



Recent advances of PGPR based approaches for stress tolerance in plants for sustainable agriculture

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ABSTRACT

The increasing worldwide population is a significant challenge for agricultural food production to feed the alarming rate of the growing world population. The enhancing community directly affected by several factors, including the limitation of agricultural land, environmental damage, and the number of biotic and abiotic stresses, which affect global food production. It is essential to increase agricultural productivity to feed an increasing population. Several approaches are needed, such as greater use of chemicals including fertilizers, pesticides, and herbicides. Several other factors, such as overcome the posture, saline, and drought land, can be improved by using stress-tolerant plant growth-promoting microorganisms. Though, many of the solutions attempted to this problem are not sustainable and are only be valid for the short term. Stresses tolerant plant growth-promoting rhizobacteria (PGPR) can produce bioactive compounds such as gibberellins and indole acetic acid. PGPR also produced several active enzymes under drought, heavy metals, and salts stress. PGPR approach can enhance plant growth and consequently crop yield with maintained eco-friendly environment. The present review focused on the recent advances of PGPR approach in concern to different biotic and abiotic stresses.

1. Introduction

The decrease in crop productivity is the incidence of various biotic and abiotic stresses. Biotic factors include stresses due to phytopathogens and pest such as fungi, nematodes, viruses, and insects. Major abiotic factors include stresses such as drought, salinity, heavy metal, flooding, high and low temperature. These stresses are major responsible factors for the reduction in crop yield. The required production of the crops worldwide needs extensive use of fertilizers, pesticides, and frequent irrigation, this ultimately depleted available soil nutrients. The loss due to stresses may reach up to 50–82% and depends on the type of stress (Christensen et al., 2007). About 7.6 million km² area is affected globally due to such unfavourable environmental factors (Christensen et al., 2007; Falkenmark, 2013). The prediction was done by 2050 that the cropping area affected by drought will be increased by two folds, and resources for water declined by 30% (Falkenmark, 2013). Salinity is a significant stress, which affects agricultural productivity in several areas worldwide. Approximately 20% of integrated

land area (450,000 km²) is affected by salinity and loss in productivity ranges from 2500 to 5000 km² (UNEP, 2009). Due to the increase in the population and rise in demand for food, there should be the utilization of salt-affected land for agricultural purpose to feed the growing population of the world. Salinity causes accumulation of ions mainly Na⁺, Cl⁻, and SO₄²⁻ increases osmotic as well as secondary stresses, cause nutritional imbalances and oxidative stress for glycophytes (Hussain et al., 2008). Plants can respond by signal transduction pathways for adjustment of the disturbed metabolism (Bartels and Sunkar, 2005). Drought has been affecting turgor pressure and decrease in biomass of plant (Bartels and Sunkar, 2005). However, drought is more injurious to plants than salinity, but the plant could be affected by both types of stresses (Hussain et al., 2008). Soil environment possesses several stresses, which influence the plant growth, are a significant obstacle for sustainable agricultural production (Fig. 1).

Mode of action of stress-tolerant PGPR includes plant growth regulators, production of protective enzymes such as glucanase, chitinase, producing the volatile antimicrobial compound, and ACC deaminase

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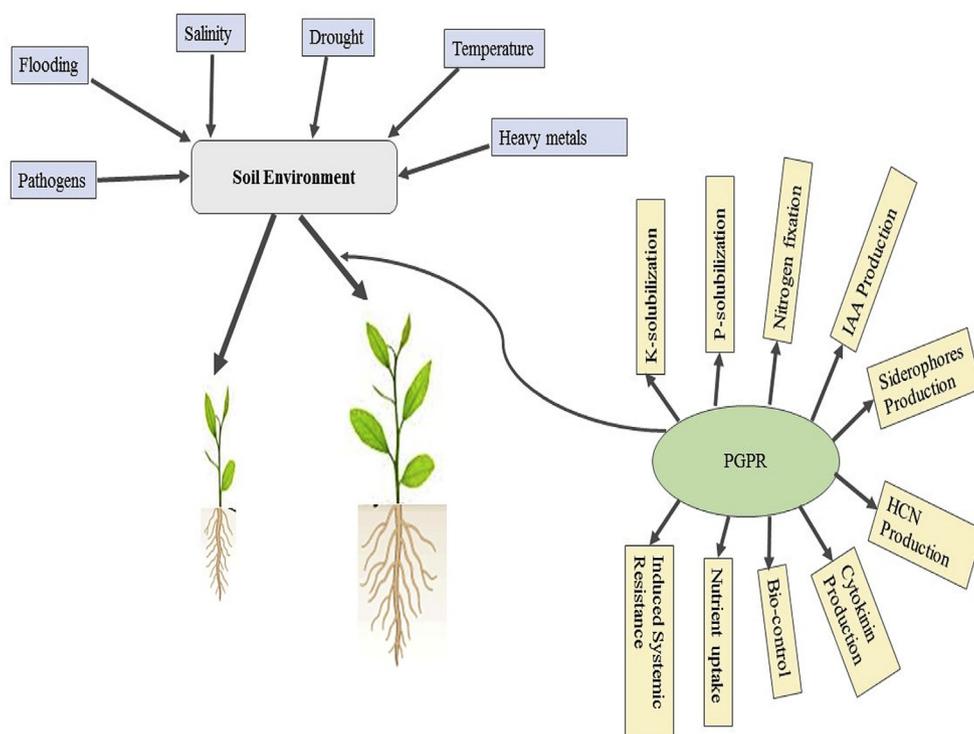


Fig. 1. Plant growth promotion activities of stresses tolerant PGPRs to enhanced the plant efficiency.

activity (García-Fraile et al., 2015). Numbers of chemicals were exuded by plant roots such as organic acids, mucilage, carbohydrates, sugars, and proteins. Rhizobacteria can use organic acids as a carbon source, which can be correlated with competence. Nature of root exudates secreted by plant in the rhizospheric region can shape the microbial community in the particular region. It is very important to understand the mechanism of microbial recruitment in the rhizosphere and effect of root exudation through plant before considering rhizobacteria for plant growth promotion (Drogue et al., 2012; Patel et al., 2017). Results obtained by Rakshapal et al. (2013) showed that the role of *Cronobacter dublinensis*, *Pseudomonas monteilii* and *Bacillus* sp. for enhancement of nutrient uptake and reduced abiotic stress in *Ocimum basilicum* L. Qudsia et al. (2013) reported the ability of *Azospirillum lipoferum* for increment of growth of maize plant as well as accumulation of free amino acids, prolines and soluble sugars under drought stress. Some PGPR such as *Pseudomonas* sp. and *Azospirillum* sp. have been reported for improved growth and biomass via regulating oxidative stress enzymes and essential nutrient availability under salinity stress (Noorieh et al., 2013). Salinity is the primary reason for the imbalance of ion flux inside the plants.

The report (Noorieh et al., 2013; Rojas-Tapias et al., 2012) suggested that there is more accumulation of Na^+ in control plants and decreased accumulation of K^+ . However, the condition was reversed after PGPR application. PGPR was reported for regulation of different stresses by abscisic acid (ABA) regulation, which was found to be involved in plant growth promotion, stomatal closure and collectively increases the efficiency of the plant during stress condition (Zhang et al., 2006; Herrera-Medina et al., 2007). PGPR application have ability to decrease the deleterious effect of ethylene produced during number of stresses such as flooding (Grichko and Glick, 2001), drought (Zahir et al., 2008), pathogenicity (Wang et al., 2000) and salinity (Nadeem et al., 2007) (Fig. 1). Tremendous work has been done to understand the mechanisms such as the physiological, molecular, and morphological effect of bacteria against biotic and abiotic stresses (Van Loon et al., 1998). The interaction between beneficial bacteria and plant depends on the composition of root and exudation pattern of roots

(Kumar et al., 2017). The exact mechanism of plant growth stimulation in the presence of microorganisms towards the rhizospheric region is still not fully explored; it depends on the type of bacterial strains and component secreted by the bacteria. The hormones are directly or indirectly related to secondary metabolites produced by microbes in different concentrations and related to plant growth promotion (Dimkpa et al., 2009). The phytohormones may act as signaling molecules and induce suppression of the phytopathogen (Sikora et al., 2007). It can enhance the availability of several minerals in the soil (Dimkpa et al., 2009). A recent report (Ghosh et al., 2019a,b) suggested the role of phytohormone secreted by rhizobacteria to cope up with water stress.

PGPR can tolerate a wide range of salinity and provide the ability to plant to withstand in saline soil conditions. The probable mechanism behind such tolerance is osmotic accumulation, hydraulic conductance, maintaining the higher osmotic conductance, photosynthetic activities and sequestering toxic Na^+ ions (Dodd and Perez-Alfocea, 2012) (Fig. 1). Nakbanpote et al. (2014) reported that the *Serratia* sp. and *Pseudomonas* sp. possess specific properties such as the production of IAA, nitrogen fixation and phosphate solubilization in 8% saline condition and tested *Pseudomonas* sp. for improved seed germination *Oryza sativa* L. cv. Salinity stress can inhibit the plant growth by causing a defect in homeostasis, water status, and distribution of ions and increase oxidative stress with higher production of ethylene (Tester and Davenport, 2003). A recent report (Ghosh et al., 2019a,b) suggested the role of rhizobacteria to reduce stress in the plant. The present review summarises the role of PGPR under various salinity stress. We have also focused the recent advanced in the area to mitigate biotic and abiotic stresses by using PGPR.

2. Stresses and PGPR

Abiotic and biotic stresses are the major regulators of crop productivity. Abiotic stresses such as drought for longer time, heavy rain and flooding, damages due to heat waves and frost will increase in the future due to climate change. Plant adapted several strategies of

adaptations required to cope up with the stresses. The evolution of better breeds of crops could overcome the significant biotic and abiotic stresses at some extents. However, developments of newer breeds against abiotic stresses are a time-consuming process. So, the alternative strategies are required to fight against biotic and abiotic stresses. Biological control mechanisms such as the use of beneficial microbes can play a significant role to combat against abiotic stresses. These microorganisms can increase plant tolerance against biotic and abiotic stresses.

2.1. Strategies of PGPR to mitigate biotic stresses

Plant-beneficial microbe interaction improves plant health, growth, and available nutrients and its assimilation and enhanced efficiency of plant against several disease-causing microorganisms (Yang et al., 2009). Direct interaction with the bioagents includes the production of several phytohormones such as cytokinin, auxins, gibberellins, and ACC-deaminase. ACC-deaminase can reduce the level of ethylene in roots of developing plants. Some other activities like symbiotic nitrogen fixation, minerals solubilization (phosphorus, potassium) and help plants to combat against stresses. The beneficial interactions of bioagents present in plants rhizosphere and, their positive effect on plant growth by the improvement of stress tolerance under hazardous environmental conditions have been broadly reviewed (Nadeem et al., 2007). A recent study showed the use of consortia of microorganism against powdery mildew of pea (Patel et al., 2015, 2017; Kumar et al., 2017).

2.1.1. Phytohormones production

Plant physiological processes, such as growth, differentiation, development, and stomatal movement, are also regulated by phytohormones (Davies, 2013). It is essential to know that two or more than two hormones are acting together. The effect of these hormones produced by PGPR can stimulate or inhibit the plant growth or involve in the regulation of plant growth (Porcel et al., 2014). Plant hormones are among the most crucial growth regulators; they are known for having a significant impact on plant's secondary metabolism, and additionally, they play a vital role in the stimulation of plant defense response mechanisms against stresses. One of the mechanisms for the improvement of plant growth and stress tolerance by beneficial microorganisms is their ability of phytohormone synthesis in the rhizosphere or root tissue.

The IAA-producing *Mycobacterium* species was reported in the rhizosphere of orchid (Tsavkelova et al., 2007), and *Azospirillum*, *Mycoplasma*, *Azotobacter*, *Rahnella*, and *Cellulomonas*, were found in the wheat rhizosphere (Egamberdiyeva, 2007). However, in the other few reports, *Pseudomonas* spp. (Lawongsa et al., 2008), *Arthrobacter* spp. (Piccoli et al., 2011), and *Enterobacter*, *Pseudomonas*, and *Stenotrophomonas* species were associated with plants that produced IAA (Khan and Doty, 2009). Mishra et al. (2017) isolated bacteria with IAA production ability from stressing environments, which were identified as *Pseudomonas* spp., and *Ochrobactrum* spp. In other studies *Bacillus megaterium*, *Pseudomonas fluorescens* G20-18, *Bacillus subtilis*, *Bacillus cereus*, *Escherichia coli*, and *Halomonas desiderata*, were reported for the synthesis of cytokinins (García de Salamone et al., 2001; Karadeniz et al., 2006; Groškinsky et al., 2016). Various root-associated microorganisms were found, involved the synthesis of stress hormone ABA. Karadeniz et al. (2006) reported that *Phaseolus vulgaris*, *B. cereus*, *Klebsiella pneumoniae*, *B. megaterium*, and *Proteus mirabilis*, as a synthesizer of ABA. Actinomycetes have also been shown to produce GB-like, IAA, and CK substances (Shutsrirung et al., 2013). Recently, few other hormones such as gibberellic acid (GA), auxin, brassinosteroids (BR), cytokinin (CK), and abscisic acid (ABA) peptide hormones have also been shown as the crucial regulators plant immunity (Bari and Jones, 2009).

2.1.2. Production of ACC-deaminase

The PGPR produces an enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase that facilitates plants for better growth (Glick, 2012) under various stresses. ACC deaminase enzyme has involved in cleaving ethylene precursor ACC to ammonia and keto-butyrate (Srivastava et al., 2014). Another plant hormone known as ethylene can regulate several processes such as abscission of leaves, fruit ripening (Reid, 1981). ACC is synthesized in the plant in response to stresses such as drought, cold, flooding, pathogen infection, and heavy metals (Glick, 2012). Plant's root colonized by PGPR with ACC deaminase activity showed more tolerant against environmental stresses (Naveed et al., 2008). Several biotic stresses can induce ethylene production in plants and started various physiological changes at molecular level not only in the regulation of plant growth but also involved in the induction of plant defense (Saleem et al., 2007). The higher production level of ethylene in the cell is sensed by trigger off different receptors, which leads to the trigger of cellular responses (Jouyban, 2012). ACC deaminase is not only the factor in changing the root morphology but nitric oxide producing bacteria such as *Azospirillum* can also change the root morphology (Creus et al., 2004; Molina Favero et al., 2008), via decreasing the level of ethylene hormone and as the indicator of general stress in plants and ethylene is the critical regulator of signal transduction pathways. Like ethylene, proline is also synthesized by the plant in response to biotic stresses, it responded towards osmotic adjustment, scavenging of free radicals for stabilization of subcellular structures (Hare and Cress, 1997). However, in pepper plant, it was accumulated without any stress in the presence of *Arthrobacter* and *Bacillus* treated plants, which ultimately concludes the role of bacteria against some of the biotic stresses (Sziderics et al., 2007).

Several databases with bacterial genomes and annotation revealed that the presence of many *acdS* genes in bacteria. However, the identity of these genes precisely is a difficult job and need more caution. Only some of the *acdS* genes are reported which, can encode active enzyme. Some genes which were tentatively reported for encoding ACC deaminase subsequently encode D-cysteine desulphydrase activity (Riemenschneider et al., 2005). A report suggested that residues of amino acids in the active sites of ACC deaminase and cysteine desulphydrase may control the reactions carried out by these enzymes. Thus, it is possible to exchange the function between these two enzymes by functional mutagenesis (Todorovic and Glick, 2008). Any bacteria growing by using nitrogen as the sole source of food have actively expressed the ACC deaminase gene (Glick, 1995). Hontzeas et al. (2005) proposed that some of ACC deaminase coding genes used horizontal gene transfer (HGT) to be evolved, by analyzing the phylogenetic relationship between all the *acdS* genes. Another report by Blaha et al. (2006) showed similar results such as HGT of ACC deaminase from Proteobacteria to bacteria. The phylogenetic study was performed with the *acdS* gene in proteobacteria, and later studies suggested that *acdR* was evolved from *acdS* by HGT (Prigent-Combaret et al., 2008). A recent report by Nasciment et al. (2012) indicated that there has the transfer of *acdS* genes during symbiosis in some *Mesorhizobium* sp. and that was based on the founding of *acdS* genes in the symbiosis islands of *M. loti* R7A, *Mesorhizobium ciceri* bv. *Biserrulae* WSM1271, *Mesorhizobium* sp. MAFF303099, *Mesorhizobium opportunistum* WSM2075T and *Mesorhizobium maustalicum* WSM2073T, nearest to the cluster of nitrogen fixation genes. These types of studies and suggestion were made that genes required for pathogenic or symbiotic interactions with eukaryotic hosts are often part of the accessory gene pool of the microbe, acquired by horizontal transfer. They may be clustered on plasmids or the chromosome as genomic islands (Finan, 2002). Most of the *acdS* and *acdR* phylogenetic analysis was based on proteobacteria, some other studies showed the presence of ACC deaminase activity by several PGPR such as Actinobacteria (Hontzeas et al., 2005; Siddikee et al., 2010) and Firmicutes (Siddikee et al., 2010; Timmusk et al., 2011).

2.1.3. Production of indole-3-acetic acid

There has been the number of mechanisms involved through PGPR for the plant growth promotion, which includes root growth, biocontrol activities, and nutrient uptake (Fig. 1). Authors (Fröhlich et al., 2012) have reported and suggested that *Pseudomonas* could be used as biocontrol PGPR or even plant pathogen.

2.1.4. PGPR against insect pests

Several chemical pesticides are in use against the insect pests. It is a well-known fact that insecticides are not suitable for the environment as it can cause a harmful effect on the human beings also. PGPR could be the alternative for these insecticides. *Bacillus thuringiensis* is a well-known PGPR against insects and is in use since so many years. A recent report suggested the use of rhizobacteria such as *Bacillus pumilus* and *B. sphaericus* against the white grubs (Coleoptera: Scarabaeidae) (Coy et al., 2019). PGPR such as *Bacillus* spp. can directly affect the insects and cause their mortality (D'Alessandro et al., 2014; Gadhave et al., 2016) and the primary mechanism is the production of volatiles. One of our very initial studies suggested the role of HCN produced by Pseudomonads against *Helicoverpa* (Patel et al., 2010).

3. Strategies used by PGPR under various abiotic stresses

Synthesis of proline has found to be increased in plants facing abiotic stress in the presence of PGPR such as *Arthrobacter*, *Burkholderia* and *Bacillus* (Sziderics et al., 2007). Recent studies have shown that phytohormones produced by root-associated microbes may prove to be crucial metabolic engineering targets for inducing host tolerance to abiotic stresses.

3.1. Under drought stress

The drought stress-tolerant plants started the synthesis of osmolytes in response to water scarcity and ultimately increased the osmotic potential of the cell (Farooq et al., 2009). Sometimes root exudates also include the osmolytes. Some of the PGPR can synthesize osmolytes and help plants to strengthen their resisting against drought stress (Fig. 1). The role of osmolyte producing rhizobacteria has been supported the plants that tolerate severe stress conditions. IAA production by PGPR may be an essential factor for the improvement of root and shoot biomass production under drought stress (Yuwono et al., 2005). ACC deaminase producing bacteria resist the plant root drying when present in the rhizospheric region of plants by affecting the ethylene signaling pathway. *Achromobacter piechaudii* having ACC deaminase activity that shown to resist against water deficit in tomato and pepper plant, leads to improvement in the biomass. Production of ethylene has found to be reduced in plants colonized with PGPR, which improved the damage due to water scarcity without influencing relative water contents of plants (Mayak et al., 2004). Maize seedlings showed improved relative water content with *Azospirillum brasilense* inoculated in plants compared to uninoculated plants. Inoculation of drought stress tolerant bacteria takes care of significant drop in water potential of plants and improves plant growth proline content in leaves and roots. The effect of rhizobacteria is more significant (75%) in the presence of water (Casanovas et al., 2002). Creus et al. (2004) suggested that the reduction in yield and higher content of Mg, K, and Ca in grains of wheat after inoculation of *Azospirillum* under water scarcity. PGPR can protect the plants under drought stress. A recent study suggests the role of PGPR, along with PGRs, provide tolerance to plants under drought stresses (Yang et al., 2016; Khan et al., 2019). PGPR have important impressions on plant growth and development. They can improve the availability of micro-nutrients to the host plant by gathering chemicals related to growth promotion. The produces exopolysaccharides (EPS), which are carbohydrates and released in the rhizosphere (Vanhaverbeke et al., 2003). Such EPS have a crucial role in the protection of the plant from desiccation (Pal and Sharma, 1999). Salicylic

acid (SA), secreted by the microorganisms, which is a well-known phenolic compound, involved in the regulation of plant growth and development and their responses to drought stress. It functions as a signaling molecule under stress induces genes that function as antioxidants, chaperones, heat shock proteins, and enzymes also induce the genes responsible for the synthesis of secondary metabolites (Jumali et al., 2011). Ethylene is known to regulate plant growth, and its production is influenced by salinity and drought (Nadeem et al., 2007) and waterlogging (Grichko and Glick, 2001).

3.2. Under heavy metal stress

Nutrient elements such as potassium, copper, iron, zinc, and phosphorus have limited mobility in soil. Insoluble form of phosphorus can be mobilized by exudate from the plants such as organic acids and phosphatases. Carbohydrates present in exudates indirectly involve in phosphorus mobilization by serving as a carbon source for microorganisms involved in phosphorus mobilization. There is increased by 52% of released carbohydrates observed in plants treated with IAA and no change in plants treated with phosphorus (Wittenmayer and Merbach, 2005). So, it could be hypothesized that IAA produced by PGPR could also mobilize phosphorus in soil and make available for plants (Fig. 1). Plants inoculated with *Mycobacterium phlei* MbP18, *Bacillus polymyxa* BcP26 and *Pseudomonas alcaligenes* PsA15 observed to promote plant growth and nutrient uptake in maize. The increase in absorption of phosphorus, nitrogen, and potassium was found in nutrient-deficient calcicols than the fertile loamy sand soil, stimulation of such uptake was detected in roots (Egamberdiyeva, 2007). Several root-colonizing bacteria can release metal-chelating compounds, which includes iron-chelating siderophores. Bacteria have siderophore producing ability that influence plant for the uptake of several metals such as zinc, iron, and copper by using the chelating mechanism of rhizobacteria (Egamberdiyeva and Kucharova, 2009; Dimkpa et al., 2009). The mechanism of acidification of the microenvironment that influencing changes in redox potential and that have also been used by microorganisms to affect the bioavailability of metals (Gadd, 2004). Metal can be mobilized by volatilization through methylation, autotrophic and heterotrophic leaching and release of chelators; however heavy metal mobility can be reduced by sorption to cell components followed by intracellular sequestration or precipitation as insoluble organic or inorganic compounds (Gadd, 2004). Barley plant surviving in cadmium contaminated soil showed 120% higher grain yield by decreased two-fold cadmium content in grains in the presence of *Klebsiella mobilis* CIAM 880. Mechanism of adaptation in plants facing several environmental stresses such as heavy metal toxicity, nutrient deficiency has been helped by phytohormones produced by PGPR (Potters et al., 2007).

3.3. Under salinity stress

The stress tolerance ability of bacterial strains provides essential benefits to plants. The strength of root-associated microbes to synthesize phytohormones is typically not hampered by high salt concentrations (Egamberdiyeva and Kucharova, 2009; Srivastava et al., 2014; Sarkar et al., 2014). Generally, irrigated water does not enter the soil that is reduced infiltration rate due to salinity and some other reason. The major obstacle to such a process to increases the availability of soluble salt in rhizospheric soil, which affects the soil-microbes-plant interaction and leading to improve plant productivity. The process is more prominent in the coastal areas, which is continually in touch of sea water, some mismanagement in the irrigation process in coastal regions and faulty practices of agriculture. The salinity is one of the major abiotic factors, affects the modern agricultural system worldwide. More than 5% of area worldwide is affected by salinity and arises due to natural processes. Accumulation of salt in arid and semiarid zones takes a long period (Bui, 2013). There are mainly two ways by

Table 1
Different stress tolerant PGPR showed their effect on varieties of plants.

PGPRs	Plant	Effect	References
<i>A. brasilense</i>	Maize	Osmolytes improved relative water content	Mayak et al. (2004)
<i>Mycobacterium phlei</i> MbP18, <i>Bacillus polymyxa</i> BcP26 and <i>Pseudomonas alcaligenes</i> PsA15	Maize	Increase in uptake of phosphorus, nitrogen and potassium	Egamberdiyeva (2007)
<i>Arthrobacter</i> and <i>Bacillus</i>	Pepper	Proline responded towards osmotic adjustment, scavenging of free radicals for stabilization of subcellular structures	Sziderics et al. (2007)
<i>Enterobacter aerogenes</i> , <i>Pseudomonas syringae</i> and <i>P. fluorescens</i>	Maize	ACC deaminase activity can induce salt tolerance in by regulation of K/Na ratios, chlorophyll and proline level	Nadeem et al. (2007)
<i>A. brasilense</i>	Tomato	Nitric oxide as a signaling molecule in IAA induced pathway which enhanced lateral root and root hair development	Molina-Favero et al. (2008)
<i>A. lipoferum</i>	Maize	Gibberellins increased ABA levels and alleviated drought stress	Cohen et al. (2009)
<i>P. fluorescens</i>	Maize	Increased proline, abscisic acid, auxin, gibberellin and cytokinin content improved plant growth	Ansary et al. (2012)
<i>Phyllobacterium brassicacearum</i> strain STM196	<i>Arabidopsis thaliana</i>	Enhanced ABA content resulted in decreased leaf transpiration	Bresson et al. (2013)
<i>A. lipoferum</i>	Maize	Increase growth and accumulation of free amino acids, prolines and soluble sugars	Qudsia et al. (2013)
<i>Bacillus subtilis</i>	<i>Platycladus orientalis</i>	Cytokinin production by PGPR elevated ABA levels in shoots and increased the stomatal conductance	Liu et al. (2013)
<i>Bacillus</i> isolate 23-B and <i>Pseudomonas</i> 6-P with <i>Mesorhizobium ciceris</i>	Chickpea	Higher proline concentration, improved germination, root and shoot length and fresh weight of the seedlings	Sharma et al. (2013)
<i>Planococcus rifietoensis</i>	Wheat	Improves plant growth and yield	Rajput et al. (2013)
<i>P. putida</i> H-2-3	Soybean	Secretion of gibberellins hormone and improved plant growth	Sang-Mo et al. (2014)
<i>B. thuringiensis</i>	<i>Lavandula dentata</i>	Decreased the glutathione reductase (GR) and ascorbate peroxidase (APX)	Armada et al. (2014)
<i>Bacillus thuringiensis</i> AZP2	Wheat	Reduction of volatile emissions and higher photosynthesis	Timmusk et al. (2014)
<i>Bacillus polymyxa</i>	Tomato	Proline accumulation improved the physiological and biochemical parameters of plants	Shintu and Jayaram (2015)
<i>P. jessenii</i> , R62, <i>P. synxantha</i> , R81 and <i>A. nitroguajacolicus</i> strainYB3, strain YB5	Rice	Accumulation of proline maintained osmotic adjustment and improved plant growth	Gusain et al. (2015)

which salinity affect the plants. Soil becomes harder and dry due to the high concentration of salt makes the roots unable to extract water, and the second one high concentration of salt is also toxic to plant cells. Root, directly in contact with salts, is majorly affected by its growth and metabolism. However, the toxic concentration of salt takes more time to be accumulated in plants. (Munns and Tester, 2008). Salinity negatively affects the plant in terms of yields by affecting panicle, tiller and spikelet of the plant as well as grain size also (Grattan et al., 2002). PGPR can solve the severity arises due to salinity. Several gram-positive and gram-negative PGPR have been reported to colonize the root of the plant and minimize the effect of salinity by different direct and indirect mechanisms (Table 1). These bacteria use their chemotaxis, and the production of exopolysaccharide, indole-3-acetic acids (IAA) and aminocyclopropane-1-carboxylate (ACC) deaminase can combat with salinity stress (Glick, 1995) (Fig. 1). PGPR can induce 'induced systemic tolerance' (IST) to resist the changes in plants to develop tolerance in plants against abiotic stresses such as salinity (Yang et al., 2009). A report by Yildirim et al. (2008) suggested that *Kocuria erythromyxa* and *Staphylococcus kloosii* can induce salt tolerance in *Raphanus sativus* by producing antioxidants for scavenging of reactive oxygen species (ROS) (Figueiredo et al., 2008). Another report by Nadeem et al. (2007) suggested that *Enterobacter aerogenes*, *Pseudomonas syringae* and *P. fluorescens* having ACC deaminase activity can induce salt tolerance in maize by regulation of K/Na ratios, chlorophyll and proline level. Hamdia et al. (2004) reported that salt tolerance in maize dependent on several mechanisms such as a high ratio of K/Na on inoculation with *Azospirillum*. M'Piga et al. (1997) reported and suggested that the role of PGPR against several phytopathogens by inducing certain defense enzymes such as peroxidase (POX), chitinase, β -1, 3-glucanase (GLU) and phenylalanine ammonia-lyase (PAL). However, IAA has activity on H^+ ATPase of the plasma membrane, induces Na^+ loading into root cells (Silva and Gerós, 2009; Cho and Hong, 1995). Another bacteria *Pseudomonas* sp. PDMZnCd2003 can produce a high concentration of IAA under salinity stress. A study showed that the characterization of IAA producing, salt-tolerant and phosphate solubilizing strain of bacteria SAL-15 also having ACC deaminase activity, improves plant growth and

yield in wheat crop (*Triticum aestivum* L. var. TJ-83) in the salinity stress conditions (Rajput et al., 2013). The molecular study showed that the changes in gene expression related to the production of ethylene reported in plants during abiotic stress having bacteria in their rhizosphere (Timmusk et al., 1999; Sziderics et al., 2007). Increase in ethylene concentration was reported in the plants facing salinity stress, due to the increase in ACC level, which leads changes in several physiological functions of plants (Table 1). Any mechanism, which can decrease the level of ethylene in plants during salinity stress, can improve plant growth. PGPR produced phytohormones such as gibberellins, indole acetic acid, abscisic acid, and cytokinins have a positive effect on root length, number of root tips and on leaf area, consequently enhanced uptake of nutrients under higher salt conditions (Egamberdiyeva and Kucharova, 2009) (Table 1). Another study (Egamberdiyeva and Kucharova, 2009) showed that *Pseudomonas extremorientalis*, *P. putida*, *P. aurantiaca*, and *P. chlororaphis*, were able to produce IAA in a 4% NaCl conditions. *Bacillus* sp. and *Pseudomonas* sp. and strains were able to produce IAA under high salt conditions (200–400 mM NaCl) and increased the plant biomass of *Sulla carnosa* under salt stress.

3.4. PGPR for the mitigation of thermal stress

In the upcoming future, increase in greenhouse gases could raise the Earth's surface temperature anywhere between 1.5 and 11 °C by 2100 (Stainforth et al., 2005). It can reduce crop productivity drastically. Recent reports suggest that PGPR also enhance the tolerance of plants to abiotic stresses such as chilling injury (Ait Barka et al., 2006), and elevated temperature stress (Ali et al., 2009). Another study suggested the role of *Pseudomonas putida* for thermal tolerance (Ali et al., 2011). PGPR can induce production of heat shock proteins in the plant and provide tolerance indirectly. A lot of work still needed to maximize the use of PGPR for thermal tolerance in the plant.

Table 2
Effect of various stresses tolerant PGPRs on crops production.

PGPRs	Crops	Stresses	Effects	References
<i>Glomus mosseae</i> <i>A. brasilense</i> Sp245	Maize Wheat	Salinity Drought	Higher accumulation of soluble sugars Higher Mg, K and Ca content in the grain and increases in water content, relative water content, water potential and apoplastic water	Feng et al. (2002) Creus et al. (2004)
<i>Glomus clarum</i> <i>Burkholderia phytofirmans</i> PsJN <i>Glomus stanticum</i> <i>Methylobacterium oryzae</i> and <i>Burkholderia</i> sp. <i>Pseudomonas fluorescens</i>	Mungbean Grapevine Soybean Tomato Groundnut	Salinity Low temperature Salinity Ni and Cd toxicity Salinity	Improved plant growth and yield Increased root growth, plantlet biomass and tolerance to cold Increased the root and shoot growth Reduced uptake and translocation Decreased endogenous ethylene levels	Rabie (2005) Ait Barka et al. (2006) Sharifi et al. (2007) Madhaiyan et al. (2007) Saravanakumar and Samiyappan (2007)
<i>Bacillus megaterium</i> and <i>Glomus</i> sp. <i>Glomus intraradices</i> BEG 123 <i>P. polymyxa</i> and <i>Rhizobium tropici</i> <i>Pseudomonas</i> sp. <i>Bacillus lentimorbus</i>	Trifolium Bean Common bean Pea Spinach, Carrots and Lettuce	Drought Salinity Drought Drought Antioxidant	IAA and proline production Greater osmotic root hydraulic conductance and increased active solute transport Increased plant growth, N content, and nodulation Decreased ethylene production Increased the antioxidant capacity, as well as plant growth	Marulanda et al. (2007) Aroca et al. (2007) Figueiredo et al. (2008) Arshad et al. (2008) Nautiyal et al. (2008)
<i>Pseudomonas</i> sp. AMK-P6 <i>Pseudomonas putida</i> P45 <i>P. fluorescens</i> Aur6 and <i>Chryseobacterium balustinum</i> Aur9	Sorghum Sunflower Rice Tomato	Heat Drought Salinity Salinity	Induction of heat shock proteins and improved plant biochemical status Increased uptake of water and nutrients from rhizosphere soil Increased productivity and quality Enhanced primary root and shoot length, fresh weight and number of leaves per plant	Ali et al. (2009) Sandhya et al. (2009) Lucas et al. (2009) Tank and Saraf, (2010)
<i>Pseudomonas fluorescens</i> , <i>P. aeruginosa</i> and <i>P. stutzeri</i> <i>Bacillus megaterium</i> <i>Pseudomonas putida</i> <i>Bacillus cereus</i>	Maize Wheat Mung bean, Chickpea and Rice	Salinity Heat Salinity	Higher root hydraulic conductance Synthesis of high-molecular weight proteins and also improved the levels of cellular metabolites Increased growth	Marulanda et al. (2010) Ali et al. (2011) Chakraborty et al. (2011)
<i>Arthro bacter</i> sp. and <i>B. subtilis</i> <i>Achromobacter piechaudii</i>	Wheat Tomato	Salinity Drought	Increased dry weight Production and excretion of glucosylglycerol (GG) were found as a remarkable mechanism for the stress protection	Upadhyay et al. (2012) Alavi et al. (2013)
<i>P. putida</i> H-2-3	Soybean	Drought	Secreted GAs and improved plant growth, induced regulation of stress hormones and antioxidants and also increased crop productivity	Sang-Mo et al. (2014)

4. Effects of PGPR on crop productivity and sustainability under stresses

Plant growth can be inhibited by various stresses like salt, drought heavy metals, flood, pathogens, temperatures, etc. that could be raised by anthropogenic activity as well as environmental stresses. Stress tolerant PGPR can minimize these stresses by using different mechanisms such as phosphate solubilization, nitrogen fixation, ACC deaminase production, and siderophore production. A PGPR *P. fluorescens* has been reported for exhibiting highest phosphate solubilization activity, siderophore production, as well as ACC deaminase production under laboratory conditions. Another report by Tank and Saraf (2010) showed that *P. aeruginosa* causes the lowest uptake of NaCl in plants so reduces the salt stress. Barley plant surviving in cadmium contaminated soil showed 120% higher grain yield in the presence of *Klebsiella mobilis* CIAM 880. ACC deaminase producing bacteria resist the plant root drying when present in the rhizospheric region of plants by affecting the ethylene signaling pathway. *Achromobacter piechaudii* have ACC deaminase activity, which caused resist against water deficit condition. There is the number of stresses tolerant PGPRs reported that have enhanced plant growth promotion in various crops (Table 2). The stress-tolerant PGPRs produced various strong, active metabolites, to protect crops and enhanced or maintained their production under as normal conditions. PGPR maintained soil texture, decrease chemicals use, control environmental pollution, and consequently balanced agriculture sustainability. This phytohormone produced by rhizobacteria and plays an important role in plant growth promotion. It is also detected in higher plants and algae. Few studies have been available to produce cytokinin from the plant-associated bacteria (Tirichine et al., 2007). Several microorganisms can synthesize cytokinin such as *Pseudomonas savastanoi* and *Agrobacterium tumefaciens* that actively involved in the formation of plant tumors (Zhang et al., 2011). The normal, natural concentration of cytokinin, getting decreases leads to stomatal closure and further leads to decreases and protect plants from water loss (Weyens et al., 2009). During drought condition that showed the effect to decrease the cytokinin concentration in plants (Hanano et al., 2006; Weyens et al., 2009). A report (Schaller, 2012) suggested that ethylene can act as a negative regulator of nodulation. Further, it is observed that PGPR containing ACC deaminase activity colonizes the rhizospheric region of plants and reduces ethylene level in plants and on bacterial infection leads to an increase in nodulation in legume plants. A report (Shaharouna et al., 2006) suggested that combined inoculation of competitive rhizobia and PGPR can increase the nodulation. Phytohormones produced by bacteria, have no direct benefits to bacteria but indirectly involve in nutrient availability for bacteria itself. Phytohormones are organic compounds which have been synthesized in specific plant parts and showed their effect in other regions of plants. ACC deaminase producing PGPR can decrease the ethylene level by decreasing ACC level in plants (Glick et al., 1998, 2007), however higher concentration of ethylene may lead to inhibition of plant growth or sometimes death. It was suggested by Glick et al. (1998) that ACC deaminase producing PGPR firstly binds on the surface of the plant on roots or seeds also reported in leaves flowers and plant's internal tissues such as endophytes. The number of photosynthetically fixed carbon has found to be exudates from plant roots (ranges 5–30%). Exudates obtained from roots contain compounds such as organic acids, large amounts of sugars, and amino acids. These compounds act as a food source to root colonizing PGPR that is the reason for the presence of several numbers of microorganisms in the rhizospheric region of plants. Auxin known as indole acetic acid (IAA) synthesized in plant shoots and basipetal transported to root tips (Overvoorde et al., 2010) in deficient concentration to stimulate the root growth and promotes the initiation of lateral roots. However, its higher concentration in root tips has an inhibitory effect on the growth of roots. The inhibition of growth can be direct or indirect effect by the promotion of ethylene synthesis (Jackson et al., 1991) due to the relationship between ethylene and auxin

precursor 1-aminocyclopropane-1-carboxylic acid (ACC) (Glick, 2003). Higher production of ethylene under the environmental stress conditions can inhibit nitrogen fixation, elongation of roots in leguminous plants (Jackson et al., 1991) and senescence of premature leaves (Ahmad et al., 2013). However, the higher concentration of ethylene can induce defoliation and other cellular processes which ultimately lead to growth inhibition of roots and shoot, and senescence of premature leaves resulting low crop yield (Li et al., 2005). Plants have the ability to synthesize 1-aminocyclopropane-1-carboxylate (ACC), the precursor for ethylene synthesis.

4.1. Mechanism adapted by PGPR to embrace the plants

PGPR can affect the plant in two ways either directly by production of phytohormones or indirectly by induction of signaling in the host plant. The direct role has been most commonly attributed to the creation of phytohormones such as gibberellins, auxins, cytokinin, and abscisic acid, fixation of biological nitrogen and phosphate solubilization, etc. However, the indirect mechanisms comprise of suppression of phytopathogens by the production of volatile HCN, siderophores, antibiotics, volatile metabolites, and ammonia, etc. Induced systemic resistance in the host plant and competition with the pathogen for space and nutrients (Glick, 1995). A bacterium can affect plant growth and development using any one of these mechanisms. During the last couple of decades, the use of PGPR for sustainable agriculture has improved enormously in various parts of the world to reduce chemical fertilizers and pesticides.

5. Conclusion

An ideal sustainable agriculture system maintains and improves human health, benefits producers and consumers both economically and spiritually, produces enough food for an increasing world population and protects the environment. One of the most critical constraints to agricultural production in the world is biotic and abiotic stress conditions prevailing in the environment. Plant-associated microorganisms can play crucial role in conferring resistance to both the stresses. Stress tolerant PGPR showed multidirectional function for enhancement of crop yield, control environmental pollution, environment eco-friendly under sustainable development through a variety of mechanisms like triggering nitrogen fixation, phosphate solubilization, providing growth hormones, siderophores, osmotic response, and nutrients and acting as biocontrol agents. Ofcourse, only PGPR can not be the solution against the different stresses but, can minimize the overuse of chemicals and pesticides. Use of the PGPR in the consortia mode could be additive to the strategie for the reduction of chemicals and prevent the human health to be compromised to residual effect of chemicals. Soil nutrient balance can also be improved by using PGPR and maintainance the agricultural lands fertile.

6. Future prospectus

The review of the literature suggests that bacterial collections from salinity, heavy metals, drought-prone areas performed better in increasing plants tolerance to that stress conditions than those that were isolated from regions that do not experience salinity, heavy metals or drought. However, such relation has been drawn from a few studies. There are needs to validate the concept in other systems also. Researchers need complementary tow requirements before the start of the experiments related to the use of PGPR for crop improvement under different stresses. The first is to simplify the system to facilitate elucidation of the essential stress-adaptive features that could be induced in plants after the treatment with beneficial microbes. Therefore, it is crucial to develop screening protocols that can be used by many scientists to evaluate PGPR-related to salinity, heavy metals, and drought adaptive features. It will help scientists create accurate data which can

be replicated with higher accuracy.

Moreover, soil sterilization may induce changes in soil physical-chemical characteristics. Such changes in the soil may affect plants response to salinity, heavy metals, and drought stress. The outcome of PGPR-mediated stress tolerance depends on the interaction between the strain of PGPR used and soil type as well as the plant's ability to benefit from PGPR populations occurring naturally in the soil. By reviewing the current leads available, the collective future research is needed in this area, particularly field studies and application of potential organisms as biofertilizers in stressed soil. The reviews regarding stress tolerance via genetic engineering and plant breeding are essential but a long drawn and expensive process. Whereas microbial inoculation to alleviate stresses in plants could be a cost-effective environment-friendly alternative which requires very less time to execute. Single or combination of efficient PGPRs can work against different stresses to increase environmental sustainability. The indigenous stress-tolerant PGPRs strains should be more suitable for the local farmers.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bcab.2019.101271>.

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