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Role of Endophytes in Agricultural Crops Under Drought Stress: Current and Future Prospects

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Abstract: Endophytic bacteria are coming in class of endosymbiotic microorganisms extensive among plants that colonize inner spaces of plant cells in all different plants. Endophytes do not cause any plant diseases or any significant morphological changes. Vast diversty of bacterial taxa and plant host associated with this plants and endophytic bacteria. For the period of last decade, new characterisitcs of the microbial diversity have developed with application of novel metagenomic analysis methods in studies of microbial endophytes. Endophytic bacteria are influenced by various environment and genetic conditions such as plant genotype, abiotic and biotic factors, microbe-microbe interactions, plant-microbe interactions. The assorted microbial community of endophytes play essential and exclusive role in the functioning of agrosystem. Plant-associated microbial communities such as plant growth promoting endophytes enhance crop productivity and provide stress resistance. Endophytic bacterial community represents a wide range of producing enzymes and metabolites that help plant to tolerate both biotic and abiotic stresses. Their roles in the management of abiotic stresses such as drought are only establishment to draw an attention. The research concerning bacterial-mediated drought tolerance in agricultural crop plants are synthesized here. Physiological traits such as relative water content and photosynthesis are measured in recent studies. Bacterial mediated drought stress tolerance and screening protocols are highlighted in present review.

Key words: Endosymbiotic; endophytes; microbial communities; abiotic stress; drought tolerance.

Introduction

Strengthening in the field of agriculture has been mainly accomplished in the 20th century through the use of farm equipment, intensive tillage, irrigation, high-yielding crop varieties, fertilizers, pesticides and other manufactured inputs [1]. This is well demonstrated by the global use of fertilizers that increased from approx. 27 to 170 million of nutrient tons over the past 50 years before 2010 [2]. However, harmful effects of the agricultural practices on soil ecology, high irrigation needs, and effect on human health, have been recognized. Therefore new environmentally gentle approaches have to be employed to maintain sustainable agricultural production and to overcome threats that lead to loss of crop yield, including plant stresses associated with hostile environmental conditions, such as drought, osmotic stress, metal stress or soil salinity, and there are biotic stress induced by plant pathogens and pests. In this regards, there is a strong case for using microorganisms for improved plant performance in integrated plant disease management systems [3].

Microorganisms can provide advantageous effects on plants directly by enhancing crop nutrition or indirectly by reducing damage caused by

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pathogens or environmental stress. Plants live in intimate association with microorganisms that fulfill important functions in agricultural ecosystems. Bacteria may exist as free-living organisms in soils or devoted to the surface of roots and it may establish symbiotic relationship with plants [4]. Endophytic bacteria are a class of endosymbiotic microorganisms that live in internal plant tissues of apparently healthy host plants [5]. Unlike phytopathogens, such bacteria do not normally cause any significant disease signs. Endophytes colonize plant apoplast, including the intercellular spaces of the cell walls and xylem vessels of plant roots, stems and leaves, and they are also found in tissues or flowers [6], fruits [7] and seeds [8]. Typically, higher density of endophyte populations is found mostly in plant roots and other below-ground tissues as compared to aboveground tissues. Arising movement of endophytic bacteria from roots to leaves of rice plants has been revealed [9]. Although endophytic bacteria are adapted to living inside specific plant genotypes, a variety of reports indicate that structure of endophytic community is influenced by abiotic and biotic factors such as environment conditions, microbe-microbe interactions and plant-microbe interactions [10].

It has been established that firm association between host-plant and endophytes is mediated through exploit of compounds produced by the microorganisms and the host cells [11,12]. Many books recorded effects of endophytic bacteria on plant health and growth. The endophytes aid nutrient availability and uptake, improve stress tolerance, and provide disease resistance [10,13]. Plant growth helping in increase the ability of endophytes for production of plant growth hormones, production of plant growth hormone alter endogenous plant by nutrients increase activity, such as nitrogen and phosphorus [14]. Plant disease resistance promoting properties are associated with the ability of endophytic bacteria to produce a wide range of compounds, such as antibiotics or chitinase enzyme, which can inhibit growth of plant pathogens and thus act as biocontrol agents [15,16,12,17].

Due to their plant growth promoting and disease control properties, endophytes can be used as bio inoculants in agriculture to promote plant growth and health. A number of registered patents that are related to application of endophytic bacteria to enhance host tolerance to fungal pathogens. They also promote plant growth for applications which are beneficial for the development of sustainable agricultural production [18].

In this review, an overview is provided for the composition of bacterial populations that are found in endosphere of major crop plants which are grown in agricultural environment. Recent advances are being analyzed in the endophytic microbiome research. Furthermore, considering a role of the endophytes in plant adaptation to stress and disease resistant, effect of agricultural practice is crucial as endophytes are having complex interactions unlike other bacterial biome.

Importance of bacterial endophytes in agricultural crops

Endophytic bacteria are very diverse as well as they play an integral role in ecosystems and plant physiology. All plant compartments, generally the intercellular and intracellular spaces of inner tissues are colonized by these bacteria. In the initial studies on diversity of endophytic bacteria were mostly based on characterization of endophytic isolates which are obtained from the plant after surface sterilization by different methods [19].

Bacillus and *Pseudomonas* are the common genera which are identified as frequently occurring in agricultural crops [20,21]. Presence of different endophytic species depends mostly on plant and bacteria genotype and biotic and abiotic environmental factors. Endophytic population is depend upon various factors like the tissue type of plants, season of isolation in a single host plant species [22,23]. A study conducted on bacterial endopyte communities revealed that although endophytic bacteria colonize entire plant, the roots usually contain higher number of species. Endophytic species mostly belong to the-, β-, and γ-proteobacteria subgroups and are closely related to epiphytic species [22]. Remarkably, the γ-proteobacteria group is the most diverse and dominant. It has been reported that most of gram-negative endophytes act as agents of biological control [24,] while among the gram-positive bacteria the dominant endophytic species primarily those belonging to the *Bacillus* species are found [25,26].

To make it more clear of the diversity of endophytic microorganisms, recently a number of studies have been focused on identification of unculturable endophytes using novel metagenomic analysis approaches. For analysis of a bacterial community many application of modern bioinformatics tools are used which are allow to analysis of its phylogenetic structure inside a variety of plant organs or tissues as well as direct amplification of microbial DNA from plant tissue samples [27,28]. Metagenomic analysis involves direct isolation of bacterial DNA, library construction and functional analysis 24, 30. To study endophytic bacterial diversity, highly specific methods should be used [31]. Initial studies on the unculturable bacterial endophyte diversity revealed technical limitation related to separation of endophytic bacteria from plant nuclei, plastids, mitochondria and plant associated microbial DNA [32]. As plant DNA is much more abundant than bacterial, it is difficult to isolate and sequence only bacterial community at high coverage.

To avoid the plant host DNA, enrichment of endophytic bacteria prior to DNA amplification should be done [32]. To eliminate interference of plant host DNA, enriched bacterial endophytes are enriched by hydrolysis of the plant cell walls, followed by differential centrifugation [30]. For bacterial DNA ratio enrichment in stems and leaves of soybean and rice, series of differential centrifugation steps were used followed by density gradient centrifugation [33]. Another technique suitable for extraction of endophytes from internal tissues of potato tubers was developed and involved overnight shaking of the small pieces of potato tubers in sodium chloride solution [34]. Even though the method allowed bacterial DNA extraction from a large amount of plant material, diversity of rare members of endophytic metagenome could be also reduced.

Bacterial endophytes interaction within population

Endophytic bacteria are known to produce a wide variety of secondary metabolites and hydrolytic enzymes. Innovation of novel endophytic metabolites and investigation of their involvement in plant metabolism is an active field of research [12]. A large number of the compounds produced by endophytes possess antibacterial or antifungal activity. So far, the main research on antimicrobial activity of endophytes has been mainly focused on impact of endophytes on pathogenic bacteria and fungi. However, an abundance of endophytic bacteria and potential of metabolic signalling suggests presence of the multidimensional network of competing and symbiotic interactions in plant endosphere, which is difficult to model in in vitro experiments. Therefore elucidation of the molecular basis for interactions among the endophytic bacteria and their effect on endophytic fungi largely remains a challenge for future research.

Recent studies have revealed that bacterial endophytes are involved in complex interactions with endophytic fungi. For example, *Burkholderia rhizoxinica* endosymbiont of endophytic fungus *Rhizopus microsporus* controls vegetative reproduction of the host fungus [35]. Endophytic bacteria identified as *Luteibacter* enhances indole-3-acetic acid (IAA) production in vitro by endophyte *Pestaliotopsis*, meanwhile bacteria alone fail to produce IAA on medium and endophytic fungi produce significantly smaller amounts of IAA in absence of the bacterium [36].

Endophytic bacterial communities and its effects on agricultural practices

The majority of bacteria in plant endosphere are assumed to have a "facultative endophyte" lifestyle and a stage in their life cycle in which they exist outside the host plants [37]. These endophytes often originate from soil, initially infecting roots of the host plant and colonizing the plant apoplast. Therefore it could be presumed that the endophytic community represents a certain subset of the wider microbial population of rhizosphere and it would reflect differences induced by agronomic practices that are characteristic of soil microbial community. However, research on the effect of agricultural practices on endophyte population dynamics is limited to several studies.

It was demonstrated that colonization ability of nitrogen-fixing endophytic bacterium *Acetobacter diazotrophicus* is largely decreased in the sugarcane plants fertilized with high levels of nitrogen 29. Analysis of the endophytic population of maize roots under treatment with herbicides and different fertilizer types revealed that microbial group-specific genetic pattern differentiated the maize plants, cultivated by using mineral fertilizer, from the plants cultivated by using organic fertilizer 20. Meanwhile, no significant effect of herbicide treatment on composition of the root endophyte population was detected. These studies did not reveal if the changes in endophyte population were a consequence of changes in overall soil microbial population upon the fertilizer treatment or the agronomic practices had a direct effect on the root endophytic community.

The importance of agricultural practices that maintain natural diversity of plant endophytic bacteria is emphasized by the observations that agricultural plants may become a niche for human pathogens and a source for outbreaks of food-borne illness [38]. Pathogenic bacteria of the family *Enterobacteriaceae* including pathogenic *Salmonella* genus strains, *Escherichia coli* and *Vibrio cholerae* strains, and the human opportunistic pathogen *Pseudomonas aeruginosa* were described as endophytic colonizers of plants [39,40,41,42]. The colonization of plants by the human pathogens may be associated with the use of manures contaminated with faecal bacteria [38], as well as the use of practices that lead to decline in soil and endophytic microbial populations and a reduced number and abundance of species antagonistic to the human pathogens [43].

Characteristics of endophytes in biotic and abiotic environmental stress with adaptation to agricultural crops

Endophytic bacteria have several beneficial effects on their host plant. Plant growth is promoted through improved nutrient acquisition, including nitrogen fixation [44] endophytes have been have produced several of plant growth enhancing substances such as cytokinins [45] and indole acetic acid (IAA) [46]. Endophytic bacteria enhance adaptation to environmental abiotic or biotic stress along with enhanced growth properties, modulation of plant metabolism and phytohormone signalling. Endophytic bacteria present a special interest for improved crop adaptation to stress as they have the advantage of being relatively protected from the harsh environment of the soil under different stress conditions i.e., draught, high salt or other stress conditions [47].

Bacterial endophyte *Burkholderia phytofirmans* PsJN enhances cold tolerance of grapevine plants by altering photosynthetic activity and metabolism of carbohydrates involved in cold stress tolerance [48]. The organism presence in the plant promoted acclimation to chilling temperatures resulting in lower cell damage, higher photosynthetic activity, and accumulation of cold-stress-related metabolites such as starch, proline, and phenolic compounds. Likewise positive effect of the bacterium on metabolic balance and reduced effect of drought stress was demonstrated in wheat plants grown under limited irrigation conditions [49]. Endophytic bacteria *Pseudomonas pseudoalcaligenes* was shown to induce accumulation of higher concentrations of glycine betain-like compounds leading to improved salinity stress tolerance in rice [50].

Water stress tolerance in maize plants was improved by addition of the abscisic acid (ABA) that is produced by endophytic *Azospirillum* spp. [51]. The effect was further improved by plant growth promoting hormones IAA and gibberellins. ABA is the phytohormone which is critical for plant growth and development. Level of ABA is known to increase under stress condition. Main function of ABA seems to be the regulation of plant water balance and osmotic stress tolerance [52].

Ethylene is another important plant hormone that is the extensively studied mediator of plant stress response signalling. Ethylene is formed from methionine via S-adenosyl-L-methionine, which is converted into 1-aminocyclopropane-1-carboxylic acid (ACC) by the enzyme ACC oxidase [53]. Stress induced accumulation of ethylene is usually deleterious to plant growth and health [54]. Endophytes may produce the enzyme ACC deaminase that has no function in bacteria but contributes to plant growth promotion and improved stress tolerance by cleaving the ethylene precursor ACC [55]. There are several reports on ACC deaminase-containing plant-associated bacteria and their role in improved plant growth and stress tolerance that was recently reviewed [55]. The effect of endophytic bacteria-derived ACC deaminase activity on salt stress was most studied. Endophytic diazotrophic *Achromobacter xylosoxidans* AUM54 isolated from *Catharanthus roseus* grown in saline soil showed ability to produce ACC deaminase and to reduce ethylene levels [56]. Halophyte plant *Limonium sinense* was naturally associated with ACC deaminase producing endophytic bacteria that might play important role in higher salinity tolerance of the plant 57. Thirteen isolates possessing ACC deaminase activity were obtained that belonged to genera: *Bacillus*, *Pseudomonas*, *Klebsiella*, *Serratia*, *Arthrobacter*, *Streptomyces*, *Isoptericola* and *Microbacterium*. The study revealed that endophytic bacteria affected plants differently under drought stress conditions as compared to other rhizospheric bacteria, such as *Pseudomonas putida* UW4 [54].

In addition, ACC deaminase producing *Pantoea agglomerans* Jp3-3 and *Achromobacter xylosoxidans* strain Ax 10 were shown to alleviate stress of *Brassica* sp. plants grown in copper-contaminated soils and improved copper uptake by the plants [58,59]. ACC deaminase producing isolates from *Commelina communis* plants grown on lead and zinc mine soils were shown to improve growth of rape plants in the lead-contaminated soil [59].

Cold resistance study of vine plants inoculated by *Burkholderia phytofirmans* PsJN revealed that the colonization of endophytic bacteria allowed higher and faster accumulation of stress related gene transcripts and metabolites leading to more effective resistance to cold stress [60]. This provided insight into the priming phenomenon implicated in stress tolerance induced by plant-associated bacteria. The protection of cucumber plants against cucumber anthracnose induced by *Pseudomonas fluorescens* strain 89B-61 was the first case demonstrating that endophytic bacteria could elicit ISR in plants [61,62]. Similar studies have proven that the ISR was induced by endophytic bacteria of genus *Bacillus*, *Pseudomonas* and *Serratia* in different plant-pathogen systems and molecular cell signalling mechanisms involved in the defense priming were previously reviewed [62].

Drought types and causes

The effects of drought are different from one region to another as it is a natural hazard. Normally, it is referred to as a creeping phenomenon which can be classified as:

1. Meteorological drought
2. Hydrologic drought
3. Agricultural drought
4. Socio-economic drought

Meteorological drought occurs when if precipitation is less than the normal season for a long period of time over a vast area. Drought affects the economy thoroughly but it may affect only a few farmers or a small community if it occurs in a small region. A method of computing numerical drought index and index number was developed by Palmer [63] for the assessment of severity of meteorological drought. If meteorological drought occurs for a long time, it may lead to hydrologic drought, which is a step ahead of meterological drought and is usually marked by a shrinkage of above ground water bodies like drying up of rivers, streams, etc., as well as a decline in ground water levels.

As compared to meteorological drought, hydrologic drought is far more reaching as it affects industry, agriculture and hydroelectric power generation and if it continues, irrigable lands have to be deserted. Another category of drought is agricultural drought, which occurs at the time of growing season when rainfall and soil moisture are not sufficient to sustain healthy crop production that causes severe wilt and crop stress. Agricultural drought is independent of meteorological drought; it may subsist even if there is no meteorological drought. Socio-economic drought is defined as the failure of water resources systems to meet water demands.

Strategies of plants to survive in water scarcity

Different mechanisms have been developed by plants to survive in water scarcity like avoidance, escape and tolerance to cell or tissue dehydration 64. In arid regions, annual plants escape against water deficit by producing seeds at the time of water availability followed by intermittent rainfall.

Drought avoidance

Plants avoid drought through changes in their anatomy, orientation and area of leaves or by increasing resistance towards stomata and cuticle to transpiration [65]. Despite water scarcity, plants can maintain their normal growth to avoid drought. This is generally achieved by increasing water use efficiency (WUE), which is measured as photosynthetic carbon gain over transpirational water loss, while high WUE may decrease development and growth rate [66].

Drought tolerance

The strategy of drought tolerance of primitive terrestrial plants remain conserved all through the evolution of angiosperms is by restricting intense levels to resurrection plants [67]. The main mechanism to sustain cell turgor is osmotic adjustment which enables water uptake, and thus helps in maintenance of plant metabolism [68].

Water stress capabilities of endophytes

Drought stress affects endophytic bacteria via osmotic stress and resource competition [69,70] and it may lead in nucleic acids damages [71] that may occur through chemical modifications like alkylation or oxidation, cross-linking, or base removal [72]. Drought stress results in an accumulation of free radicals due to conformational protein changes, restricted enzyme efficiency, and changes in electron transport chains [73].

To survive drought and protect cell structures and organelles, bacteria employ a variety of physiological mechanisms including accumulation of compatible solutes, exopolysaccharide production, and the production of spores [74,69,75]. Accumulation of compatible solutes such as proline, glycine betaine and trehalose increases thermotolerance of enzymes which can inhibits proteins thermal denaturation and helps maintain membrane integrity [76,74,69]. Bacteria also synthesize heat shock proteins (HSPs) that recognize and bind to other proteins if they are in non-native conformations [36,77]. Alternatively, some bacteria store high quantities of ribosomes, which allow them to respond with rapid protein synthesis when the stress is released [78]. Other mechanisms that help bacteria to combine with water stress include increased efficiency of microbial cells [79] and the production of extracellular polymeric substances (EPS). EPS serve to protect the cell as well as the local environment in which the cell is embedded [80]. For example, many of the compatible solutes i.e., proline and glycine betaine that help bacteria to cope with drought stress also help plants to tolerate drought stress.

PGP trait improve physiological processes connected with drought stress

Rooting characteristics for water uptake

Among the many adaptive traits that plants possess to endure drought, root system architecture is one of the most important [26,57,81]. Roots show morphological plasticity in response to soil physical conditions [82,83,91], that allows plants to adapt better to the chemical and physical properties of the soil, particularly under drought conditions [26,57]. Specific root traits associated with maintaining plant productivity under drought conditions include increases in numbers of roots with smaller diameters and a deeper root system [85,86,87,88]. A correlation between a deep and prolific root system with drought resistance has been established in several crops including soybeans [89], chickpea (*Cicer arietinum* L.) [90], maize [91]; and wheat (*Triticum aestivum* L.) [92]. Similarly, increases in numbers of roots with small diameters enable plants undergoing drought to increase hydraulic conductance by increasing the surface area in contact with soil water as well as increasing the volume of soil that can be explored for water 88. From these studies, it can be argued that plants with a more prolific and deeper root system would be able to tolerate drought stress better than plants with fewer roots, as roots are the only organ capable of extracting water from the soil profile [93].

Shoot growth characteristics

Treatment of plants with PGPR leads to increase shoot growth. Subsequently, under drought stress, plants inoculated with effective PGPR strains could maintain near-normal shoot growth rates, resulting in increased crop productivity. For example, it was showed that inoculation of corn plants with plant growth-promoting *Bacillus* spp. improved shoot growth [94]. In this study, under drought stress conditions, all the plants inoculated with the tested *Bacillus* spp. showed significantly greater shoot length and dry biomass compared to non-inoculated plants. Similarly, also studied that under drought stress, wheat plants treated with PGPR had 78 % higher biomass than non-treated plants and moreover it was confirming the potential of PGPR to enhance plant performance under drought stress [95]. In addition to, results showed that pepper plants treated with *Bacillus licheniformis* K11 and exposed to drought stress had 50 % higher biomass than non-treated plants [117]. The plant shoot length was also increased. Increases in shoot and plant growth under drought stress as a result of PGPR treatment have also been reported in other crops including sorghum (*Sorghum bicolor* L.) [96], sunflower (*Helianthus annuus* L.) [97], wheat [98], green gram (*Vigna radiata* L.) [99], mung bean (*Vigna radiata L.*) [100] and maize [49,101].

Relative water content in plants under drought condition

Relative water content (RWC) in plant leaves is considered one of the best criteria for measuring plant water status because it is involved in the metabolic activity in tissues. It has been observed that species that are better adapted to dry environments have high RWC [102]. Therefore, an increase in RWC should be considered an important drought tolerance enhancement strategy. RWC could be used as a parameter in screening PGPR for drought stress alleviating potential. Indeed, many studies investigating the ability of PGPR to help plants tolerate drought stress have measured RWC in treated and non-treated plants under drought stress. Several studies have shown that under drought stress, PGPR-treated plants maintained relatively higher RWC compared to non-treated plants, leading to the conclusion that PGPR strains that improve survival of plants under drought stress generally increase RWC in the plants. For example, it was reported that sorghum plants treated with PGPR, *Bacillus* spp strain KB 129 under drought stress showed 24 % increase in RWC over plants that were not treated with PGPR [96]. Studies reported above have indicated that higher RWC may help plants counteract the oxidative and osmotic stresses caused by drought stress, potentially contributing to greater productivity under stress.

Osmotic adjustment for drought tolerance

Osmotic adjustment is one of the key adaptations at the cellular level that helps plants tolerate drought-induced damage [85,103]. It protects enzymes, proteins, cellular organelles and membranes against oxidative damage [81,103]. Osmotic adjustment is the active accumulation of organic and inorganic solutes, also referred to as compatible solutes [104], in response to drought stress [105]. They include ammonium compounds such as glycine betaine, sugars (e.g. sucrose), organic acids (e.g. malate), inorganic ions (e.g. calcium), and non-protein amino acids (e.g. proline). Drought stress is often accompanied by an increase in compatible solutes, specifically proline [103].

Antioxidant metabolism

One of the inevitable consequences of drought stress is enhanced production of a variety of reactive oxygen species (ROS), such as hydrogen peroxide (H2O2), singlet oxygen (1O2), superoxide radical (O2-), and the hydroxyl radical (HO*) [106]. These ROS slow down normal plant metabolism through oxidative damage to lipids, proteins and other macromolecules and may ultimately cause cell death [103,107].

Plant growth and development substances

Plant growth and development including shoot growth is under the control of plant growth regulators and several phytohormones, including auxins, gibberellins (GAs), cytokinins (CKs), ethylene (ET), and abscisic acid (ABA) 103. GAs and CKs promote plant growth while ethylene and abscisic acid inhibit growth [108]. Drought stress leads to an increase in the concentrations of substances that inhibit growth, thereby allowing the plants to regulate their water budget [103]. PGPR treatment promotes plant growth in the presence of drought stress by manipulating and modifying the phytohormone content [109]. Such modifications include decreasing ET production [14,109] and changing the balance of CKs and ABA [51,110] or IAA signaling [111.] These modifications have all been associated with drought stress tolerance when PGPR are applied and may contribute to the observed bacterial-mediated drought tolerance.

Auxin

Auxin, also referred to as indole-3-acetic acid (IAA), is an important regulator of plant growth and development, which influences a large number of diverse cellular functions including differentiation of vascular tissues, initiation of lateral and adventitious roots, stimulation of cell division, elongation of stems and roots, and orientation of root and shoot growth in response to light and gravity [54]. Treatment of clover (*Trifolium repens L.*) plants with PGPR (*P. putida* and *B. megaterium*) increased shoot and root biomass and water content under drought stress, and these increases were correlated with increased IAA production also elicited by the applied PGPR [112].

Ethylene and ACC deaminase

Ethylene (ET) is synthesized at higher rates as a result of several stress signals, including mechanical wounding, chemicals and metals, flooding, extreme temperatures, pathogen infection and drought [113]. 1-Aminocyclopropane-1- carboxylate (ACC) is the immediate precursor of ET in higher plants. Its regulation has been suggested as the principal mechanism by which bacteria exert beneficial effects on plants under abiotic stress, including drought stress [114].

Abscisic acid

Abscisic acid plays important roles in many physiological processes in plants and is crucial for the response to environmental stresses such as drought [51,115]. Elevated ABA contents in plant organs under drought stress result in physiological changes that modulate plant growth [103]. PGPR that elevate the concentrations of ABA can enhance plants' ability to tolerate drought stress. It was showed that *Bacillus* sp. treated lettuce (*Lactuca sativa L.*) plants had increased amounts of ABA when compared to non-treated plants [116].

Conclusion

A wide range of diversity of endophytic bacterial organisms isolated from a variety of agricultural plants suggests that the bacteria play a vital role in harmonizing plant physiology and functioning of agroecosystems. Composition of the endosphere microbial populations depends mostly on plant and bacteria genotype, biotic and abiotic environmental factors. Several studies demonstrate beneficial effects of the endophytic bacteria on plant growth and adaptability to biotic or abiotic stresses.

This review of the literature indicates that certain strains of PGPR can help plants tolerate drought stress. Some of the physiological mechanisms that have been anticipated include modifications in root construction which results in better water and nutrient uptake, with positive effects on the overall plant growth, increase in relative water content, increase in several organic and inorganic solutes as well as an increase in the synthesis of osmolytes including proline, increase in antioxidant enzymes that scavenge for reactive oxygen species, and manipulation of phytohormones including IAA, ABA, and CK. The research that has been published so far offers a glimpse into the intricate, complex and intriguing mechanisms underlying bacterial-mediated drought tolerance. New studies on these mechanisms will help improve strategies for the use of PGPR in mediating drought tolerance.

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