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Alleviation of Drought Stress by Plant Growth Promoting Rhizobacteria (Pgprs) In Crop Plants: A Review

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Abstract

Drought stress is the major constrain among all stresses, which affects the agricultural production worldwide. The food production is get reduced due to drought stress which unable to feed an ever-increasing population. The development of drought resistant plant variety or transgenic plant to increase food production is costly and time consuming, so any sustainable way is required. The use of plant growth promoting rhizobacteria (PGPRs) for improvement of plant growth is sustainable and inexpensive way. PGPRs provide various direct mechanisms like phytohormone synthesis, phosphate solubilisation, nitrogen fixation, exopolysaccharide production and indirect mechanism like HCN, ACC deaminase, siderophore, antibiotics production which enhance the plant growth under abiotic stress. Due to their multiple traits, the search for suitable and rhizosphere competent PGPR becomes interesting and can be used as inoculants for bio fertilization and biocontrol purposes in agriculture, forestry, and environmental rehabilitation.

Keywords: Plant growth promoting rhizobacteria (PGPR); Drought stress; ACC deaminase; Reactive oxygen species; Exopolysaccharide; Antioxidants; IAA

Introduction

As the world's population increasing continuously and the environment gets damaged due to adverse condition like global warming, it is impossible to produce sufficient food to feed the population. For instance, the world's population which is currently 7.8 billion will increase up to around 10 billion in 2050, the increasing population also increase demand of food, mostly it required more than double amount of food [1-4]. To fulfil their need of food demand, it is absolutely indispensable to increase the agriculture production either by using more land for crop production or by means of different types of chemical fertilizers, pesticides, insecticides etc. But the availability of land area is limited due to urbanization and industrialization while available area already under cultivation is simultaneously losing fertility due to different anthropogenic activity7 like use of chemical fertilizers, pesticides. In recent time, majority of the world is facing climate change due to global warming which leads to different stress conditions like severe drought, very high temperature, salinity, soil acidity etc., and ultimately decreases agricultural production. Low water availability and extreme temperature adversely affect to the plant growth and reduce the food production. In past decades, the intensity of drought stress increased and became most destructive abiotic stress that affect world's food security. It is expected that by 2050, serious plant growth problems generated for more than 50% of the arable lands by drought stress [5,6]. Severe drought reduced gross primary productivity of Europe by 30% in 2003 [7] and maize production of United States by 25% in 2010 [8]. According to published data from 1980 to 2015, drought stress reduced the 21% wheat yield and 40% maize yield worldwide [9].

Plant growth and development under drought stress

As plants are sessile, their normal physiological functions and metabolism easily get affected by abiotic stresses such as extreme temperatures, excess water flooding or deficient, salinity, as well as heavy metal. High temperature generates excessive heat which produces reactive oxygen species (ROS) and further leads to degradation of membranes, denaturation of proteins as well as nucleic acids while at low temperature plants get dehydrated due to the freezing condition. Inadequate nutrients in soil, change in pH or microbial community of soil also affect the growth as well as development of plant. The availability of water is the prominent factor responsible for the promotion of growth and survival of plant as it adversely affects the normal metabolic processes of plant [10]. Among all abiotic stress, drought stress has major effect on the normal growth and metabolism [11,12], physiological, biochemical and morphological characteristics of plant [13,14]. Insufficient water availability generates osmotic stress and cell dehydration which hinder the cell division and cell elongation [15]. Drought stress also affects various physiological characteristics like relative water content (RWC), stomatal conductance, transpiration rate, relative electrical conductivity, maximum quantum efficiency of photosystem II (Fv/Fm ratio), leaf water potential, net CO2 assimilation rate, malondialdehyde (MDA) content, turgor pressure etc. Furthermore, drought stress declines the photosynthetic capacity of plant cells due to stomata closure which reduces the availability of CO2 and also due to reduced turgor pressure and oxidative stress via ROS which reduced the chlorophyll content in leaves [16-19]. Several species like sweet corn, sunflower mung bean Paulownia imperialis bean and Carthamus tinctorius has been studied with decreased chlorophyll content under drought stress. Growth of several species such as barley maize rice and wheat has been reduced under drought stress. Water conservation occurs in plant tissue due to less availability of water under drought and salt stress, which results in low gas exchange and stomatal conductance in leaves that cause damage and death of tissues. As plant uptake the nutrient from soil through root by osmosis, the diffusion rate as well as availability and transportation of many nutrients like S, Mg, Ca, P and nitrate is reduced in drought stress [20-32]. Drought also induces the generation of reactive oxygen species (ROS) such as hydrogen peroxide, hydroxyl radicals, superoxide radicals, singlet oxygen that diminishes the antioxidative defence and produce oxidative stress This oxidative stress with high concentration of ROS causes various changes in plant like degradation of proteins, lipids and nucleic acids, cell membrane degradation, lipid peroxidation [33-35]. Overproduction of ROS in chloroplast, mitochondria lead to reduction in CO2 uptake and affect the rate of photosynthesis Seed germination and plant growth require enough quantity of water but in drought condition plant size, leaf area and size remain small and seedling development either stop completely or occurs delay. Drought stress also affect to the various plant’s biochemical activities like nitrate reductase activity due to limited uptake of nitrate from the soil by plant roots it enhances the synthesis of ethylene, a plant growth hormone which adversely affect to root and shoot growth of the plant [36-40]. Finally, the quantity and quality of plant growth is negatively affected by the drought stress, so to overcome this problem and increase the food production to fulfil the requirement of increasing population, the alleviation of drought stress is important.

Microbial biome thriving under drought stress

Enormous number of microorganisms exists in the rhizosphere and on the root surface which have a substantial influence on the growth pattern of plant by producing different plant hormones and metabolites The microbial community in rhizosphere may get change under the influence of drought stress, like, population of gram-positive bacteria such as actinobacteria, Bacillus, Pseudomonas get enhanced in comparison with gram-negative bacteria such as Bacteroidetes, Proteobacteria The change in community of the root associated bacteria in rhizosphere and rhizoplane may lead to stress adapted bacterial colonization that enhance tolerance against drought stress Altered distribution of bacteria in rhizosphere and root associated soil was observed and compared to uncultivated soil of drought sensitive pepper plant (capsicum annuum L.) indicates effect of metabolic activity of plant on the microbial community [41-45]. In another study, pepper plants inoculated with drought tolerant bacteria which were isolated from desert revealed a more resistance against drought situation as compared to uninoculated plant. The root growth increased by 40% in inoculated plant which enhanced water uptake capability of plant Salicornia, a halotolerant plant and their rhizobacterial microbiome showed tolerance against abiotic stress by performing various plant growth promoting (PGP) traits and high colonization with root indicating that halotolerant bacteria isolated from saline environment are potent to enhance plant growth under both salinity and drought stress The growth of Brassica rapa is reduced with change in chlorophyll content, number of flowers and leaf with their simplified indigenous microbial community as compared to complex indigenous rhizobacterial community. This suggest that microorganisms present in soil help to mitigate the effect of abiotic stress by modulating plant growth promoting traits .Comparatives studies of microbial diversity in two soil samples one from agriculture soil and another from Egypt desert soil showed difference in microbial population for instance, extremophiles were present in desert soil while absent in agriculture soil, whereas agriculture soil was found to be rich with Bacillus sp. and Paenibacillus sp. which promotes plant growth [46-50]. This suggests that microbiome of soil vary with variation in soil pH, salinity, water content, temperature, metal ion concentration and it is unique to each ecosystem. The synergistic interaction between plants and microbiome of rhizosphere helps to mitigate abiotic stress by a different mechanism [51-53]. Among them, plant growth promoting rhizobacteria (PGPR) can facilitate the plant growth via different mechanism such as directly modulate the plant hormone level and enhance uptake of micronutrient or indirectly prevent the deleterious effect of plant pathogen by producing antagonistic response or by inducing resistance to pathogen . PGPR cleave 1-aminocyclopropane-1-carboxylate (ACC), a precursor of plant ethylene by producing ACC deaminase and modulate the level of ethylene in a plant in response to stress condition [54-56]. Inoculation of ACC deaminase producing Pseudomonas lini and Serratia plymuthica significantly increased leaf relative water content, plant height, ROS scavenging enzymes, root and shoot dry weight, soil aggregate stability, regulating IAA and ABA level, reducing malondialdehyde in jujube plant and alleviate the adverse effect of drought stress. The drought sensitive wheat (Triticum aestivum L.) when treated with Streptomyces pactum Act12 under drought stress, it shows increased growth of wheat by increasing 21.3% fresh shoot weight, 10.3% shoot length, 13.6% root length. It also increases total soluble sugar content, proline and also upregulate the expression of drought resistance related genes like SnRK2, EXPA2, P5CS in addition decrease the malondialdehyde content around 20.5% in wheat [58].Microorganisms also exist as an endophyte which colonize stems, leaves, roots, tubers and other organelles of the plant and provide protection to plant against environmental stress by employing various mechanisms [57-60]. Endophytes helps plant to survive in drought stress by enhancing relative water content, antioxidants and root growth in addition to releasing various growth regulating substances like IAA, ABA, ACC deaminase . The extent of colonization by endophytes to host plant organs and tissues indicate the ability of PGPR to adapt specific ecosystem and make favorable environment for their existence. According to Chen et al, the endophytic bacterium Pantoea alhagi, which is isolated from wheat enhance the drought tolerance as well as root length and plant growth by adopting mechanisms like production of siderophores, IAA, ammonia. Khan et al. reported that, when plants inoculated with drought resistant endophytic bacteria Pseudomonas azotoformans ASS1 isolated from Alyssum serpyllifolium leaves, enhance chlorophyll content, peroxidase, proline, catalase, superoxide dismutase and decrease the malondialdehyde content in plant under drought stress.

PGPR mitigating drought stress

Various microorganisms can be used to increase plant growth under different stress conditions inexpensively. These beneficial microorganisms can be used as bioinoculants to enhance plant growth which mainly colonize the rhizospheric area and they can be classified into three major categories: i) Plant growth promoting rhizobacteria (PGPR) ii) Arbuscular mycorrhizal fungi (AMF) and iii) Nitrogen fixing rhizobia [61-66]. Plant growth-promoting rhizobacteria (PGPR) are the soil bacteria occupying on the surface of plant roots (rhizoplane), within root tissues (endophytes) or in soil near root area (rhizosphere) that can boost plant growth under various abiotic stresses. In rhizosphere, plant and their associated bacteria establish mutually beneficial relationship for instance PGPRs use plant root exudate for their requirement of carbon, enzymes, nutrient, hormones to derive nourishment and in return they enhance the availability and uptake of nutrients for plants and promote healthy plant growth [67-72]. Plant roots make the rhizosphere a niche for microbial activity and sustain the soil fertility by interacting with both soil and microorganisms Different genera of PGPR decrease the damage caused by environmental stresses and increase the tolerance in plants towards stress condition by adapting different direct mechanisms such as, production of phytohormones, phosphate solubilization, nitrogen fixation, iron sequestration, exopolysaccharide production and indirect mechanisms such as production of hydrogen cyanide (HCN), siderophore production, synthesis of ACC deaminase, production of antibiotics, Induced systemic resistance (ISR), production of lytic enzymes, production of osmo-protectants and antioxidants production (Figure 1).

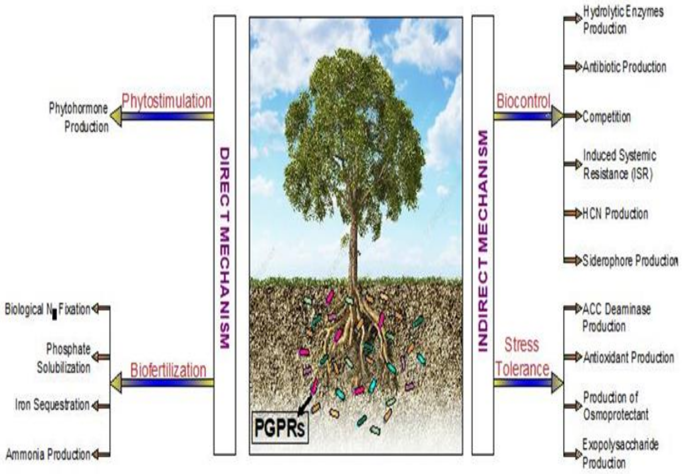

Figure 1: *Mechanisms used by PGPRs to enhance plant growth.*

Inoculation of PGPRs provides benefits for the plant growth such as increase in chlorophyll content, root growth, leaf area, grain size, germination rate, tolerance against environmental stress . PGPRs belongs to various genera including Bacillus, Acinetobacter, Enterobacter, Rhizobium, Serratia, Paenibacillus, Azospirillum, Enterobacter, Bradyrhizobium, Burkholderia, Azotobacter, Pseudomonas, Arthrobacter, Klebsiella, Streptomyces etc. [73-77]. Many PGPRs are used as bioinoculants to enhance crop production in unfavorable condition as they possess multiple plant growth promoting (PGP) traits (Table 1). Recently, PGPRs have been utilized for growth of several crops like wheat, maize, potato, chickpea, Foxtail millet, and sunflower and enhance agricultural sustainability. The expression of multiple PGP traits by PGPRs such as production of osmolytes, antioxidants, ACC deaminase, exopolysaccharide, volatile compounds help plants to tolerate drought stress. These bacteria may also have capability for N2

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fixation, solubilizing phosphate, siderophore production which help in plant growth.

Table 1*:* *Mitigation of drought stress in plants by PGPRs using different mechanisms.*

Bacterial Strains (PGPR)	Test Crop	Mechanism of Action	Effects of PGPR Inoculation	References
Bacillus spp. 12D6 and Enterobacter spp. 16i	Wheat & Maize	IAA synthesis	IAA enhanced the root length, root diameter and surface area, root branching	Jochum et al., 2019
Enterobacteria lignolyticus strain TG1	Tea	IAA synthesis	IAA increased root biomass, root length, shoot biomass and shoot length of tea plant	Dutta et al., 2015
Azospirillum brasilense	Arabidopsis thaliana	Abscisic acid (ABA) production	Increased the resistance towards drought and other abiotic stress as compared to Arabidopsis mutant aba2-1, defective in ABA biosynthesis	Cohen at al., 2015
Sphingomonas sp. LK11	Soya bean	Osmolyte Synthesis	Improved plant growth through accumulation of free amino acids and soluble sugars	Asaf et al. 2017
Bacillus subtilis, Bacillus thuringiensis, and Bacillus megaterium	Chickpea	Osmolyte Synthesis, Antioxidative activity	Higher soluble sugar content maintains water balance and photosynthetic efficacy as well as enhanced leaf chlorophyll, proline content and reduced the lipid peroxidation, antioxidant enzyme like SOD, CAT, POD, APX activities	Khan et al., 2019
Raoultella planticola	Maize	Osmolyte Synthesis	Accumulation of higher choline and GB content in plant cells promoted seed germination by providing osmo-regulation	Niu et al., 2017
Pseudomonas lini and Serratia plymuthica	Jujube	ACC Deaminase, Antioxidative activity	Increased leaf relative water content, plant height, ROS scavenging enzymes, root and shoot dry weight, regulating IAA and ABA level, reducing malondialdehyde	Zhang et al., 2020
Enterobacter HS9 and Bacillus G9	Velvet bean (Mucuna pruriens)	ACC Deaminase	Reduced the ethylene production by reducing concentration of ACC in the roots and leaves and improved root and shoot length as well as biomass	Saleem et al., 2018
Pseudomonas aeruginosa, Enterobacter cloacae, Achromobacter xylosoxidans and Leclercia adecarboxylata	Maize	ACC Deaminase	Enhanced root and shoot length, dry and fresh weight of root and shoot, amount of nitrogen, potassium as well as phosphorous and improved the plant growth with reducing accumulation of ethylene	Danish et al., 2020a

Pseudomonas aeruginosa PM389, Bacillus endophyticus J13, Bacillus tequilensis J12 and Pseudomonas aeruginosa ZNP1	Arabidopsis thaliana	exopolysaccharide (EPS) synthesis	Fresh weight (FW), dry weight (DW) and plant water content (PWC) increased significantly under osmotic stress as compared to no stress condition	Ghosh et al., 2019
Bacillus cereus strain P2 and Planomicrobium chinenese strain P1	Wheat	exopolysaccharide (EPS) synthesis	Increased leaf protein content, sugar content, shoot and root dry as well as fresh weight, relative water content and soil moisture content & reduced lipid peroxidation, phenolic content of leaves and the activity of antioxidant enzymes like catalase, peroxidase, ascorbate peroxidase	Khan and Bano, 2019
Pseudomonas putida strain GAP-P45	Sunflower	exopolysaccharide (EPS) synthesis	Formation of biofilm on the surface of roots of sunflower seedings and Improved RAS/RT, root aggregation, high relative water content of leaves, plant biomass & provide the drought resistance	Sandhya et al., 2009
Proteus penneri (Pp1), Pseudomonas aeruginosa (Pa2), and Alcaligenes faecalis (AF3)	Maize	exopolysaccharide (EPS) synthesis	Improved soil moisture content, leaf area, relative water content of leaves, root and shoot length, dry and fresh weight of root as well as shoot	Naseem and Bano, 2014
Bacillus subtilis HAS31	Potato	Antioxidative activity	Showed increase leaf area, tuber number, dry mass, total soluble sugar, proline, total protein, leaf relative water content, membrane stability, MDA and ROS production, tuber yield and higher enzymatic activity of POD, SOD and CAT	Batool et al., 2020
Pseudomonas putida GAP-P45	Arabidopsis thaliana	Antioxidative activity	Reduced the accumulation of ROS and reduced the activities of all ROS scavenging enzymes	Ghosh et al., 2018

Production of Growth regulators

Plant produced various phytohormones such as cytokinin, auxins, ethylene, gibberellins and abscisic acid (ABA) which play a significant role in plant growth and development and help to escape or tolerate the stressful abiotic conditions by modifying nutrient allocation, source/sink transition [84-86]. PGPRs also synthesize various phytohormones including cytokines, gibberellins, and IAA, which further simulate plant growth under unfavourable environmental conditions [78-88]. They have an ability to manipulate plant hormone balance and even modify the plant hormone crosstalk by altering root to shoot signaling and hormone concentration to provide protection against abiotic stress .The most prominent and physiologically active phytohormone, which regulate the various developmental processes in plant either directly or indirectly are auxins. In auxins, the most important plant growth promotor is Indole-3-acetic acid (IAA), which is produced by both plants as well as PGPRs and essential for rhizobacteria – plant interactions [89-90]. IAA is the most abundant phytohormones secreted by the bacteria which is produced by around 80% of rhizospheric bacteria. IAA play important role in different plant activities like, cell division, cell and tissue differentiation, lateral and adventitious root initiation and development, vegetative growth, seed and tuber germination, fruit development, leaf formation, abscission, embryo development etc. In microorganisms, IAA mainly synthesized via tryptophan dependent pathway. IAA production is a direct mechanism of PGPR by which they enhance the growth of root system by increasing number as well as surface area of root tips, adventitious root differentiation from stem and thereby promoting uptake of water and minerals more efficiently under drought stress [91-93].Wheat plant inoculated with Bacillus subtilis (LDR2) under drought stress, it enhanced IAA content (80%), total biomass, Fv/Fm value, net CO2 assimilation, stomatal conductance, transpiration rate and decreased the ABA as well as ACC content. It also downregulates the AUX/IAA1 gene expression and upregulate the TaCTR1 and TaDREB2 gene expression in wheat plant under drought stress as compared to uninoculated plant. According to Jochum et al. [94], Bacillus spp. 12D6 and Enterobacter spp. 16i increased the root length, root diameter and surface area, root branching by excreting IAA in wheat and maize plant under water deficit condition as compared to the control. Inoculation of wheat plant with IAA rhizobacterial strain of genus Bacillus, Enterobacter, Moraxella and Pseudomonas lead to significant improvement of root growth, shoot length, number of tillers and spikelet, spike length and grain weight under drought conditions as compared to control condition. Combinations of PGPRs significantly improved yield parameters in wheat plant as compared to single PGPR [95]. PGPR isolated from rhizosphere of tea plant Enterobacteria lignolyticus strain TG1 produced a noteworthy amount of IAA (92.5 ± 0.2 μg mL−1). When this PGPR under greenhouse conditions inoculated with three different important tea clones TV1, TV19 and TV20, it showed increase root biomass (4.3-fold), root length (2.2-fold), shoot biomass (3.1-fold) and shoot length (1.6-fold) in contrast to control plants. In plants, at low concentration, IAA promote the elongation of primary root, while at higher concentration it stimulates lateral root formation with decreasing primary root length and also increase the growth of root hairs. Abscisic acid (ABA) is a plant stress hormone which plays vital role in plant growth under environmental stresses by modulating physiological process. ABA regulates water content of plants under water deficit conditions by regulating opening and closing of stomata in response to various signals like ROS, nitric oxide etc. ABA also play role in growth of root branching to improve water uptake and induces leaf growth by providing water movement. For long term response, ABA also regulates the expression of stress responsive genes. When Arabidopsis plant inoculated with ABA producing Azospirillum brasilense, it increased the resistance towards drought and other abiotic stress as compared to Arabidopsis mutant aba2-1, defective in ABA biosynthesis and wild type plant [96-99].

Osmolyte Synthesis (Osmoregulation)

Under drought stress, plant adjust their physiology and metabolism such as protection of membrane integrity, cellular osmotic adjustment, stabilization of proteins/enzymes, and detoxification of ROS by regulating the secretion of several compatible solutes. They are highly soluble, low molecular weight compounds and nontoxic at high cellular concentrations. These solutes include soluble sugars (e.g., trehalose, sucrose), polyamines, glycine betaines, polyhydric alcohols, organic acids (e.g., malate), inorganic ions (e.g., calcium), quaternary ammonium compounds, water stress proteins (e.g., dehydrins), proline and other amino acids which are useful for plant growth and to adapt stress conditions. PGPRs also secrete osmolytes, which synergistically act with plant's osmolytes further to boost plant growth under stress condition [100-102]. These compatible solutes protect the genetic material, proteins, enzymes, membranes and organelles in plant against oxidative stress due to drought condition. It has been suggested that proline protect different proteins like chaperones from degradation and/or mis-folding under water stress condition by forming a protective layer around them and by maintaining their integrity. Plants store some ions and metabolites like proline in their vacuoles, which help plants to maintain high turgor pressure, decrease the osmotic potential as well as maintain their physiological and metabolic activity. Proline also provide stability to the cell membrane by interacting with membrane phospholipids. It also regulates cytosolic pH and NAD/NADPH ration under drought stress. Inoculation of Arabidopsis thaliana with PGPR Pseudomonas putida GAP-P45 modulate the proline metabolism by modulating the gene expression of both proline catabolic and biosynthetic activity under water stress [103-106]. Soya bean plants shows increased drought tolerance when inoculated with endophyte Sphingomonas sp. LK11 isolated from the leaves of Tephrosia apollinea, which produces sugars and amino acids like proline, glutamate and glycine . Shahzad et al. Reported that when rice plants inoculated with endophytic bacteria Bacillus amyloliquefaciens enhanced content of amino acids like proline, cysteine, aspartic acid, glutamic acid etc. Apart from proline, PGPRs also synthesize other osmolytes like soluble sugar such as trehalose (α-D-glucopyranosyl-1, 1-α-D-glucopyranoside), proteins such as dehydrins. The concentration of these osmolytes synthesized by PGPR are increased under drought stress and prevent the cell destruction and cell death. Sugar content in the leaves of plant is reduced under extreme stress condition and it leads to destructive for the macromolecules in cell and cell membrane. In this type of condition, trehalose or sucrose, a non-reducing disaccharide produced by PGPR act as an osmo-protectant and protect the plant from cell membrane and macromolecules degradation by stabilizing degrading enzymes .In chickpea plant, the photosynthetic efficacy and water balance maintained by inducing higher soluble sugar accumulation by the application of combination of plant growth regulators and consortium of PGPRs as, Bacillus subtilis, Bacillus thuringiensis and Bacillus megaterium. It also enhanced leaf chlorophyll as well as proline content and reduced the lipid peroxidation, antioxidant

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enzyme activities which creates drought tolerance in chickpea plant [107-109]. Elevated sugar level in leaves because activation and expression of several genes involved in photosynthesis and as a result it increases the rate of photosynthesis in leaves under drought condition. To cope up with the water stress condition, high sugar levels in leaves act as signalling molecule and control several physiological processes such as flowering, germination, photosynthesis, senescence. Trehalose biosynthesis gene transformed Azospirillum brasilense inoculated with maize plant, 85% maize plants survived under drought stress as compared to wild type strain only 55% plants were survived. It significantly increases total biomass (73%), as well as length and biomass of root and leaf under water deficit condition by producing higher level of trehalose in maize plant inoculated with transformed strain in contrast to inoculation with wild type strain. Choline also plays an important role to develop water stress resistance in plant, mainly by synthesis and accumulation of glycine betaine (GB) by acting as osmo-protectant. GB can be synthesized by plant, animal and microorganisms by utilizing choline or glycine as a precursor molecule with diverse mechanism. GB protect the plants under different environmental stress condition by various mechanisms such as, it plays vital role in maintaining the ROS level under control by stabilizing the activities of ROS scavenging enzymes, it function as chemical chaperone and protect the activities of malate dehydrogenase and Rubisco enzyme under salt stress, GB also serve as molecular chaperones which regulate the denaturation and disaggregation of proteins as well as assist refolding of proteins and provide thermal stability to them [110-114]. Plant growth promoting rhizobacteria Raoultella planticola inoculated in roots of two maize variety Zheng Dan 958 (drought tolerant) and Jun Dan 20 (drought sensitive), it was found that it accumulates higher choline and GB content in plant cells and promoted seed germination by providing osmo-regulation under drought stress. This higher GB content was regulated by activity of key enzymes such as, phosphor-ethanolamine N-methyltransferase (PEAMT), choline monooxygenase (CMO), and betaine aldehyde dehydrogenase (BADH) are involved in the synthesis of GB in chloroplast. When maize plant inoculated with three PGPR strains i.e., Klebsiella variicola F2 (KJ465989), Raoultella planticola YL2 (KJ465991) and Pseudomonas fluorescents YX2 (KJ465990) under varying degree of drought stress, it enhanced the leaf relative water content and dry matter weight with greater osmotic regulation as compared to control inoculated plant through the improved content of choline and GB in plant cells.

Upregulation of ACC deaminase

Environmental factors including temperature, light, nutrition, various biotic and abiotic stress as well as concentration and presence of other phytohormones affect the synthesis of ethylene in a plant [115-118]. Ethylene is a phytohormone which is concerned with several physiological processes in plants like abscission, fruit ripening, leaf and flower senescence, aging, initiation of root and root nodule formation. Ethylene is synthesized from its precursor 1-aminocyclopropane-1 carboxylate by ACC-oxidase which is produced from S-adenosylmethionine (S-AdoMet) by 1-aminocyclopropane-1- carboxylate synthase (ACS). Under environmental stress conditions like salinity, drought, water logging, heavy metal contamination, synthesis of ACC has been reported to increase further increasing the concentration of ethylene which reduce the vegetative growth of plant by restraining root and shoot development process and leaf expansion. Plant use ACC deaminase produced by PGPR in rhizosphere to degrade the ACC, resulting in reduction of ethylene production and aid the normal vegetative growth and development of plant root and shoots. ACC deaminase produced by PGPR converts Plant ACC (the precursor of ethylene) into ammonia and α-ketobutyrate, there by halting ethylene production and enhancing growth of plant even under environmental stress condition [119 - 126].ACC deaminase producing bacterial strain Enterobacter mori, E. asburiae and E. ludwigii alleviate the effect of water stress on wheat by reducing the release of ethylene in leaves of wheat concomitantly reducing the activity of ACC synthase and ACC oxidase activity as compared to non-stress condition [127]. When velvet bean (Mucuna pruriens) inoculated with ACC deaminase producing rhizobacteria Enterobacter HS9 and Bacillus G9, it significantly reduced the ethylene production around 50% by reducing concentration of ACC in the roots and leaves and improved root and shoot length as well as biomass of velvet bean under severe drought stress condition while greater concentration of ACC was found in root and leaf of uninoculated plant. According to Zarei er al, sweet corn plant inoculated with combination of four ACC deaminase producing bacteria Pseudomonas fluorescents strains i.e., P. fluorescens P1, P. fluorescens P3, P. fluorescens P8, P. fluorescens P14 under water stress condition. The result showed significant increase in total sugar content, chlorophyll content, proline, photochemical efficiency of photosystems, root growth, catalase and peroxidase activity along with it also increased the yield traits like canned seed (27%) and ear yield (44%). When maize plant inoculated with plant growth-promoting rhizobacteria Pseudomonas aeruginosa, Enterobacter cloacae, Achromobacter xylosoxidans and Leclercia adecarboxylata, it showed increase in root and shoot length, dry and fresh weight of root and shoot, amount of nitrogen, potassium as well as phosphorous and improved the plant growth with reducing accumulation of ethylene in plant which indicates ACC deaminase producing ability of PGPRs [128-130]. Furthermore, Danish et al, inoculated maize plant with Pseudomonas aeruginosa, Enterobacter cloacae, Achromobacter xylosoxidans and Leclercia adecarboxylata with timber waste biochar, which further increase the plant growth by increasing photosynthetic rate, stomatal conductance, content of chlorophyll and carotenoids, grain yield as compared to control plant.

P1 are studied for their EPS producing capacity. Under non-stress condition all four strain secrete same level of EPS while under osmotic stress condition EPS production by Pseudomonas aeruginosa ZNP1 was increased about 2.5-fold and Bacillus endophyticus J13 was increased about 1.5-fold. There is no change in EPS level in case of Bacillus tequilensis J12 while it is adversely affected in case of Pseudomonas aeruginosa PM389. When Arabidopsis thaliana inoculated with all these four stains separately under osmotic stress and normal condition, the fresh weight, dry weight and plant water content increased significantly under osmotic stress as compared to no stress condition.

EPS producing bacteria, Pseudomonas putida strain GAP-P45 when inoculated with sunflower plant, it increased RAS/RT, root aggregation, high relative water content of leaves, plant biomass in addition it also forms biofilm on the surface of roots of sunflower seeding and provide the drought resistance to sunflower plants . When wheat plant treated with EPS-producing bacteria Bacillus cereus strain P2 and Planomicrobium chinenese strain P1 under drought stress, it showed increase in leaf protein content (56%), leaf sugar content (69%), shoot and root dry weight as well as fresh weight, relative water content and soil moisture content. On the other hand, it reduced lipid peroxidation, phenolic content of leaves and the activity of different antioxidant enzymes like catalase, peroxidase, ascorbate peroxidase [131-140]. Maize plant inoculated with EPS producing rhizobacterial strains Proteus penneri (Pp1), Pseudomonas aeruginosa (Pa2), and Alcaligenes faecalis (AF3) showed increase soil moisture content, leaf.

Rhizobacterial exopolysaccharide (EPS) synthesis

Lack of irrigation and inadequate rainfall severely affects agriculture production. Water stress leads to inadequate soil moisture, alters the physicochemical and biological properties of soil often resulting in decreased soil microbial activity, affecting functional niche and also reduce the growth and production of crop plants. Water unavailability alters soil structure indirectly as microorganism's consumption rate of proteins and polysaccharides from soil changes in absence of water. In this type of unfavourable environmental condition where water availability is scanty, PGPRs secrete high molecular weight complex organic compound termed exopolysaccharide (EPS), in the environment. EPSs are synthesized by bacteria during late logarithmic or stationary phase of growth and present on the outer surface of the bacterial cell which provides stability to the cell membrane against environmental stress condition and enables their survival. EPS play important role in surface attachment, biofilm formation, bioremediation, plant-microbes interaction, protection, microbial aggregation and root adhering soil per root tissue (RAS/RT) ratio. EPS provides the protection to the microbes against desiccation by increasing water retention and by regulating diffusion of organic carbon, it also prevents the soil drying by holding the water in soil surrounding the plant root. Under water stress condition, plants showed increase in proteins, proline, and sugar, several compatible solutes, relative water content as well as activity of different antioxidant enzymes when inoculated with EPS producing bacteria. When sunflower plant treated with EPS-producing rhizobacterial strain YAS34 under drought stress, it exhibited significant increase in RAS/RT ratio in rhizosphere [136,137]. According to Ghosh et al, four bacterial strains, namely, Pseudomonas aeruginosa PM389, Bacillus endophyticus J13, Bacillus tequilensis J12 and Pseudomonas aeruginosa ZNP1 are studied for their EPS producing capacity. Under non-stress condition all four strain secrete same level of EPS while under osmotic stress condition EPS production by Pseudomonas aeruginosa ZNP1 was increased about 2.5-fold and Bacillus endophyticus J13 was increased about 1.5-fold. There is no change in EPS level in case of Bacillus tequilensis J12 while it is adversely affected in case of Pseudomonas aeruginosa PM389. When Arabidopsis thaliana inoculated with all these four stains separately under osmotic stress and normal condition, the fresh weight, dry weight and plant water content increased significantly under osmotic stress as compared to no stress condition. EPS producing bacteria, Pseudomonas putida strain GAP-P45 when inoculated with sunflower plant, it increased RAS/RT, root aggregation, high relative water content of leaves, plant biomass in addition it also forms biofilm on the surface of roots of sunflower seeding's and provide the drought resistance to sunflower plants . When wheat plant treated with EPS-producing bacteria Bacillus cereus strain P2 and Planomicrobium chinenese strain P1 under drought stress, it showed increase in leaf protein content (56%), leaf sugar content (69%), shoot and root dry weight as well as fresh weight, relative water content and soil moisture content. On the other hand, it reduced lipid peroxidation, phenolic content of leaves and the activity of different antioxidant enzymes like catalase, peroxidase, and ascorbate peroxidase. Maize plant inoculated with EPS producing rhizobacterial strains Proteus penneri (Pp1), Pseudomonas aeruginosa (Pa2), and Alcaligenes faecalis (AF3) showed increase soil moisture content, leaf area, relative water content of leaves, root and shoot length, dry and fresh weight of root as well as shoot under water stressed condition [138-141].

Antioxidative defense System in Stress Management

Under optimal growth condition, plant cells produce minimal amount of reactive oxygen species (ROS). While in water deficient condition, various oxidative pathways in plants leads to generation of ROS namely, hydrogen peroxide (H_2O_2), super oxide free radicals (O_2-), hydroxyl radicals (OH-), alkoxy radicals (RO) and singlet oxygen (O-). This ROS cause oxidative damage and hinder the normal functions of plant cells by reacting with the

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macromolecules like deoxyribonucleic acid (DNA), proteins, and lipids and even causes their denaturation or degradation. ROS enhances the lipid peroxidation of membrane phospholipids and damage the cell and organelle membrane by producing malondialdehyde, a final product of peroxidation under stressful condition. An antioxidative system plays a crucial role to cope up with ROS and for maintenance of physiological system in plant cells. Under drought condition, to reduce the oxidative damage and accumulation of ROS in plant cells, plant develop antioxidative defense system consisting of various enzymatic and non-enzymatic mechanism. Various PGPRs also synthesize such antioxidative molecules to protect the plants against various oxidative stress conditions. Antioxidative enzymatic mechanism developed under adverse environmental condition includes superoxide dismutase (SOD), glutathione reductase (GR), catalase (CAT), peroxidase (POD), glutathione peroxidase (GPX) and ascorbate peroxidase (APX). Plants also developed some non-enzymatic mechanism including ascorbic acid, cysteine and glutathione which generate tolerance against oxidative damage and provide protection to plant cells [143-145].Five drought tolerant plant growth promoting Pseudomonas spp. Strains i.e., P. putida strain GAP-P45, P. syringae strain GRFHYTP52, P. stutzeri strain GRFHAP-P14, P. monteilli strain WAPP53 and P. entomophila strain BV-P13 inoculated with maize plant, it showed increase in relative water content of leaves, proline (up to 6.3 fold), starch, protein, root length (37.12 – 48.08%), shoot length (36.06 – 44.11%), total dry biomass (37.80 – 60.36%), soluble sugar, RAS/RT ratio (26.0 – 56.72%), leaf water potential, soil aggregate (27 ± 1 – 70 ± 3%) and significantly lower the activity of antioxidant enzymes such as CAT, SOD, APX, GPX with decreasing electrolyte leakage as compared to uninoculated plant under drought stress. According to Khan et al. [109], when chickpea plant inoculated with consortium of Bacillus subtilis, Bacillus thuringiensis, and Bacillus megaterium under drought stress, it decreased the activity of antioxidant enzymes like, SOD, CAT, POD, and APX and promoted the plant growth by increasing the protein, chlorophyll, sugar content. As it compared to uninoculated plant activity of SOD, CAT, POD and APX get elevated in response to drought stress. Potato plant showed increase leaf area, tuber weight, tuber number, dry matter production, total soluble sugar, proline, total protein with less decrease in chlorophyll content, leaf relative water content, membrane stability, MDA and ROS production, tuber yield and higher enzymatic activity of POD, SOD and CAT, when inoculated with drought tolerant plant growth-promoting rhizobacteria (PGPR) Bacillus subtilis HAS31 under drought stress as compared to uninoculated plant. Drought mitigating PGPR Pseudomonas putida GAP-P45 reduced the accumulation of ROS and also significantly reduced the activities of all ROS scavenging enzymes in Arabidopsis thaliana under water stressed condition as compared to uninoculated plant [146,147].

Volatile organic compound secretion

In addition to various mechanism describe above, PGPR in rhizosphere also produce some gaseous organic compounds known as volatile organic compounds (VOCs) to enhance the growth of plant and to provide protection against stress condition. These VOCs are low molecular weight (<300 Da) containing organic compounds which get evaporated at normal temperature and pressure [148]. When PGPRs release VOCs in soil, it stimulates plant defense system against bacterial and fungal pathogens by evoking an induced systemic resistance/tolerance (ISR/IST) response in plants [149-151]. VOCs produced from rhizobacteria can maintain plant health by interacting with plant roots. This microbial volatile organic compound (mVOCs) includes alcohols, sulfides, pyrazines, alkanes, ketones, benzenoids, terpenes [152-155]. Microbial VOCs can provide protection to plants against phytopathogens as well as stress caused by drought and heavy metal by signalling inhibiting microbial growth and activity like raising pH of medium, biofilm formation, modifying drug resistance or by eliciting ISR and IST in plants. These VOCs could be used as alternative technique for sustainable crop improvement because of their eco-friendly nature. Bacteria are the predominant microbes in soil which generate induced systemic resistance in plant by producing large variety of VOCs. Bacterial VOCs includes alkanes, ketones, terpenoids, sulfur compounds, esters and also ammonia, alcohols, phenazine-1-carboxylic acid, HCN which comprises antifungal activity that contribute to the biocontrol activity of PGPRs. Hydrogen cyanide (HCN) is blocking the cytochrome oxidase and there by inhibit electron transport chain and energy supply to the cells, and leading to death of cells especially all aerobic microorganisms at pico-molar concentration.

Co-inoculation of PGPR

Single strain of PGPR provide benefit to the plant against drought stress by generating tolerance or resistance against them. In addition to this, the combination of more than one PGPR or with mycorrhizae provide better protection to the host plant against different stress condition and promote plant growth as compared to single PGPR strain. Dasgupta et al. studied PGPR from the Rhizosphere of Sesbania bispinosa and selected 12 isolates. From that three-strain showed PGPR traits that are Escherichia coli DACG2, Pseudomonas fluorescens strain DACG3 and Burkholderia sp. DACG1. The combination of all three strain gives maximum rates of plant height, number of leaves, pod bearing branches and seed weight in pot study as compared to single inoculant and double inoculants. Co-inoculation of tobacco (Nicotiana tabacum L.) with plant growth promoting rhizobacteria, Bacillus methylotrophicus and Arbuscular mycorrhizal fungi, Glomus versiforme significantly increased growth and biomass of tobacco plant by improving accumulation of flavonoids (71.74%), phenol (57.85%), indole-3-acetic acid (IAA) (54.41%), total chlorophyll (67.96%), PSII efficiency (33.43%), abscisic acid (ABA) (67.71%), caretonoids (56.88%), photosynthesis (53.22%). The co-inoculation of AMF and PGPR also enhanced antioxidant enzymatic activity and plant nutrition status as well as reduced the lipid peroxidation and electrolyte leakage in tobacco plant, which showed drought tolerance as compared to uninoculated plant.

Molecular approach employed to study alleviation of drought stress

Todays, several molecular techniques are developed to increase crop production under different environmental stress condition. For example, genetic modification in which addition or deletion is carried out in the genes which involved in stress tolerance and generate the stress resistant variety of crops. Gene expression technique is used to understand the response of microorganisms in contrast to various environmental conditions. Nowadays, several techniques such as hybridization-based microarray technique, RNA sequencing are developed to understand and evaluate the transcriptome, which is the set of all the transcript expressed in particular cell or organism at specific developmental stage under different environmental stress condition. Various molecular approaches were used to check the expression of genes linked with physiological functions in regard to stress tolerance generated by PGPR under drought stress condition.

Challenges in exploitation of PGPR

The use of PGPR as a bioinoculants to enhance the growth of plant by providing various benefits like synthesis of plant growth promoting substances, nutrient mobilization, protection against pathogen by producing HCN, antibiotics or by induced systemic resistance. The use of PGPR is also eco-friendly because they also restore the fertility of soil without damaging the environment as like chemical fertilizers which produce lots of pollution in environment. PGPR also helps to mitigate the effect of different environmental stress condition like drought, salinity and increase the plant growth [156-166]. There are also some drawbacks besides these benefits in contrast to utilization and commercialization of PGPR for sustainable agricultural development. The result derived by experiments which carried out in green house and in vitro condition is not often sustainable under field condition and consistency is not maintained because in field they are exposed to natural environmental conditions which are not present in green house or in vitro. Moreover, the other factors like soil pH, soil structure and texture, nutrient availability, mineral composition also vary under field condition which alters the efficacy of microbes. This is a drawback for usage of beneficial PGPR in agriculture to enhance the crop production. Therefore, to overcome this limitation, before final application in field in presence of natural indigenous microflora under stress condition, it is important to determine efficiency of PGPR strains in pot experiments by using sterilized and unsterilized soil and test whether they will compete with the indigenous microbes that are present in natural environment and able to establish their population on plant root as well as in rhizosphere. Before selecting any bacterial strain for bio fertilizer formulation, it requires to check the localization of the bacteria after the inoculum applied to plant, whether PGPRs to be systemic and spread in all the tissues of plant or remain localized near the root of host plant. When Brachypodium inoculated with B. subtilis strain B26, it spread systemically inside whole plant and it was recovered from stems, roots, blades as well as seeds, which indicates that the bacterium is able to migrate in aerial organs and tissues of the plant and also able to transmit in next generation of plant via seeds [167]. Sometimes, extreme condition like drought, heat may affect the ability of the PGPR strain like denature and degrade their macromolecules and cell membrane, except they have ability to form endospore or form biofilm. Because of this excessive heat, the population of PGPR get reduce if they do not have any protection. Therefore, enough quantity of PGPRs with physical protection used to formulate the bio-inoculant which prevent rapid reduction of PGPRs population [168]. PGPR strain is more effective when it is used in consortium as compared to single strain. But some strain may become antagonist when used in consortium due to its incompatibility, which perform excellent when used alone. So, it needs to check their effect in vitro or in green house study before applied to field study. The choice of PGPR is also a challenge, mostly these PGPR strain choose for formulation which must have two or more PGP trait because it is more suitable to promote plant growth under stress condition.

Future research perspective

Agricultural production is badly affected by the changing climate. The use of microbes- plant interaction is best approach to increase agricultural production for continuously increasing population under global climate change. Though, to reduce the use of chemical fertilizers and pesticides and to enhance plant growth under stress condition, formulation of microbial bio-inoculant is needed. Therefore, research should be carried out to isolate best PGPR strains with longer shelf-life from stress affected soil which can be used as bio fertilizer for the growth of crop under stress condition [16]. Sometimes, the beneficial activity of isolated PGPR also get affected by extreme condition like salinity, drought, extreme temperature, heavy metal ions, pH when applied to field condition which reduced their efficacy and also their life span. When bacteria are encapsulated with nanoparticles, the adhesive capacity of cells towards plant roots get increased along with stability towards heat, desiccation, and UV inactivation get increased. As reported by Danielsson et al. (169], when beneficial PGPR Bacillus amyloliquefaciens strain UCMB 5513 encapsulated with titania

(TiO2) nano particle, it gets adhered to the plant root and protect the plant Brassica napus from fungal infection by acting as biocontrol agent. Therefore, research effort should be focused on the development of nanoparticles, which can be used with PGPR in the formation of bio fertilizers. Due to advancement in omics technology like genomics, proteomics, transcriptomics, metabolomics, it can be possible to identify genes which is responsible for drought tolerances as well as different proteins like heat shock proteins, chaperones, which gives protections to plants and microbes against stressful condition, and also can be transferred to beneficial PGPR which enhances their ability to survive in various adverse condition. By using molecular techniques like microarray, RNA sequencing, the function of different upregulated or down regulated genes can be studied out under abiotic stress. The overexpression of genes responsible for production of osmolytes like trehalose, proline which reduced the effect of ROS can enhance the tolerance towards stress condition of bacterial strains as well as plants.

Conclusions

Drought stress severely reduce the plant growth and production by generating ROS species, higher amount of ethylene, which cannot feed the ever-increasing population of the world. The development of drought resistance species of crop by genetic engineering and conventional breeding is essential to increase production but it is costly and time-consuming process [170,171], on the other hand Plant genetic engineering is faster to develop transgenic crop but success of a transgenic crop is not decided until its commercialization. Whereas the use of PGPRs is an effective, eco-friendly and inexpensive way to improve growth and development of crop under abiotic stress. PGPRs provides benefits to crop plant different mechanisms like by N2 fixation, phosphate solubilization, IAA synthesis, siderophore production, in addition to all of these, they also produce osmolytes and antioxidants which is used to reduced detrimental effect of ROS on plant growth and ensuring plant survival under drought stress. Therefore, there is a requirement of identification of efficient strain of PGPR with desired trait and understanding the molecular mechanism of plant-microbes interaction for better considerate of microbe's utilized pathways for sustainable enhancement of plant growth and survival under abiotic stress.

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