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Microbial inoculants for drought stress tolerance

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Abstract

Temperature, rain, humidity, wind, and solar radiation are all climatic factors that affect agricultural activities. While some agricultural areas of the world are irrigated, the vast majority rely on natural rainfall patterns. Farmers will consume more water as a result of climate change and experience less water availability, resulting in a decrease in production capacity. As one of the most important natural phenomena affecting agricultural productivity, drought is a limiting environment for plant growth. Bacteria have been shown to reduce water stress in these plant species and promote greater growth by regulating gene expression and the integration of hormones. Phytohormones modulation, stress-induced enzymatic apparatus, and metabolites are integrated into the root-to-shoot phenotypic changes in growth rate, architecture, hydraulic conductivity, water conservation, plant cell protection, and damage restoration. By demonstrating how plant growth-promoting bacteria can mitigate plant stress and provide examples of technology conversion in agroecosystems, this review illustrates how water stress can be mitigated.

Keywords: Sustainable agriculture; Biofertilizers; PGPB; Endophytic bacteria; Abiotic stress; Inoculant

1. Introduction

Agricultural systems are directly affected by climate changes and global demands for food, fiber, and energy, which compromise food security and agroecosystem sustainability [1] (Malhi *et al.* 2021). Due to fossil fuel demands associated with industrialization and urbanization, deforestation and intensive land use, which have increased greenhouse gas emissions, food chain production activities contribute significantly to global climate change trends. In this century, changes in temperature and precipitation regimes will be a significant constraint on food production. Abiotic factors account for about half of agricultural productivity losses, while biotic factors account for about 30% [2,3]. Agriculture faces a number of challenges under global climate change scenarios and economic constraints, including increasing crop yields or mitigating crop losses [4] (Ashraf, 2010). As a result of an external factor that alters plant physiology, stress can be defined as any adverse change that occurs. In addition to temperature, drought, salinity, flooding, and heavy metals, abiotic stressors reduce plant productivity. An integrative approach to developing drought-tolerant varieties has been used in several studies by combining conventional breeding tools with modern breeding techniques [4]. The use of plant breeding has been widely applied to select genotypes that are tolerant to diverse environmental stresses. Furthermore, several studies have been conducted to unravel the molecular bases and morpho-physiological traits associated with drought tolerance [5,6]. Environmental stresses can be mitigated by plant growth-promoting bacteria (PGPB) through two pri-mary mechanisms, including water conservation mechanisms and protection recovery mechanisms [7,8,9]. Drought mitigating bacteria are being converted into a sustainable solution for agroecosystems, resulting in increased interest [10,11]. The most feasible bi-ological technology for biotic and abiotic crop protection is microbial inoculants [12,13]. Using complex molecular machinery that is mediated by

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phytohormonal signaling, an induced enzymatic pool, and metabolites, this review examines how bacterial inoculants alleviate plant water stress to increase soil water accessibility and reduce plant water loss. It will also demonstrate how catalytic proteins and metabolites are coordinated to prevent damage to plant cells and trigger repair mechanisms that increase plant tolerance for water scarcity. Additionally, past and current drought stress mitigation strategies, technological applications, and future prospects for bacterial inoculants will be discussed.

2. Adaptation mechanisms of plants to drought

The greatest threat to global agricultural quality and productivity is drought, which limits plant growth and development. It is defined as a meteorological phenomenon characterized by prolonged periods of sub-normal rainfall that compromises soil moisture for a given crop [14]. Consequently, a decrease in water availability impacts plant growth and development negatively, affecting plant life cycles [15]. The water potential of the soil decreases during drought periods, thereby affecting the plant's water potential as well. In order to maintain the balance between soil, plants, and the atmosphere, plants' response to drought is a complex phenomenon involving a variety of molecular, biochemical, and physiological changes. Researchers conducted studies on grape leaves and demonstrated that the stomata completely closed before cavitation occurred, thus preventing cavitation and embolism [16,17]. CO_2 influx decreases simultaneously, directly affecting photosynthetic capacity, while photorespiration increases simultaneously. Reduced carbon incorporation into plant biomass under water scarcity influences plant drought responses. To increase plant resilience to water stress, two main approaches must be interconnected. A combination of morpho-physiological mechanisms are employed to increase plant water status, primarily through hormonal signaling mechanisms (i.e. auxin, cytokinin, gibberellin) [18,19,20]. As well as signaling stress, they are essential for growth and development. In drought conditions, abscisic acid (ABA), a stress hormone, is present in significant amounts. In addition to regulating several genes, it promotes stomatal closure and dehydration tolerance [21,22]. A process known as osmotic adjustment can also be used to maintain cell turgor by modulating a cell's osmolarity by increasing solute concentrations within the cell (soluble sugars and glycine) [23]. These solutes prevent plant cells from becoming toxic during droughts in addition to main-taining turgor pressure [23]. The osmotic adjustment of pea roots [24] and sorghum [25] has been reported. In subsequent studies [26,27,28,29,30], osmotic adjustment mechanisms were demonstrated to maintain plant turgor [26,27,28,29,30]. It is important to note, however, that plant species/cultivars and the duration of stress events determine the degree of response to osmotic adjustment. As a result of the application of organic compounds as foliar sprays, plants are able to tolerate stress conditions better, which results in an increase in osmolytes accumulation, such as when sugar beets (*Beta vulgaris* var. saccharifera L.) [31], *Catharanthus roseus* [32], *Brassica* spp. [33], and *Raphanus sativus* L. [34]. Protecting and repairing machinery are associated with water conservation [10]. Similarly to other abiotic stresses, water deficit causes a decrease in electron transport chain activity, causing plant tissue to photooxidize [35]. As a result, the Rubisco enzyme activity declines and the PSII membrane complex is damaged, repressing photosynthetic activity [36]. An important photoprotective response to drought occurs in plants, as well as a number of molecular and biochemical mechanisms that lead to non-photochemical quenching (NPQ) of chlorophyll fluorescence. Induction of reactive oxygen species (ROS) is one of these well-studied mechanisms that can lead to membrane peroxidation and oxidative damage, impairing cellular functions [37]. Various enzymes are involved in plants' antioxidant defense system in order to reduce oxidative damage (superoxide dismutase (SOD), peroxidase (POX), catalase (CAT), and glutathione reductase (GR). As a result, drought tolerance correlates positively with antioxidant response. Plant species that are more tolerant display better antioxidant responses, resulting in higher levels of antioxidative enzyme activity, which protects the plant from oxidative damage [38]. Conversely, species whose enzyme activity machinery is less sensitive to drought show no such changes. Drought increases the activity of antioxidant enzymes, as shown in several studies. These antioxidant responses can differ between cultivars, as found in rice *Oryza sativa* L. [39], *Triticum aestivum* L. [40], and *Hordeum vulgare* L. [41]. Researchers have shown that drought-tolerant cultivars produce less ROS and oxidative stress than drought-sensitive cultivars as a result of their research. Through breeding and genetic engineering, these differences between drought-sensitive and drought-tolerant genotypes can be used to develop more resistant crops [42,43]. ROS play a critical role in maintaining cellular processes, but when they exceed normal levels, they have a toxic effect. It is therefore important to maintain a balance between cytostatic and cytotoxic ROS levels [35,36]. Plant fitness under environmental stress can be enhanced by microbial communities at the rhizosphere, root-shoot surfaces, and inner tissues (endophytes), in addition to the molecular, biochemical, and physiological responses triggered by drought [44,45]. In natural conditions, scientists are able to understand and enhance drought tolerance through the study of plant-bacteria interactions. In order to reduce the impact of drought on food security and agricultural production, researchers can gain insight into plant-microbe interactions that can lead to the development of drought-tolerant crops.

3. Growth-Promoting Bacteria in Plants

As a group of organisms, soil bacteria communities have the greatest diversity, abundance, and physiological activity, with bacterial phylotypes ranging from 102 to 106 per gram [46]. A new ecological niche is created when seeds or other reproductive plant structures are sown through the soil as the soil microbes act as a "seed bank" of species richness [47]. As described by the authors, rhizospheres are soil perimeters enriched with carbon exudates (including organic acids, amino acids, sugars, flavonoids), mucilaginous matrixes, and detached root cap cells. This environment is highly active and conducive to plant recruitment of taxa capable of colonizing the rhizosphere [48,49,50]. It is important to note that in the rhizosphere, beneficial and pathogenic microorganisms compete for colonization of plant tissues, modulating nutrient flux through the soil-plant system and affecting the growth of plants [51]. Bacteria have played a crucial role as the most common and active fraction interacting with plant hosts among such microorganisms [52]. It has been reported that biofertilizers, biostimulants, and bioprotections enhance plant growth, prevent pathogens, and mitigate environmental stresses, according to several reports. *Klebsiella*, *Paraburkholderia*, *Azospirillum*, *Herbaspirillum*, *Gluconacetobacter*, *Serratia*, *Azotobacter*, and many others belong to the PGPB family in addition to *Pseudomonas* and *Enterobacter*. Plant growth is promoted by these microorganisms in two ways: (1) biolog-ical nitrogen fixation; (2) indirect mechanisms: reducing damage caused by pathogens and/or environmental stresses by producing hormones (indole-3-acetic acid, gibberellic acid, and cytokinin, such as zeatin) and acquiring essential nutrients; and (3) indirect mechanisms: relating to biocontrol, which involves mitigating damage caused by path-ogens and environmental stresses [13, 53,54,55,56,57,58,59] (Figure 1).

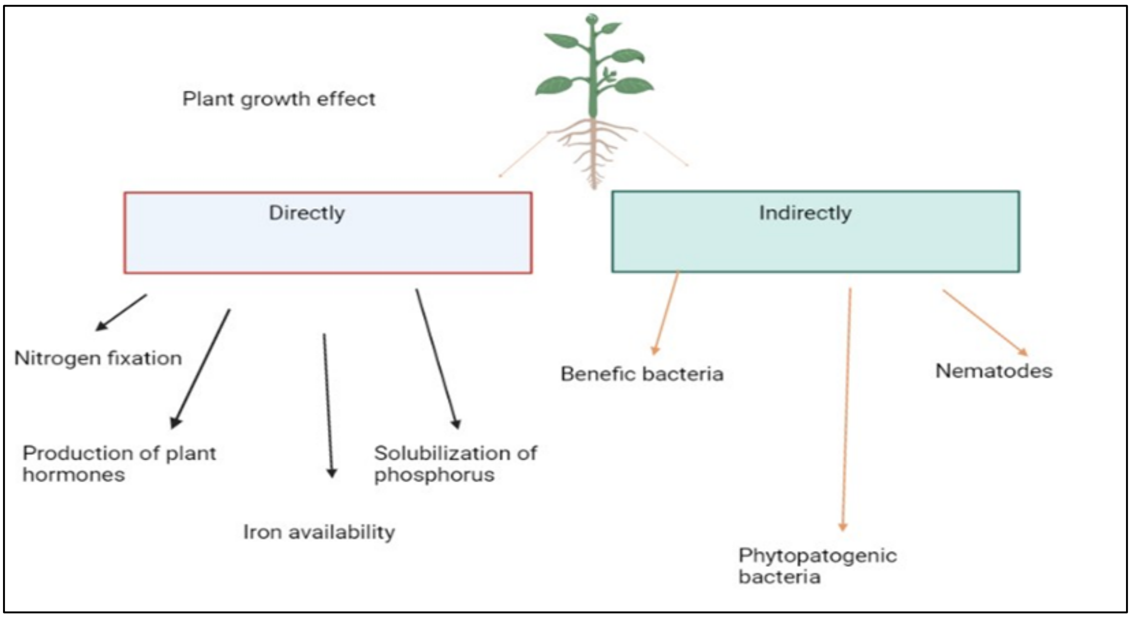

Figure 1 Plant growth is facilitated by PGPB, which produces siderophores, increases iron availability, and produces hormones like auxins, gibberellins, and cytokinin which influence plant hormone balance. By utilizing the nitrogenase enzyme complex and solubilizing inorganic phosphate in the soil, biological nitrogen fixation (BNF) occurs, as well as siderophores are produced. Plant pathogens and nematodes are repelled by PGPB by occupying niches and producing substances that repel them.

To reduce damage caused by environmental stress on plants, several mechanisms have already been identified in the reactions and interactions between PGPB and plants [60,61]. In addition to producing hormones (auxin, cytokinin, abscisic acid), exopolysac-charides and beneficial enzymes, including 1-aminocyclopropane-1-carboxylate deami-nase (ACC deaminase), trehalose and volatile organic compounds, as well as osmoregulation, there are also responses related to osmoregulation. PGPB resists drought by a variety of mechanisms as shown in Table 1.

Table 1 Bacterial genera and species that are drought resistant

Microorganisms	Plant	Method of action	References
Azospirillum sp.	Wheat	Auxin and N concentrations are highest	[62]
Bacillus sp.	Grass	Antioxidant system response and early proline accumulation	[63]
Streptomyces sp.	*Tomato*	Increasing the content of different sugars	[64]
Pseudomonas sp.	*Arabidopsis*	Exopolysaccharide, gibberellic acid, abscisic acid, and indole acetic acid deaminase activity are higher	[65]
Enterobacter sp.	*Bean*	Increase the levels of proline, malondialdehyde, and antioxidant enzymes	[66]
Azospirillum brasilense	*Wheat*	A decrease in H_2O_2 accumulation and a decrease in the production of proline and catalase as well as peroxidase activity	[67]

4. Plant Growth-Promoting Bacteria (PGPB) and stress tolerance

4.1. Plant morpho-physiological traits are modulated by bacterial phytohormones

A complex network of plant hormones is necessary for beneficial microorganisms to promote plant growth. PGPB's interaction with plants results in a number of changes, including changes in hormonal homeostasis, as well as responses to biotic and abiotic stimuli [68,69,70]. Some microorganisms can affect hormone concentrations, locations, and signaling in plants [71,72,73]. Plant hormones play an important role in promoting plant growth through beneficial microorganisms (Figure 2).

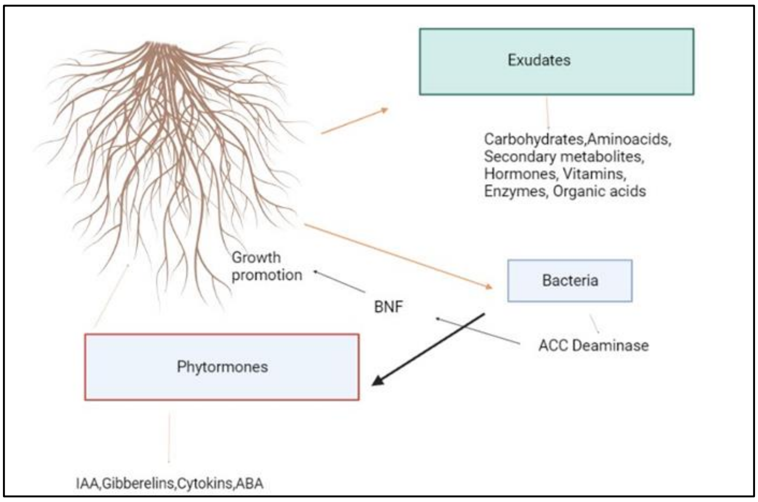

Figure 2 Microorganisms and plants produce metabolites that act as signaling molecules and substrates when they interact. Besides fixing nitrogen and solubilizing nutrients (phosphate and iron), microorganisms also produce hormones, which stimulate plant growth. A dashed line indicates a positive relationship between plants and bacteria. Abbreviations: 1-aminocyclopropane-1 carboxylate deaminase; BNF, biological nitrogen fixation

Plant hormone auxin has a number of functions including cell division, expansion, and differentiation [74]. Seeds and tubers are stimulated by auxinic activity, xylem and roots are developed at a faster rate, vegetative growth processes are controlled, lateral and adventitious roots are formed, light, gravity, and flowering are mediated, and synthesis of photosynthesis, pigments, metabolites, and resistance to stressful conditions are all affected [75]. A number of PGPBs regulate auxin balance, which affects the growth rate and architecture of roots [76,77,78,79]. Microbes inoculate crops in such a way as to modify root anatomy and biochemistry through the modulation of phytohormones [80,81,82,83,84]. As a matter of interest, these plant-growth promotion effects are crucial to increasing water availability in environmental scarcity situations with a low soil matrix water potential. By increasing root formation (root ramification), root hair density, and root hair length (specific surface enhancement), absorptive root structures increase water uptake. This results in an increase in root surface, volume, and biomass. Additionally, the root system's hydraulic conductivity is modulated by changes in the organization pattern of epidermal, cortical, and vascular root tissue systems [85]. Variables include the number and arrangement of cell layers, water flux resistance, metaxylem size, diameter, and dis-tribution, and water channel transmembrane transporters (such as aquaporin). Additionally, auxin signaling activates electrogenic transmembrane pumps (P-type H^+ ATPase at the plasma membrane and V-type H^+ ATPase at the vacuolar membrane) which create electrochemical gradients to facilitate secondary nutrient transport. Furthermore, P-type pumps acidify the apoplast microenvironment near the meristematic tip of recently di-vided cells, which promotes growth of the root axes and tissue proliferation [86,87]. The inoculation of bacteria facilitates plant growth under appropriate water availability or alleviates water scarcity negative effects by modulating auxin signaling and balance. When drought occurs, abscisic acid (ABA), a stress hormone, is detected significantly. ABA promotes stomatal closure and regulates genes involved in dehydration tolerance [22]. The ability of some plants to cope with abiotic stresses is attributed to exogenous ABA provided by bacteria of a particular genus, according to Cohen and collaborators [88]. When maize plants were inoculated with Azospirillum brasilense strains Ab-V5 and Ab-V6, they recovered better from a prolonged drought [89]. Microorganisms and plants interact to control the hormonal balance of ABA in plants, thus promoting plant growth even under stressful conditions. Bashan and collaborators [90], demonstrated that inocu-lating maize plants with *Azospirillum* and *Herbaspirillum* directly alters molecular, bio-chemical, and physiological processes. PGPB inoculation also induces the accumulation of ABA in *Vitis vinifera* plants, according to Salomon and collaborators [91]. Under water scarcity, bacterial-inoculated plants generate convergent action mechanisms to improve water use efficiency as a result of complex crosstalk between auxin and ABA. In plants, auxiliary signals contribute to water uptake and transport, while ABA signals reduce transpiration losses. Dual-mode actions increase plant tissue water content under stressful conditions. When plants are exposed to severe drought, they display a survival phenotype, and when they are exposed to mild drought, microbial inoculation promotes their growth and development [92]. A number of experiments have shown significant increases in fresh biomass under greenhouse and field conditions despite a non-significant accumulation of dry biomass due to microbial inoculation. Due to the increased water content in plants' bodies, inoculating them with bacteria improved their fitness in water-scarce environments. As a result of its integrative role in water conserva-tion in plant cells and tissues, neither the auxin–ABA signaling network nor the osmo-regulation mechanism can be considered separately. However, changes in plant micro-structure would increase plant water storage and circulation if they were based on plant phenotypic plasticity [93]. Plant cells vacuolize more, specialized cells for water storage increase, and apoplastic and symplastic compartment volumes change [94,95]. This in-tegrated mechanism of plant water conservation also stimulates plant response enzy-matic-metabolic machinery that protects cells and restores damage (i.e., ROS produced as a consequence of damage to biological membranes and biomolecules). When atmospheric temperatures rise and soil water availability declines, leaf water potential decreases, reducing stomatic conductance and transpiration and decreasing photosynthetic rates until the stomata are completely closed, preventing water loss in plant tissue and reducing photosynthetic activity [96,97,98,99]. The inoculation of bacteria can increase net photosynthetic activity to some extent compared with non-inoculated plants with similar stomatic conductance values. Inoculated bacteria are believed to increase water use effi-ciency by increasing carbon dioxide influx or reducing respiration rates at a similar rate to water loss from leaf blade substomatic chambers, which leads to an additional acquisition of carbon to meet the energetic requirements needed to restore cell homeostasis [100,101]. Plant growth and development are influenced by ethylene gas, another phytohormone, in several ways, but the underlying mechanism remains unclear. In addition to initiating roots, inhibiting root elongation, promoting fruit ripening, causing flower wilting, stimulating seed germination, promoting leaf abscission, and responding to biotic and abiotic stresses, it also stimulates flower wilting, stimulates seed germination, stimulates leaf abscission, and activates plant hormone synthesis. In response to stressful conditions, plants can increase ethylene synthesis. In order to synthesize ethylene, 1-aminocyclopropane-1-carboxylate is required. The first component of this hormone is methionine, which is converted by SAM synthase (SAM synthase) into S-adenosylmethionine (SAM) and ACC synthase into ACC. In response to this, ACC concentrations increase, and so do ethylene levels. However, at high concentrations, ACC inhibits crop growth and yield. Honma and Shimomura first characterized 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase) in PGPB [102], under stressful conditions, it promotes plant growth. According to Glick et al. [103], PGPB syn-thesizes and secretes auxin, which promotes plant growth when tryptophan is present. Also, auxin induces S-adenosylmethionine to be converted into ACC by 1-aminocyclopropane-1-carboxylate synthase (ACC synthase). A plant exudes ACC to maintain a balance between the internal and external concentration of ACC, which in turn decreases the outside concentration of ACC. Due to ACC's role as a precursor to ethylene, a reduction in ACC directly leads to a decrease in plant ethylene levels, which promotes plant growth even under limited conditions [104]. As a result of bacteria containing this enzyme, plants can withstand both biotic and abiotic stresses [105]. Inoculation of bacteria that synthesize ACC deaminase under abiotic stress is an excellent growth promoter for plants [106,107,108,109].

4.2. Biosynthetic Bacteria and Induced Accumulation in Plants

Osmolytes are synthesized by plant growth-promoting bacteria and secreted together with other exuded compounds [110]. In addition to osmolytes produced by plants (such as glycine-betaine, soluble sugars, trehalose, and proline), plant-produced osmolytes serve as osmoprotectants. Plants are more likely to tolerate water stress when these microbes accumulate osmolytes [111,112,113,114,115,116]. Under water deficit conditions, plants inoculated with PGPB may be able to tolerate stress, maintain cell turgor and membrane stability, and prevent electrolyte leakage due to increased proline levels. Plants produce proline as a result of *Arthrobacter* sp. and *Bacillus* spp. inoculated [117]. The drought-tolerant strains of *Bacillus* spp. There was an increase in proline, sugars, and free amino acids in sunflowers (*Helianthus annuus* L.) and maize (*Zea mays* L.) when antioxi-dant enzyme activity was reduced. When Aridopsis thaliana was inoculated with *Azospirillum baldaniorum* strain Sp 245 under water deficit conditions, proline levels and relative water content were increased, improving the plants' performance under drought conditions [118]. A plant cell's cytoplasmatic compartment has an increased osmolyte content as a result of bacterial inoculants (secreted by microbes or induced by microbes), resulting in a decrease in osmotic pressure, preventing water efflux. To balance water and flux within the plant body, phytohormonal imbalances serve as an orchestrated connection mechanism. The improved hydrated microenvironment promotes photosynthesis recovery, thus protecting subcellular compartments from damage [119].

4.3. A self-protective and water-retaining property of bacterial exopolysaccharides

As well as being highly heterogeneous, exopolysaccharides (EPSs) have a high molecular weight. It has been demonstrated that microorganisms in extreme environ-ments secrete a variety of monosaccharides, soluble in water and composed of sugar residues [120], as a means of protecting themselves. Thus, EPS synthesis is one of the most common mechanisms for bacterial self-defense. To grow, adhere to solid surfaces, and survive harsh conditions, bacteria synthesize this compound, which accounts for 40% to 95% of the bacteria's weight. Furthermore, they are essential for forming and maintaining biofilm architecture, retaining water, absorbing nutrients, and ensuring survival in harsh environments [121]. In stressful conditions, EPS is beneficial for both bacteria and plants [122]. Due to their ability to increase soil water retention capacity, bacteria that synthesize exopolysaccharides are essential for promoting plant growth under stressful conditions, such as drought. It is noteworthy that these bacteria are more advantageous and have gained prominence in being used as bio-inoculants for drought tolerance in plants [123]. EPSs have been found to be secreted by bacteria from the genera *Bacillus*, *Pseudomonas*, and *Azospirillum* as well as other microorganisms under water stress [124,125]. Moreover, these compounds can also act as emulsifiers and mitigate ROS-induced effects, as well as alter root structure. Additionally, plants inoculated with bacteria capable of synthesizing EPS accumulate more proline, sugars, and free amino acids, as well as more biomass, leaf area, and protein content [118].

4.4. The role of volatile organic compounds in drought bioprotection by bacteria

Many publications have discussed the potential of PGPB to increase crop yields. As plants develop, they release low molecular weight lipophilic compounds (300 moles. L^{-1}) as a response to biotic and abiotic stress and as a result of gaseous organic compounds (VOCs) [17]. Plants release volatile organic compounds during stressful periods, reducing ROS effects and increasing membrane protection. As a signal molecule, VOCs emitted by microorganisms can be found in the rhizosphere [21]. The first demonstration of this mechanism was made when *Bacillus subtilis* was inoculated into *Arabidopsis thaliana* [26]. The compounds are synthesized by many bacteria, including *Burkholderia*, *Pantoea*, *Serratia*, *Chromobacterium*, *Arthrobacter*, *Proteus*, *Bacillus*, *Fusarium*, *Pseudomonas*, *Alternaria*, and *Laccaria*. As a result of modulating essential nutrients, hormonal balance, metabolism, and sugar concentrations [28], these organisms release a variety of compounds that are specific to different metabolic pathways, signaling a variety of plant physiological processes and promoting growth. These studies [88,90,91,92] demonstrated that VOCs can be effective for promoting plant growth by using *A. thaliana*. It has already been demonstrated by some researchers [97,98,99] that these compounds promote plant growth and reduce stress, but most of these studies have been conducted in controlled laboratory settings. Because these compounds are highly biodegradable and reactive, agriculture does not commonly use them. Further research is needed into these compounds, their perception mechanisms in plant tissues, and their application techniques [100].

4.5. Mechanisms of bacterial protection and repair in drought-stressed plant tissue

It has been shown that drought stress leads to the generation of reactive oxygen species (ROS) within subcellular compartments, causing free radicals and redox imbalances (oxidative damage) that damage macromolecules (such as biological membranes) and compromise plant health. There is a differential tolerance to drought stress in plant tissues that is influenced by antioxidant enzymes [37,40,42]. Plant antioxidant enzymes are modulated by bacterial inoculants, which decrease ROS levels, thereby enhancing crop protection. Researchers have found that under stressful conditions, enzymatic antioxidants (such as ascorbate peroxidase, catalases, peroxidases, glutathione reductase, superoxide dismutase) and nonenzymatic antioxidants (such as ascorbic acid, flavonoids, and phenolic compounds) are more effective. ROS accumulation impairs photosynthetic activity, compromising antenna harvesting, electron transport, enzyme activity, and chloroplast membrane function [45]. Inoculating *Bacillus pumilus* improved the photosynthetic efficiency of *Glycyrrhiza uralensis* under drought stress [55,56,57]. *Bacillus* inoculation maintained chloroplasts and mitochondrial integrity. Plants can benefit from a combination of beneficial bacteria and bioactive products to boost their antioxidant response. A combination of humic acids and diazotrophic bacteria enhanced drought stress recovery in sugarcane [62]. Inoculating leaves with bacteria preserved their water potential and increased relative water content, while humic acids activated antioxidant enzymes to mitigate water stress.

5. Drought Stress Mitigation Using Microbial Inoculants in Agroecosystems

In current times, industrial fertilizers, mainly derived from nonrenewable resources, pose a significant environmental problem. They contribute significantly to the degradation of the ozone layer, greenhouse gas emissions, low-efficiency recovery by plants, as well as the high cost of production. In order to reduce agriculture's environmental impact on local and global levels, bioinoculants and other biological products have become increasingly important as sustainable technologies [64]. Bioinputs include formulations containing live microorganisms (fungi, bacteria, and algae) and/or their metabolites that are used to fertilize, stimulate, and protect agroecosystems [12,17,21]. It is possible to inoculate plant surfaces, soil, or seeds with bioinoculants (delivering niches) in various physicochemical formulations (microbiological composition, carriers, and additives), as well as to apply them at the right time, depending on the crop's physiological state. By colonizing plant surfaces, interiors, or rhizospheres, microorganisms boost plant growth: (a) enhancing nutrient availability in the plant-soil system (i.e., biological nitrogen fixation, mineral solubilization, organic compound mineralization); and (b) enhancing nutrient absorption through hormonal action (auxin, cytokinin, gibberellin, abscisic acid) that results in changes in plant morphology that improves nutrient utilization [12,26,32]. The first microbial inoculants used in agriculture were introduced by Nobbe and Hiltner (1895), who introduced "Nitragin," which contains rhizobia. In addition, numerous studies have examined the use of microorganisms as bioinoculants for the promotion of plant growth in sugarcane, rice, soybeans, beans, chickpeas, tomatoes, maize, tropical fruits, and wheat, among others [12,17,19,44,66,78]. A rapid increase in farmers' adoption of bioinoculants has been observed [12], leveraging innovation and technologies to fulfill the growing demand for bioproducts. It is estimated that *Bradyrhizobium* spp. and *Azospirillum brasilense* are used mainly as biofertilizers in global agriculture [12]. Plant growth is primarily promoted by nitrogen fixation and increased nutrient uptake by roots (Figure 3). There are, however, a variety of side effects associated with commercial inoculants, such as an "increase in water absorption and saline stress" and "produces phytohormones that promote root development, which increases water and nutrient absorption and improves resistance to drought and salinity." However, some mechanisms do not directly promote plant growth promotion, despite the fact that microbial inoculations provide complementary effects on soil nutrient availability and root uptake. The plants, however, rely heavily on them to protect themselves from adverse environmental conditions, mitigating biotic and abiotic stresses. These mechanisms include ACC deaminase activity, ROS-enzyme synthesis, EPSs, volatile organic compounds, and osmolytes, as well as induced systemic resistance [36,45,48,59]. In previous technological attempts, bacteria were collected under non-selective pressure conditions that were used to screen candidate strains. A better-performing isolate was screened and further evaluated in a greenhouse and an open field using assays involving water activity reduction (i.e. osmotic active molecules) [88,92], or studies involving progressive cell-bacterium dissection [97,102]. In bacterial selection programs, plant-growth-enhancing traits and water deficit tolerance traits have also been regarded as addictive traits. Plants adapted to harsh environments have emerged with a new generation of microbial products based on microbe-driven selection for rhizospheres, rhizoplanes, and inner tissues. As abiotic stress affects bacteria cell phenology, an increasing number of studies have been conducted [66]. The secondary metabolites of a halotolerant PGPR could induce tomato salinity stress tolerance by producing auxin and ACC-deaminase [73,76].

By analyzing the entire genomes of bacterial candidates for inoculant formulations, it is possible to conduct phenotypic screening. In *Bacillus altitudinis* (strain FD48), previously shown to induce antioxidant stress in rice under drought, genes related to distinct mechanisms of water stress evaluation were discovered. Jochum and colleagues [88] proposed a bacterial bioprospecting screen that combines effective root colonization and drought stress mediation to design microbial products for drought stress. PGPBs were selected from perennial grass rhizospheres in a semi-arid environment, prescreened in the laboratory for desired plant phenotypes (delayed symptoms of water scarcity), and (c) bacteria isolates were selected to be formulated and delivered as soon as water stress was detected (rapid colonizers and adequate crop protection). As a result of bioprospecting, another sudamerican commercial bacterial inoculant that relieves plant water stress was developed. Using rhizobacteria for drought-tolerant plant growth, researchers led by Melo [90] examined cacti-associated bacteria from semi-arid environments.

Figure 3 Inoculation of different strains of *Azospirillum* sp., *Bacillus* sp. and *Streptomyces* sp., in the growth promotion of water-stressed lettuce plants

6. Conclusions

Plant survival and resilience under stress is influenced by a series of physiological, biochemical, and molecular complex network responses. It is well known that there are two core mechanisms: one that conserves plant water and one that protects and restores plant damage. In addition to reducing drought stress in plants, bacteria that promote plant growth have also been shown to be effective. In order to increase crop yields by using strategies and techniques that support water deficits, it is still necessary to have a comprehensive understanding of these response mechanisms triggered by microorgan-isms. However, with current technological advancements, we are able to formulate, apply, and design bacterial inoculants that can help plants cope with droughts. In our knowledge, microbial bacteria can mitigate the adverse effects and reduce agricultural productivity. Inoculants for drought stress mitigation should be designed according to the main mechanisms that enhance plant–microbe interactions under drought tolerance. The survival and efficacy of bacterial inoculum are affected by field conditions. A bacterial cell maintains its viability by accumulating osmoprotectants, antioxidants, genes related to stress, and essential proteins. Microorganisms can produce and/or modulate several hormonal classes, which are regulated by changes in concentrations, locations, and signaling of hormones, which affect plant concentrations and balances, making it important to characterize drought-induced responses molecularly, and identify hormonal homeostasis. By altering plant structural changes triggered by ABA signaling, it is also possible to increase plant water content during water shortages in inoculated plants. Inoculating plants with BPCV could increase plant response under drought conditions or increase agricultural productivity by altering the hormonal balance of ABA in plants, since abscisic acid is a sign of plant stress. Using this information, we can select stress-tolerant microorganisms and improve the use of BPCVs to reduce the damage ob-served in agricultural production systems. New generations of bacterial inoculants aimed at mitigating water stress in plants could benefit from recent initiatives involving bacterial bioprospection under appropriate selective pressure (arid environments). This involves the distinct soil-plant compartments (rhizosphere, rhizoplane, and inner tissue) under intense selective pressure and constant water deficits. We also selected bacteria strains that produced exopolysaccharides (EPSs) under osmotic stress as well as batch reactor growth media and inoculant formulations that stimulated EPS secretion. In EPS systems that are rich in microenvironments, water is trapped and desiccation is reduced, allowing bacteria to thrive. A formulation containing synthetic microbial communities was developed using metataxonomic and metagenomic data gathered from plant micro-biomes cultivated in drought-stressed environments. Furthermore, proper formulations contain additives or carriers that promote bacteria's survival or protect plants from abiotic stressors (humic substances).

Compliance with ethical standards

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Disclosure of conflict of interest

The author declares no conflict of interest.

Statement of ethical approval

The present research work does not contain any studies performed on animal/humans subjects.

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