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A review of endophytic bacteria and plants: Natural partners against the challenges of drought

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Abstract

Drought stress, driven by climate change and exacerbated by global warming and rainfall anomalies, poses significant threats to agricultural productivity and food security. It leads to profound morphological, physiological, and biochemical changes in plants, impacting growth and yield. Traditional strategies for drought mitigation, such as water-efficient irrigation and genetic engineering, face limitations due to technical challenges and resource de mands. Endophytic bacteria, a subset of plant growth-promoting rhizobacteria (PGPR), offer a promising, sustainable alternative to improve plant drought tolerance. These microorganisms establish symbiotic relationships within plant tissues, enhancing nutrient acquisition, modulating phytohormones, scavenging reactive oxygen species (ROS), and influencing gene expression to promote plant growth and stress resistance. This paper explores the mechanisms by which endophytic bacteria improve drought tolerance, including nutrient acquisition, stomatal closure regulation, osmotic adjustments, and biochemical changes. Examples from various crop studies demonstrate the potential of these bacteria to enhance drought resilience. The findings highlight endophytic bacteria as a vital tool in sustainable agriculture, offering solutions to mitigate the adverse effects of drought stress while supporting global food security.

Keywords: Climate change, drought stress, endophytes, bacteria, plant growth promoting

Introduction

Drought, a critical consequence of climate change, poses severe challenges to agriculture by reducing water availability essential for plant growth. It diminishes crop yield and quality, threatening global food security as water constitutes 80–95% of plant biomass (Farooq *et al*., 2012) [6]. The greenhouse effect, caused by gases like carbon dioxide and methane, exacerbates climate shifts, increasing the frequency of droughts (Majumder, 2010)[13].

Traditional strategies to mitigate drought include efficient irrigation, breeding drought-resistant crops, and genetic engineering. However, these methods are often costly, time-consuming, and complex (Niu *et al*., 2018). An innovative alternative is the use of plant growth-promoting rhizobacteria (PGPR), particularly endophytic bacteria. Endophytic bacteria form symbiotic relationships within plant tissues, enhancing stress tolerance by improving nutrient acquisition, producing phytohormones, and mitigating competition from other plants. These microorganisms offer a sustainable approach to improving plant resilience against drought, highlighting their potential in modern agriculture (Afzal *et al*., 2019; Morales-Cedeño *et al*., 2021) [1, 14].

Drought stress and its impact on plants

Drought is one of the most severe environmental stressors affecting plant productivity, particularly in drought-prone areas where it poses a major threat to global food security and has historically caused significant famines. With 80–95% of plant fresh biomass being water, insufficient rainfall can severely limit plant growth and development, hindering their life cycles (Farooq *et al*., 2012) [6]. Factors such as uneven rainfall distribution, evapotranspiration, and soil water-holding capacity contribute to the unpredictable nature of drought (Seleiman *et al*., 2021) [23]. Besides reducing crop yields, drought exacerbates soil erosion, deteriorates water quality, and increases the frequency of disasters such as floods, fires, and disease outbreaks. Economically, drought has led to significant losses; for instance, the prolonged drought in California caused $3.8 billion in agricultural damages between 2014 and 2016, while Spain's Ebro River Basin experienced losses of approximately $0.57 billion during the 2005 drought (Fadiji *et al*., 2022). [5] Additionally, the United Nations predicts that by 2030, drought could displace 700 million people globally, affecting 55 million annually.

Causes of drought stress

Drought stress is primarily attributed to climate change, with rising air temperatures and increased atmospheric CO2 levels disrupting rainfall patterns and distribution. Insufficient rainfall remains the primary cause of drought stress (Seleiman *et al*., 2021) [23]. Global warming, driven by industrialization and the combustion of fossil fuels, has steadily increased greenhouse gas concentrations. These gases trap infrared radiation, causing global surface temperatures to rise. Between 1880 and 2012, temperatures increased by 0.85°C, with further warming of at least 0.2°C per decade anticipated (IPCC, 2014). This warming intensifies drought by reducing soil moisture and increasing water loss at the plant level (Seleiman *et al*., 2021) [23]. Rainfall anomalies, influenced by human activities such as deforestation, industrialization, and urbanization, also play a critical role in altering water availability. The distribution and intensity of rainfall significantly impact drought conditions and the management of water resources (Konapala *et al*., 2020) [9].

Impact of drought stress on plants

Drought stress affects plants through physiological, morphological, and biochemical changes that help them adapt to water scarcity (Basu *et al*., 2016; Wahab *et al*., 2022) [3, 32]. Physiologically, plants close their stomata to conserve water, reducing transpiration and protecting against pathogen invasion. However, this also limits photosynthetic capacity by reducing leaf number and photosynthesis per unit area (Santos *et al*., 2022) [21]. Plants utilize osmotic regulation, accumulating osmolytes such as sugars and amino acids to maintain cellular water potential and prevent dehydration (Yang *et al*., 2021a) [34]. Reactive oxygen species (ROS) are also produced during drought, potentially causing cellular damage. Plants mitigate this through antioxidant defenses (Garg & Manchanda, 2009) [7]. Morphologically, drought stress impacts seed germination, reducing water uptake and seedling vigor, which hinders early growth stages in crops like rice and maize. Leaves also experience reduced cell development, abscission, and diminished mitosis, which decreases leaf area and biomass, ultimately affecting photosynthetic efficiency. Root architecture adapts by increasing root biomass and water absorption capacity, as seen in plants like Catharanthus roseus and Helianthus annuus, which develop deeper and more robust root systems under drought conditions (Sharma *et al*., 2021; Wahab *et al*., 2022) [32] Biochemically, drought stress reduces photosynthetic pigments, including chlorophyll and carotenoids, impairing the photosynthetic process (Wahab *et al*., 2022) [32]. It also affects starch production by disrupting the Calvin cycle and enzymatic activity, altering energy metabolism. Plants respond by accumulating biochemicals such as proline, proteins, and carbohydrates, which mitigate oxidative stress and enhance drought tolerance. Enzymatic antioxidants, including catalase and superoxide dismutase, play a crucial role in maintaining redox balance and mitigating ROS damage during drought (Garg & Manchanda, 2009; Wahab *et al*., 2022) [7, 32].

Importance of developing drought-tolerant strategies for agriculture

Developing drought-tolerant strategies is crucial for mitigating the impact of drought on agriculture and ensuring global food security amid growing populations and climate change. Severe yield losses in staple crops like wheat and maize have been attributed to drought, with reductions of up to 21% and 40%, respectively, reported globally (Fahad *et al*., 2017) [29]. By 2050, drought is expected to impact more than half of the world's arable land (Fadiji *et al*., 2022) [5]. Water shortages, exacerbated by reduced rainfall, highlight the need for crops capable of sustaining yields under limited water availability, particularly in arid and semi-arid regions (Ahluwalia *et al*., 2021). Technological advancements, including molecular biology and systems modeling, have enabled the development of crops with enhanced drought tolerance. These strategies allow farmers to optimize water use, reduce environmental impacts, and maintain agricultural productivity. Sustainable approaches such as breeding drought-tolerant crops and employing innovative techniques are essential for resource-efficient farming practices and long-term food security (McMillen *et al*., 2022).

Mechanisms of drought stress tolerance in plants

Plants have evolved diverse strategies to cope with drought stress, including aversion, escape, and tolerance mechanisms (Seleiman *et al*., 2021) [23]. Stomatal closure, regulated by abscisic acid (ABA), conserves water during drought. Recent studies have explored molecular mechanisms of ABA-induced stomatal closure, identifying key proteins such as SnRK2 kinases and PP2C phosphatases that enhance water use efficiency (Hsu *et al*., 2021). Osmotic regulation involves accumulating solutes like trehalose and mannitol to maintain cellular water potential, turgor pressure, and photosynthetic efficiency under water-deficient conditions (Yang *et al*., 2021) [34].

Free radical scavenging and antioxidant defense mechanisms protect plants from oxidative stress caused by ROS during drought. Endogenous antioxidants, including catalase and superoxide dismutase, mitigate cellular damage, while exogenous antioxidants from plant-derived phytochemicals further enhance defenses (Trivedi & Jana, 2019) [28]. Gene expression modulation also plays a critical role; dehydration-tolerant plants exhibit upregulated genes, such as LEA proteins, which stabilize cellular structures and enhance drought resilience. Transcriptome profiling has identified genes linked to photosynthesis and stress response pathways, providing insights into plant adaptability (Ramanjulu & Bartels, 2002; Mikołajczak *et al*., 2022).

1. Microbial interactions

Microorganisms, particularly endophytic bacteria and fungi, provide an eco-friendly alternative to agrochemicals for improving plant drought tolerance, especially in crops like wheat (Allagulova *et al*., 2020). Plant growth-promoting microorganisms (PGPM) enhance drought resistance by producing phytohormones, antioxidants, and xeroprotectants while inducing plant stress tolerance mechanisms (Hanaka *et al*., 2021). Studies confirm the efficacy of PGPM applied in the rhizosphere or within plant tissues, offering cost-effective and practical solutions to mitigate drought stress (Abhilash *et al*., 2016; Hanaka *et al*., 2021). Advancing sustainable strategies requires understanding the interactions between microorganisms and plants during drought and refining PGPM application methods (Allagulova *et al*., 2020; Hanaka *et al*., 2021). Fungi demonstrate superior drought tolerance compared to bacteria due to traits like osmolyte production, thick cell walls, and melanin. Their long hyphae structures allow them to absorb water from distant soil sources, enabling survival and development under extreme drought conditions (Hanaka *et al*., 2021).

1.1 Plant growth-promoting fungi

Fungi exhibit significantly greater drought tolerance than bacteria due to their diverse defenses, including osmolyte production, thick cell walls, and melanin. Filamentous fungi, with their long hyphae, can transport water and solutes over large distances and thrive in arid conditions. These traits enable fungi to support essential processes like polymer breakdown and nutrient cycling, such as carbon and nitrogen (Hanaka *et al*., 2021).

Arbuscular mycorrhizal fungi (AMF)

Approximately 80% of terrestrial plants form symbiotic relationships with arbuscular mycorrhizal fungi (AMF), significantly improving plant growth, water uptake, and drought resistance (Tang *et al*., 2022). Under drought conditions, AMF enhances the absorption of critical minerals like phosphorus and produces phytohormones, such as auxins and cytokinins, that help plants withstand drought stress (Branco *et al*., 2022; Li *et al*., 2019; Tang *et al*., 2022).

AMF also modulates the expression of stress-related genes responsible for antioxidants and osmolytes, protecting plants from dehydration. Additionally, it regulates aquaporins, proteins crucial for water transport, aiding plants in maintaining hydration during drought. Common AMF genera like *Glomus, Rhizophagus, Funneliformis,* and *Claroideoglomus* are known to enhance plant growth and drought tolerance through both physiological and biochemical mechanisms (Tang *et al*., 2022; Branco *et al*., 2022).

1.1.1 Endophytic fungi

Additionally, endophytic fungi live naturally inside plant tissues without harming the host plant. It has been discovered that these fungi significantly contribute to improving plants' ability to withstand drought stress. It serves a similar AMF function (Verma *et al*., 2022) [31].

1.2 Plant growth-promoting bacteria

Plant growth-promoting bacteria (PGPB) enhance plant development and protect against abiotic stressors by producing metabolites and hormones, aiding nutrient uptake, and promoting soil health (Figure 1.3) (Orozco-Mosqueda *et al*., 2020). These bacteria are a sustainable alternative to pesticides, with applications in farming and environmental management (Orozco-Mosqueda *et al*., 2020; Verma *et al*., 2022) [31].

PGPB have been shown to boost chlorophyll content by up to 280% in garden peas and increase biomass in black gram under drought stress. Key bacterial groups include *Rhizobium, Bacillus,* and *Pseudomonas,* each supporting plant resilience through unique mechanisms (Poria *et al*., 2022; Pellegrini *et al*., 2023) [16].

Endophytic bacteria

De Bary developed the term "endophyte" in 1866 (Pandey *et al*., 2019), [15] which Endophytes are microorganisms that live in plant tissues' interiors without harming their hosts. Internal colonists with seemingly neutral behavior as well as symbionts are included in this description (White *et al*., 2019) [33]. It is estimated that the over 300,000 plant species that exist on Earth serve as a host to one or more endophytes. Fungi and bacteria are both possible endophytes (Afzal *et al*., 2019) [1]. Endophytes have the potential to be environmentally benign ways to enhance agricultural production without excessively relying on synthetic fertilizers and pesticides, as shown by the way they promote plant growth and fitness (Pandey *et al*., 2019) [15]. Endophytic bacteria are being researched for their possible use in agriculture as a natural alternative to chemical fertilizers and pesticides. They have been identified in a number of plant species, including crops, trees, and medicinal plants (Soppa, 2014) [26]. A biphasic life cycle is shared by the majority of endophytic bacteria, which rotates between plant and soil habitats (Afzal *et al*., 2019) [1].

1. Colonization of endophytic bacteria on plant

A variety of distinct bacterial features influence the bacteria's ability to colonize the host in an endophytic fashion. These characteristics, which are referred to as colonization qualities together, control the entire colonization process of plants. Communication between the two couples is extremely complicated throughout the colonization process. The process often begins at the roots and needs endophytic bacteria to recognize certain substances in the root exudates (Afzal *et al*., 2019) [1]. Endophytic bacteria can also be found in the aerial sections of plants, such as stems, leaves, flowers, and cotyledons, however this is less common. Endophytic bacteria may now systematically infect the surrounding plant tissues after they have entered the roots (Fig 1) (Afzal *et al*., 2019; Poria *et al*., 2022; Singh *et al*., 2017) [1, 16, 25].

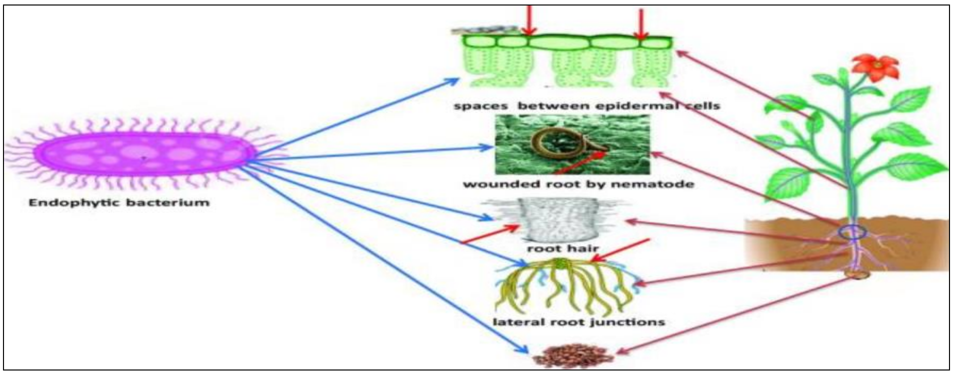

Fig 1: Routes of entry of endophytic bacteria (Singh *et al*., 2017)

1.1 Rhizosphere colonization by the endophytic bacteria

The region of the soil immediately next to the root that is directly impacted by the plant's root exudates known as the rhizosphere. A variety of organic acids, amino acids, sugars, and other tiny compounds that are secreted by plant roots and function as potent chemo-attractants of the soil microbiota are known as root exudates. As a result, the chemical content of the exudates produced by the roots might range significantly depending on the plant species or even variation, which attracts a particular microbial diversity. the ability of the soil microbiota to recognize specific chemical cues enables it to effectively colonize particular rhizospheres and plant root (Santoyo *et al*., 2021) [22].

Endophytic bacteria compete fiercely for resources and space in the rhizosphere during colonization. And bacterial rhizosphere population can be between 107 and 109 cfu/g of the rhizosphere soil, whereas the bacterial rhizoplane population is between 105 and 107 cfu/g fresh weight (Afzal *et al*., 2019). [1] Motility, the capacity to degrade plant cell walls, and the ability to scavenge reactive oxygen species are all characteristics that are necessary for the colonization and establishment of endophytic bacteria in the rhizosphere (Liu *et al*., 2017) [12].

1.2 Root colonization by the endophytic bacteria

Plant roots are colonized by bacterial endophytes, which produce subpopulations with 105–107 cfu/g of fresh weight. Proteobacteria, Actinobacteria, and to a lesser extent Bacteroidetes and Firmicutes dominate the root endophytic microbiome because plant roots serve as "gatekeepers" that separate soil bacteria from the rhizosphere and rhizoplane (Liu *et al*., 2017) [12]. Through polysaccharides, pili, and adhesins, bacteria cling to cell surface structures and travel to root entrance sites by twitching motility. Pectinases and cellulases, in particular, are cell-wall-degrading enzymes that aid in bacterial invasion and dissemination within plants (Fig 2)(Afzal *et al*., 2019; Liu *et al*., 2017) [1, 12].

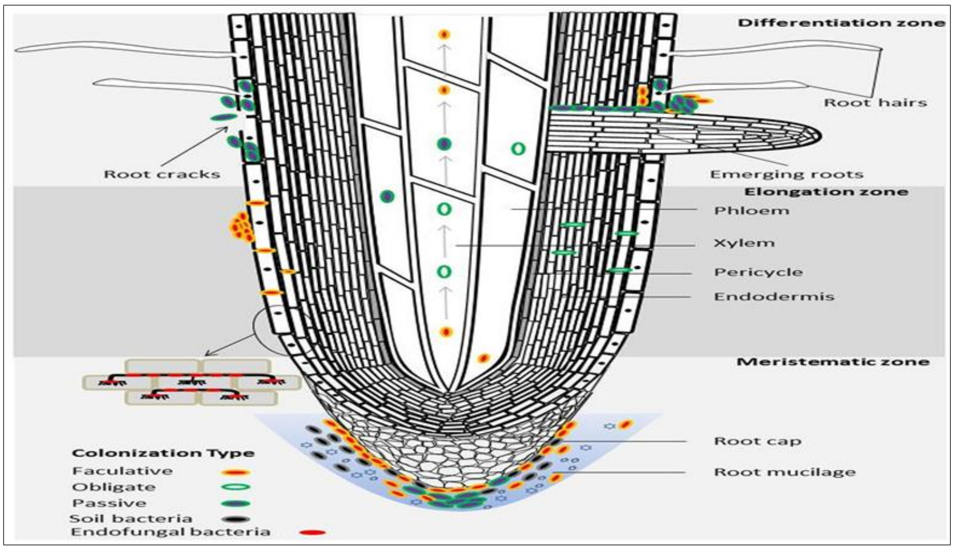

Fig 2: Schematic representation of the bacterial distribution and colonization patterns in the endosphere of a plant root. The emerging sites of lateral roots are among the hotspots of bacterial colonization. Arrows represent the translocation of bacteria inside the xylem and phloem. Endophytic bacteria may engage in different lifestyles as depicted by different colored ovals (Liu *et al*., 2017)

1.3 Systemic Colonization of Aerial Plant Tissues by The Endophytic Bacteria

In natural settings, endophytic bacteria can invade above-ground tissues and reach stem and leaf population densities of 103–104 cfu/gfw. However, physiologic needs restrict colonization of aerial vegetative portions. While movement across xylem components happens through perforated plates, movement inside plants is assisted by flagella and the plant transpiration stream. Endophytic bacteria often colonize leaf tissues via plant roots, although they can also enter leaves through stomata on the leaves (Afzal *et al*., 2019) [1]. Bacterial populations are often bigger in roots and smaller in stems and leaves, despite the fact that endophyte populations vary in different plants depending on a variety of conditions.Furthermore, the species, genotype, tissue, development stage, specialization, variances in the colonization process, and mutual exclusion of various bacterial populations all affect the population density of endophytic bacteria found in plants (Lacava & Azevedo, 2013) [11].

2. Diversity of Endophytic Bacteria

The diversity of endophytic bacteria in plants is influenced by various factors, including the host plant's age, genotype, location, and tissue type, as well as environmental conditions and soil type (Afzal *et al*., 2019; Reinhold-Hurek & Hurek, 2011) [1]. Endophytic bacterial communities can vary significantly within the same plant species grown in different soils. Proteobacteria, including α-, β-, and γ-Proteobacteria, are the most commonly isolated phylum, with γ-Proteobacteria being the most diverse. Other frequently identified groups include Actinobacteria, Bacteroidetes, and Firmicutes, while less common phyla such as Acidobacteria, Planctomycetes, and Verrucomicrobia are also occasionally observed (Afzal *et al*., 2019; Reinhold-Hurek & Hurek, 2011) [1]. The most frequently isolated genera include *Bacillus*, *Pseudomonas*, *Burkholderia*, *Microbacterium*, *Micrococcus*, *Pantoea*, and *Stenotrophomonas*, *with Bacillus and Pseudomonas* being the dominant genera (Table 1.3) (Afzal *et al*., 2019) [1].

Table 1: Diversity of endophytic bacteria isolated from some agronomic and wild plants

Some common endophytic bacterial genera isolated from agronomic plants	
PLANT	**Endophytic bacterial genera**
Alfalfa	*Bacillus, Erwinia, Microbacterium, Pseudomonas, Salmonella.*
Rice	*Agrobacterium, Azoarcus, Azorhizobium, Azospirillum, Bacillus, Bradyrhizobium, Burkholderia, Chromobacterium, Enterobacter, Herbaspirillum.*
Wheat	*Bacillus, Burkholderia, Flavobacterium, Klebsiella, Microbispora, Micrococcus, Micromonospora, Mycobacterium, Nacardiodes, Rathayibacter, Streptomyces.*
Some common endophytic bacterial genera isolated from wild plants	
PLANT	**Endophytic bacterial genera**
Mammillaria fraileana (cactus) (wild rocky habitat)	*Azotobacter vinelandii, Bacillus megaterium, Enterobacter sakazakii, Pseudomonas putida.*
Elymus mollis (sand dunes)	*Acinetobacter, Arthrobacter, Chryseobacterium, Enterobacter, Exiguobaterium, Flavobacterium, Klebsiella, Pedobacter, Pseudomonas, Stenotrophomonas.*
Calystegia soldanella (sand dunes)	*Acinetobacte, Arthrobacter, Chryseobacterium, Curtobacterium, Enterobacter, Microbacterium, Pantoea, Pedobacter, Pseudomonas, Stenotrophomonas.*

3. Mechanisms of Endophytic Bacteria to Plant Growth Promotion

Endophytic bacteria promote plant growth through various mechanisms that involve nutrient acquisition and the production or modulation of phytohormones.

3.1 Nutrient Absorption

Endophytic bacteria enhance the uptake of key nutrients, such as iron (Fe) and zinc (Zn), and are commonly found in genera like *Bacillus, Micrococcus, Staphylococcus, Pseudomonas*, *Pantoea,* and *Kosakonia,* particularly in wheat plants (Makar & Romanyuk, 2022). Their nutrient acquisition mechanisms include:

- **Nitrogen**: These bacteria exhibit nitrogenase activity to fix atmospheric nitrogen and supply it to host plants. For example, species like *Azoarcus sp.*, *Azospirillum brasilense*, *Burkholderia spp.*, and *Herbaspirillum seropedicae* significantly improve host plant biomass (Afzal *et al*., 2019; Bhattacharjee *et al*., 2008) [1].

- **Phosphorus**: Most soil phosphorus exists in insoluble forms. Endophytic bacteria solubilize these compounds by releasing acid phosphatase, improving phosphorus availability to plants. Between 59% and 100% of endophytic populations show phosphate solubilization capabilities, enabling better growth without nutrient supplements (Afzal *et al*., 2019) [1].

- **Iron**: Iron often exists in insoluble forms (ferric Fe^{3+}), inaccessible to plants. Endophytic bacteria produce siderophores—iron-chelating compounds that bind ferric ions—facilitating plant uptake through ligand exchange and root chelation (Afzal *et al*., 2019; Ma *et al*., 2016) [1].

3.2 Production and Modulation of Phytohormones

Endophytic bacteria regulate host plant metabolism and stress response by producing phytohormones like abscisic acid (ABA), cytokinins, ethylene, gibberellins, and indole-3-acetic acid (IAA) (Afzal *et al*., 2019; Hsu *et al*., 2021) [1]. Key pathways include:

1. **Indole Acetic Acid (IAA) Modulation**:
   a. IAA is a critical auxin for cell communication, root formation, and stress tolerance. Endophytic bacteria regulate IAA levels to enhance root growth and control ethylene production, supporting overall plant development (Afzal *et al*., 2019) [1].

2. **Ethylene Regulation**:
   a. Ethylene regulates plant responses to stress but can hinder growth when produced excessively. Endophytic bacteria with ACC deaminase hydrolyze ACC (an ethylene precursor), reducing ethylene levels and enhancing plant growth under stress (Afzal *et al*., 2019; Sun *et al*., 2016) [1, 27].

3. **Gibberellin and Cytokinin Production**:
   a. Endophytic bacteria, such as *Azospirillum lipoferum*, produce gibberellins that aid drought-stressed maize recovery. Additionally, cytokinin-like compounds from bacteria like *Paenibacillus polymaxa* support plant development by breaking seed dormancy and inducing hydrolytic enzymes for germination (Afzal *et al*., 2019; ALKahtani *et al*., 2020) [1, 2].

3.3 Biochemical Changes

3.3.1 Photosynthetic Pigments

Photosynthetic pigments, such as chlorophyll and carotenoids, are essential for plants as they play a key role in photosynthesis by capturing light and producing energy. Chlorophyll is crucial for the photosynthetic process, while carotenoids act as antioxidants and contribute to stress tolerance. Drought stress negatively affects these pigments by causing their degradation and photo-oxidation, leading to oxidative stress in plants. Chlorophyll is particularly sensitive to soil dehydration, while carotenoids help plants resist drought by enhancing their stress response mechanisms (Zhang *et al*., 2021) [36].

Beneficial bacteria, like *Bacillus subtilis*, can improve pigment content under drought conditions. Studies have shown increased chlorophyll levels in rice and higher carotenoid levels in tomatoes after bacterial inoculation, leading to better growth and enhanced drought tolerance (Ruiz-Cisneros *et al*., 2021; Sa *et al*., 2023) [19].

3.3.2 Phenolic and Flavonoids Content

Phenolic compounds and flavonoids are key antioxidants in plants, protecting against oxidative stress by reducing reactive oxygen species (ROS). Phenolic compounds include non-flavonoids (e.g., phenolic acids) and flavonoids, which are further divided into subtypes like flavonols and flavones. These compounds play a critical role in plant defense under abiotic stress, particularly in slow-growing species adapted to long-term stress like drought (Varela *et al*., 2016) [30].

Drought stress typically increases the production of phenolics and flavonoids as a defense mechanism. Beneficial bacteria, such as *Bacillus subtilis* and *Bacillus halotolerans*, further enhance these levels. For example, inoculation with *Bacillus halotolerans* increased flavonoids to 3.89 mg catechin equivalent/g fresh weight under drought conditions, while *Bacillus subtilis* raised phenolic content in tomatoes from 0.42 to 0.90 mg GAE/g (Ruiz-Cisneros *et al*., 2021) [19].

3.3.3 Soluble Proteins

Late embryogenesis abundant (LEA) proteins are hydrophilic and thermally stable proteins that play a critical role in plant dehydration tolerance. These proteins, highly abundant during seed development, are regulated by developmental stages, ABA, and dehydration signals. LEA proteins stabilize membranes and functional proteins during water loss by forming α-helix structures under stress, protecting intracellular metabolism and enhancing drought resistance (Rashid *et al*., 2022) [17].

Beneficial bacteria, such as *Bacillus megaterium*, further enhance drought tolerance. For instance, wheat plants inoculated with *Bacillus megaterium* under drought stress showed a 136% increase in protein content, alongside improvements in water retention, chlorophyll, carotenoids, and proline levels, highlighting the role of LEA proteins in mitigating stress (Yang *et al*., 2021b) [35].

3.3.4 Enzymatic Antioxidants

Plants use antioxidant systems, both enzymatic and non-enzymatic, to protect against reactive oxygen species (ROS) damage. Non-enzymatic antioxidants, such as ascorbate, glutathione, carotenoids, and flavonoids, directly neutralize ROS or act as enzyme substrates. Enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), which collectively maintain ROS at balanced levels. SOD removes superoxide radicals (O_2^-), converting them into hydrogen peroxide (H_2O_2), while CAT and POD eliminate H_2O_2, forming key defenses against oxidative stress. Together, these systems mitigate ROS damage and enhance plant adaptation to drought stress (Yang *et al*., 2021b) [35].

Bacterial inoculation, particularly with *Bacillus spp.*, has been shown to boost peroxidase activity. For example, treated plants exhibited higher peroxidase activity (0.106–0.271 nmol) compared to 0.021 nmol in untreated controls, highlighting the role of bacteria in enhancing enzymatic defenses under stress conditions (Kawas *et al*., 2017) [8].

3.4 Resistance to Phytopathogens

By inhibiting the growth of phytopathogens and plant pests, endophytic bacteria indirectly promote the growth of the host plant. They are capable of producing chemicals such antibiotics, poisons, siderophores, hydrolytic enzymes, and antimicrobial volatile organic compounds that can combat phytopathogens (Afzal *et al*., 2019; Sheoran *et al*., 2015). [1] Endophytic bacteria can target both bacterial and fungal diseases. The most often reported genera of bacteria for their antibiotic action against phytopathogens include *Actinobacteria, Bacillus, Enterobacteor, Paenibacillus, Pseudomonas,* and *Serratia*.(Afzal *et al*., 2019) [1].

Finally the ability of roots to adapt to the characteristics of the soil and boost hydraulic conductivity makes root architecture an essential adaptive attribute for plant drought resistance. In times of drought, deeper roots produce bigger harvests. Plant hormones, ammonia, and nutrient bioavailability are all produced by endophytic bacteria, which increases root length and density. Under the stress of dryness, they also increase suitable solutes like sugars and proline. A plant's ability to respond to environmental stress, including drought stress, can be determined by its relative water content, also known as relative water turgidity (Ullah *et al*., 2019) [29]. Endophytic bacteria work to alleviate drought stress with all the aforementioned mechanism (mechanism of host plant growth promotion) and summarized in (Fig 3) (Ullah *et al*., 2019) [29].

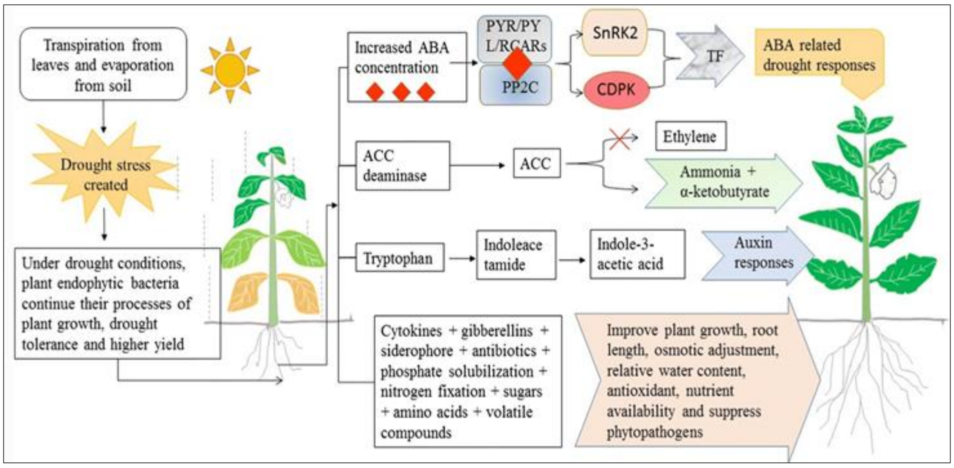

Fig 3: Enhancing drought tolerance by regulating various processes in plants via Endophytic bacteria (Ullah *et al*., 2019)

Numerous crops have been discovered to be able to withstand drought during the past ten years because to endophytic bacteria. *Azospirillum lipoferum* preserved RWC and reduced drought stress in *maize* when it was derived from sugar cane roots. *Trifolium avense*'s relative water content, chlorophyll content, SOD, POD, CAT, proline, and plant biomass were all elevated by *Pseudomonas azotoformans*. Switch grass's starch content, yield, total soluble sugars, and drought-responsive genes were all boosted by *Bacillus subtilis*(Ullah *et al*., 2019) [29]. Endophytic bacteria that can withstand drought have demonstrated promising outcomes in several applications. 26 endophytic bacteria were identified from a study on *Ricinus communis* plants and tested for abilities to withstand drought stress and foster plant development. 22 of them shown drought tolerance up to a minimum water potential of -0.001 MPa, while five of them demonstrated the greatest tolerance up to -1.09 MPa(Trivedi *et al*., 2018) [28]. In Indonesia, 21 drought-resistant endophytic bacteria from healthy tomato plants were discovered, increasing the viability and strength of the seeds (La Fua *et al*., 2021) [10]. And 26 highly osmotolerant endophytic bacteria were discovered in Rajasthan, India, and tested for growth in 30% PEG 6000. In order to increase Cluster bean yield in dry and semi-arid areas, two promising isolates were found (Rathi *et al*., 2018) [18]. Two endophytic bacterial isolates from Algerian prickly pear roots, *Pseudomonas putida* and *P. brassicacearum*, were discovered to stimulate durum wheat development and lessen the signs of drought stress in seedlings treated with these bacteria (Draou *et al*., 2022) [4].

Conclusions

Endophytic bacteria play a critical role in improving plant drought tolerance by enhancing physiological processes like photosynthesis, reactive oxygen species regulation, and osmolyte accumulation. They also optimize root architecture, increasing water and nutrient uptake, which is especially beneficial for crops in drought-prone areas. Studies demonstrate their broad applicability across crops like maize and wheat, offering a sustainable solution for resource-limited regions. Future research should focus on field-scale applications and combining these bacteria with other drought mitigation strategies to maximize benefits for sustainable agriculture.

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