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Applications of inoculants to treat drought stress in plants

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Abstract All climatic factors, including temperature, rainfall, humidity, wind, and solar radiation, significantly influence agricultural activities. These environmental conditions determine the types of crops that can be grown, the length of growing seasons, and the overall productivity of agricultural systems. While some agricultural areas around the world rely on artificial irrigation, the vast majority still depend heavily on natural rainfall patterns. This reliance makes agriculture particularly vulnerable to climate variability and change. Climate change is expected to increase the frequency and severity of extreme weather events, such as droughts and heatwaves, which will lead to higher water demands from crops while simultaneously reducing water availability. This imbalance between water supply and demand is likely to result in reduced crop yields and lower production capacity in many regions. One of the most critical challenges faced by agriculture under climate change is drought. Drought stress severely limits plant growth and productivity by affecting physiological and biochemical processes. However, plant growth-promoting bacteria (PGPB) offer a promising solution to this issue. These beneficial microbes enhance plant tolerance to drought by regulating gene expression and modulating hormone activity in plants. They also influence the stress-induced enzymatic system, alter phytohormone levels, and contribute to the accumulation of protective metabolites. These mechanisms are expressed through phenotypic changes in plant architecture, growth rate, root-to-shoot ratio, hydraulic conductivity, and water conservation abilities. Additionally, PGPB support plant cell protection under stressful conditions. This review aims to highlight the role of plant growth-promoting bacteria in mitigating the adverse effects of climate-induced stress on crops. By exploring how these microorganisms interact with plants to enhance resilience, it provides insight into potential applications of microbial biotechnology in agroecosystems. Ultimately, the integration of such microbial strategies into farming practices can contribute to more sustainable and climate-resilient agriculture.

Keywords: sustainable agriculture, biofertilizers, PGPB, endophytic bacteria, abiotic stress, inoculant

1. Introduction

Climate change and global demands for food, fiber, and energy directly affect agricultural systems, compromising food security and agroecosystem sustainability (Gullino et al., 2018). Deforestation and intensive land use, which have resulted in increased greenhouse gas emissions, have contributed significantly to global climate change trends due to fossil fuel demand from industrialization and urbanization. Food production has been significantly affected by changes in temperature and precipitation regimes during this century. According to Foley et al. (2011), biotic factors account for approximately 50% of agricultural productivity losses, whereas abiotic factors account for 30% (Junaid et al., 2024). In addition to reducing crop losses and increasing crop yields, agriculture also faces several challenges under climate change scenarios (Ashraf, 2010). Stress refers to any adverse change in plant physiology caused by external factors. Temperature, drought, salinity, flooding, and heavy metals are not the only abiotic stressors that can reduce plant productivity. Several studies have combined conventional breeding tools with modern breeding techniques to develop drought-tolerant varieties (Ashraf, 2010). A wide range of environmental stresses have adapted to plants through plant breeding. The morphophysiological traits associated with drought tolerance have also been explored in several studies (Akhtar & Siddiqui, 2009; Rao & Chaitanya, 2016). The two primary mechanisms by which plant growth-promoting bacteria (PGPB) mitigate environmental stresses are water conservation and protection recovery mechanisms (Berg, 2009; Broeckling, 2008; Li et al., 2021). The conversion of drought-mitigating bacteria to a sustainable solution for agroecosystems is of increasing interest (Deubel et al., 2000; Rasheed et al., 2022). Biological inoculants are the most effective biotic and abiotic crop protection technology (Gull et al., 2004; Poudel et al., 2021). This review examines how bacterial inoculants reduce soil water loss by increasing soil water accessibility through phytohormonal signaling, an induced enzymatic pool, and metabolites. A demonstration of how catalytic proteins and metabolites work together to prevent damage to plant cells and activate repair mechanisms that increase plant tolerance to water scarcity is also presented. In addition, drought stress mitigation strategies, technological applications, and potential future applications of bacterial inoculants are discussed.

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2. Drought-Adapted Mechanism of Plants

Agricultural quality and productivity are threatened by drought, which inhibits plant growth and development. A prolonged period of subnormal rainfall compromises the soil moisture for a given crop (Duponnois et al., 2006). Water availability negatively affects plant growth and development and affects plant life cycles (Dutton & Evans, 1996). As a result of drought periods, the soil water potential decreases, which affects the water potential of the plant. The response of a plant to drought is a complex process that involves a variety of molecular, biochemical, and physiological changes. Researchers have demonstrated that in grape leaves, the stomata are completely closed before cavitation occurs, thus preventing cavitation and embolism (Cochard et al., 2002; Hochberg et al., 2017). Photorespiration increases simultaneously with CO2 influx, directly affecting photosynthetic capacity. The drought response of plants is influenced by reduced carbon incorporation into the plant biomass when water is scarce. To increase plant resilience to water stress, two main approaches must be used. Hormonal signaling mechanisms (e.g., auxin, cytokinin and gibberellin) are primarily used to increase plant water status (Habibi et al., 2011; Iqbal et al., 2022; Bandurska, 2022). In addition to signaling stress, they also play important roles in growth and development. The stress hormone abscisic acid (ABA) is present in significant amounts during drought conditions. Henri et al. (2008) and Hilda & Fraga (2000) demonstrated that it regulates several genes and promotes stomatal closure and hydration tolerance. Osmotic adjustment can also be used to maintain cell turgor by increasing solute concentrations within the cells (soluble sugars and glycine) by modulating the osmolarity of the cell (Turner, 2017). During drought, these solutions prevent plant cells from becoming toxic and maintaining turgor pressure (Turner, 2017). Sorghum and pea roots have been studied for their osmotic adjustment (Constable & Hearn, 1978). Several subsequent studies (Hinsinger, 2001; Igual et al., 2001; Hayat et al., 2012; Chen & Jiang 2010; Kathiresan et al., 1995) have demonstrated that osmotic adjustment mechanisms maintain plant turgor (Hinsinger, 2001; Igual et al., 2001; Hayat et al., 2012; Kathiresan et al., 1995). Osmotic adjustment is determined by the species and cultivar of plants as well as the duration of the stress event. The application of organic compounds as foliar sprays improves plant tolerance to stress conditions, resulting in the accumulation of osmolytes, such as sugar beets (*Beta vulgaris* var. *Saccharifera L.*) (Hussein et al., 2019), *Catharanthus roseus* (Chang et al., 2014), Brassica species (Alam et al., 2014), and *Raphanus sativus L*. (Akram et al., 2016). Water conservation is associated with the protection and repair of machinery (Deubel et al., 2000). Like other abiotic stresses, plant tissue photooxidizes when water deficit decreases electron transport chain activity. (Khan et al., 2007). Consequently, Rubisco enzyme activity decreases, and the PSII membrane complex is damaged, repressing photosynthetic activity (Kim et al., 1998). A number of molecular and biochemical mechanisms lead to nonphotochemical quenching (NPQ) of chlorophyll fluorescence in plants in response to drought. An important mechanism for membrane peroxidation and oxidative damage is the induction of reactive oxygen species (ROS) (Sohbat, 2022). Superoxide dismutase (SOD), peroxidase (POX), catalase (CAT), and glutathione reductase (GR) are enzymes involved in plant antioxidant defense systems. Therefore, drought tolerance was positively correlated with the antioxidant response. More tolerant plant species have higher levels of antioxidant enzyme activity, which protects them from oxidative damage (Hernández et al., 2012). In contrast, species with less sensitive enzyme activity machinery showed no such changes. Several studies have shown that drought increases antioxidant enzyme activity. These antioxidant responses can differ among cultivars, such as *Oryza sativa* L. (Pyngrope et al., 2013), *Triticum aestivum* L. (Sheoran et al., 2015), and *Hordeum vulgare* L. (Harb et al., 2015). According to previous studies, drought-tolerant cultivars produce less ROS and oxidative stress than do drought-sensitive cultivars. Drought-resistant crops can be developed through breeding and genetic engineering by leveraging the genetic differences between drought-tolerant and drought-sensitive genotypes (Kpomblekou & Tabatabai, 1994; Lee & Pankhurst, 1992). Despite their importance in cellular function, ROS can be toxic when their levels exceed normal levels. Therefore, a balance between cytostatic and cytotoxic ROS levels should be maintained (Khan et al., 2007; Kim et al., 1998). The rhizosphere, root shoots, and inner tissues of plants (endophytes) can increase plant fitness under environmental stress, in addition to the molecular, biochemical, and physiological responses triggered by drought (Nahas, 1996; Nihorimbere et al., 2011). By studying plant–bacteria interactions under natural conditions, scientists can increase drought tolerance. Researchers can develop drought-tolerant crops by gaining insight into how plant–microbe interactions can impact food security and agricultural production.

3. The Growth-Promoting Bacteria in Plants

Phylotype counts in soil bacterial communities range from 102 to 106 per gram, with soil bacteria exhibiting the greatest diversity, abundance, and physiological activity (Fierer & Jackson, 2006). Soil microbes act as "seed banks" for species richness when seeds or other reproductive plant structures are sown in the soil (Ponmurugan & Gopi, 2006). Rhizospheres are soil perimeters enriched with carbon exudates (including organic acids, amino acids, sugars, and flavonoids), mucilaginous matrixes, and detached root caps. Several factors make this environment conducive to plant recruitment by taxa capable of colonizing the rhizosphere (Sashidhar & Podile, 2010; Rokhzadi et al., 2008; Jjemba & Alexander, 1999). In the rhizosphere, beneficial and pathogenic microorganisms compete for the colonization of plant tissues, modulating nutrient flux through the soil–plant system and affecting plant growth (Rokhzadi & Toashih, 2011). Among such microorganisms, bacteria play a crucial role as the most common and active fraction that interacts with plant hosts (Rosas et al., 2006). Several studies have reported that biofertilizers, biostimulants, and bioprotections increase plant growth, prevent pathogens, and mitigate environmental stresses. A number of bacteria, such as *Klebsiella, Paraburkholderia, Azospirillum, Herbaspirillum, Gluconacetobacter, Serratia,* and *Azotobacter*, belong to the PGPB family, as do Pseudomonas and Enterobacter. Plant growth is promoted by these microorganisms in two ways: (1) biological nitrogen fixation; (2) indirect mechanisms, such as reducing damage caused by pathogens and/or environmental stresses by producing hormones (indole-3-acetic acid, gibberellic acid, and cytokinins, such as zeatin) and acquiring essential nutrients; and (3) indirect mechanisms, such as biocontrol, which involves mitigating damage caused by pathogens and environmental stresses (Poudel et al., 2021; Nahas, 1996; Rokhzadi & Toashih, 2011; Olivares et al., 2017; Kumar & Verma, 2018; Etesami & Maheshwari, 2018; Saikia & Jain, 2007; Schroth & Hancock, 1981) (Figure 1).

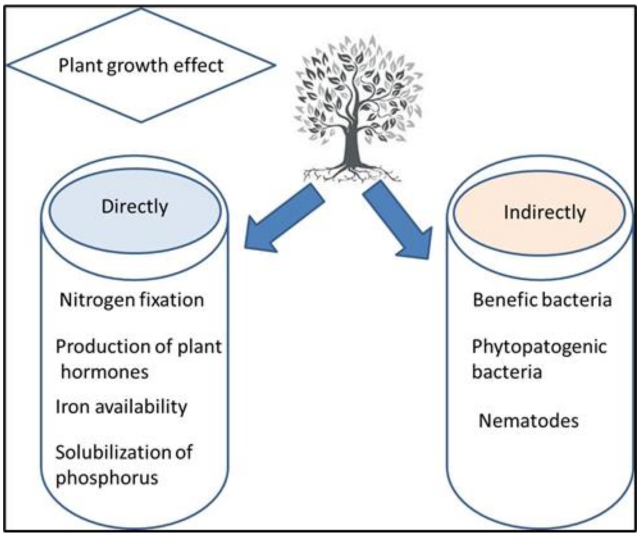

Figure 1 Auxins, gibberellins, and cytokinin, which regulate plant hormone balance, are produced by PGPB. It also produces siderophores and increases iron availability. Solubilizing inorganic phosphate in the soil and using nitrogenase enzymes results in biological nitrogen fixation (BNF) and siderophores. PGPB repels pathogens and nematodes by occupying niches and producing repelling substances.

Several mechanisms have been identified in the reactions and interactions between PGPB and plants (Shanmugam & Veeraputhran, 2000; Shehata & El-Khawas, 2003) to reduce the damage caused by environmental stress to plants. In addition to producing hormones (auxin, cytokinin, and abscisic acid), exopolysaccharides and beneficial enzymes, such as 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase), trehalose, and volatile organic compounds, as well as osmoregulation, are also involved in osmoregulation. As shown in Table 1, PGPB resist drought through a variety of mechanisms.

Table 1 Species and genera of bacteria that are drought resistant.

Microorganisms	Plant	Method of action	References
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	(Kasim et al., 2021)
Enterobacter sp.	Bean	Increase the levels of proline, malondialdehyde, and antioxidant enzymes	(Ahmed et al., 2021)
Pseudomonas sp.	Arabidopsis	Exopolysaccharide, gibberellic acid, abscisic acid, and indole acetic acid deaminase activity are higher	(Yasmin et al., 2022)
Streptomyces sp.	Tomato	Increasing the content of different sugars	(Abbasi et al., 2020)
Bacillus sp.	Grass	Antioxidant system response and early proline accumulation	(Moreno-Galván et al., 2020)
Azospirillum sp.	Wheat	Auxin and N concentrations are highest	(Arzanesh et al., 2011)

4. PGPBs and Stress Tolerance in Plants

4.1. Bacterial phytohormones modulate plant morphophysiology

Beneficial microorganisms promote plant growth by secreting complex plant hormone networks. When PGPB interact with plants, they respond to abiotic and biotic stimuli, including hormonal homeostasis (Sundara et al., 2022; Bashan et al., 2004; Tambekar et al., 2009). A variety of microorganisms can affect hormone concentrations, locations, and signaling in plants (Tambekar et al., 2009; Pantoja-Guerra et al., 2023; Sgroy et al., 2009). Beneficial microorganisms utilize plant hormones to promote plant growth (Figure 2).

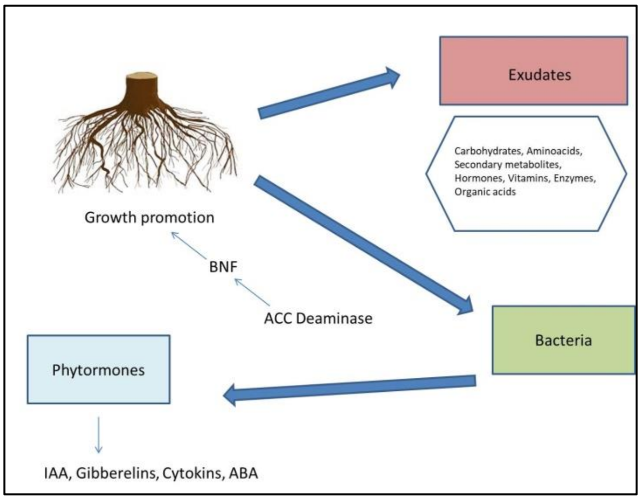

Figure 2 Metabolites are signaling molecules and substrates produced by microorganisms and plants. In addition to fixing nitrogen and soluble nutrients (phosphate and iron), microorganisms produce hormones that stimulate plant growth. Plants and bacteria have a positive relationship when the dashed line indicates this relationship. Abbreviations: 1-aminocyclopropane-1 carboxylate deaminase; BNF, biological nitrogen fixation.

The plant hormone auxin plays a number of roles in cell division, expansion, and differentiation (Tao et al., 2008). In addition to stimulating seed and tuber development, auxinic activity regulates xylem and root development; controls vegetative growth processes; leads to the formation of lateral and adventitious roots; regulates light, gravity, and flowering; and influences photosynthesis, pigmentation, metabolites, and resistance to stress (Vazquez et al., 2000). Pantoja-Guerra et al. (2023; Vazquez et al., 2000; Valente et al., 2020; Ahmed and Hasnain, 2010) reported that PGPB affect the auxin balance, which in turn affects the root growth rate and architecture (Pantoja-Guerra et al., 2023; Vazquez et al., 2000). Microbial inoculation of crops alters root anatomy and biochemistry by modulating phytohormones (Rokhzadi & Toashih, 2011; Saikia & Jain, 2007; Etesami & Maheshwari, 2018; Pantoja-Guerra et al., 2023; Valente et al., 2020). Plant growth-promoting effects are crucial for increasing water availability in situations where the soil matrix water potential is low. Absorptive root structures increase water uptake by increasing root formation (root ramification), root hair density, and root hair length (specific surface enhancement). As a result, the root surface area, volume, and biomass increased. The organizational patterns of epidermal, cortical, and vascular root tissue systems also modulate the hydraulic conductivity of the root system (Mohammadi Alagoz et al., 2022). The number and arrangement of cell layers, water flux resistance, metaxylem size, diameter, and distribution, as well as transmembrane transporters (such as aquaporins), play a significant role in these processes. Auxin signaling also activates electrogenic transmembrane pumps (P-type H+ ATPases in the plasma membrane and V-type H+ ATPases in the vacuolar membrane) that facilitate secondary nutrient transport. P-type pumps acidify the apoplastic microenvironment near the meristematic type of recently divided cells, promoting root axis growth and tissue proliferation (Whitela, 2000; Xiao et al., 2008). Inoculation with bacteria facilitates plant growth when water availability is appropriate or ameliorates the negative effects of water scarcity. The stress hormone abscisic acid (ABA) was detected in significant amounts during drought. Becker et al., (2003) reported that ABA regulates genes linked to dehydration tolerance and stomatal closure. In some plants, exogenous ABA supplied by bacteria of a particular genus allows them to cope with abiotic stress (Cohen et al., 2008). Prolonged drought was better tolerated by maize plants inoculated with *Azospirillum brasilense* strains Ab-V5 and Ab-V6 (Hungria et al., 2010). The hormonal balance of ABA in plants is controlled by microorganisms and plants, thereby promoting plant growth under stress conditions. Using *Azospirillum* and *Herbaspirillum* infections of maize plants, Bashan et al. (2004) demonstrated direct alterations in molecular, biochemical, and physiological processes. Salomon et al. (2014) reported that inoculation with PGPB induced ABA accumulation in *Vitis vinifera* plants. Owing to the complex crosstalk between auxin and ABA, bacterium-inoculated plants generate convergent action mechanisms that improve water use efficiency under water scarcity. ABA signals reduce transpiration losses in plants, whereas auxiliary signals facilitate water uptake and transport. Stressed plant tissues contain more water because of dual-mode actions. Plants display a survival phenotype when exposed to severe drought, and microbial inoculation leads to growth and development in plants exposed to mild drought (Yahya & Azawi, 1998). In the greenhouse and field experiments, microbial inoculation resulted in a significant increase in fresh biomass, despite the lack of significant accumulation of dry biomass. By increasing the amount of water in plant bodies, bacteria can improve their ability to survive in water-scarce conditions. Owing to their integrated roles in water conservation in plant cells and tissues, neither auxin–ABA signaling nor osmoregulation can be considered separately. In contrast, if changes in plant microstructure are based on phenotypic plasticity, plant water storage and circulation increase (Zaddy & Perevolosky, 1995). In plant cells, vacuoles are larger, water-storing cells are more numerous, and apoplastic and symplastic compartment volumes appear to change (Mohammadi Alagoz et al., 2022; Zaddy et al., 1993). The integrated mechanism of plant water conservation also stimulates enzyme-metabolic machinery that protects cells and repairs damage (e.g., ROS produced by damaged biological membranes). In response to rising atmospheric temperatures and decreasing soil water availability, leaf water potential decreases, stomatal conductance and transpiration decrease, and photosynthetic rates decrease until the stomata are completely closed, preventing water loss and reducing photosynthetic activity (Bhat et al., 2010; Bisleski, 1973; Brundrett & Abbott, 1995; Champawat & Pathak, 1993). Compared with noninoculated plants, inoculated plants with bacteria presented increased net photosynthetic activity to some extent. By increasing carbon dioxide influx or reducing respiration rates at a rate similar to that of water loss from leaf blade substomatic chambers, inoculated bacteria are believed to increase water use efficiency. Thus, additional carbon must be acquired to meet the energy requirements required to restore cell homeostasis (Naveed et al., 2014; Aguiar et al., 2016). Phytohormones such as ethylene gas affect plant growth and development in a variety of ways, although their mechanisms are unknown. In addition to initiating root growth, 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, seed germination, leaf abscission, and plant hormone production. The synthesis of ethylene can increase in plants under stressful conditions. The ethylene reaction was triggered by a 1-aminocyclopropane-1-carboxylate. The first component of this hormone is methionine, which is converted to S-adenosylmethionine (SAM) and ACC by SAM synthase. The ACC and ethylene levels increased. However, high ACC concentrations inhibit crop growth and yield. As described by Honma and Shimomura (Honma & Shimomura, 1978), ACC deaminase promotes plant growth under stressful conditions. PGPB synthesizes and secretes auxin when tryptophan is present in the soil (Glick et al., 1998), which promotes plant growth. In addition, S-adenosylmethionine is converted to ACC by an enzyme called 1-aminocyclopropane-1-carboxylate synthase (ACC synthase). To regulate the balance between internal and external ACC concentrations, plants release ACC into their surroundings, thereby lowering its external levels. Since ACC serves as a precursor to ethylene, reducing its concentration leads to decreased ethylene production, which in turn promotes plant growth under stressful or limited conditions (Duchense et al., 1989). Plants tolerate biological and abiotic stresses owing to the presence of bacteria containing this enzyme (Duchense et al., 1989). An excellent growth promoter for plants is the inoculation of bacteria that synthesize ACC deaminase under abiotic stress conditions (Arzanesh et al., 2011; Ahmed et al., 2021; Glick et al., 1998; Duchense et al., 1989).

4.2. Induced accumulationof plant-derived bacteria

In combination with other exuded compounds, osmolytes are synthesized by plant growth-promoting bacteria (Dumas et al., 1994). Plant-produced osmolytes, such as glycine-betaine, soluble sugars, trehalose, and proline, also serve as osmoprotectants. Microbes that accumulate osmolytes are more able to tolerate water stress in plants (Shehata & El-Khawas, 2003; Moreno-Galván et al., 2020; Abbasi et al., 2020; Sundara et al., 2022; Bashan et al., 2004). In plants inoculated with PGPB, turgor and membrane stability are maintained under water deficit conditions, and electrolyte leakage is prevented. Plants produce proline as a result of *Arthrobacter* sp. and *Bacillus* spp. inoculation (Sziderics et al., 2007). When antioxidant enzyme activity in sunflower (*Helianthus annuus* L.) and corn (*Zea mays* L.) was reduced, drought-tolerant strains of *Bacillus* spp. presented increased proline, sugar, and free amino acid contents. As a result of inoculating *Aridopsis thaliana* with Azospirillum baldaniorum strain Sp245, proline levels and relative water content increase, improving plant performance under drought conditions (Cohen et al., 2008). Bacterial inoculants (secreted by microbes or induced by microbes) increase the osmolyte content of a plant's cytoplasmic compartment, reducing osmotic pressure and preventing water loss. Phytohormonal imbalances serve to balance water and flux within the plant body. A hydrated microenvironment promotes photosynthesis recovery, protecting subcellular compartments from damage (Vardharajula et al., 2011).

4.3. Bacterial exopolysaccharides possess self-protective and water-retaining properties

Exopolysaccharides (EPSs) are highly heterogeneous and have high molecular weights. Research has shown that microorganisms in extreme environments secrete water-soluble monosaccharides composed of sugar residues to protect themselves (Ghosh et al., 2019). The synthesis of EPS is a key bacterial self-defense mechanism. To grow, adhere to solid surfaces, and survive harsh conditions, bacteria synthesize this compound, which accounts for 40% to 95% of their dry weight. EPS also play crucial roles in forming and maintaining biofilm architecture, retaining water, absorbing nutrients, and ensuring survival in harsh environments (Fa Yuan et al., 2008). Ghosh et al. (2019) demonstrated that EPS benefits both bacteria and plants under stressful conditions.

Under drought-stressed conditions, exopolysaccharide-producing bacteria promote plant growth by increasing soil water retention. Recently, these bacteria have gained prominence and are being used as bioinoculants to increase drought tolerance in plants (Ojuederie et al., 2019). *Bacillus, Pseudomonas*, and *Azospirillum*, along with other microorganisms, secrete EPS under water stress (Ghosh et al., 2019; Ojuederie et al., 2019). Additionally, these compounds can act as emulsifiers, mitigate ROS-induced damage, and alter root structure. Furthermore, plants inoculated with EPS-producing bacteria accumulate relatively high levels of proline, sugars, free amino acids, biomass, leaf area, and protein.

4.4. The role of volatile organic compounds in the protection of bacteria from drought

Plant growth-promoting bacteria (PGPB) have been discussed in numerous publications as potential enhancers of crop yield. Plants emit low-molecular-weight lipophilic compounds (approximately 300 g/mol) in reaction to both biotic and abiotic stresses, as well as to the presence of gaseous organic substances known as volatile organic compounds (VOCs). Under stressful conditions, plants release VOCs that reduce ROS-induced effects and protect membranes. Rhizospheres contain VOCs emitted by microorganisms as signal molecules (Brilli et al., 2019). This mechanism was demonstrated for the first time when *Bacillus subtilis* was inoculated into *Arabidopsis thaliana* (Ryu et al., 2003). Many bacteria produce these compounds, including *Burkholderia, Pantoea, Serratia, Chromobacterium, Arthrobacter, Proteus, Bacillus, Fusarium, Pseudomonas, Alternaria*, and *Laccaria*.

By modulating essential nutrients, hormonal balance, metabolism, and sugar concentrations (Hart & Reader, 2002), these organisms release a variety of compounds that function in specific metabolic pathways, signaling diverse physiological processes and promoting plant growth. Multiple studies (Brilli et al., 2019; Ryu et al., 2003; Blom et al., 2011; Subrahmanyam et al., 2020) have demonstrated that VOCs effectively promote growth in *Arabidopsis thaliana*. Several studies (Jeffries, 1987; Khan et al., 2008; Cho et al., 2008) have demonstrated that these compounds can enhance plant growth and alleviate stress; however, the majority of this research has been carried out in controlled laboratory environments. The agricultural application of these compounds is limited because of their high biodegradability and reactivity. Further studies are needed to investigate these compounds as well as their perception mechanisms in plant tissues (Ali et al., 2022).

4.5. Plant tissue damaged by drought: Mechanism of bacterial protection and repair

In response to drought stress, reactive oxygen species (ROS) are generated within subcellular compartments, leading to free radical and redox imbalances that cause oxidative damage, which harms macromolecules (such as biological membranes) and compromises plant health. Differential drought tolerance in plant tissues is influenced by antioxidant enzymes (Sohbat, 2022; Sheoran et al., 2015; Harb et al., 2015). Bacterial inoculants modulate plant antioxidant enzymes, decreasing ROS levels and enhancing crop protection. Under stress-induced conditions, enzymatic antioxidants (such as ascorbate peroxidase, catalase, peroxidase, glutathione reductase, and superoxide dismutase) and nonenzymatic antioxidants (such as ascorbic acid, flavonoids, and phenolic compounds) play more significant roles. Photosynthetic activity is impaired by ROS accumulation, which affects light-harvesting complexes, electron transport, enzyme activity, and chloroplast membrane function. According to El-Komy & Hesham (2004), El-Komy et al. (2003), and Zhang et al. (2019), inoculation with *Bacillus pumilus* improved photosynthesis in *Glycyrrhiza uralensis* under drought stress. Bacillus inoculation prevented chloroplast damage and mitochondrial dysfunction. The combination of bioactive products with beneficial bacteria can increase a plant's antioxidant response. Aguiar et al. (2016) reported that humic acids and diazotrophic bacteria effectively enhanced drought stress recovery in sugarcane. Humic acids activate antioxidant enzymes to mitigate water stress when applied in conjunction with bacterial inoculation. In addition, bacterial inoculation in leaves preserves the leaf water potential while increasing the relative water content.

5. Mitigating Drought Stress in Agriculture Via Microbial Inoculants

A major environmental problem in today's world is the production of industrial fertilizers, most of which are derived from nonrenewable resources. In addition to contributing to the depletion of the ozone layer, greenhouse gas emissions, low recovery efficiency, and high production costs, they also contribute to the degradation of the ozone layer. The use of bioinoculants and other biological products has become increasingly important as sustainable technologies to reduce the environmental impact of agriculture (Fulchieri & Frioni, 1994). Agroecosystems are fertilized, stimulated, and protected by formulations containing live microorganisms (fungi, bacteria, and algae) and their metabolites (Gull et al., 2004; Valente et al., 2020; Fulchieri & Frioni, 1994). Various physicochemical formulations (microbiological compositions, carriers, and additives) are available for inoculating plant surfaces, soil, or seeds with bioinoculants (delivering niches), as well as the timing of the application, depending on the crop's physiological condition. By colonizing plant surfaces, interiors, or rhizospheres, microorganisms increase plant growth by (a) increasing nutrient availability in the plant–soil system (i.e., biological nitrogen fixation, mineral solubilization, and organic compound mineralization) and (b) enhancing nutrient absorption through hormonal action (auxin, cytokinin, gibberellin, and abscisic acid), which results in changes in plant morphology that improve nutrient utilization (Gull et al., 2004; Kumar & Verma, 2018; Valente et al., 2020). Bittencourt et al. (2023) introduced the first microbial inoculant used in agriculture, "Nitragin," which contains rhizobia. A number of studies have also examined the use of microorganisms as bioinoculants in sugarcane, rice, soybeans, beans, chickpeas, tomatoes, maize, tropical fruits, and wheat (Gull et al., 2004; Hungria et al., 2010; Patil & Medhane, 1994; Khan et al., 2016; McA Fee & Fortin, 1986; De Souza et al., 2016; Baldotto et al., 2010). The adoption of bioinoculants by farmers has increased rapidly (Gull et al., 2004), leveraging innovation and technology to meet the growing demand for bioproducts. In agriculture worldwide, *Bradyrhizobium* spp. and *Azospirillum brasilense* are primarily used as biofertilizers (Gull et al., 2004). Nitrogen fixation and nutrient uptake by roots are the primary factors that promote plant growth (Figure 3). However, commercial inoculants are associated with a variety of side effects, including "increased water absorption and saline stress" and "produces phytohormones that promote root development, which improves water and nutrient absorption, as well as drought and salinity resistance". Although microbial inoculation has complementary effects on soil nutrient availability and root uptake, some mechanisms do not directly promote plant growth. In addition to mitigating biotic and abiotic stresses, plants also rely heavily on them to protect themselves from adverse environmental conditions. Among these mechanisms are ACC deaminase activity, ROS-enzyme synthesis, EPSs, volatile organic compounds, and osmolytes, as well as induced systemic resistance (Kim et al., 1998; Nihorimbere et al., 2011; Moreno-Galván et al., 2020; Salomon et al., 2014; Garg et al., 2001). The screening of candidate strains was performed under nonselective pressure conditions in previous technological attempts. Using assays involving water activity reduction (i.e., osmosis-active molecules) (Ghosh et al., 2019; Ali et al., 2022) or progressive cell–bacterium dissections (Geurts & Bisseling, 2002; Khosro & Yousef, 2012), a better-performing isolate was screened and further evaluated in a greenhouse and open field. Additionally, plant growth-enhancing traits and water deficit tolerance traits have been regarded as addictive traits in bacterial selection programs. New microbial products have emerged in hardy plants because of microbe-driven selection in rhizospheres, rhizoplanes, and inner tissues. The effects of abiotic stress on bacterial cell phenology have been increasingly studied (Kavamura et al., 2013). Induced salinity stress tolerance in tomato might be achieved through the production of auxin and ACC deaminase by halotolerant PGPR (Kang et al., 2019; Narayanasamy et al., 2023). Phenotypic screening can be performed by analyzing the entire genomes of bacterial candidates for inoculant formulations. Genes involved in water stress evaluation were discovered in *Bacillus altitudinis* (strain FD48), which was previously shown to induce antioxidant stress in rice under drought. Using a combination of effective root colonization and drought stress, Jochum and colleagues (Jochum et al., 2019) proposed a bacterial bioprospecting screen for designing drought stress-mediating microbial products. In a semiarid environment, perennial grass rhizospheres were selected and screened in the laboratory for desired plant phenotypes (delayed symptoms of water scarcity), and (c) bacterial isolates were selected for formulation and delivery as soon as water stress was detected (rapid colonizers and adequate crop protection). Using bioprospecting, another South American commercial bacterial inoculant was developed to relieve plant water stress. Researchers led by de Nessner Kavamura et al. (2013) examined cacti-associated bacteria from semiarid environments via rhizobacteria for the growth of drought-tolerant plants.

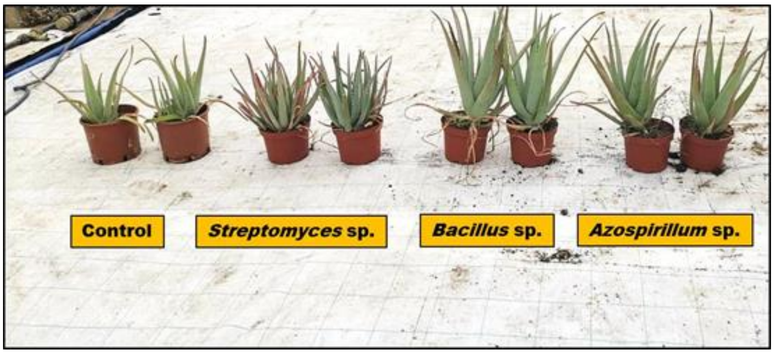

Figure 3 Inoculation of different strains of Azospirillum sp., Bacillus sp. and Streptomyces sp. promotes the growth of water-stressed aloe plants.

6. Conclusions

Plant survival and resilience under stress are governed by a complex interplay of physiological, biochemical, and molecular responses. One set of mechanisms focuses on conserving water, while another is dedicated to protecting plant tissues and repairing damage. In addition to reducing drought stress in plants, bacteria that increase plant growth have been shown to be effective. Microorganisms trigger a variety of responses that are critical to understanding the mechanisms that increase crop yields in the face of water deficit. However, with the advancement of technology, bacterial inoculants can be formulated, applied, and designed to help plants survive drought. To the best of our knowledge, the adverse effects of drought stress can be mitigated or reduced by microbial bacteria. A plant–microbe interaction that enhances drought tolerance should be considered when designing inoculants to mitigate drought stress. Field conditions affect bacterial inoculum survival and effectiveness. Osmoprotectants, antioxidants, stress-associated genes, and essential proteins maintain bacterial cell viability. Several classes of hormones can be produced and/or modulated by microorganisms and are regulated by changes in their concentrations, locations, and signaling. Because drought-induced responses affect plant hormonal concentrations and balance, identifying hormonal homeostasis and characterizing drought-induced responses at the molecular level are essential. The plant water content can also be increased by altering the structural changes induced by ABA signaling during water shortages in inoculated plants. Plants inoculated with PGPR may be able to respond more effectively under drought conditions or produce more crops by altering the hormonal balance of abscisic acid in the plant, since abscisic acid is known to signal stress in plants. In agricultural production systems, we can reduce damage by using PGPR and stress-tolerant microorganisms. Recent initiatives involving bacterial bioprospecting under appropriate selective pressure (in arid environments) could help develop new bacterial inoculants aimed at mitigating water stress in plants. Plant compartments (rhizosphere, rhizoplane, and inner tissue) are under intense selective pressure and are subjected to constant water deficit. Additionally, we selected strains of bacteria that secreted exopolysaccharides (EPSs) under osmotic stress and used batch reactor growth media and inoculant formulations that stimulated EPS secretion. EPS-rich systems create microenvironments that trap water and reduce desiccation, which helps bacteria grow. Using metataxonomic and metagenomic data collected from drought-stressed plant microbiomes, a formulation containing synthetic microbial communities was developed. Additionally, proper formulations contain additives that promote bacterial survival or protect plants from abiotic stressors such as humic substances.

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Ethical Considerations

Not applicable.

Conflict of Interest

The authors declare that they have no conflicts of interest.

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References

Abbasi, S., Sadeghi, A., & Safaie, N. (2020). *Streptomyces alleviate drought stress in tomato plants and modulate the expression of transcription factors ERF1 and WRKY70 genes. Scientia Horticulturae, 265*, 109206. https://doi.org/10.1016/j.scienta.2020.109206

Aguiar, N. O., Medici, L. O., Olivares, F. L., Dobbss, L. B., Torres-Netto, A., Silva, S. F., Novotny, E. H., & Canellas, L. P. (2016). *Metabolic profile and antioxidant responses during drought stress recovery in sugarcane treated with humic acids and endophytic diazotrophic bacteria. Annals of Applied Biology, 168*, 203–213. https://doi.org/10.1111/aab.12256

Ahmed, A., & Hasnain, S. (2010). *Auxin-producing Bacillus sp.: Auxin quantification and effect on the growth of Solanum tuberosum. Pure and Applied Chemistry, 82*, 313–319. https://doi.org/10.1351/PAC-CON-09-02-06

Ahmed, B., Shahid, M., Syed, A., Rajput, V. D., Elgorban, A. M., Minkina, T., Bahkali, A. H., & Lee, J. (2021). *Drought tolerant Enterobacter sp./Leclercia adecarboxylata secretes indole-3-acetic acid and other biomolecules and enhances the biological attributes of Vigna radiata (L.) R. Wilczek in water deficit conditions. Biology, 10*, 1149. https://doi.org/10.3390/biology10111149

Akhtar, M. S., & Siddiqui, Z. A. (2009). *Effect of phosphate solubilizing microorganisms and Rizobium sp. on the growth, nodulation, yield and root-rot disease complex of chickpea under field condition. African Journal of Biotechnology, 8*, 3489–3496. http://www.academicjournals.org/AJB

Akram, N. A., Waseem, M., Ameen, R., & Ashraf, M. (2016). *Trehalose pretreatment induces drought tolerance in radish (Raphanus sativus L.) plants: Some key physio-biochemical traits. Acta Physiologiae Plantarum, 38*, 3. https://doi.org/10.1007/s11738-015-2018-1

Alam, M. M., Nahar, K., Hasanuzzaman, M., & Fujita, M. (2014). *Trehalose-induced drought stress tolerance: A comparative study among different Brassica species. Plant Omics, 7*, 271–283. https://www.pomics.com/hassanuzzaman_7_4_2014_271_283.pdf

Alam, S., Khalil, S., Ayub, N., & Rashid, M. (2022). *In vitro solubilization of inorganic phosphate by phosphate solubilizing microorganism (PSM) from maize rhizosphere. International Journal of Agriculture and Biology, 4*, 454–458. http://www.ijab.org

Ali, B., Wang, X., Saleem, M. H., Sumaira Hafeez, A., Afridi, M. S., Khan, S., Zaib Un, N., Ullah, I., & Amaral Júnior, A. T. D. (2022). *PGPR-mediated salt tolerance in maize by modulating plant physiology, antioxidant defense, compatible solutes accumulation and bio-surfactant producing genes. Plants, 11*, 345. https://doi.org/10.3390/plants11030345

Arzanesh, M. H., Alikhani, H. A., Khavazi, K., Rahimian, H. A., & Miransari, M. (2011). *Wheat (Triticum aestivum L.) growth enhancement by Azospirillum sp. under drought stress. World Journal of Microbiology and Biotechnology, 27*, 197–205. https://doi.org/10.1007/s11274-010-0444-1

Ashraf, M. (2010). *Inducing drought tolerance in plants: Recent advances. Biotechnology Advances, 28*, 169–183. https://doi.org/10.1016/j.biotechadv.2009.11.005

Baldotto, L. E. B., Baldotto, M. A., Canellas, L. P., Bressan-Smith, R., & Olivares, F. L. (2010). *Growth promotion of pineapple 'Vitória' by humic acids and Burkholderia spp. during acclimatization. Revista Brasileira de Ciência do Solo, 34*, 1593–1600. https://doi.org/10.1590/S0100-06832010000500012

Bandurska, H. (2022). *Drought stress responses: Coping strategy and resistance. Plants, 11*, 922. https://doi.org/10.3390/plants11070922

Bashan, Y., Holguin, G., & De-Bashan, L. (2004). *Azospirillum-plant relationships: Physiological, molecular, agricultural, and environmental advances. Canadian Journal of Microbiology, 50*, 521–577. https://doi.org/10.1139/w04-035

Becker, D., Hoth, S., Ache, P., Wenkel, S., Roelfsema, M. R., Meyerhoff, O., Hartung, W., & Hedrich, R. (2003). Regulation of the ABA-sensitive Arabidopsis potassium channel gene GORK in response to water stress. *FEBS Letters, 554*(1–2), 119–126. https://doi.org/10.1016/S0014-5793(03)01118-9

Berg, G. (2009). *Plant-microbe interactions promoting plant growth and health: Perspectives for controlled use of microorganisms in agriculture. Applied Microbiology and Biotechnology, 84*, 11–18. https://doi.org/10.1007/s00253-009-2092-7

Bhat, M. I., Rashid, A., Faisul-Ur, R., Mahdi, S. S., Haq, S. A., & Raies, A. B. (2010). *Effect of Rhizobium and vesicular-arbuscular mycorrhizae fungi on green gram (Vigna radiata L. Wilczek) under temperate conditions. Research Journal of Agricultural Sciences, 1*, 113–118. https://www.scirp.org/reference/referencespapers?referenceid=669377

Bisleski, R. L. (1973). *Phosphate transport and phosphate availability. Annual Review of Plant Physiology, 24*, 225–252. https://doi.org/10.1146/annurev.pp.24.060173.001301

Bittencourt, P. P., Alves, A. F., Ferreira, M. B., da Silva Irineu, L. E. S., Pinto, V. B., & Olivares, F. L. (2023). Mechanisms and applications of bacterial inoculants in plant drought stress tolerance. *Microorganisms, 11*(2), 502. https://doi.org/10.3390/microorganisms11020502

Blom, D., Fabbri, C., Connor, E. C., Schiestl, F. P., Klauser, D. R., Boller, T., Eberl, L., & Weisskopf, L. (2011). *Production of plant growth modulating volatiles is widespread among rhizosphere bacteria and strongly depends on culture conditions. Environmental Microbiology, 13*, 3047–3058. https://doi.org/10.1111/j.1462-2920.2011.02582.x

Brilli, F., Loreto, F., & Baccelli, I. (2019). *Exploiting plant volatile organic compounds (VOCs) in agriculture to improve sustainable defense strategies and productivity of crops. Frontiers in Plant Science, 10*, 264. https://doi.org/10.3389/fpls.2019.00264

Broeckling, C. D. (2008). *Root exudates regulate soil fungal community composition and diversity. Applied Environmental Microbiology, 74*, 738–744. https://doi.org/10.1128/AEM.02188-07

Brundrett, M. C., & Abbott, L. K. (1995). *Mycorrhizal fungus propagules in the jarrah forest. I. Spatial variability in inoculum levels. New Phytologist, 131*, 461–469. https://doi.org/10.1111/j.1469-8137.1995.tb03083.x

Champawat, R. S., & Pathak, V. N. (1993). *Effect of vesicular-arbuscular mycorrhizal fungi on growth and nutrition uptake of pearl millet. Indian Journal of Mycology and Plant Pathology, 23*, 30–34. https://doi.org/10.1104/pp.102.3.771

Chang, B., Yang, L., Cong, W., & Tang, Z. (2014). *The improved resistance to high salinity induced by trehalose is associated with ionic regulation and osmotic adjustment in Catharanthus roseus. Plant Physiology and Biochemistry, 77*, 140–148. https://doi.org/10.1016/j.plaphy.2014.02.001

Chen, H., & Jiang, J. G. (2010). *Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environmental Reviews, 18*, 309–319. https://doi.org/10.1139/A10-014

Cho, S. M., Kang, B. R., Han, S. H., Anderson, A. J., Park, J. Y., Lee, Y. H., Cho, B. H., Yang, K. Y., Ryu, C. M., & Kim, Y. C. (2008). *2R, 3R-butanediol, a bacterial volatile produced by Pseudomonas chlororaphis O6, is involved in induction of systemic tolerance to drought in Arabidopsis thaliana. Molecular Plant-Microbe Interactions, 21*, 1067–1075. https://doi.org/10.1094/MPMI-21-8-1067

Cochard, H., Coll, L., Le Roux, X., & Améglio, T. (2002). *Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. Plant Physiology, 128*, 282–290. https://pmc.ncbi.nlm.nih.gov/articles/PMC148995/

Cohen, A. C., Bottini, R., & Piccoli, P. N. (2008). *Azospirillum brasilense Sp 245 produces ABA in chemically-defined culture medium and increases ABA content in Arabidopsis plants. Plant Growth Regulation, 54*, 97–103. https://doi.org/10.1007/s10725-007-9232-9

Constable, G. A., & Hearn, A. B. (1978). *Agronomic and physiological responses of soybean and sorghum crops to water deficits I. Growth, development and yield. Functional Plant Biology, 5*, 159–167. https://doi.org/10.1071/PP9780159

De Souza, R., Schoenfeld, R., & Passaglia, L. M. P. (2016). *Bacterial inoculants for rice: Effects on nutrient uptake and growth promotion. Archives of Agronomy and Soil Science, 62*, 561–569. https://doi.org/10.1080/03650340.2015.1065973

Deubel, A., Gransee, G., & Merbach, W. (2000). *Transformation of organic rhizodeposits by rhizoplane bacteria and its influence on the availability of tertiary calcium phosphate. Journal of Plant Nutrition and Soil Science, 163*, 387–392. https://doi.org/10.1002/1522-2624(200008)163:4

Duchense, L. C., Peterson, R. L., & Ellis, B. E. (1989). *The future of ectomycorrhizal fungi as biological control agents. Phytoprotection, 70*, 51–57. https://doi.org/10.1007/978-3-642-85063-9_3

Dumas, G. E., Guillaume, P., Tahiri, A. A., Gianinazzi-Pearson, V., & Gianinazzi, S. (1994). *Changes in polypeptide patterns in tobacco roots by Glomus species. Mycorrhiza, 4*, 215–221. https://link.springer.com/book/10.1007/978-94-017-0776-3

Duponnois, R., Kisa, M., & Plenchette, C. (2006). *Phosphate solubilizing potential of the nemato fungus Arthrobotrys oligospora. Journal of Plant Nutrition and Soil Science, 169*, 280–282. https://doi.org/10.1002/jpln.200520551

Dutton, V. M., & Evans, C. S. (1996). *Oxalate production by fungi: Its role in pathogenicity and ecology in the soil environment. Canadian Journal of Microbiology, 42*, 881–895. https://doi.org/10.1139/m96-114

El-Komy, H. M., Hamdia, M. A., & El-Baki, G. K. A. (2003). *Nitrate reductase in wheat plants grown under water stress and inoculated with Azospirillum spp. Biologia Plantarum, 46*, 281–287. https://doi.org/10.1023/A:1022819114860

El-Komy, M., & Hesham, A. (2004). *Coimmobilization of Azospirillum lipoferum and Bacillus megaterium for successful phosphorus and nitrogen nutrition of wheat plants. Food Technology and Biotechnology, 43*, 19–27. https://www.ftb.com.hr/images/pdfarticles/2005/January-March/43-19.pdf

Etesami, H., & Maheshwari, D. K. (2018). *Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: Action mechanisms and future prospects. Ecotoxicology Environment Safety, 156*, 225–246. https://doi.org/10.1016/j.ecoenv.2018.03.013

Fa Yuan, W., & Zhao Yong, S. (2008). *Biodiversity of arbuscular mycorrhizal fungi in China: A review. Advances in Environmental Biology, 2*, 31–39. https://www.aensiweb.com/old/aeb/2008/31-39.pdf

Fierer, N., & Jackson, R. B. (2006). *The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences of the USA, 103*, 626–631. https://doi.org/10.1073/pnas.0507535103

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., & West, P. C. (2011). *Solutions for a cultivated planet. Nature, 478*, 337–342. https://doi.org/10.1038/nature10452

Fulchieri, M., & Frioni, L. (1994). *Azospirillum inoculation on maize (Zea mays): Effect on yield in a field experiment in Central Argentina. Soil Biology and Biochemistry, 26*, 921–924. https://doi.org/10.1016/0038-0717(94)90308-5

Garg, S., Bhatnagar, A., Kalla, A., & Narula, N. (2001). *In vitro nitrogen fixation, phosphate solubilization, survival and nutrient release by Azotobacter strains in an aquatic system. Bioresource Technology, 80*, 101–109. https://doi.org/10.1016/s0960-8524(01)00081-5

Geurts, R., & Bisseling, T. (2002). *Rhizobium nod factor perception and signalling. The Plant Cell, 14*, S239–S249. https://doi.org/10.1105/tpc.002451

Ghosh, D., Gupta, A., & Mohapatra, S. (2019). A comparative analysis of exopolysaccharide and phytohormone secretions by four drought-tolerant rhizobacterial strains and their impact on osmotic-stress mitigation in *Arabidopsis thaliana*. *World Journal of Microbiology and Biotechnology, 35*(90). https://doi.org/10.1007/s11274-019-2659-0

Glick, B. R., Penrose, D. M., & Li, J. (1998). A model for the lowering of plant ethylene concentrations by plant growth-promoting bacteria. *Journal of Theoretical Biology, 190*, 63–68. https://doi.org/10.1006/jtbi.1997.0532

Greacen, E. L., & Oh, J. S. (1972). Physics of root growth. *Nat. New Biol., 235*, 24–25. https://doi.org/10.1038/newbio235024a0

Gull, M., Hafeez, F. E., Saleem, M., & Malik, K. A. (2004). Phosphorus uptake and growth promotion of chickpea by co-inoculation of mineral phosphate solubilizing bacteria and a mixed rhizobial culture. *Australian Journal of Experimental Agriculture, 44*, 623–628. https://doi.org/10.1071/EA02218

Gullino, P., Luca, B., & Federica, L. (2018). Linking multifunctionality and sustainability for valuing peri-urban farming: A case study in the Turin Metropolitan Area (Italy). *Sustainability, 10*(5), 1625. https://doi.org/10.3390/su10051625

Habibi, A., Heidari, G., Sohrabi, Y., Badakhshan, H., & Mohammadi, K. (2011). Influence of bio, organic and chemical fertilizers on medicinal pumpkin traits. *Journal of Medicinal Plants Research, 5*, 5590–5597. http://www.academicjournals.org/JMPR

Harb, A., Awad, D., & Samarah, N. (2015). Gene expression and activity of antioxidant enzymes in barley (*Hordeum vulgare* L.) under controlled severe drought. *Journal of Plant Interactions, 10*, 109–116. https://doi.org/10.1080/17429145.2015.1033023

Hart, M. M., & Reader, R. J. (2002). Host plant benefit from association with arbuscular mycorrhizal fungi: Variation due to differences in size of mycelium. *Biology and Fertility of Soils, 36*, 357–366. https://doi.org/10.1007/s00374-002-0539-4

Hayat, S., Hayat, Q., Alyemeni, M. N., Wani, A. S., Pichtel, J., & Ahmad, A. (2012). Role of proline under changing environments: A review. *Plant Signaling & Behavior, 7*, 1456–1466. https://doi.org/10.4161/psb.21949

Henri, F., Laurette, N. N., Annette, A., John, Q., Wolfgang, M., François-Xavier, E., & Dieudonné, E. (2008). Solubilization of inorganic phosphates and plant growth promotion by strains of *Pseudomonas fluorescens* isolated from acidic soils of Cameroon. *African Journal of Microbiology Research, 2*, 171–178. https://www.internationalscholarsjournals.com/articles/solubilization-of-inorganic-phosphates-and-plant-growth-promotion-by-strains-of-pseudomonas-fluorescens-isolated-from-ac.pdf

Hernández, I., Cela, J., Alegre, L., & Munné-Bosch, S. (2012). Antioxidant defenses against drought stress. In R. Aroca (Ed.), *Plant responses to drought stress: From morphological to molecular features* (pp. 231–258). Springer. https://doi.org/10.1007/978-3-642-32653-0_9

Hilda, R., & Fraga, R. (2000). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances, 17*, 319–359. https://doi.org/10.1016/s0734-9750(99)00014-2

Hinsinger, P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: A review. *Plant and Soil, 237*, 173–195. https://doi.org/10.1023/A:1013351617532

Hochberg, U., Windt, C. W., Ponomarenko, A., Zhang, Y. J., Gersony, J., Rockwell, F. E., & Holbrook, N. M. (2017). Stomatal closure, basal leaf embolism, and shedding protect the hydraulic integrity of grape stems. *Plant Physiology, 174*, 764–775. https://doi.org/10.1104/pp.16.01816

Honma, M., & Shimomura, T. (1978). Metabolism of 1-aminocyclopropane-1-carboxylic acid. *Agricultural and Biological Chemistry, 42*, 1825–1831. https://doi.org/10.1080/00021369.1978.10863261

Hungria, M., Campo, R. J., Souza, E. M., & Pedrosa, F. O. (2010). Inoculation with selected strains of *Azospirillum brasilense* and *A. lipoferum* improves yields of maize and wheat in Brazil. *Plant and Soil, 331*, 413–425. https://doi.org/10.1007/s11104-009-0262-0

Hussein, H. A. A., Mekki, B. B., Abd El-Sadek, M. E., & El Lateef, E. E. (2019). Effect of L-ornithine application on improving drought tolerance in sugar beet plants. *Heliyon, 5*, e02631. https://doi.org/10.1016/j.heliyon.2019.e02631

Igual, J. M., Valverde, A., Cervantes, E., & Velázquez, E. (2001). Phosphate-solubilizing bacteria as inoculants for agriculture: Use of updated molecular techniques in their study. *Agronomie, 21*, 561–568. https://hal.science/hal-00886151/document

Iqbal, S., Wang, X., Mubeen, I., Kamran, M., Kanwal, I., Díaz, G. A., Abbas, A., Parveen, A., Atiq, M. N., & Alshaya, H. (2022). Phytohormones trigger drought tolerance in crop plants: Outlook and future perspectives. *Frontiers in Plant Science, 12*, 3378. https://doi.org/10.3389/fpls.2021.799318

Jeffries, A. (1987). Use of mycorrhiza in agriculture. *Critical Reviews in Biotechnology, 5*, 319–357. https://doi.org/10.3109/07388558709079476

Jjemba, P. K., & Alexander, M. (1999). Possible determinants of rhizosphere competence of bacteria. *Soil Biology and Biochemistry, 31*, 623–632. https://doi.org/10.1016/S0038-0717(98)00168-0

Jochum, M. D., McWilliams, K. L., Borrego, E. J., Kolomiets, M. V., Niu, G., Pierson, E. A., & Jo, Y. K. (2019). Bioprospecting plant growth-promoting rhizobacteria that mitigate drought stress in grasses. *Frontiers in Microbiology, 10,* 2106. https://doi.org/10.3389/fmicb.2019.02106

Junaid, M. D., Gokce, A. F., & Bostani, R. (2024). Global agricultural losses and their causes. *Bulletin of Biological and Allied Science Research, 9*(1), 66. https://doi.org/10.54112/bbasr.v2024i1.66

Kang, S. M., Shahzad, R., Bilal, S., Khan, A. L., Park, Y. G., Lee, K. E., Asaf, S., Khan, M. A., & Lee, I. J. (2019). Indole-3-acetic-acid and ACC deaminase producing *Leclercia adecarboxylata* MO1 improves *Solanum lycopersicum* L. growth and salinity stress tolerance by endogenous secondary metabolites regulation. *BMC Microbiology, 19*, 80. https://doi.org/10.1186/s12866-019-1450-6

Kasim, W. A., Osman, M. E. H., Omar, M. N., & Salama, S. (2021). Enhancement of drought tolerance in *Triticum aestivum* L. seedlings using *Azospirillum brasilense* NO40 and *Stenotrophomonas maltophilia* B11. *Bulletin of the National Research Centre, 45*, 95. https://doi.org/10.1186/s42269-021-00546-6

Kathiresan, G., Manickam, G., & Parameswaran, P. (1995). Efficiency of phosphobacteria addition on cane yield and quality. *Cooperative Sugar, 26*, 629–631. https://www.academia.edu/77310716/Bacterial_biofertilizers_for_sustainable_crop_production_a_review

Kavamura, V. N., Santos, S. N., Silva, J. L. D., Parma, M. M., Ávila, L. A., Visconti, A., Zucchi, T. D., Taketani, R. G., Andreote, F. D., & Melo, I. S. D. (2013). Screening of Brazilian cacti rhizobacteria for plant growth promotion under drought. *Microbiological Research, 168*, 183–191. https://doi.org/10.1016/j.micres.2012.12.002

Khan, A. L., Halo, B. A., Elyassi, A., Ali, S., Al-Hosni, K., Hussain, J., Al-Harrasi, A., & Lee, I. J. (2016). Indole acetic acid and ACC deaminase from endophytic bacteria improves the growth of *Solanum lycopersicum*. *Electronic Journal of Biotechnology, 21*, 58–64. http://dx.doi.org/10.1016/j.ejbt.2016.02.001

Khan, I. A., Ayub, N., Mirza, S. N., Nizami, S. M., & Azam, M. (2008). Synergistic effect of dual inoculation (vesicular-arbuscular mycorrhizae) on the growth and nutrient uptake of *Medicago sativa*. *Pakistan Journal of Botany, 40*, 939–945. https://www.researchgate.net/publication/235913809_Synergistic_Effect_of_Dual_Inoculation_Vesicular_Arbuscular_Mycorrhizae_on_the_Growth_and_Nutrients_Uptake_of_Medicago_sativa

Khan, M. S., Zaidi, A., & Wani, P. A. (2007). Role of phosphate-solubilizing microorganisms in sustainable agriculture: A review. *Agronomy for Sustainable Development, 27*, 29–43. https://doi.org/10.1051/agro:2006011

Khan, N., & Bano, A. (2019). Exopolysaccharide producing rhizobacteria and their impact on growth and drought tolerance of wheat grown under rainfed conditions. *PLoS ONE, 14*, e0222302. https://doi.org/10.1371/journal.pone.0222302

Khosro, M., & Yousef, S. (2012). Bacterial biofertilizers for sustainable crop production: A review. *ARPN Journal of Agricultural and Biological Science, 7*, 307–316. https://www.arpnjournals.com/jabs/research_papers/rp_2012/jabs_0512_396.pdf

Kim, K. Y., Jordan, D., & McDonald, G. A. (1998). Effect of phosphate-solubilizing bacteria and vesicular-arbuscular mycorrhizae on tomato growth and soil microbial activity. *Biology and Fertility of Soils, 26*, 79–87. https://doi.org/10.1007/s003740050347

Kpomblekou, K., & Tabatabai, M. A. (1994). Effect of organic acids on release of phosphorus from phosphate rocks. *Soil Science, 158*, 442–453. https://journals.lww.com/soilsci/abstract/1994/15860/effect_of_organic_acids_on_release_of_phosphorus.6.aspx

Kumar, A., & Verma, J. P. (2018). Does plant—microbe interaction confer stress tolerance in plants: A review? *Microbiological Research, 207*, 41–52. https://doi.org/10.1016/j.micres.2017.11.004

Lee, K. E., & Pankhurst, C. E. (1992). Soil organisms and sustainable productivity. *Australian Journal of Soil Research, 30*, 855–892. http://dx.doi.org/10.1071/SR9920855

Li, C., Li, L., Reynolds, M. P., Wang, J., Chang, X., Mao, X., & Jing, R. (2021). Recognizing the hidden half in wheat: Root system attributes associated with drought tolerance. *Journal of Experimental Botany, 72*, 5117–5133. http://dx.doi.org/10.1093/jxb/erab124

Malhi, G. S., Kaur, M., & Kaushik, P. (2021). Impact of climate change on agriculture and its mitigation strategies: A review. *Sustainability, 13*, 1318. https://doi.org/10.3390/su13031318

McAfee, B. J., & Fortin, J. A. (1986). Comparative effects of the soil microflora on ectomycorrhizal inoculation of conifer seedling. *New Phytologist, 108*, 108–443. https://doi.org/10.1111/j.1469-8137.1988.tb04185.x

Mohammadi Alagoz, S., Zahra, N., Hajiaghaei Kamrani, M., Asgari Lajayer, B., Nobaharan, K., Astatkie, T., Siddique, K. H. M., & Farooq, M. (2022). Role of root hydraulics in plant drought tolerance. *Journal of Plant Growth Regulation, 1–16*. https://research-repository.uwa.edu.au/en/publications/role-of-root-hydraulics-in-plant-drought-tolerance

Moreno-Galván, A. E., Cortés-Patiño, S., Romero-Perdomo, F., Uribe-Vélez, D., Bashan, Y., & Bonilla, R. R. (2020). Proline accumulation and glutathione reductase activity induced by drought-tolerant rhizobacteria as potential mechanisms to alleviate drought stress in Guinea grass. *Applied Soil Ecology, 147*, 103367. https://doi.org/10.1016/j.apsoil.2019.103367

Nahas, E. (1996). Factors determining rock phosphate solubilization by microorganisms isolated from soil. *World Journal of Microbiology and Biotechnology, 12*, 18–23. https://doi.org/10.1007/BF00327716

Narayanasamy, S., Thankappan, S., Kumaravel, S., Ragupathi, S., & Uthandi, S. (2023). Complete genome sequence analysis of a plant growth-promoting phylloplane *Bacillus altitudinis* FD48 offers mechanistic insights into priming drought stress tolerance in rice. *Genomics, 115*, 110550. https://doi.org/10.1016/j.ygeno.2022.110550

Naveed, M., Mitter, B., Reichenauer, T. G., Wieczorek, K., & Sessitsch, A. (2014). Increased drought stress resilience of maize through endophytic colonization by *Burkholderia phytofirmans* PsJN and *Enterobacter* sp. FD17. *Environmental Experimental Botany, 97*, 30–39. https://doi.org/10.1016/j.envexpbot.2013.09.014

Nessner Kavamura, V., Santos, S. N., da Silva, J. L., Parma, M. M., Aparecida Ávila, L., Visconti, A., Zucchi, T. D., Gouvêa Taketani, R., Andreote, F. D., & de Melo, I. S. (2013). Screening of Brazilian cacti rhizobacteria for plant growth promotion under drought. *Microbiological Research, 168*(3), 183–191. https://doi.org/10.1016/j.micres.2012.12.002

Nihorimbere, V., Ongena, M., Smargiassi, M., & Thonart, P. (2011). Beneficial effect of the rhizosphere microbial community for plant growth and health. *Biotechnologie Agronomie Société et Environnement, 15*, 327–337. https://popups.uliege.be/1780-4507/index.php?id=7578

Nivetha, N., Lavanya, A. K., Vikram, K. V., Asha, A. D., Sruthi, K. S., Bandeppa, S., Annapurna, K., & Paul, S. (2021). PGPR-mediated regulation of antioxidants: Prospects for abiotic stress management in plants. In *Plant Stress Physiology: From Genomics to Systems Biology* (pp. 471–497). Springer. https://doi.org/10.1007/978-981-16-1350-0_23

Ojuederie, O. B., Olanrewaju, O. S., & Babalola, O. O. (2019). Plant growth promoting rhizobacterial mitigation of drought stress in crop plants: Implications for sustainable agriculture. *Agronomy, 9*, 712. https://doi.org/10.3390/agronomy9110712

Olivares, F. L., Busato, J. G., De Paula, A. M., Da Silva Lima, L., Aguiar, N. O., & Canellas, L. P. (2017). Plant growth promoting bacteria and humic substances: Crop promotion and mechanisms of action. *Chemical and Biological Technologies in Agriculture, 4*, 30. https://doi.org/10.1186/s40538-017-0112-x

Pantoja-Guerra, M., Valero-Valero, N., & Ramírez, C. A. (2023). Total auxin level in the soil–plant system as a modulating factor for the effectiveness of PGPR inocula: A review. *Chemical and Biological Technologies in Agriculture, 10*, 6. https://doi.org/10.1186/s40538-022-00370-8

Patil, P. L., & Medhane, N. S. (1994). Seed inoculation studies in gram (Cicer arietinum L.) with different strains of Rhizobium sp. *Plant and Soil, 40*, 221–223. https://doi.org/10.1007/bf00011425

Ponmurugan, P., & Gopi, G. (2006). Distribution pattern and screening of phosphate solubilizing bacteria isolated from different food and forage crops. *Journal of Agronomy, 5*, 600–604. https://doi.org/10.3923/ja.2006.600.604

Poudel, M., Mendes, R., Costa, L. A. S., Bueno, C. G., Meng, Y., Folimonova, S. Y., Garrett, K. A., & Martins, S. J. (2021). The role of plant-associated bacteria, fungi, and viruses in drought stress mitigation. *Frontiers in Microbiology, 12*, 3058. https://doi.org/10.3389/fmicb.2021.743512

Pyngrope, S., Bhoomika, K., & Dubey, R. S. (2013). Oxidative stress, protein carbonylation, proteolysis and antioxidative defense system as a model for depicting water deficit tolerance in Indica rice seedlings. *Plant Growth Regulation, 69*, 149–165. https://doi.org/10.1007/s10725-012-9758-3

Rao, D. E., & Chaitanya, K. V. (2016). Photosynthesis and antioxidative defense mechanisms in deciphering drought stress tolerance of crop plants. *Biologia Plantarum, 60*, 201–218. https://doi.org/10.1007/s10535-016-0584-8

Rasheed, A., Mahmood, A., Maqbool, R., Albaqami, M., Sher, A., Sattar, A., Khosa, G. B., Nawaz, M., Hassan, M. U., & Al-Yahyai, R. (2022). Key insights to develop drought-resilient soybean: A review. *Journal of King Saud University – Science, 34*, 102089. https://doi.org/10.1016/j.jksus.2022.102089

Rodríguez, H., & Fraga, R. (1999). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances, 17*, 319–339. https://doi.org/10.1016/s0734-9750(99)00014-2

Rokhzadi, A., & Toashih, V. (2011). Nutrient uptake and yield of chickpea (Cicer arietinum L.) inoculated with plant growth promoting rhizobacteria. *Australian Journal of Crop Science, 5*, 44–48. https://www.scirp.org/reference/referencespapers?referenceid=3777753

Rokhzadi, A., Asgharzadeh, A., Darvish, F., Nourmohammadi, G., & Majidi, E. (2008). Influence of plant growth-promoting rhizobacteria on dry matter accumulation and yield of chickpea (Cicer arietinum L.) under field condition. *Agricultural and Food Sciences, 3*, 253–257. https://www.semanticscholar.org/paper/Influence-of-plant-growth-promoting-rhizobacteria-Rokhzadi

Rosas, S. B., André, S. J. A., Rovera, M., & Correa, N. S. (2006). Phosphate-solubilizing *Pseudomonas putida* can influence the rhizobia–legume symbiosis. *Soil Biology and Biochemistry, 38*, 3502–3505. https://doi.org/10.1016/j.soilbio.2006.05.008

Ryu, C. M., Farag, M. A., Hu, C. H., Reddy, M. S., Wei, H. X., Paré, P. W., & Kloepper, J. W. (2003). Bacterial volatiles promote growth in *Arabidopsis*. *Proceedings of the National Academy of Sciences, 100*, 4927–4932. https://doi.org/10.1073/pnas.0730845100

Saikia, S. P., & Jain, V. (2007). Biological nitrogen fixation with non-legumes: An achievable target or a dogma. *Current Science, 92*, 317–322. https://www.researchgate.net/publication/255620954_Biological_nitrogen_fixation_with_non-legumes_An_achievable_target_or_a_dogma

Salomon, M. V., Bottini, R., De Souza Filho, G. A., Cohen, A. C., Moreno, D., Gil, M., & Piccoli, P. (2014). Bacteria isolated from roots and rhizosphere of *Vitis vinifera* retard water losses, induce abscisic acid accumulation and synthesis of defense-related terpenes in in vitro cultured grapevine. *Physiologia Plantarum, 151*, 359–374. https://doi.org/10.1111/ppl.12117

Sashidhar, B., & Podile, A. R. (2010). Mineral phosphate solubilization by rhizosphere bacteria and scope for manipulation of the direct oxidation pathway involving glucose dehydrogenase. *Journal of Applied Microbiology, 109*(1), 1–12. https://doi.org/10.1111/j.1365-2672.2009.04654.x

Schroth, M. N., & Hancock, J. G. (1981). Selected topics in biological control. *Annual Review of Microbiology, 35*, 453–476. https://doi.org/10.1146/annurev.mi.35.100181.002321

Sgroy, V., Cassán, F., Masciarelli, O., Del Papa, M. F., Lagares, A., & Luna, V. (2009). Isolation and characterization of endophytic plant growth-promoting (PGPB) or stress homeostasis-regulating (PSHB) bacteria associated to the halophyte *Prosopis strombulifera*. *Applied Microbiology and Biotechnology, 85*, 371–381. https://doi.org/10.1007/s00253-009-2116-3

Shanmugam, P. M., & Veeraputhran, R. (2000). Effect of organic manure, biofertilizers, inorganic nitrogen and zinc on growth and yield of rabi rice. *Madras Agricultural Journal, 87*(2), 87–90. https://doi.org/10.29321/MAJ.10.A00426

Shehata, M. M., & El-Khawas, S. A. (2003). Effect of biofertilizers on growth parameters, yield characters, nitrogenous components, nucleic acids content, minerals, oil content, protein profiles and DNA banding pattern of sunflower (*Helianthus annuus* L. cv. Vedock) yield. *Pakistan Journal of Biological Sciences, 6*, 1257–1268. https://doi.org/10.3923/pjbs.2003.1257.1268

Sheoran, S., Thakur, V., Narwal, S., Turan, R., Mamrutha, H. M., Singh, V., Tiwari, V., & Sharma, I. (2015). Differential activity and expression profile of antioxidant enzymes and physiological changes in wheat (*Triticum aestivum* L.) under drought. *Applied Biochemistry and Biotechnology, 177*, 1282–1298. https://doi.org/10.1007/s12010-015-1813-x

Sohbat, Z. I. (2022). Non-photochemical quenching of chlorophyll fluorescence and its components: Recent advances. *Journal of Life Science & Biomedicine, 4*, 76–86. https://jlsbjournal.org/uploads/public_files/2022-07/10_chap.pdf

Subrahmanyam, G., Kumar, A., Sandilya, S. P., Chutia, M., & Yadav, A. N. (2020). Diversity, plant growth promoting attributes, and agricultural applications of rhizospheric microbes. In *Plant Microbiomes for Sustainable Agriculture* (pp. 1–52). https://doi.org/10.1007/978-3-030-38453-1_1

Sundara, B., Natarajan, V., & Hari, K. (2022). Influence of phosphorus solubilizing bacteria on the changes in soil available phosphorus and sugarcane yields. *Field Crops Research, 77*, 43–49. https://doi.org/10.1016/S0378-4290(02)00048-5

Sziderics, A. H., Rasche, F., Trognitz, F., Sessitsch, A., & Wilhelm, E. (2007). Bacterial endophytes contribute to abiotic stress adaptation in pepper plants (*Capsicum annuum* L.). *Canadian Journal of Microbiology, 53*, 1195–1202. https://doi.org/10.1139/W07-082

Tambekar, D. H., Gulhane, S. R., Somkuwar, D. O., Ingle, K. B., & Kanchalwar, S. P. (2009). Potential Rhizobium and phosphate solubilizers as biofertilizers from saline belt of Akola and Buldhana district, India. *Research Journal of Agriculture and Biological Sciences, 5*, 578–582. https://www.aensiweb.net/AENSIWEB/rjabs/rjabs/2009/578-582.pdf

Tao, G., Tian, S., Cai, M., & Xie, G. (2008). Phosphate solubilizing and mineralizing abilities of bacteria isolated from soils. *Pedosphere, 18*, 515–523. https://doi.org/10.1016/S1002-0160(08)60042-9

Turner, N. C. (2017). Turgor maintenance by osmotic adjustment, an adaptive mechanism for coping with plant water deficits. *Plant, Cell & Environment, 40*, 1–3. https://doi.org/10.1111/pce.12839

Valente Lima, J., Tinôco, R. S., Olivares, F. L., Moraes, A. J. G. D., Chia, G. S., & Silva, G. B. D. (2020). Hormonal imbalance triggered by rhizobacteria enhances nutrient use efficiency and biomass in oil palm. *Scientia Horticulturae, 264*, 109161. https://doi.org/10.1016/j.scienta.2019.109161

Vardharajula, S., Zulfikar Ali, S., Grover, M., Reddy, G., & Bandi, V. (2011). Drought-tolerant plant growth promoting *Bacillus* spp.: Effect on growth, osmolytes, and antioxidant status of maize under drought stress. *Journal of Plant Interactions, 6*, 1–14. https://doi.org/10.1080/17429145.2010.535178

Vazquez, P., Holguin, G., Puente, M., Cortes, A. E., & Bashan, Y. (2000). Phosphate solubilizing microorganisms associated with the rhizosphere of mangroves in a semi-arid coastal lagoon. *Biology and Fertility of Soils, 30*, 460–468. https://doi.org/10.1007/s003740050024

Whitelaw, M. A. (2000). Growth promotion of plants inoculated with phosphate solubilizing fungi. *Advances in Agronomy, 69*, 99–151. https://doi.org/10.1016/S0065-2113(08)60948-7

Xiao, C. Q., Chi, R. A., Huang, X. H., & Zhang, W. X. (2008). Optimization for rock phosphate solubilization by phosphate-solubilizing fungi isolated from phosphate mines. *Ecological Engineering, 33*, 187–193. https://doi.org/10.1016/j.ecoleng.2008.04.001

Yahya, A., & Azawi, S. K. A. (1998). Occurrence of phosphate solubilizing bacteria in some Iranian soils. *Plant and Soil, 117*, 135–141. https://doi.org/10.1007/BF02206266

Yasmin, H., Bano, A., Wilson, N. L., Nosheen, A., Naz, R., Hassan, M. N., Ilyas, N., Saleem, M. H., Noureldeen, A., & Ahmad, P. (2022). Drought-tolerant *Pseudomonas* sp. showed differential expression of stress-responsive genes and induced drought tolerance in *Arabidopsis thaliana*. *Physiologia Plantarum, 174*, e13497. https://doi.org/10.1111/ppl.13497

Zaddy, E., & Perevolosky, A. (1995). Enhancement of growth and establishment of oak seedlings by inoculation with *Azospirillum brasilense*. *Forest Ecology and Management, 72*, 81–83. https://www.academia.edu/33819891/

Zaddy, E., Perevolosky, A., & Okon, Y. (1993). Promotion of plant growth by inoculation with aggregated and single-cell suspension of *Azospirillum brasilense*. *Soil Biology and Biochemistry, 25*, 819–823. https://doi.org/10.1007/s00248-004-0148-x

Zhang, W., Xie, Z., Zhang, X., Lang, D., & Zhang, X. (2019). Growth-promoting bacteria alleviates drought stress of *Glycyrrhiza uralensis* through improving photosynthesis characteristics and water status. *Journal of Plant Interactions, 14*, 580–589. https://doi.org/10.1080/17429145.2019.1680752