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Plant Growth-Promoting Rhizobacteria: An Emerging Method for the Enhancement of Wheat Tolerance against Salinity Stress-(Review)

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Abstract

Salinity is a major threat to crop productivity and agriculture development worldwide. Intensive research has been conducted to overcome such problem focusing primarily on efficient resource management and crop improvement. However, such approaches take a long time and are considerably expensive. Therefore, there is an urgent need to develop new economical methods that are effective in ameliorating the adverse effects of high salinity levels in the soil. The isolation and use of halotolerant Plant Growth-Promoting Rhizobacteria (PGPR), from natural saline habitats, are needed to reduce the adverse effects of salinity on crop species. The ability of PGPR to provide plants with necessary nutrients is considered a promising substitute to chemical fertilizers and organic alternatives to promote growth and improve the yield of crops. PGPR have been reported to enhance germination, and to delay leaf senescence at various salinity levels. Several bacterial activities and mechanisms have been identified including the increase in nutrient availability through biological nitrogen fixation, inorganic phosphate solubilization, and siderophore production, which result in the improvement of nutrient availability and plant hormonal activities. The present review gives an update of scientific progress regarding PGPR utilization for improving staple food crops such as wheat.

Keywords: Halotolerant Plant Growth Promoting, 1-aminocydopropane-1-carboxylic acid (ACC) deaminase, Durum Wheat, Endophyte, Salinity.

1. Introduction

Crop productivity is severely affected by several biotic and abiotic stresses including drought, salinity, extreme temperatures, and pathogens, which can limit growth and development of any given crop. Salinity is an adverse condition affecting crop productivity in arid and semi-arid areas around the world where it caused an annual loss of 1-2% of arable land (Shrivastava and Kumar, 2015). Salinity alters cellular metabolism causing many physiological, morphological, biochemical, and molecular changes in plants. It also affects all aspects of plant growth and development from seed germination up to reproductive growth (Gupta and Huang, 2014). Salinity impact on plant growth and development is mainly attributed to changes in the osmotic status of plants, which has an immediate impact on water availability, accumulation of toxic ions such as Na^+ and Cl^- in the cells, and nutrient imbalances (Munns and Tester, 2008).

Wheat (*Triticum spp.*) is considered one of the most important crops in the world; it is a staple food for over 35 % of the world's population where it provides more calories and proteins than any other cultivated crop (FAOSTAT, 2017). Durum wheat (*T. turgidum subsp. durum*) forms about 10 % of all wheat cultivated areas in the world. Indeed, it is a major cereal crop in the Mediterranean region (Kabbaj *et al.*, 2017). Several studies indicate that the wild progenitor of modern durum wheat is widely distributed in the Jordan Valley region on the eastern side of the Dead Sea with archeological evidences of durum wheat utilization near the Dead Sea region as far back as 9500 years ago (Weide, 2015). High genetic diversity in Jordanian germplasm is considered a valuable resource to improve durum wheat tolerance against different abiotic stresses including drought, heat, and salinity (Abdel-Ghani, 2009; Abu-Romman, 2016; Jaradat, 1992).

High-salt stress has more pronounced effects on durum-wheat growth and development compared with other cereals. This is mainly attributed to its inability to exclude Na^+ from its tissues (Roy *et al.*, 2014). Several approaches have been used to reduce salinity effects on durum wheat, including proper soil practices, irrigation managements, traditional breeding and genetic engineering (Katerji *et al.*, 2009).

The rhizosphere environment harbors many microorganisms that can play a major role in enhancing

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plant productivity under saline conditions (Etesami and Beattie, 2018). In such environments, Plant Growth-Promoting Rhizobacteria (PGPR) are considered beneficial microorganisms that possess many growth-promoting traits, which are crucial to improving plant growth and the yield of crops, either directly or indirectly. They can also help in alleviating the adverse effects of many stresses, including salinity. The direct plant-growth promotion occurs when PGPR facilitate the plant nutrients' uptake from the surrounding environments by phosphorus solubilization, nitrogen fixation, and/or by producing siderophore to sequester iron (Etesami and Beattie, 2018). Furthermore, PGPR can modulate plant growth by promoting the production and regulation of phytohormones, such as Indole Acetic Acid (IAA) (Arshadullah *et al.*, 2017), or by lowering plant ethylene production by the activity of the 1-Aminocyclopropane-1-carboxylate (ACC) deaminase enzyme (Glick, 2014). On the other hand, indirect plant-growth promotion by PGPR occurs when they limit or prevent plant damage caused by various pathogenic agents such as bacteria, fungi, and nematodes (Compant *et al.*, 2005). This review focuses on the soil salinity problem as a challenge to improve crops, primarily wheat productivity. It discusses the utilization of PGPR as a strategy to mitigate soil salinity-stress and identifies the mechanisms to cope with such stresses.

2. Soil Salinity: A Global Problem

Soil salinity is a major problem affecting crop productivity in arid and semi-arid areas around the globe with salinity-affected soils covering more than 7 % of total arable lands of the world (Rasool *et al.*, 2013). Climate change and human activities result in increased salt accumulation in the soil; high rates of evapotranspiration, improper drainage and limited leaching of mineral salts from the soil surface result in increased salinity levels in arid and semi-arid regions (Mohan *et al.*, 2017). According to the United States Department of Agriculture (USDA), a given soil with an Electrical Conductivity (EC) of 4 dS m^{-1} is considered as saline soil. The inhibitory effect of excess salt in the soil can impact many plant cellular, physiological, biochemical and molecular processes that will hinder plant growth and eventually reduce crop production (Sairam and Tyagi, 2004).

3. Effect of Soil Salinity on Crop Plants

Plant growth and development are affected by salinity stress at different growth stages including germination, vegetative growth and reproductive development (Shrivastava and Kumar, 2015). Such adverse effects are mainly attributed to changes in cellular water and ionic status in growing plants (Munns and Tester, 2008). Plants are generally divided into four groups according to their salinity tolerance as follows: sensitive, moderately-sensitive, moderately- tolerant and tolerant. Many of the cereal crops are considered sensitive to high salt stress; bread wheat plants can withstand a salinity level up to 6 dSm^{-1}, while maize plants are considered less tolerant and are negatively affected at levels higher than 2 dSm^{-1}. Under salinity stress, the yield of many cereals, such as wheat, rice, and barley, is reduced significantly (Arshadullah *et al.*, 2017).

Salinity can have enormous negative effects on the morphological and physiological properties in wheat. It affects wheat-seed germination, seedling growth, water-uptake, photosynthesis, nutrient uptake, enzymatic activities and yield. Several studies revealed diverse effects of salt stress on different wheat species and cultivars, by which some were found tolerant, while others were susceptible (Hasanuzzaman *et al.*, 2017). Bread wheat (*T. aestivum*) showed moderate salinity-tolerance responses, while durum wheat (*T. turgidum subsp. durum*) was found more sensitive due to its inability to exclude Na^+ from its tissue (Roy *et al.*, 2014). High salinity levels were found to reduce the growth and development of eight Jordanian durum wheat genotypes when compared with non-saline treatments (Abdel-Ghani, 2009); three lines showed low values of susceptibility indices for germination, seminal root length and grain yield.

4. Amelioration of Soil Salinity

Several strategies can be adopted to manage the deleterious effects of soil salinity on plants such as leaching the excess of soluble salts from the soil, conventional plant breeding and genetic improvement aiming for tolerant varieties; however, all of these strategies have their own limitations. Plant breeding is a relatively slow process depending often on laborious programs, whereas genetically-modified crops are promising, but the limited success to find major genetic determinants of salt tolerance in plants and its acceptance by the general public are quite challenging (Key *et al.*, 2008).

Other tools used for salinity amelioration include the application of biochar, which is a charcoal-derived material that can adsorb Na^+ (Akhtar *et al.*, 2015), seed priming with plant growth-promoting substances, such as salicylic acid (Azooz, 2009), and the application of polyamines (Roychoudhury *et al.*, 2011).

Plant salt-tolerance can be improved by the application of eco-friendly strategies and through the use of beneficial microorganisms. The free-living or root-colonizing beneficial bacteria known as PGPR, which reside in the rhizosphere region, have many beneficial effects on plants (Arshadullah *et al.*, 2017). They comprise 2-5 % of the total rhizospheric bacteria surrounding a given plant-root system (Katiyar *et al.*, 2016). PGPR may possess multiple plant growth-promoting traits, which increase plant growth and the yield of crops, and can help in alleviating the effects of abiotic and biotic stresses through direct or indirect mechanisms (Numana *et al.*, 2018).

5. Plant Growth-Promoting Rhizobacteria

PGPR are composed of different groups of soil-living bacteria, which enhance plant growth through different mechanisms; they may be free-living or may colonize plant roots (Numana *et al.*, 2018). The rhizosphere is a region that extends only a few mm from the root system and is directly affected by the plant-root activity. In this region, the bacterial communities are the most dominant living organisms typically ranging from 10^6 to 10^9 CFU g^{-1} of a rhizospheric soil. Bacterial concentrations in the rhizosphere is generally higher than in bulk soils as a result of chemical signals and exudates produced by the roots, which support bacterial growth and their metabolism (Ahemad and Kibret, 2014). In general, PGPR are classified into two main groups according to their degree of proximity to the roots of their host plant: (1) Rhizospheric bacteria that live outside plant roots and include free-living rhizobacteria, which exist in the soil near the root system (rhizosphere), or bacteria colonizing the root surface (rhizoplane), and (2) Endophytic bacteria or endophytes that live inside plant-root tissues and include bacteria which inhabit intercellular spaces, specialized root structures (nodules), or in the vascular system (Menendez and Garcia-Fraile, 2017).

Most of rhizospheric bacteria belong to several phyla including: Cyanobacteria, Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria; in addition to several bacterial genera including: *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, and *Serratia* (Bhattacharyya and Jha, 2012). On the other hand, dominant endophytic bacterial phyla include: Proteobacteria, Actinobacteria and to a lesser extent Bacteroidetes and Firmicutes. The most common genera of bacterial endophytes include: *Pseudomonas, Bacillus, Burkholderia, Stenotrophomonas (Xanthomonas), Micrococcus, Pantoea* and *Mycobacterium*; endophytic bacteria enter into a plant tissue through primary and/or lateral root cracks, wounds, lenticels, and germinating radicles (Chaturvedi *et al.*, 2016). Upon their entrance into a plant tissue, the endophytes may become localized at the place of entry or spread systematically throughout the plant (Glick, 2014).

Compared to the rhizospheric bacteria, endophytes have many advantages to plants as they are able to colonize the internal tissues conferring growth-promoting abilities; this is mainly attributed to the internal protective environment inside the plant compared to its surfaces (Santos *et al.*, 2018). Furthermore, endophytic bacteria can utilize carbon sources and other metabolites provided by the plants compared with rhizospheric bacteria that don't have access to such resources. The localization of endophytes in special plant tissues like nodes and xylem vessels allow them to grow in low O_2 environment, which is necessary for their nitrogenase enzyme activity (Yousaf *et al.*, 2017). Furthermore, the ability of endophytic bacteria to fix nitrogen by nitrogenase or to produce growth regulators inside plant tissue helps plants to survive against multiple stresses when compared with rhizospheric bacteria (Santoyo *et al.*, 2016).

6. Growth-Promoting Mechanisms of PGPR under Stress Conditions

In general, PGPR are composed of a mixed group of unrelated taxa that promote plant growth under stress conditions through different mechanisms (Lugtenberg and Kamilova, 2009). Specific beneficial compounds, synthesized by PGPR, have a direct growth-promoting activity, which enhances the uptake of nutrients and minerals from the surrounding environment (Gouda *et al.*, 2018); growth-promotion mechanisms involve nitrogen fixation, inorganic phosphorus mobilization, and sequestering micronutrients by siderophores' production, and modulation of the levels of phytohormones. PGPR can improve plant growth by altering plant-hormone levels; by increasing the production of auxins, cytokinins and gibberellins, or decreasing ethylene production through the activity of ACC deaminase (Glick, 2014). Such alterations in phytohormones lead to increased root length, and/or the number of root hairs that enhance the nutrient uptake by plants. Furthermore, indirect growth-promoting activities of PGPR involve control against plant pathogens by the production of inhibitory substances (Egamberdieva and Lugtenberg, 2014).

6.1. PGPR Enhance Plant Nutrients Uptake

The ability of plants to adapt to soil salinity is highly affected by their mineral nutritional status. Under saline conditions, cellular nutritional imbalance results from the effect of salinity on nutrient availability and their uptake, transport, and distribution within the plant. It may also cause physiological disorders associated with major nutrients resulting in the development of deficiency symptoms (Grattan and Grieve, 1998). Such nutritional imbalance eventually hinders plant growth and development and subsequently their yield. Soil salinity results in osmotic- pressure changes and ionic strength in stressed plants that dramatically affect the cellular processes. Stressed plants were found to require higher amounts of nutrients to reduce the adverse effects of salinity stress (Khoshgoftarmanesh *et al.*, 2010). PGPR have been proven to be effective in circulating nutrients in the rhizosphere, and thereby increase their availability for plants, and subsequently reduce the need for chemical fertilizers. Under saline conditions, PGPR can increase nutrients' uptake and plant growth by different mechanisms such as atmospheric nitrogen fixation, solubilization of phosphorus, and sequestering iron by the production of siderophores (Ahemad and Kibret, 2014).

6.1.1. Biological Nitrogen Fixation

Nitrogen is an essential nutrient for plant growth and productivity. It is needed for the cellular synthesis of proteins, enzymes, chlorophyll, DNA and RNA. Although atmospheric nitrogen accounts for about 78 % of N_2, plants are unable to use it in this form. Nitrogen-fixing bacteria convert N_2 into ammonia, thus making it available for plants. Globally, the Biological Nitrogen Fixation (BNF) process accounts for approximately two-thirds of fixed nitrogen, and it is considered the most important feature in PGPR (Raymond *et al.*, 2004). In this perspective, N_2-fixing PGPR can form a symbiotic relationship with plants; members of the family rhizobiaceae form symbiosis with leguminous plants (e.g. *Rhizobia*) and non-leguminous trees (e.g. *Frankia*). The non-symbiotic nitrogen-fixing PGPR group includes endophytes or free-living bacteria such as cyanobacteria (e.g. *Azospirillum spp., Azotobacter spp., Gluconacetobacter diazotrophicus* and *Azocarus*) (Riggs *et al.*, 2001). In non-leguminous plants, diazotrophs can fix N_2 through the formation of a non-obligate interaction with the host plants (Glick *et al.*, 1999). Strains of diazotrophic bacteria, such as *Azotobacter*, *Azospirillum, Bacillus* and *Paenibacillus,* have gained economic importance due to their nitrogen-fixation ability as they possess the *nif* gene cluster (Goswami *et al.*, 2016). The ability of *Providencia spp.* AW4 and *Brevundimonas diminuta* AW7 strains to fix atmospheric nitrogen has been associated with higher yields and plant height in wheat plants (Rana *et al.*, 2011).

6.1.2. Phosphate Solubilization

Phosphorus (P) is a macronutrient, which is abundant in soils in both organic and inorganic forms, and is considered the second most important growth-limiting nutrient after nitrogen. However, the majority of inorganic P present in the soil is found in insoluble forms, which are not available for plants (Zaidi *et al.*, 2009). Plants can absorb P in two soluble forms: the monobasic (H_2PO^{-4}) and the dibasic (HPO_2^- ions). High-salt stress results in phosphate- deficiency symptoms due to its effect on P uptake and accumulation in plant tissues. To overcome such P limitation in soils, farmers use phosphate fertilizers that are considerably expensive and environmentally undesirable. An alternative solution to overcome low P levels in soils is the use of PGPR that possess a phosphate-solubilizing activity, known as Phosphate Solubilizing Bacteria (PSB); PSB can help in providing available forms to the plants, and act as a good substitute to chemical fertilizers (Richardson *et al.*, 2009). The solubilization of inorganic P results from the action of low molecular-weight organic acids synthesized by various by PSB; these organic acids decrease the pH in the soil surrounding roots, and catalyze the conversion of inorganic phosphate forms to free phosphate ready-to-use by plants (Zaidi *et al.*, 2009). Many *Pseudomonas, Bacillus, Rhizobium, Burkholderia, Agrobacterium, Achromobacter Micrococcus, Aerobacter, Flavobacterium* and *Erwinia spp.* are PSB that can solubilize inorganic phosphate compounds such as tricalcium phosphate, dicalcium phosphate, hydroxyl apatite and rock phosphate (Rodríguez *et al.*, 2006). Several strains of PGPR have been found to be very efficient in phosphorus-solubilization under high-saline conditions (Upadhyay *et al.*, 2012).

6.1.3. Production of Siderophores

Iron is considered an essential micronutrient for plant growth and development. It is a constituent of many cellular enzymes involved in many biochemical reactions such as photosynthesis and respiration (Abbas *et al.*, 2015). It is one of the most abundant minerals on earth; however, it is inaccessible for direct assimilation by plants. Under aerobic conditions, the reduced ferrous (Fe^{2+}) form is considered unstable, and is oxidized to ferric (Fe^{3+}) form, which is unstable and form insoluble ferric hydroxide that is unavailable to living organisms. Therefore, the amount of soluble Fe in the soil can hardly maintain microbial and plant growth. In saline soils, Fe availability is much lower than in non-saline conditions, which suppresses plant growth and development (Abbas *et al.*, 2015). To overcome such limitation in Fe supply, PGPR secrete siderophores, small iron-binding proteins, which can bind Fe^{+3} with a very high affinity to allow its acquisition by microbial cells (Saha *et al.*, 2016). The ability of PGPR to produce siderophores is considered crucial in determining the ability of PGPR to enhance plant growth and development under stress conditions (Saraf *et al.*, 2014). Siderophores produced by PGPR enhance the iron uptake by plants, but the cellular mechanisms involved in providing plants with Fe are not fully understood yet (Menendez and Garcia-Fraile, 2017). Furthermore, siderophore- production by PGPR helps in the Fe uptake even in the presence of heavy metals such as nickel and cadmium (Dimkpa *et al.*, 2008). It also reduces the impact of other harmful microorganisms and soil-borne pathogens such as bacteria, fungi, and nematodes (Haas and Défago, 2005).

There are many studies on the ability of PGPR producing siderophores to promote the growth of many plants, siderophores production by endophytic *Streptomyces* strains promoted the growth of *Azadirachta indica* plant (Verma *et al.*, 2011). *Phyllobacterium endophyticum* PEPV15, a siderophore-producing strain, promoted the growth and quality of strawberry plants (Flores-Felix *et al.*, 2015). The production of siderophores by the *Chryseobacterium sp.* strain C138 enabled the growth of tomato plants under an iron-limited supply (Radzki *et al.*, 2013). Furthermore, halotolerant PGPR and siderophores produced from different bacterial species enhanced salinity tolerance in different plant species (Menendez and Garcia-Fraile, 2017).

6.2. Phytohormones and PGPR

Phytohormones are small organic molecules that play a major role in plant growth development and enable plants to tolerate different stress conditions (Shaterian *et al.* 2005). PGPR are known to produce or alter the concentrations of different plant-growth hormones such as auxin, gibberellin, cytokinins and ethylene in host plants (Kumar and Sharma, 2017). Under salinity, PGPR can alter the phytohormone status, hence modulating plant growth and development by regulating various cellular and molecular responses. They were found to alter the levels of IAA (Vessey, 2003), gibberellic acid, cytokinins and ethylene (Kaushal and Wani, 2016). The effect of IAA-producing PGPR on plants was reflected in enhanced growth and development under stress conditions (Vessey, 2003). They increased root length, root surface area and the number of root hairs that enhanced the nutrients' uptake and improved plant tolerance against different stresses (Ramos-Solano *et al.*, 2008). On the other hand, PGPR modulated the levels of ethylene, an important phytohormone that accumulates under salinity and may have negative effects on plant growth and development (Goswami *et al.*, 2016). Several PGPR strains have been found to ameliorate salt-stress conditions by reducing ethylene levels in stressed plant through the production of ACC deaminase, which cleaves ACC, the immediate precursor for ethylene production in plants and alleviates its inhibitory effects on plants (Glick, 2014).

6.2.1. IAA-producing PGPR

Under normal conditions, IAA is involved in root initiation, cell division, and cell enlargement. Its production is inhibited under saline conditions. The decrease in IAA levels in the roots of stressed plants results in impaired germination, plant growth and development (Pérez-Alfocea *et al.*, 2010). The production of IAA is considered an important growth-prompting trait in PGPR that is commonly found in more than 80 % of the bacteria existing in the rhizosphere (Spaepen *et al.*, 2007). Many PGPR expressed the ability to affect the endogenous levels of IAA and had remarkable effects on plant growth under saline conditions (Jha and Saraf, 2015). IAA produced by PGPR affects the root system by increasing its growth, the number of lateral roots, and surface area, which subsequently leads to an increase in nutrient absorption and an improvement of plant growth and development (Ramos-Solano *et al.*, 2008).

To produce IAA, most of PGPR utilize L-tryptophan that is secreted by the roots as a precursor (Jha and Saraf, 2015). Auxin-production by PGPR is considered an important factor responsible for establishing the plant-microbe symbiotic relationship, enhancing plant growth and development and helping in alleviating adverse effects of salinity stress on plant growth (Ahmed and Hasnain, 2014). Halotolerant PGPR, capable of IAA production, enhance plant growth under salinity conditions through maintaining the auxin supply in the rhizosphere to help plant root and shoot growth under stress conditions (Albacete *et al.*, 2008). Halotolerant *Azospirillum brasilense* strain NH, associated with wheat plants, was able to produce auxin under high-salt stress of 200 mM NaCl (Nabti *et al.*, 2007). Similarly, halotolerant strains of PGPR including *Serratia plymuthica* RR2-5-10, *S. rhizophila* e-p10, *Pseudomonas fluorescens* SPB2145 and *P. chlororaphis* TSAU13 produced auxin under saline conditions, and enhanced plant tolerance to such adverse conditions (Egamberdieva, 2012). The effect of several auxin-producing PGPR strains (*Pseudomonas*; *P. aureantiaca* TSAU22, *P. extremorientalis* TSAU6 and *P. extremorientalis* TSAU20) on wheat at 100 mM NaCl level was reflected in significantly improved root and shoot (Egamberdieva and Kucharova, 2009). One *Streptomyces* isolate was able to produce IAA in the presence of salt stress and improved significantly wheat growth and development (Sadeghi *et al.*, 2012). Ramadoss *et al.* (2013) found that the inoculation of wheat with IAA-producing halotolerant PGPR ameliorated salt stress in wheat seedlings and increased the root length. Similarly, wheat plants inoculated with *Halobacillus sp.* SL3 and *Bacillus halodenitrificans* PU62 had a significant increase (90 %) in root elongation and in dry weight (17.4 % increase) at 320 mM NaCl stress compared with non-inoculated plants. In order to have a significant impact on plant growth under salinity, it is important to select PGPR with a capability to produce high levels of phytohormones under stress (Paul and Lade, 2014).

6.2.2. ACC deaminase-producing PGPR

Few PGPR were able to cleave ACC into ammonia and ketobutyrate and reduce the level of the ethylene precursor in plants under stress conditions (Glick *et al.*, 2007). Plants under stress conditions, such as salinity, drought, temperature extremes, flooding, pathogen infections, and nutritional stress, synthesize significant amounts of ethylene that have deleterious effects on plants (Bhattacharyya and Jha, 2012). As a consequence of prolonged stress, ethylene negatively affects plant growth and other cellular processes, leading to defoliation, chlorosis, reduced crop performance and senescence in plants that lead to the death of plant tissue (Bhattacharyya and Jha, 2012). ACC deaminase-producing PGPR were able to counteract the effects of the ACC hormone, and subsequently improve plant growth and development under stress conditions (Glick *et al.*, 2007). They also showed positive effects on root elongation, shoot growth, and increased the N, P, and K uptakes in various crops including wheat, tomato, rice among others under salt-stress conditions (Nadeem *et al.*, 2007; Glick, 2014; Cardinale *et al.*, 2015). Siddikee *et al.* (2010) reported that halotolerant-bacteria strains, belonging to different genera (*Bacillus, Brevibacterium, Planococcus, Zhihengliuella, Halomonas, Exiguobacterium, Oceanimonas, Corynebacterium, Arthrobacter* and *Micrococcus)* improved salinity tolerance in plants via ACC deaminase activity. PGPR with ACC deaminase- activity can hydrolyze ACC, the ethylene precursor in plants, to ammonia and α-ketobutyrate, thereby lowering the level of ethylene, improving tolerance against different stresses and subsequently promoting growth (Glick *et al.*, 2007).

6.3. PGPR and Plant Pathogens

In nature, plants are attacked by different types of pathogens including viruses, bacteria, fungi and nematodes, in addition to insects, which cause significant reduction in the yield of any given crop (Haggag *et al.*, 2015). Pathogens contribute to about a 15 % worldwide loss of global food production (Strange and Scott, 2005). Several PGPR were found to decrease or prevent the deleterious effects of pathogens on plants through the production of antibiotics and antifungal metabolites. They can also induce systemic resistance, competition with harmful microbes on invasion sites, and the sequestering of iron from the rhizosphere region (Glick *et al.*, 1999). The utilization of PGPR as a biocontrol agent seems to be a good strategy to reduce the negative impact of such pathogen on plant production (Rebib *et al.*, 2012).

7. Screening of Halotolerant PGPR from Saline Environments

The ability of PGPR, isolated from harsh environments to withstand different stresses, might indicate their abilities to improve stress tolerance in inoculated plants. Only PGPR isolated from stressful environments have the ability to withstand stress conditions, and may promote plant growth and development as they are well-adapted to such conditions (Shrivastava and Kumar, 2015). For salinity stress, most of microbial taxa that show improved tolerance for increased-salinity environments can be divided into two groups (Zahran, 1997): Halophiles which need salt for growth and are sub-classified into slight, moderate, and extreme halophiles; and the halotolerant group that includes microbes with no specific requirement for salt but may grow under normal conditions and saline conditions (up to 33% NaCl). The halotolerant group is sub-classified into slightly halotolerant, moderately halotolerant and extremely halotolerant.

The ability of halotolerant PGPR to promote growth in plants reflects their ability to deploy different cellular mechanisms and alter morphology as well as physiology to colonize roots and improve the plant tolerance to high-salt concentration (Miransari, 2017). The major salinity-tolerance mechanisms of halotolerant PGPR include: a reduced-salt uptake due to the structural properties of their membranes or cell wall, maintenance of intracellular ion hemostasis by the action ions antiporters and transporters, biosynthesis of compatible solutes such as sucrose and glycine betaine, biosynthesis of enzymes that are resilient to high levels of salt, and the production of exopolysaccharides that can form hydrating biofilms. The isolation of indigenous halotolerant PGPR from stressful environments and the assessment of their stress tolerance mechanisms and growth-promoting traits are important to enable their use as bio-fertilizers for stressed crops (Etesami and Maheshwari, 2018).

Several genera of halotolerant PGPR with plant promoting-growth activities have been isolated from a wide range of habitats including saline soils (Shi *et al.*, 2012; Ruppel *et al.*, 2013). Zhu *et al.* (2011) isolated *Kushneria sp.* YCWA18, a halotolerant PGPR that can grow on media containing 20 % NaCl and was found to possess high phosphorus-solubilizing ability; Tiwari *et al.* (2011) isolated several halotolerant PGPR that were able to tolerate up to 25 % of NaCl and included different genera: *Bacillus pumilus*, *Pseudomonas mendocina*, *Arthrobacter sp.*, *Halomonas sp.*, and *Nitrinicola lacisaponensis*. These strains were found to possess different plant growth-promoting traits including P solubilization and IAA production, siderophores and ACC deaminase activities. Other examples of halotolerant PGPR isolated from the rhizosphere of different crops growing under saline conditions including *Bacillus megaterium* from maize (Marulanda *et al.*, 2010); *Pseudomonas pseudoalcaligenes, P. syringae, P. fluorescens, Enterobacter aerogenes* and *Bacillus pumilus* from rice (Jha *et al.*, 2011); *Azospirillum brasilense* from barley (Omar *et al.*, 2009); *Pseudomonas syringae, P. fluorescens,* and *Enterobacter aerogenes* from maize (Nadeem *et al.*, 2007). In wheat, it was reported that halotolerant PGPR isolated directly from the plants grown in a saline soil were able to increase plant growth (Egamberdieva *et al.*, 2008).

8. Mitigation of Salt Stress in Wheat by PGPR

Wheat (*Triticum spp.*) is considered as one of the most important crops in the world. It is a staple food for over 35 % of the world's population where it provides more calories and proteins than any other crop. The wheat plant is a monocotyledonous plant that belongs to the Poaceae family within the Triticeae tribe that includes many domesticated cereals. The average global production of wheat was estimated at 729 million metric tons; of which, only twenty-eight million metric tons were produced from west Asia (FAOSTAT, 2015).

Wheat species show different responses to salinity stress. Bread wheat (*T. aestivum*) has moderate-tolerance responses, while durum wheat (*T. turgidum subsp. durum*) is considered salt- sensitive. This is attributed mainly to its inability to exclude Na^+ from its tissue (Roy *et al.*, 2014). The utilization of PGPR to improve plant growth and tolerance against multiple stresses is an effective and eco-friendly approach (Shrivastava and Kumar, 2015). The mitigation of the effects of salts on wheat by halotolerant PGPR at early stages can improve the chance of establishing a successful crop and improve the yield (Etesami and Beattie, 2018). Several studies (Etesami and Beattie, 2018; Etesami and Maheshwari, 2018; Shrivastava and Kumar, 2015) have been conducted in order to understand the role of halotolerant PGPR in alleviating the devastating effects of salinity and the mechanisms involved in the alleviation and promotion of growth in different plant species including wheat. Such studies have focused on the isolation of halotolerant PGPR directly from saline soils, the rhizosphere of different plants species (Siddikee *et al.*, 2011; Ruppel *et al.*, 2013) and from endophytic bacteria in the roots of different plant species (Bacilio *et al.*, 2004). However, there have been few reports on the effects of halotolerant PGPR on durum-wheat growth under saline conditions, while most reports are related to bread wheat.

Several PGPR strains, which belong to different genera, were isolated from saline habitats and possessed growth-promoting traits which improved wheat tolerance against saline conditions (Table 1). For instance, the inoculation of wheat with four selected PGPR strains (*Pseudomonas fluorescens* 153 and 169 as well as *P. putida* 4 and 108) alleviated the negative effect of salinity on plants (Abbaspoor *et al.*, 2009). Upadhyay *et al.* (2011) reported that the inoculation of wheat plants with *Bacillus subtilis* and *Arthobacter* sp. (two halotolerant PGPR) improved the growth under different salinity levels. Several PGPR strains from the genus *Pseudomonas*, that had the ACC-deaminase enzyme, improved wheat plant growth substantially under saline conditions (Egamberdieva and Kucharovaes, 2009). *Klebsiella* strains, with IAA-producing capabilities, increased root length and shoot height of inoculated wheat seedlings significantly compared with non-inoculated control (Sachdev *et al.*, 2009). Ramadoss *et al.* (2013) isolated eighty-four halotolerant bacterial strains from saline habitats, from which 25 % enhanced wheat germination and seedling growth at 20 % NaCl level. Five extremely halotolerant isolates of *Bacillus* and *Hallobacillus* possessed several growth-promoting activities such as IAA production, siderophore production, ACC deaminase activity and P solubilization. Chakraborty *et al.* (2011) isolated several highly-halotolerant PGPR from which *Bacillus cereus* showed increased height, number, and length of leaves of different plants. Abbas *et al.* (2015) reported positive effects of IAA-producing PGPR on wheat under saline conditions. Wheat seeds inoculated with the siderophore-producing *P. putida* and *P. aeruginosa* had higher germination percentages, and increased shoot height, shoot and root length, chlorophyll content, spikelets weight, grain yield, and iron content (Sarode *et al.*, 2013). Egamberdieva (2009) found that both IAA and ACC deaminase-producing PGPR improved wheat growth under salinity stress. The nitrogen-fixing *Pantoea agglomerans* Lma2 strain, isolated from wheat rhizosphere, was able to produce IAA, siderophores, solubilize P and was found to enhance growth in the presence of salt (Silini-Cherif *et al.*, 2012). Orhan (2016) isolated eighteen indigenous halotolerant bacteria from saline soils of the East Anatolian region in Turkey; eight isolates promoted wheat growth in a hydroponic culture under high salt-stress conditions (200 mM NaCl). Pande *et al.* (2016) found that wheat plants' germination and growth under saline conditions improved when they were inoculated separately with six strains of ACC deaminase-producing PGPR.

There have been a few studies for evaluation the effects of salt-tolerant PGPR on seeds and seedling growth under salinity stress on durum wheat. The inoculation of durum wheat cultivar (*Triticum durum* var. *waha*) with *A. brasilense* NH strain, isolated from a saline soil in northern Algeria, improved the growth under salt-stress conditions (Nabti *et al.,* 2007) even under high salt stress (160 and 200 mM NaCl). *A. brasilense* NH enhanced the restoration of complete vegetative growth and grain production compared with control plants. Similarly, the *Azotobacter chroococcum* AZ6 strain, isolated from rhizospheric soils surrounding durum-wheat plants cultivated in an arid location in Algeria, was inoculated in wheat seedling under salt stress, and the negative effects on plant growth parameters such as root length, plant height, fresh shoot and root weight and dry shoot and root weight were reduced (Silini *et al.*, 2016).

Table 1. The ability of some PGPR strains to promote growth in wheat plants

PGPR strains	PGP traits	Results of inoculation with PGPR	References
Providencia spp. AW4, *Brevundimonas diminuta* AW7	Nitrogen fixation	Increased yield and plant height	Rana *et al.* (2011)
Azotobacter chroococcum AZ6	Nitrogen fixation	Improved the growth under salt-stress conditions	Silini *et al.* (2016)
Pantoea agglomerans Lma2	Nitrogen fixation, siderophores, phosphate solubilization	Enhanced growth in the presence of salt	Silini-Cherif *et al.* (2012)
Azospirillum brasilense NH	Auxin production	Improved the growth under salt-stress conditions	Nabti *et al.* (2007)
Pseudomonas aureantiaca TSAU22, *P. extremorientalis* TSAU6 and *P. extremorientalis* TSAU20	Auxin production	Improved root and shoot growth	Egamberdieva and Kucharova, 2009
Bacillus pumilus	Auxin production, increase of phenolic and flavonoid quercetin	Increased shoot and root length and biomass	Tiwari *et al.* (2011)
Halobacillus sp. SL3 and *Bacillus halodenitrificans* PU62	Auxin production	Increased root elongation and dry weight	Ramadoss *et al.* (2013)
Klebsiella strains	Auxin production	Increased root and shoot length	Sachdev *et al.* (2009)
Pseudomonas putida and *P. aeruginosa*	Siderophore production	Increased germination percentages, shoot and root length, chlorophyll content, spikelets weight, grain yield, and iron content.	Sarode *et al.* (2013)
Bacillus subtilis and *Arthobacter sp.*	Change the activity of antioxidant enzymes	Improved growth under different salinity levels	Upadhyay *et al.* (2011)
Pseudomonas fluorescens 153, 169, *Pseudomonas putida* 108, 4	Undefined traits	Increased shoot growth and grain yield	Abbaspoor *et al.* (2009)

9. Formulation and Commercialization of PGPR

The utilization of PGPR as an agricultural practice is expected to have huge impacts on crop productivity in the near future (Glick, 2014). Recently, PGPR have been utilized commercially in various formulated products as biofertilizers and biocontrol agents (Jha and Saraf, 2015; Goswami *et al.*, 2016). Several bacterial biofertilizers are available in different forms in the market. For instance, it is possible to produce dry powders of Gram-positive spore-forming bacteria, which are known to be resistant to desiccation and heat stress (Kamilova *et al.*, 2015). Nowadays, several companies have become successful in commercializing spore-forming bacterial strains as PGPR-based biofertilizers such as *Bacillus licheniformis* SB3086 that can act as a phosphate-solubilizer strain and an effective biocontrol agent against the Dollar spot disease (Goswami *et al.*, 2016). The same strain is currently distributed as a commercial biocontrol product, known as “EcoGuard”. A bioformulation of *Pseudomonas aureofaciens*, which is commercialized by “Ecosoil” (www.ecosoil.com), is currently used as a natural biocontrol agent against different fungal diseases caused by *Pythium aphanidermatum* and *Microdochium patch* (pink snow mold). The “AgBio” product is a commercial formulation of *Streptomyces griseoviridis* strain K61, which is known to inhibit fungal and bacterial diseases that cause seed, root, and stem rotting, and the wilting of different crops.

Further development in biofertilizer formulations with an improved shelf life and more efficient strains is required. Several challenges faced the developers due to the multiplicity of biotic and abiotic stresses that plants encounter during their life cycle. The variability of climatic conditions and the severity of stresses and genetic variation (crop species and cultivars) cause variabilities in the responses of these microorganisms and also disparities in the potentiality of PGPR-based biofertilizers (Kamilova *et al.*, 2015).

10. Conclusion

The rhizosphere is a dynamic environment that enables the existence of symbiotic relationship between plants and other living organism including PGPR. Such beneficial microorganisms exert numerous benefits on plant growth and development which include improved tolerance against different abiotic stresses including salinity and induced resistance against different pathogens. The present review discussed the potential use of PGPR as biostimulants to ameliorate the inhibitory effects of high salinity-stress on plant growth and development with special emphasis on wheat plants. Plant growth-promoting traits, such as nitrogen fixation, phosphate immobilization, siderophore production, are unique properties of many halotolerant PGPR that can improve nutrients’ availability of stressed plants in saline soils. Furthermore, the ability of halotolerant PGPR to synthesize several phytohormones that can be utilized by plants to mitigate salinity stress conditions, and the ability of PGPR to induce resistance mechanisms were also discussed. Commercialized products that relay on PGPR are considered eco-friendly alternatives to the use of chemical fertilizers and pesticides. New formulations and commercial products that use PGPR are expected to have a positive impact on crop productivity and yield of many crops, in addition to securing food supplies to growing populations around the globe.

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