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Review Paper

The Role of Plant Growth-Promoting Rhizobacteria in Alleviating the Adverse Effects of Drought, Heat and Salinity Stresses in Crop

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Review ARTICLE

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ABSTRACT

Climate change and various abiotic stresses, especially, drought, salinity and heat stress on the one hand, and the issue of providing adequate quality food for the growing population of the world on the other hand, has made it necessary to revise the methods of crop production. In these conditions, the use of plant growth-promoting rhizobacteria (PGPR) in the agro ecosystems is useful and profitable due to the efficiency of these organisms in regulating plant growth and strengthening the plant's natural defense system. In this paper, considering the importance of modulating the negative effects of abiotic stresses using an environmentally friendly approach to achieve a healthy and sustainable crop system, the mechanisms of modulating abiotic stresses by growth-promoting rhizobacteria have been reviewed and the results of several studies have been presented. Growth promoting rhizobacteria through modification of plant hormone levels, restricting ethylene production, maintaining ion balance, osmolytes accumulation during stress, induction of antioxidant enzymes synthesis and removal of reactive oxygen species, production of extracellular polymeric substances, and improving the uptake of mineral elements and water, moderate the adverse effects of abiotic stresses on plant growth. By identifying useful and native rhizobacteria to each region and investigating the ability of these bacteria in producing the 1-aminocyclopropane-1-carboxylate (ACC) deaminase, balancing the plant hormones levels, producing siderophores, and enhancing solubility of mineral, the field will be provided for the successful use of these microorganisms.

KEYWORDS: *Abiotic stress, Beneficial microorganisms, Exopolysaccharides, Phytohormones, Sustainable agriculture.*

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1. BACKGROUND

Food is one of the basic human needs that plays an important role in the health and development of human societies. The United Nations has predicted that the world's population will reach more than 10 billion people by the year 2100, and providing food for this growing population will lead to increased pressure on agricultural fields and the destruction of these fields, and in this situation, it is likely that food supply will to face danger for all the people of the world (Glick, 2014, Pereira and Castro, 2014). In addition, climate change along with the increase in ambient temperature is one of the major problems of agriculture in many regions of the world, including Iran. Due to climate change caused by natural processes and human interventions, the occurrence of abiotic stresses, especially heat and drought, is intensified, and due to the decrease in the production of agricultural products, future food security will be seriously affected (Etesami and Maheshwari, 2018). Considering the changing weather pattern, to reduce the risk of production and achieve a stable yield, it is particularly important to investigate different solutions to deal with or minimize the adverse effects of abiotic stress with an environmentally friendly approach. In recent years, researchers around the world are seriously looking for possible solutions to reduce the adverse effects of abiotic stresses on the production of crop plants and increase the tolerance of plants to abiotic stresses through environmentally friendly solutions. In this regard, the role of beneficial soil microorganisms in improving plant growth in variable and stressful environmental conditions by strengthening the plant's natural defense system has been considered (Chatterjee *et al*., 2019). Plant growth-promoting rhizobacteria (PGPR) are a group of bacteria that have a positive effect on the growth of plants through several different mechanisms (Besharati, 2023). *Achromobacter*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Klebsiella*, *Microbacterium*, *Paenibacillus*, *Pantoea*, *Pseudomonas*, *Serratia*, *Streptomyces,* etc. are among the growth-promoting bacteria inhabit in the rhizosphere. These bacteria are used as inoculants for biostimulation, biocontrol and biofertilization (Numan *et al*., 2018). PGPR by stimulate the biological fixation of nitrogen and increase the absorption and availability of nutrients, the production of plant growth regulators (such as gibberellin, cytokinin and auxin), the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, the secretion of group B vitamins, nicotinic acid, pantothenic acid, and biotin, promote the growth of plants (Goswami and Deka, 2020). In general, the positive effect of bacteria on the growth and development of plants is classified into two groups of direct and indirect mechanisms. Directly, all kinds of growth-promoting bacteria stimulate and increase the growth of plants by using biological nitrogen fixation mechanisms, increasing the absorption and availability or solubilization of nutrients, production of plant growth regulators, production of siderophores, sulfur oxidation, and ACC-deaminase production. Indirectly, by using different antagonistic mechanisms, they neutralize or moderate the harmful effects of plant diseases and thereby increase plant growth. Competition for absorption of materials and occupation of suitable sites for the activity of pathogens, antibiotics production, pathogen cell walls destroying enzymes (such as chitinase), increasing the Induced systemic resistance (ISR), hydrogen cyanide (HCN) production, and volatile compounds production are among the most important mechanisms used in this method (Besharati, 2023). The presence of bacteria in the mineral cycles in the plant rhizosphere is very important. Rhizobacteria by increasing the availability of nutrients such as nitrogen (biofixation of atmospheric nitrogen), phosphorus (transformation of insoluble phosphorus into available form for plants through acidification, chelation, ion exchange, the release of compounds that dissolve minerals, release of organic and inorganic acids, and mineralization of organic phosphates through phosphatases), potassium (transforming inorganic potassium into plant-absorbable potassium), iron (through secretion of siderophore as an iron-chelating agent), manganese (Mg), zinc (Zn) and copper (Cu) (through secretion of chelating agents such as phenolic compounds and organic acids that form soluble complexes with elements such as Mg, Fe, Cu and Zn and prevent their precipitation) in the soil, reducing the plants' need for chemical fertilizers (Bhodiwal and Barupal, 2022, Vocciante *et al*. 2022, Etesami and Naheshwari, 2018). Increasing the chemical fertilizer use efficiency is one of the positive results of seed inoculation with growth-promoting bacteria, as a result of which it is possible to reduce the use of chemical fertilizers and achieve a stable and favorable yield (Akbari and Mojtabaie Zamani, 2020). In addition to increasing the chemical fertilizer use efficiency and increasing the effect of chemical fertilizers on plant growth, growth-promoting rhizobacteria play a role in improving soil structure and permeability due to the creation of bonds between soil particles (Wu *et al*., 2005). By balancing the level of plant hormones in the plant, these bacteria help to improve the development of the root system by affecting the size and external and internal morphology of the roots. PGPR reduce the growth of main root, increase the number, and/or length of lateral roots, and stimulate root hair elongation, which ultimately increases plant production due to more effective absorption (Grover *et al*., 2021). In addition to the positive effect on the growth and yield of plants in normal environmental conditions, these microorganisms moderate the unfavorable environmental conditions caused by stress and improve the growth of plants in these conditions (Vocciante *et al*., 2022). Therefore, one of the methods used to improve stress tolerance in plants is seed inoculation or treating plants with natural compounds or biological agents such as bacteria (Goswami and Deka, 2020, Chatterjee *et al*., 2019).

2. OBJECTIVES

The present review discussed the role of PGPR in alleviating the adverse effects of drought, heat, and salinity stresses in crop plants.

3. EVIDENCE ACQUISITION

This research was conducted based on the published findings of valid scientific research.

4. RESULT AND DISCUSSION

So far, increased tolerance to abiotic stresses such as drought (Chatterjee *et al*., 2019, Gontia-Mishra *et al*., 2016, Kumar *et al*., 2016, Kang *et al*., 2014), salinity (Numan *et al*., 2018, Sharma *et al*., 2016, Upadhyay *et al*., 2012, Yao *et al*., 2010), heat (Sarkar *et al*., 2018, Eisvand *et al*., 2018; Abd El-Daim *et al*., 2014; Ali *et al*., 2011), cold (Subramanian *et al*., 2016; Mishra *et al*., 2011), heavy metal (Etesami, 2018) and waterlogging (Barnawal *et al*., 2012), as a result of seed inoculation with plant growth-promoting rhizobacteria, has been reported in various types of research worldwide. In Iran, also, the possibility of alleviating abiotic stresses such as drought, salinity, and heat with the use of PGPR has been investigated (Table 1).

Table 1. Effects of PGPR on modulating abiotic stresses in crop plants in some research carried out in Iran

Abiotic stress	Crop	PGPR and Effect	Reference
Drought	Canola (*Brassica napus* L.)	Inoculation of canola cultivars with *Enterobacter* sp. S16-3 not only improved height and root length, but also increased biological yield by 57.5 %. Bacterial inoculation also increased chlorophyll content and the concentration of proline under different stress conditions. Inoculated canola cultivars had better growth characteristics and biological yield than non-inoculated plants in drought stress.	Kazemi Oskuei *et al.* (2021)
	Canola (*Brasica napus* L.)	The application of *Pseudomonas fluorescens, Pseudomonas putida* bacteria individually had a significant effect on formation of final yield, relative water content, and stress relief, but the combination of two strains had an antagonistic effect.	Arvin *et al.* (2018)
	Chickpea (*Cicer arientum*)	Seed bacterial inoculation with *Mesorhizobium* resulted in increased leaf area index, net assimilation rate, crop growth rate, yield components, grain yield, and increased drought tolerance.	Nemati *et al.* (2017)
	Maize (*Zea mays*)	The effect of inoculation of native isolates of *Azotobacter* isolated from arid and semi-arid regions of Iran under drought stress conditions was investigated on the growth of maize in greenhouse conditions. Inoculation with Azc10 resulted in significant increase in shoot dry weight compared to control. This isolate increased the shoot yield by about 20% compared to non-inoculated treatment under drought stress conditions.	Khosravi, (2019)
	Maize (*Zea mays*)	*Pseudomonas fluerescens* strain 93, *Bacillus lentus* strain P5 and *Penicillium radicum* with the phosphate solubilizing ability in the soil led to an increase in the tolerance of corn to drought stress.	Ghasemi *et al.* (2011)
	Rice (*Oryza sativa* L.)	The application of *Azospirillum lipoferum* and *Pseudomonas fluorescence* individually had a significant effect on paddy yield in which the maximum grain yield was obtained by the combination of *Azospirillum + Pseudomonas* and the minimum grain yield was obtained by no bacterium application. These bacteria were effective in significantly improving rice paddy yield under water deficit conditions	Niknejad *et al.* (2017)
	Soybean (*Glycine max*)	*Rhizobium japonicum* led to a 17% increase in root colonization and an increase in soybean yield under drought stress conditions.	Nakhzari *et al.* (2019)
	Wheat (*Triticum aestivum* L.)	20 isolates of *Pseudomonas* were studied in terms of the important characteristics of plant growth promoter (including production of ACC-deaminase, hydrogen cyanide and siderophore, ability to dissolve inorganic phosphate, growth hormone production) and drought tolerance in laboratory conditions. Four strains that were superior to others based on growth-promoting properties and drought tolerance were selected for inoculation. These strains were effective in modulating drought stress.	Safari, (2019)

Table 1. (Continued)

Abiotic stress	Crop	PGPR and Effect	Reference
Drought	Wheat (*Triticum aestivum* L.)	*Pseudomonas vancouverensis* strain 26 and *Pseudomonas korensis* strain 104 were effective in modulating drought stress by increasing potassium solubility in soil.	Kordzangeneh and Marashi, (2018)
	Wheat (*Triticum aestivum* L.)	The combined use of *Pseudomonas fluerescens*, *Azospirillum lipoferum*, and *Azotobacter chroococcum* bacteria, increased the content of chlorophyll a, b, grain yield, and harvest index.	Mozafari *et al.* (2015)
Heat stress in grain filling period due to delay in planting	Wheat (*Triticum aestivum* L.)	By inoculating the seeds with *Pseudomonas putida* and *Pantoea agglomerans*, on both planting dates (optimum and late planting date), increased the number of grains per spike by 4.6%, grain yield by 7.6%, and biological yield by 7%. In this research, the effect of phosphate solubilizing bacteria on mitigating the effect of heat stress was not proven, and the positive effect of bacteria was the same on both planting dates.	Aslani and Mojtabaie Zamani, (2021)
	Wheat (*Triticum aestivum* L.)	The use of phosphate solubilizing bacteria (*Bacillus* and *Pseudomonas*) combined with the foliar application of zinc significantly reduced the adverse effects caused by the delay in planting and the grain yield increased. This is while the consumption of each of these factors alone did not have such an effect on the grain yield on the late planting date.	Kamaei *et al.* (2018)
Salinity	Canola (*Brasica napus* L.)	Inoculation with *Pseudomonas fluerescens* containing the ACC-deaminase gene led to an increase in leaf and root dry weight, leaf area, and root length and finally improved the growth of canola in salt stress.	Bazyar *et al.* (2015)
	Canola (*Brasica napus* L.)	*Sinorhizobium meliloti* strain 29 and 103 and *Rhizobium leguminosarum biovar phaseoli* strain 307, 281, 266, 258 with ACC-deaminase-producing gene and phosphate solubilizing ability played a role in modulating salinity.	Saghafi *et al.* (2015)
	Rye (*Secale cereale* L.)	The co-application of *Pseudomonas fluerescen*s and *Azospirillum lipoferum* led to an increase in the activity of antioxidants catalase, peroxidase, polyphenol oxidase, and a decrease in sodium in roots and shoots and an increase in chlorophyll a, b and total chlorophyll content.	Moradi *et al.* (2018)
	Triticale (× *Triticosecale*)	The co-application of *Pseudomonas putida* strain 186 and *Azotobacter chroococcum* strain 5 led to an increase in yield by increasing the photochemical efficiency of photosystem II, the relative water content, and the chlorophyll content.	Kheirizadeh *et al.* (2019)
	Wheat (*Triticum aestivum L.*)	Using *Bacillus amyloliquefaciens* under salt stress increased the proline and catalase activity, and changed the pattern of protein bands in both sensitive and resistant wheat genotypes. Applying this bacterium without harming the environment can be a practical method to control salinity stress and maintain optimal yield.	Faramarzi *et al.* (2022)

Table 1. (Continued)

Abiotic stress	Crop	PGPR and Effect	Reference
Salinity	Wheat (*Triticum aestivum* L.)	The isolates collected from the rhizosphere soils of saline-tolerant plants with the ability to produce auxin and siderophore, and phosphate solubilizing ability were effective in modulating the adverse effect of salinity in the growth period of wheat.	Safdarian *et al.* (2018)
	Wheat (*Triticum aestivum* L.)	The inoculation with *Pseudomonas fluorescens* and *Pseudomonas putida* compared to the control (without inoculation) increased root volume by 83% and 25%, and root dry weight by 38% and 7% in salinity stress, respectively. Both bacteria increased shoot dry weight and were effective in modulating salinity stress.	Soltani Toolarood *et al.* (2019)

In these studies, the use of growth-promoting bacteria has led to the alleviation of the adverse effects of stress, which promises the success of using these useful soil microorganisms in farms and achieving healthy and sustainable production. It is not yet known exactly how bacteria affect tolerance to abiotic stress in plants, and the plant's response to these bacteria includes a set of complex mechanisms with molecular and biochemical changes (Abd El-Daim *et al*., 2018). PGPR through modification of plant hormone levels, restricting ethylene production, maintaining ion balance (increasing potassium absorption and limiting sodium and chloride absorption), osmolytes accumulation during stress, induction of antioxidant enzymes synthesis and removal of reactive oxygen species (ROS), production of extracellular polymeric substances and improving the uptake of mineral elements and water, moderate the adverse effects of abiotic stresses on plant growth (Bhagat *et al*., 2021, Goswami and Deka, 2020, Etesami and Maheshwari, 2018, Numan *et al*., 2018). One of the reasons for growth reduction under abiotic stresses is the reduction of auxin, brassinosteroid, gibberellin, and cytokinin hormones in the plant. PGPR by changing the hormone content in plants, production of indole acetic acid (IAA), gibberellin, and other plant hormones, increased root length and the root contact surface, which leads to improved uptake of water and nutrients (Grover *et al*., 2021, Goswami and Deka, 2020). Some PGPR can increase the level of these plant hormones, especially auxin and cytokinin, in the plant and improve the uptake of water and mineral elements by increasing the growth of the root system and increasing the effective absorption level of the root (Numan *et al*., 2018). Yao *et al*. (2010) investigated the efficiency of PGPR strains in balancing the level of plant hormones under abiotic stress conditions and increasing tolerance to stress. They observed that inoculation of cotton with *Pseudomonas putida* led to an increase production of endogenous IAA and promoted the growth of cotton seedlings growing under salt stress. They considered the increase in root growth and absorption of Mg^{2+}, Ca^{2+}, and K^{+} as the reasons for the increase in plant growth. Egamberdieva (2009) reported that priming of wheat plants with different strains of *Pseudomonas* (with the ability to produce IAA) resulted in a significant increase in root and shoot growth of wheat seedlings (40% and 52%, respectively) compared with the control plants under salt stress conditions. In another study, Kang *et al*. (2014) considered the increase in gibberellin production in soybeans inoculated with *Pseudomonas putida* as one of the reasons for improved growth under drought stress conditions. Kordzangeneh and Marashi (2018) investigated the effect of Petabarvar biofertilizer (containing *Pseudomonas koreensis* and *Pseudomonas vancouverensis*) in three irrigation regimes (irrigation after 60, 90 and 120 mm of evaporation from the evaporation pan) on wheat yield. They observed that in the three irrigation regimes, the application of 75% potassium sulfate fertilizer coupled with bacterial inoculation resulted in a significant rise in grain yield compared to when no bacteria were present (100% application of potassium sulfate chemical fertilizer). They considered the increase in bioavailability of K^+ due to increasing potassium solubility in soil and the production of growth-regulating hormones by these bacteria as effective factors in improving yield under normal conditions and drought stress. Increased production of growth-regulating hormones in plants inoculated with PGPR, and as a result, increased root growth and improved uptake of water and nutrients despite the occurrence of abiotic stress, have been reported in the conditions of salinity stress (Sharma *et al*., 2016) and heat stress (Ali *et al*., 2011). Ali *et al*. (2011) to study of the effect of thermotolerant *Pseudomonas putida* strain AKMP7 on the alleviation of heat stress in wheat isolated these bacteria from the sorghum rhizosphere soil sample collected from the semi-arid region with high temperature. The results showed that bacterial inoculation of wheat seed with strain AKMP7 significantly increased the length of the root and shoot, the dry biomass, the number of tillers and spikes, the number of grains per spike, and the 100-grain weight. Inoculation reduced membrane injury and improved the levels of cellular metabolites like proline, chlorophyll, sugars, starch, amino acids, and proteins compared to the control. In this study, the production of phytohormones and the stimulation of root growth (which leads to an increase in the uptake of water and minerals), the production of iron-chelating siderophores, the increase in the content of chlorophyll and the increase in the stability of cell membrane as the reasons for heat tolerance in wheat plants inoculated with bacteria (*Pseudomonas putida*) became known. Ethylene is an essential hormone for plant growth and development, but its high concentration is problematic for plant growth in stressful conditions. Due to the production of stress-related ethylene, the growth and yield of plants under different stress conditions of drought, salinity, the toxicity of elements and lack of the balance of nutritional elements decreases (Numan *et al*., 2018). The production of 1-Aminocyclopropane-1-carboxylic acid (ACC) deaminase is one of the most important physiological characteristics of growth-promoting rhizobacteria. By preventing the production of ethylene in stressful conditions, this enzyme increases the growth of roots and shoots (Goswami and Deka, 2020). Researchers have shown that the bacteria that have the ACC-deaminase, decompose ACC, an ethylene precursor, into ammonia and alpha-ketobutyrate, and use it as a source of nitrogen. In this way, the surface of ethylene produced decreases under stress conditions (Glick, 2014). Reduction of ethylene production as a result of increased production of ACC-deaminase by PGPR is known as one of the most important reasons for improving the growth and development of the root system under stress conditions. According to the report of Saghafi *et al*. (2015), the inoculation of rapeseed with ACC deaminase-producing bacterial strains led to a significant increase in the amount of chlorophyll in leaves under salinity stress conditions and moderated the adverse effects of salinity stress on growth indices. They stated that under salinity stress, ethylene production causes leaf aging, and if there are ACC deaminase-producing bacterial strains and ethylene synthesis inhibition, chlorophyll decomposition will be prevented. Modification of the adverse effects of drought stress in pea plants inoculated with *Pseudomonas putida* as a result of increasing the activity of ACC-deaminase has also been reported by Kumar *et al*. (2016). Cheng *et al*. (2007) observed that the growth of canola plants inoculated with *Pseudomonas putida* was significantly higher than the growth of plants inoculated with a mutant *Pseudomonas putida* lacking ACC-deaminase. In their research, they proved the role of this enzyme in reducing ethylene production and increasing plant growth. Maintaining ion balance during stress is one of the other effects of using PGPR to moderate stress, especially salinity stress. In salty environments where the concentration of sodium is high, plants absorb large amounts of Na^+ instead of K^+ and Ca^{+2}, and this leads to an increase in Na^+ and a decrease in K^+ and Ca^{+2} in plant roots. A decrease in the amount of potassium in the root leads to a decrease in the transfer of nitrate from the xylem to the leaves, and instead of nitrate, Na^+ and Cl^- are transferred to the leaves and accumulate there (Moradi *et al*., 2018). The ability of different strains of *Pseudomonas* bacteria to alleviate salinity stress by reducing Na^+ absorption has been reported by different researchers (Goswami and Deka, 2020, Sharma *et al*., 2016). According to Yao *et al*. (2010), *Pseudomonas putida* increases the absorption of Ca, K, and Mg by the plant and decreases the absorption of Na. In the study of Moradi *et al*. (2018), the highest concentration of sodium in the roots and shoots of rye was obtained under the conditions of salt stress and no seed inoculation with bacteria. The lowest amount of sodium in the roots and shoots was obtained in the treatment of seed inoculation with *Azospirillum* and *Pseudomonas*. In the research of Saghafi *et al*. (2015), the inoculation of canola with *rhizobia* under the salinity, significantly increased the Chlorophyll (8.34%), leaf area (17%), relative water content (8.78%), shoot and root fresh weight (20.4 and 49% respectively), compared to un-inoculated control. Also, inoculation decreased the uptake of Na^+ (29%) and enhanced the accumulation of N, P, K, Fe, Zn, Cu, and Mn in the shoot compared to the control. The role of PGPR in the accumulation of osmolytes in stress conditions has been reported by different researchers. Accumulation of compatible solutes like sugars and proline in leaves under abiotic stresses is one of the adaptive mechanisms that regulate the permeability of the cell membrane and the movement of water through the cells and tissues (Ashraf and Foolad, 2007). In wheat plants treated with rhizobacteria, the accumulation of proline and soluble sugars has been reported as one of the important strategies for salt tolerance (Upadhyay *et al*., 2012). Proline accumulated during salt stress not only provides tolerance but also serves as an important source of organic nitrogen during stress (Numan *et al*., 2018). In the conditions of drought stress, Ansary *et al*. (2012) reported that inoculation of corn plants with *Pseudomonas* led to an increase in proline in the plant, and the production biomass, relative water content, and leaf water potential of corn plants enhanced. Proline accumulation in leaves as one of the defense solutions to prevent the leakage of electrolytes from the membrane and to maintain the stability of the cell membrane in heat stress conditions has also been introduced (Sarkar *et al*., 2018). The difference between wheat plants inoculated with *Pseudomonas putida* and non-inoculated in heat tolerance is related to their ability to accumulate carbohydrates, amino acids, and proteins under heat stress conditions (Ali *et al*., 2011). In inoculated wheat with *Pseu-*

domonas putida, proline, as one of the organic molecules whose accumulation increases in most plant cells in abiotic stresses, increased significantly (Ali *et al*., 2011). About sorghum seedlings exposed to heat stress, similar results have been obtained regarding the accumulation of cellular osmolytes (Ali *et al*., 2009). Under stress conditions, the production of reactive oxygen species (like singlet oxygen, superoxide radical, hydroxyl radical and hydrogen peroxide) increases, which leads to the destruction of lipids, proteins, DNA, RNA, and cell death. There is significant evidence that in plants inoculated with PGPR, the oxidative stress caused by other stresses has been controlled by manipulating the antioxidant defense system and removing ROS (Etesami and Maheshwari, 2018). For example, the inoculation of wheat with *Pseudomonas aeruginosa* led to an increase in the biomass of the inoculated plants compared to the control plants, and it was found that this bacterium increased the activity of superoxide dismutase, catalase, peroxidase and non-enzymatic antioxidant compounds such as ascorbic acid and phenols (Islam *et al*., 2014). However, in some studies, the levels of antioxidants decreased in the conditions inoculated with PGPR, which indicates that the plants inoculated with bacteria experienced less stressful conditions compared to the control plants (Ali *et al*., 2011). Changes in the level of antioxidant enzymes in plant cells and ROS removal in soybean inoculated with *Pseudomonas putida* in drought stress conditions have been reported by Kang *et al*. (2014). Abd El-Daim *et al*. (2014) investigated the effect of *Azospirillum* and *Bacillus* on improving heat tolerance in wheat and reported that seed inoculation with bacteria is a promising strategy for improving heat tolerance in wheat. In the inoculated plants, the production of ROS was controlled, and as a result, oxidative stress and cell damage were reduced. Sarkar *et al*. (2018) by investigating the effect of *Bacillus safensis* and *Ochrobactrum pseudogrignonense*, on mitigating the effects of heat stress on the growth of two wheat cultivars, reported that high temperature causes the accumulation of ROS in the cell and the damage to thylakoid membranes. In a defense reaction, the scavenging activity of antioxidants and the amount of osmolytes such as proline and glycine betaine increased. PGPR priming, especially *B. safensis* improved the heat stress tolerance level of wheat seedlings. In seed inoculation treatment with PGPR, restored chloroplast structure and the activity of catalase, superoxide dismutase, and ascorbate peroxidase antioxidants increased compared to non-inoculation conditions. They considered the mitigation of adverse effects of heat stress in PGPR priming as a result of reducing the ROS production, less membrane damage, maintenance of chloroplast structure, enhanced chlorophyll content, increased expression of enzymatic antioxidants and accumulation of osmolytes (Sarkar *et al*., 2018). Some PGPR support plant growth under stress conditions by producing extracellular polymers such as exopolysaccharides. Exopolysaccharides play a significant role in improving soil structure (improved soil aggregation, increased the percentage of stable soil aggregates, and improved soil permeability), which can help to retain more water in the soil. On the other hand, exopolysaccharides are hydrated compounds including 97% water in a polymer matrix. Therefore, they can protect the plant against desiccation (due to the formation of hydrophilic biofilms on the root surface) and guarantee the survival of the plant under drought stress (Etesami and Maheshwari, 2018). Exopolysaccharide-producing microbes help in increasing nutrient uptake by roots, soil stability, soil fertility, plant biomass, chlorophyll content, root and shoot length, surface area of leaves, and maintain metabolic and physiological activities during drought stress (Bhagat *et al*., 2021). Under saline conditions, exopolysaccharides due to their anionic property, can bind free Na^+ ions thus preventing Na^+ ions from being absorbed by the plant (Upadhyay *et al*., 2012). This issue is considered as one of the reasons for the decrease in the ratio of absorbed sodium to potassium in plants inoculated with rhizobacteria under salt stress conditions. Exopolysaccharide-producing microbes can induce the production of new types of cellular proteins such as heat shock proteins and alleviate adverse effect of heat stress (Bhagat *et al*., 2021). Increasing the solubility of phosphate and potassium, biofixation of atmospheric nitrogen, production of Fe, Mn, Zn and Cu chelating siderophores, and finally improving the soil permeability, aggregate stability and root growth are among the properties of growth promoting rhizobacteria. These bacteria by helping the plant root to uptake water and nutrients, can moderate adverse effects of abiotic stress (Etesami and Maheshwari, 2018, Kumar *et al*., 2016, Sharma *et al*., 2016). The application of manure in combination with biofertilizers (including *Azotobacter*, *Azospirillum*, *Bacillus* and *Pseudomonas*) to achieve maximum grain yield under end-season drought stress conditions was useful (Namarvari *et al*., 2012). In this research, in three irrigation regimes (complete irrigation, interruption of irrigation from anthesis to maturity and interruption of irrigation from spike emergence to maturity), the highest wheat grain yield was reported in the Integrated system (manure with biofertilizer). They considered the possible improvement of vital soil processes and the increase of soil fertility in the integrated system as the reason for achieving a suitable culture medium for maximum dry matter production. Khalilzadeh *et al*. (2018) also stated that by inoculating wheat seeds with *Azotobacter chroococcum* and *Pseudomonas putida*, reduced the adverse effects of salinity stress on grain yield and many physiological traits of wheat. Inoculated plants with the mentioned bacteria under salinity stress had a significantly higher grain filling rate. The improvement of chlorophyll index and quantum yield in inoculation conditions compared to non-inoculation and the sufficient assimilate supply and large partitioning capacity as the reasons for increasing the grain filling rate and grain yield was introduced. The positive effects of the PGPR (*Pseudomonas* and *Bacillus*) on the number of spikes per area, the number of grains per spike, 1000-grain weight and finally grain yield in conditions of late planting date and occurrence of heat stress in grain filling period by Eisvand *et al*. (2018) has also been reported. In their research, with the inoculation of wheat seeds compared to the non-inoculation, the number of grains per spike increased by 17% on the optimum planting date and 15.8% on the late planting date. This increase was the most important reason for the increase in grain yield as a result of bacterial inoculation. They cited the supply of phosphorus as a necessary element in metabolic processes, and its role in increasing the quantum efficiency of photosystem II as the reasons for the increase grain yield.

5. CONCLUSION

The findings of various researches have shown the positive and strong effect of PGPR in moderating the adverse effects of various environmental stresses, especially drought and salinity. PGPR can help humans in producing stable and healthy products in stressful environment conditions by regulating plant growth, strengthening the natural defense system, and facilitating the uptake of water and essential mineral elements for plant growth. One of the most important effects of PGPR is the effect on the structure and morphology of plant roots under stress conditions. ACC deaminase-producing bacteria by ethylene synthesis inhibition under stress conditions and IAA-producing bacteria by balancing the level of auxin in the plant, can increase the growth of root and improve uptake of nutrients and water. By identifying beneficial soil micro-organisms and investigating how these organisms affect the rhizosphere, while taking advantage of the relevant ecological relationships, it is possible to achieve sustainable production in stressful environmental conditions.

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