan, 2011; Zhang et al., 2011).

11. Nitrogen fixation

Among these processes, nitrogen fixation is one of the most important processes. The adverse effects of salt stress on nitrogen fixation may be due to salt-induced effect on the activity of rhizobia for infection of legumes, effect on the growth and development of nodules and, finally direct effect on the activity of nodules for nitrogen fixation (Bouhmouch et al., 2005). Although rhizobium is more tolerant to salinity than a host plant, a great magnitude of variability among rhizobial strains with respect to salinity tolerance has been observed. Salinity stress is believed to significantly reduce the nitrogenase activity in microorganisms (Rai and Tiwari, 1999). However, it is also generally reported that the biosynthesis of nitrogenase is inhibited more than nitrogenase activity (Tripathi et al., 2002). In addition to non-leguminous plants, the AM fungus has great potential to improve nodulation, and hence nitrogen fixation in legumes. Increased phosphorus and other nutrients as well as synergistic interactions with other rhizospheric microorganisms could be very effective for enhancing nitrogen fixation under stressful environments for achieving maximum grain yield of legumes. Some studies conducted have shown that inoculation of AM fungus with nitrogen fixer bacteria together was very effective for enhancing nitrogen fixation in legumes (Lesueur and Sarr, 2008; Rabie et al., 2005). As AM fungi exist naturally in stressful environments like salinity (Evelin et al., 2009) so their association with plants could be very effective for improving growth and vigor of plants under stress conditions (Kumar et al., 2010). Most of the legumes are known to be salt sensitive (Munns, 2002). Garg and Chandel (2011) observed that symbiotic association of pigeon pea (Cajanus cajan) with G. mosseae led to a significant improvement in plant dry mass and nitrogen-fixing potential of nodules under salt stress. The application of AM fungus with PGPR is also found to enhance nitrogen fixation ability of plants. For example,dual application of P. Putida strain R-20 with AM fungus enhanced growth and nodulation of sub clover (Meyer and Linderman, 1986). Higher leghemoglobin content was observed in mycorrhizal plants (Garg and Manchanda, 2008). Mycorrhizal plants also possess a higher nitrogenase activity.

12. Inducing stress tolerance through combined inoculation of PGPR and mycorrhizae (PGPR–mycorrhizae interactions)

Beside powerful effect of dual inoculation of PGPR and mycorrhizae to enhance plant growth under normal conditions, the interactions between them could be very useful to reduce the negative impact of a stress on plant growth and development. High concentration of sodium in saline soil caused a negative impact on essential nutrients uptake and dual inoculation of PGPR and mycorrhizae proved helpful for providing nutrients to plants subjected to saline environment (Gamalero et al., 2010). A pot study carried out by Shirmardi et al. (2010) on sunflower (Helianthus annuus L.) under salinity stress is an evidence of this claim. They found that inoculation with PGPR and mycorrhizal fungus significantly enhanced the uptake of essential nutrients. Although they observed that mycorrhizae enhanced the uptake of phosphorus however, they demonstrated that due to small soil volume in pots, hyphae could not work properly and hence did not show their full potential. The recent results of Najafi et al. (2012) have shown the positive effects of PGPR–mycorrhizae interactions with barley root enhanced the water and nutrition absorption. The major impact of drought on plant growth is the non availability of water. The dual inoculation of PGPR and mycorrhizae increased colonization and biological grain yield of barley under field conditions. This association is also useful for protecting the plant from deleterious impact of plant pathogens. The effectiveness of co-inoculation was depending upon mycorrhizal species. This positive effect dual inoculation of PGPR and mycorrhizal fungi might be due to combination of certain mechanisms and also the synergistic effect of these populations on one another. However, the selection of these combinations and their effectiveness under natural soil environment still needs further investigation.

13. Future perspective

Salt stress causes huge losses of agriculture productivity worldwide. Therefore, plant biologists aimed at overcoming severe environmental stresses needs to be quickly and fully implemented. The stress-induced negative impact on plant growth can be alleviated and/or minimized by naturally occurring microorganisms including bacteria and fungi whether applied singly or in combination. Although a number of studies revealed the effectiveness of sole application of PGPR or mycorrhizae for improving plant growth under stress conditions, however, a number of researchers have reported more usefulness of dual inoculation compared to that of individual inoculation. The role of PGPR and mycorrhizae for nutrient acquisition is well defined in the above discussion. Identification of genes controlling stress tolerance traits of PGPR and mycorrhizae would enhance our knowledge about the molecular basis of the stress tolerance mechanisms. Selection of microorganisms from stressed ecosystems may contribute to the concept of biotechnology application in agriculture.

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