Beneficial microbes in agriculture under abiotic stress conditions: An overview

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Abstract
In agriculture, the demand is increasing for environment friendly, ecologically compatible techniques which can provide food for our growing population by raising both the quality and quantity of farm produce. Here, using plant beneficial microbes enables plants to tackle disease-causing organisms and insects, and withstand abiotic stress. Objective of this review is to focus on the emergence of the agriculturally important micro-organisms in order to establish an ideal agricultural system which supports efficient use of nutrients and energy recycling, and thereby preserves natural resources in the ecosystem as the environment conditions continue to aggravate due to climate change. This review gives a brief overview of the beneficial aspects of microbes in agriculture and several stress situations related to the climate change.

Keywords: Agriculture, beneficial microorganisms, climate change, stress

Introduction
Microbial ecosystem is the greatest unexplored biodiversity resource on earth (Gibbons, 2015)\(^{[26]}\). They represent world’s largest mass on earth. Although, microorganisms are smallest forms of life, they are known to play a vital role in every continuum of existence. Therefore, in today’s biological science, microbial ecology based research has become a prominent field. Organisms within the vast resources of microbial diversity are bacteria, fungi, algae, protozoa, actinomycetes, and infectious agents such as viruses (Jacoby et al., 2017)\(^{[31]}\). Microbial populations interact and associate by different means in different activities. Climate change is one of the most significant issues impacting life on planet earth. Climate change affects plants defenses (Odelade and Babalola, 2019)\(^{[29]}\). Different regulators for plant growth are produced from soil microorganisms, such as bacteria, fungi and algae (Gouda et al., 2018)\(^{[28]}\). Plant growth-promoting rhizobacteria (PGPR) is responsible for production of various phytohormones such as indole acetic acid (IAA), gibberellic acid, and cytokinines (Sharma et al., 2014)\(^{[74]}\) and essential metabolites such as siderophores, HCN, and antibiotics. PGPR has also been reported as being affective in enhancing availability of P in soil. The source of P (organic or mineral), host plant, microbial mixture, pH, anions, and cations, etc., determines P solubility in soil (Niu et al., 2010; Salimpour et al., 2010)\(^{[56, 68]}\).
Ectorhizospheric strains of *Pseudomonas*, *Bacillus*, *Rhizobium*, *Enterobacter*, and endosymbiotic rhizobia constitute effective phosphate solubilizer for enriching P soils (Khan *et al.*, 2009) [36]. Adequate supply of P allows crops such as cereals and legumes to form seeds and mature early (Sharma *et al.*, 2013) [75]. In mobilization of insoluble K in soil for plants, some effective microorganisms such as *Bacillus* mucilaginosus, *Acidithiobacillus ferrooxidans*, *Arthrobacter* sp., *Azotobacter* sp., *Bacillus* edaphicus, *Frateuria* sp., *Klebsiella* sp., *Paenibacillus* sp., *Pseudomonas* sp., and *Rhizobium* sp. (Liu *et al.*, 2012) [43] play a very important role. Beneficial microorganisms can suppress phytopathogens growth in a variety of ways, such as competing for nutrients and space, limiting pathogens' supply of available nutrients (Köhl *et al.*, 2019; Rana *et al.*, 2016) [39, 64].

### Plant Growth Regulators

Soil microorganisms have the ability to synthesize different metabolites which may affect the properties of soil. Plant growth and chemical composition and their wellbeing are considered as one of the most significant soil fertility factors (Odelade and Babalola 2019) [57]. Different regulators for plant growth are produced from soil microorganisms, such as bacteria, fungi and algae (Goudaa *et al.*, 2018) [28]. Plant growth-promoting rhizobacteria (PGPR) is responsible for the production of various phytohormones such as indole acetic acid (IAA), gibberellic acid, and cytokinines (Sharma *et al.*, 2014) [74] and essential metabolites such as siderophores, HCN, and antibiotics. In the rhizosphere, several pathogenic, symbiotic, and free-living species of rhizobacteria acted along with PGPRs (Rachel *et al.*, 2018). Fungi also play important role by bio-controlling parasitic spores, sclerotia, or hynphae of pathogenic fungi (Mejia *et al.*, 2008) [49]. This biocontrol process involves enzymes including chitinases, proteases, and gluconases. This beneficial plant growth association of fungi is termed mycoparasitism (Köhl *et al.*, 2019) [39].

### Phosphorus Solubilization

Unsolubilized phosphate is not taken up by plants but some rhizobacteria solubilize phosphate which is readily taken up by plants. Microorganisms solubilizing phosphorus (MSPs) play an important role in solubilization and mineralization (Sharma *et al.*, 2013) [75]. The phosphate solubilization process involves a decrease in soil pH due to organic acid production by the microbial communities accompanied by the acid phosphatase discharge of organic phosphorus. Phosphorus solubilizing efficiency is achieved when co-inoculated with other beneficial bacteria or mycorrhizal fungi (Mohammadi 2012) [50]. Bacterial efficacy in phosphorous solubilization is higher than fungi.

PGPR has also been reported as being effective in enhancing the availability of P in soil. These bacteria, for example, can generate enzymes (phosphatases) (less than plants) and products such as organic products such as organic acids (carboxylic acids), protons, etc. that can increase the availability of P in the soil by influencing mineral P sources such as rock phosphate (Sharma *et al.*, 2014) [74]. The source of P (organic or mineral), host plant, microbial mixture, pH, anions, and cations, etc., determines the P solubility in soil (Niu *et al.*, 2010) [56]. Ectorhizospheric strains of *Pseudomonas*, *Bacillus*, *Rhizobium*, *Enterobacter*, and endosymbiotic rhizobia constitute effective phosphate solubilizer for enriching P soils (Khan *et al.*, 2009) [36].

Phosphate-solubilizing bacteria (PSB) remain 1-50 percent of the population in normal soil, while phosphate-solubilizing fungi (PSF) have a population of only 0.1-0.5 percent (Panhwat *et al.*, 2011) [59]. Many studies have shown that the use of PSM has increased production, yield and quality of crops, including apple, walnut rice, mustard, palm oil, maize and chili, wheat, sugar beet, sugar cane, chickpea, soybean, peanut and legumes, and potatoes. When applied to crop plants, PSMs have shown to enhance P uptake, growth and yield (Vikram *et al.*, 2008) [94]. Adequate supply of P allows crops such as cereals and legumes to form seeds and mature early [Sharma *et al.*, 2013] [75]. It induces early maturing and promotes the growth of deeper and more abundant roots by young plants [Mehrvaz *et al.*, 2008] [48].

### Potash Mobilization

The third basic nutrient that plants need is potassium. Microorganisms play an important role in making insoluble forms of potassium available through mineralisation. K is Earth's seventh most abundant element "Total K content in soils ranges between 0.04 and 3% K. While K is present in the soil as an abundant element, only 1-2% of this element is available to plants (Sattar *et al.*, 2018) [71]. The remainder are related to other minerals and are therefore not accessible to plants. Large quantities of Potassium in the soil are present as a fixed source (not available indirectly to the plant) due to the imbalanced use of fertilizers, the large increase in crop yield, depleting soil Potassium and the depletion of Potassium in the soil system. As a result, Potassium deficiency has been identified in most crop plants (Xiao *et al.*, 2017). Another study showed that potassium was solubilized by *Bacillus*, *Clostridium* and *Thiobacillus* (Groudev 1987) [29]. In mobilization of insoluble K in the soil for plants, some effective microorganisms such as *Bacillus* mucilaginosus, *Acidithiobacillus ferrooxidans*, *Arthrobacter* sp., *Azotobacter* sp., *Bacillus* edaphicus, *Frateuria* sp., *Klebsiella* sp., *Paenibacillus* sp., *Pseudomonas* sp., and *Rhizobium* sp. (Liu *et al.*, 2012) [43] play a very important role. Inoculation of various plants with potassium solubilising bacteria generally showed significant increase in seedling vigor, germination rate, plant growth, yield (Anjanadevi *et al.*, 2016) [7].

### Biofertilizer and Biopesticide

Biofertilizer helps in improving soil fertility by fixing atmospheric nitrogen, both in conjunction with and without plant roots, solubilizing insoluble soil phosphates and producing plant growth regulator in the soil. The application of bio-fertilizers play important role in raising soil fertility, production attributing characters and there by final production has been documented by many workers. In addition, their application reduces the use of chemical fertilizers and improves soil biota. Microbial biofertilizer is the application of living microorganisms to seed, plant surface or soil to encourage microbial growth and nutrient supply for plants in the rhizosphere (Bhattacharyya and Jha 2012) [12]. Microbial biopesticides helps in plant growth by production of antibiotics, siderophores, HCN, production of hydrolytic enzymes, and acquired and induced systemic resistance against pathogen (Rana *et al.*, 2016, Chandler *et al.*, 2008) [64, 15]. An important bacterial species called *Rhizobium* exhibits symbiotic relationships with leguminous plants (Shridhar 2012; Wang and Martínez-Romero 2000) [76, 96]. Biofertilizer application is the only alternative for improving soil organic carbon to maintain soil quality and potential productivity in
agriculture. Organic farming, a system of production which tends to avoid the use of chemicals and is heavily dependent on biopesticides and biofertilizers. Best for sustainable agriculture are microbial biofertilizers and biopesticides (Bhardwaj et al. 2014) [11]. Other bacterial species, e.g., Bacillus, Mesorhizobium, Acetobacter, Azospirillum, Aspergillus, Rhizobium, Bradyrhizobium, Azorhizobium, Azotobacter, Allorhizobium, Penicillium, Pseudomonas, etc., also have potential plant growth-promoting capacity (Vessey 2003) [93].

**Microbial Antagonism**

Beneficial microorganisms can suppress phytopathogens growth in a variety of ways, such as competing for nutrients and space, limiting pathogens’ supply of available nutrients (Köhl et al., 2019) [19]. Disease-suppressive soil microflora is generally dominated by antagonistic microorganisms capable of producing a variety of antibiotics (Gómez Expósito, R, 2017) [27]. Aspergillus, Penicillium, Trichoderma, and antagonistic actinomycetes are known as a potent center for developing varying mode of action for various antibiotics (Zivkovic et al., 2010) [100]. Most Trichoderma strains are highly opportunistic attackers (Kubicek, 2019) [40]. In soil-borne plant pathogens, antibiotics produced by antagonistic microbials have biostatic and biocidal effects.

**Rhizosphere Microbes Improves Plant Stress Tolerance**

### Salinity Tolerance

Salinity is considered enemy of intensive farming (Machado et al., 2017) [44]. Salinity can have significant impact on agriculture, biodiversity and environment (Shrivastava et al., 2015). High salt concentrations in soil decrease seed germination and plant growth (Orlovsky et al., 2016) [56]. A.chroococcum inoculation significantly reduces impact of salt stress on plant growth parameters such as root length, plant height, fresh shooting, root weight, dry shooting and root weight (Prajapati et al., 2008) [61]. Azospirillum inoculation can affect variety of salt-stressed maize (Khan et al., 2019) [38]. Secondary inoculation with Azospirillum may result in prolonged root exudation of plant flavonoids for salt-stressed plants following inoculation with Rhizobium (Dardanelli et al., 2008) [19]. Therefore, co-inoculation of plants with different bacterial species will increase resistance against abiotic stress. Two PGPR B. megaterium and Enterobacter sp. induce salt tolerance, and consequently improve growth of salt stressed okra plants (Gouda et al., 2018) [28]. However, most other species of Azospirillum can only tolerate 2 percent of NaCl (Fukami et al., 2018) [25]. (Ramadoss et al., 2013) [63] reported halotolerant bacteria Hallobacillus sp. SL3 and Bacillus halodenitrificans PU62 have potential to enhance growth of plants under saline stress. In addition, soil bacteria also gave transgenic pea a positive relationship and increased tolerance for salt stress (Ali et al., 2015) [6]. (Vega et al., 2020) [92] stated that inoculation of crops with natural halotolerant PGPR strains like S. equorum strain EN21, with its high quorum quenching ability, could be an effective biocontrol strategy for both saline and non-saline soils. Another strain P. geniculate MF-84 decreases Na+ uptake and increases K+ and Ca2+ uptake in maize roots suggesting MF-84’s function in maintaining ionic balance / homeostasis in plant roots under higher salt conditions. This strain not only helps to mitigate salt toxic effects but also increases plant growth and decreases crop losses due to salinity (Singh et al., 2020) [60]. (Sadd et al., 2019) [67] reported that P. polyxynxa, B. nakamura and B. pacificus were effective in colonizing the wheat plant rhizosphere and in protecting wheat plants from destruction to salt stress. Such PGPRs also ameliorated the reduction of proline accumulation in shoots, increased RWC, electrolyte leakage and enzymatic activity, improved antioxidant enzymes, growth and wheat yield under saline stress. Direct mechanisms including phytohormone formation (e.g., auxins, cytokinin, ethylene, and gibberellins), nitrogen fixation, nutrient mobilization, and synthesis of siderophores (Egamberdieve et al., 2017) [22] lead to an increase in root volume, surface area and root number through nutrient uptake there. Main indirect mechanism involves reducing incidence of diseases causing plant pathogens. ACC deaminase is produced by root colonizing rhizobacteria which converts ACC into ammonia and alpha ketobutyrate and lower ethylene. Physical and chemical changes caused by PGPR contribute to mediated systemic tolerance (IST), improved salinity stress tolerance. They promote growth of root and shoot and reduce susceptibility of fungi like Fusarium solani to cotton plant disease.

**Fig 1:** Plant Microbe interaction under abiotic stress Drought Stress Tolerance
Paenibacillus sp., Bacillus sp. and some other gram-positive bacterial isolates were found to be successful in increasing the drought resistance of plants (Timmusk et al., 2014) [86]. Drought stress on plants can lead to stomatal closure to mitigate water loss by increasing levels of abscisic acid (ABA) in leaves along with other compounds such as ethylene, salicylic acid, etc. PGPR has beneficial effects on plant drought tolerance due to changes in hormonal content ABA, ethylene and cytokinine (Cohen et al., 2008) [18]. Drought stress limits crop growth, yield and changes plant chemistry, particularly in arid and semi-arid regions (Emerson et al., 2014; van der Weijde et al., 2016) [23, 62, 90]. It also affects soil microbiota directly or indirectly by producing osmotic stress, contributing to microbial cell death. However, dry plants seem to favor higher bacterial and fungal levels, and increased soil fungal / bacterial proportions (Naylor et al., 2018) [54]. Thus, plant inoculation with beneficial native microorganisms may increase drought tolerance of plants growing in arid or semi-arid areas. Stimulating with rhizosphere bacteria is a novel and successful way to increase the efficiency of water usage by plants in extreme conditions (Timmusk et al., 2014) [86]. Under low water potential, microbes have evolved to survive by forming thick walls or entering a dormant phase, accumulating osmolytes, producing exopolysaccharides. Such microbes provide nutrient and better environmental conditions for continuous growth of plants, regardless of water content. PGPR also has the ability to synthesize plant hormones, which promote plant growth and division under stress. IAA, the most active auxin controlling differentiation of vascular tissue, adventitious and lateral root differentiation, cell division, and shoot growth during drought stress (Guan et al., 2019) [30]. ABA is an effective growth regulator in the event of drought stress. Concentration of ABA increases when seed or plant is inoculated with PGPR, and controls plant physiology to withstand drought stress. ABA relieves stress from drought by controlling transcription of drought-related gene and root hydraulic conductivity (Jiang et al., 2013) [33]. Drought stress tolerant and PGPR increase biomass, water potential, decreasing water loss under stress conditions in maize plants. These inoculants reduce antioxidant activity and also boost proline, free amino acid, and plant sugar production (Vardharajula et al., 2011) [91]. (Silva et al., 2020) [78] studied that inoculation of strain G diazotrophicus Pal5 favored red rice plants by promoting different root growth and developmental mechanisms against drought stress, enabling root development and improving biochemical composition.

Table 1: Microbe-mediated abiotic stress tolerance in plants.

| Abiotic stress | Microorganism | Plant | Reference |
|----------------|---------------|-------|-----------|
| Salinity       | Glomus fasciculatum | Phragmites australis | (Figueiredo et al., 2008) [24] |
|                | Glomus intraradices | Glycine max | (Al-Garni, 2006) [5] |
|                | Azospirillum brasilense and Pantocea dispersa (Co-inoculation) | Capsicum annuum | (del Amor and Cuadra-Crespo, 2012) [21] |
|                | Glomus intraradices BAFC 3108 | Lotus glaber | (Sannazzaro et al., 2006) [70] |
|                | Glomus clarium | Vigna radiata | (Kaya et al., 2009) [35] |
|                | Glomus etunicatum | Capsicum annuum Triticum aestivum | (Zhang et al., 2008) [101] |
|                | Bacillus subtilis | Arabidopsis | (Aroca et al., 2008) [9] |
|                | Glomus intraradices BEG121 Pseudomonas putida (Co-inoculation) | Lactuca sativa Gossypium hirsutum | (Yao et al., 2010) [99] |
|                | Azospirillum brasilense strain Rs-198 | Phaseolus vulgaris | (Dardaneli et al., 2008) [109] |
|                | Bacillus subtilis | Lactuca sativa | (Arkhipova et al., 2007) [8] |
|                | Bacillus subtilis GB03 | Arabidopsis thaliana | (Zhang et al., 2008) [101] |
|                | Pseudomonas simiae | Glycine max | (Vaishnav et al., 2016) [39] |
|                | Pseudomonas syringae DC3000, Bacillus sp. strain L81, Arthrobacter oxidans Root-associated plant growth-promoting rhizobacteria (PGPR) | Arabidopsis thaliana Oryza sativa | (Jha et al., 2014) [32] |
|                | Cyanobacteria and cyanobacterial extracts | Oryza sativa Triticum aestivum Zea mays Gossypium hirsutum | (Singh, 2014) [79] |
|                | Pseudomonas koreensis strain AK-1 | Glycine max L. Merril | (Kasotia et al., 2015) [34] |
|                | Burkholderia phytofirmans.enterobacter sp. FD17 | Zea mays | (Naveed et al., 2014) [53] |
|                | Bacillus thuringiensis A2P2 | Triticum aestivum | (Timmusk et al., 2014) [48] |
|                | Pseudomonas chlororaphis O6 | Arabidopsis thaliana | (Cho et al., 2008) [46] |
|                | Pseudomonas putida strain GAP-P45 | Helianthus annuus | (Sandhya et al., 2009) [69] |
|                | Bacillus licheniformis strain K11 | Capsicum annuum | (Lim and Kim, 2013) [42] |
|                | Rhizobium tropici and Paenibacillus polymyxa (Co-inoculation) | Phaseolus vulgaris | (Figueiredo et al., 2008) [24] |
| Heat           | Bacillus amyloliquefaciens, Azospirillum brasilense | Triticum aestivum | (Abd El-Daim et al., 2014) |
|                | Curvularia protuberata isolate Cp4666D | Dichanthium lanuginosum Solanum lycopersicum | (De Zellicourt et al., 2013) [20] |
| Cold           | Burkholderia phytofirmans PsJN | A. thaliana | (Su et al., 2015) [82] |
|                | Pseudomonas vaucherensis Ob155-gfp | Pseudomonas frederiksbergensis OS261-gfp | (Subramanian et al., 2015) [83] |
Cold Tolerance
Organisms adapted to cold constitute a large part of the earth's biomass. In biogeochemical cycles, they play important roles. These bacteria synthesize cold shock proteins (CSPs) and cold acclimatizing proteins (Caps) when faced with low temperatures. Cold shock proteins (CSP) are 7-10 kD in size and are adequate for the functioning of RNA chaperones because they contain nucleic acid binding activity. The CSP chaperone function is considered essential for promoting growth during stress acclimation as well as during times of high metabolism.

The tolerance of transgenic rice, maize and arabidopsis for various abiotic stresses such as cold, heat and water deficiency has been shown to increase yields in field conditions due to the expression of bacterial CSPs (Castiglioni et al., 2008) [13]. They can also produce housekeeping proteins under cold conditions. Some earlier findings suggest effective introduction of cold-tolerant rhizobacteria (Rani et al., 2013; Suyal et al., 2014) [65, 65], (Selvakumar et al., 2013) [72] revealed rock phosphate solubilization using Himalayan-isolated psychrotolerant Pseudomonas sp. from India. (Majeed et al., 2015) [46] examined the overall impact of crop yield boosting rhizobacteria extracted from Kashmir’s wheat rhizosphere in Himalayan area. Furthermore, seven diazotrophs were isolated from rhizospheric soil, and their proteom was recently published (Tomer et al., 2017) [87].

The temperature resistant microbes were shown to exhibit low-temperature plant growth properties. (Yadav et al., 2019) [98] reported that, Brevundimonas terrae, Pseudomonas cedrina, Arthrobacter nicotianae adapted for low temperature shows ability to promote multifunctional growth of plants. PGPR isolated from root nodule of pea plant growing at low temperature has an effective low temperature biofertilizer ability (Meena et al., 2015) [47], These studies verified that the protein family can offer broad stress resistance, which also correlates into increased grain yields under both controlled stress and natural environment.

Heat Tolerance
The rising climate crisis already has a serious influence on global agricultural development, as heat waves trigger reduction in yield which is a major risk for ensuring food security (Ray et al., 2019) [60]. Rising temperatures impact photosynthesis, plant water interactions, flora and fruit in warm and subtropical plants. For nitrogen fixation, elevated temperatures in the soil is a major restriction to leguminous plants.

Genetic advances can impart a resistance for heat stress on crops, but bacteria and fungi can be a more environmentally sustainable solution in overcoming this challenge. PGPR also improves plant resistance to temperature stress in recent studies. Crop treatment with PGPR strains that colonize roots greatly improves tolerance for heat stress (Abd El-Daim et al., 2014) [11], (Srivastava et al., 2008) [81] extracted Pseudomonas putida NBRI0987 from drought impacted chickpea rhizosphere.

This microorganism observed over development of stress sigma (S) (RpoS) when grown under high temperature stress at 40°C versus 30°C. A thermotolerant Pseudomonas sp. strain AMK-P6 induced thermotolerance in sorghum seedlings due to synthesis of high molecular weight protein in leaves and improved plant biomass as well as biochemical status in terms of proline, sugar, amino acid and chlorophyll content (Ali et al., 2009) [4], (Nehra et al., 2007) [55] reported Rhizobium sp mutants which are heat-resistant / heat-tolerant. (Cajanus) can tolerate thermal stress and be more efficient in fixing atmospheric N2 than parent strain under natural high temperature conditions. In addition, Pseudomonas putida strain AKMP7 thermotolerant inoculation decreases heat stress and thus increases the development of the wheat plant in the face of heat stress (Ali et al., 2011) [3]. The bacterial heat-shock reaction isn't restricted just to variations in the temperature and is a universal stress response because other environmental adjustments including heavy metal additions, contaminants, ethanol, deprivation, high osmolarity or the relation with eukaryotic hosts activate several thermal-shock proteins. (Mahmood et al., 2014) [45].

Conclusion
Climate change already shows its damaging effect on Earth. The prospect of climate change is going to be more dangerous and we need to act immediately. As a result there is an emerging interest in different climate change adaptation approaches, microbial mitigation and adaptation. The role of microbes among scientific community is not that well known. But recently, diverse promising aspects of microbes have been discovered to cope with changing environments due to climate change. Some of them were discussed in this review. Further progression this direction will come from microbial community, diagnosis and physiology study, and DNA sequencing research. Most definitely, the Earth's sustainability will depend greatly on how effectively the microbial life can be utilized under rising environmental stress conditions. To contribute to the development of PGPR mediated strategies for abiotic stress, in depth knowledge of the PGPR associated mechanism is extremely essential. Some changes in root architecture induced by PGPR are important in increasing the tolerance to stress in plants and therefore requires thorough study. In addition, the clarification of the underlying mechanism in PGPR’s abiotic stress alleviation needs to be further elucidated, and much more needs to be revealed about PGPR mediated stress tolerance in plants.

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