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Microbial approaches for stress tolerance in plants

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Abstract
Climate change has intensified several abiotic stresses such as drought, salinity, extreme temperatures, posing serious threats to global agriculture and food security. Conventional methods of reducing these stressors are frequently expensive, time-consuming, and unsustainable for the environment. In this context, plant growth-promoting microorganisms (PGPM) including rhizobacteria, mycorrhizal fungi, endophytes, and actinomycetes have emerged as eco-friendly and effective alternatives. These microbes enhance plant stress tolerance through diverse mechanisms such as ACC deaminase activity, phytohormone production, osmolyte accumulation, antioxidant enzyme stimulation, and modulation of stress-responsive genes. Under drought and salinity stress, PGPM improve water retention, ion balance, and root architecture, while under temperature and heavy metal stress, they stabilize proteins, detoxify metals, and protect cellular functions. The application of microbial consortia and bioinoculants has shown promise in improving plant resilience under multiple stress conditions. Furthermore, advanced multi-omics technologies—including genomics, transcriptomic, proteomics, and metabolomics—offer deeper insights into plant-microbe interactions, enabling the development of next-generation bioinoculants. Despite demonstrated benefits, challenges such as field variability, strain compatibility, and formulation stability remain. Addressing these gaps through integrated field research, omics-based strain selection, and innovative formulation strategies will pave the way for climate-smart, sustainable agriculture.

Keywords: Climate resilience, Abiotic Stress, Bioinoculants, PGPM

1. Introduction

In an era where climate change intensifies environmental challenges, abiotic and biotic stresses threaten global agriculture with staggering losses, reducing crop yields by up to 50% and costing billions annually [1, 2]. Drought alone slashes global maize and wheat production by 20-40%, incurring losses of approximately $10 billion yearly in developing nations, while salinity affects 800 million hectares of arable land, diminishing yields of crops like rice by up to 70% [3, 2]. Biotic stresses, such as fungal pathogens, further exacerbate the crisis, with diseases like rice blast causing $66 billion in annual losses [4]. These issues highlight the pressing need for sustainable solutions to protect food security and ecosystem resilience. Abiotic pressures including drought, salinity, heat, cold, and heavy metal contamination, as well as biotic difficulties like infections and pests, have become much more frequent and severe due to climate change, endangering the world's food supply. Without the adoption of resilient techniques, crop yields for basic grains such as rice, wheat, and maize are predicted to decrease by 20-50% by the year 2100 [5]. These challenges are exacerbated by climate change, which intensifies stress frequency and severity, threatening food security [6]. Traditional solutions, such as breeding stress-resistant cultivars or employing chemical inputs, are frequently costly, time-consuming, and environmentally unsustainable. As a result, microbial approaches leveraging beneficial microorganisms, including bacteria, fungi, and actinomycetes, have gained attention as eco-friendly and effective strategies to enhance stress tolerance in plants [7].

Plant Growth-Promoting Rhizobacteria (PGPR) play a key role in improving plant stress tolerance through various mechanisms including production of phytohormones, ACC deaminase activity, siderophore production, and induced systemic tolerance [8, 9]. They colonize the root system and help in better water and nutrient uptake, which enhances drought and salinity tolerance. For instance, Bacillus spp. And Pseudomonas spp. Have been shown to induce systemic tolerance in plants against salinity and drought stress through modulation of antioxidant enzymes and osmolyte accumulation [10]. Similarly, *Azospirillum brasilense* improved drought resistance in maize by enhancing root architecture and proline content [11]. Mycorrhizal fungi, especially Arbuscular Mycorrhizal Fungi (AMF), form symbiotic associations with plant roots and significantly improve nutrient uptake (especially phosphorus) under stress conditions [12]. AMF enhance plant tolerance to salinity and drought by maintaining better osmotic balance and reducing oxidative damage [13]. Endophytic fungi and bacteria also contribute to stress tolerance. For example, *Piriformospora indica*, an endophytic fungus, enhances drought and heat tolerance by increasing antioxidant activity and maintaining hormonal balance [14]. Microbial inoculants also assist in heavy metal stress tolerance. Certain strains of Rhizobium, Pseudomonas, and Bacillus can immobilize or transform toxic metals like cadmium and lead, thereby reducing their bioavailability to plants [15, 16].

Moreover, microbes can trigger plant defence systems by activating genes related to stress tolerance, resulting in better plant health under unfavourable conditions [17]. Recent advances in microbial biotechnology and metagenomics have helped identify novel microbes and their stress-related genes, which can be further used to develop bioformulations [18]. These bacteria aid in hormone regulation, osmolyte synthesis, antioxidant enzyme activity, nutrient solubilization, and induced systemic resistance [9]. Unlike chemical treatments, microbial techniques are inexpensive, environmentally safe, and long-lasting, making them ideal for sustainable agriculture. These microorganisms interact with plants through symbiotic or associative relationships, promoting growth, enhancing nutrient uptake, and mitigating stress effects via mechanisms like phytohormone production, antioxidant activity, and modulation of stress-related gene expression [7, 19]. The use of microbes offers a cost-effective, environmentally sustainable solution to improve stress resilience in agriculture and bioremediation.

Hence, this review is planned with the following objectives:

To identify and study different types of helpful microbes that support plants during stressful conditions like drought.

To understand how these microbes help plants deal with problems such as lack of water, salty soil, extreme temperatures, and harmful metals - both at the physiological and molecular level.

To collect and review recent studies on using mixtures of microbes (called microbial consortia) and special microbial products (bioinoculants) to protect plants from stress.

To explore how advanced techniques like genomics and proteomics (multi-omics) help us learn more about how plants and microbes work together during stress.

2. Plant-microbe interactions under abiotic stress

The relationships between microbes and plants are dynamic and intricate, particularly when abiotic stress is present. A varied community of microorganisms interacts with plants in the rhizosphere, the soil zone around plant roots, frequently increasing the plants' resistance to challenges including salinity, drought, heavy metals, and extreme temperatures. Actinomycetes, arbuscular mycorrhizal fungi (AMF), endophytic bacteria, and plant growth-promoting rhizobacteria (PGPR) are examples of beneficial microorganisms that each play a unique role in minimizing the negative effects of abiotic stress and improving plant health. These microbes help plants survive and adapt to environmental stress conditions through a variety of direct and indirect mechanisms, including phytohormone production, increased nutrient uptake, antioxidant activity, and induced systemic resistance [20-22]. Direct mechanisms that improve nutrient availability include nitrogen fixation, siderophore production, and phytohormone production (such as auxins, gibberellins, and cytokinins). Indirect mechanisms involve induced systemic resistance (ISR), antioxidant enzyme activation, and modulation of stress-related gene expression [23].

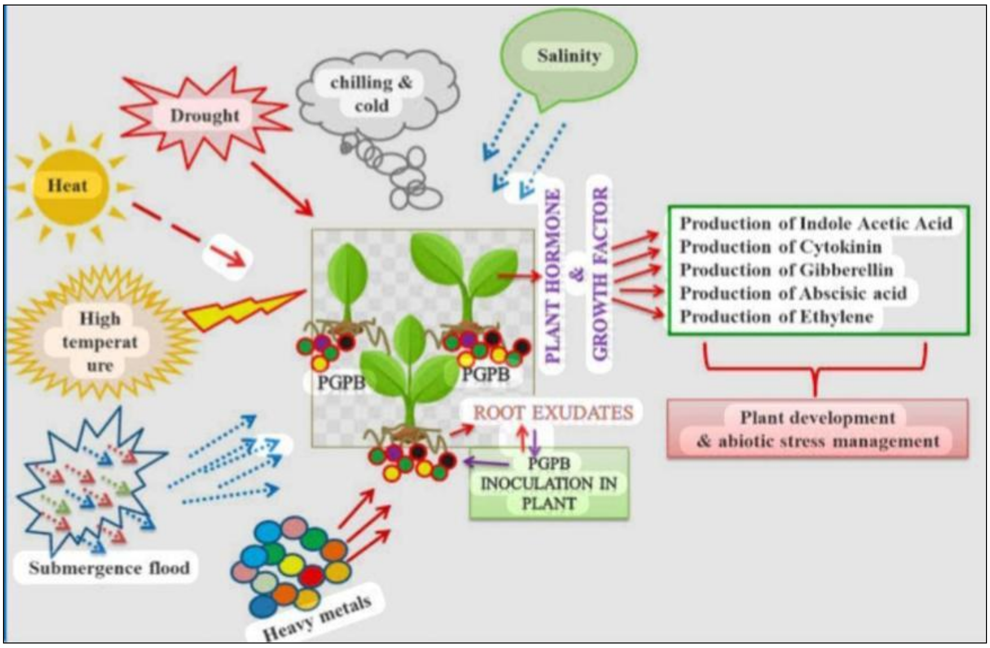

Fig 1: Mechanisms by which plant growth-promoting bacteria alleviate abiotic stress in plants through hormone regulation and modulation of stress-responsive genes [22, 23].

2.1 Drought Stress

Under stress, microbial inoculation leads to enhanced root architecture, improved water uptake, and increased chlorophyll content. For example, *Azospirillum* spp. And Bacillus spp. Are Drought stress is a major abiotic limitation that affects plant growth, production, and physiology. It reduces water availability, inhibits root elongation, limits nutrient uptake, and leads to the accumulation of reactive oxygen species (ROS), which induce oxidative damage at the cellular level. PGPM promote plant drought tolerance through a variety of biochemical, physiological, and molecular pathways that improve water-use efficiency, root growth, and cellular homeostasis.

2.1.1 ACC deaminase activity: regulation of ethylene levels

Plants create high quantities of ethylene during drought stress, which limits root elongation and shoot development. PGPM such as Azospirillum, Pseudomonas, and Bacillus spp. Produce the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which degrades ACC, the precursor of ethylene. This decrease in ethylene levels promotes root and shoot growth under stressful conditions [27].

2.1.2 Exopolysaccharide (EPS) production

Some PGPM produce exopolysaccharides (EPS), which form a protective biofilm around plant roots. This biofilm promotes soil aggregation, increases water retention, and decreases evapotranspiration, allowing the plant to stay hydrated even during drought circumstances [28].

2.1.3 Osmoprotectant Accumulation

PGPM promote the synthesis of compatible solutes and osmoprotectants like proline, glycine betaine, and trehalose. These compounds are essential for osmotic adjustment, cell turgor maintenance, protein stabilization, and membrane protection against desiccation-induced damage [29].

2.1.4 Improved Root Morphology

Rhizobacteria and arbuscular mycorrhizal fungi produce phytohormones such as indole-3-acetic acid (IAA), which promote root growth and branching, hence increasing root surface area and depth. This increases the plant’s ability to explore a larger soil volume for moisture and nutrients [30].

2.1.5 Mycorrhizal Associations

Arbuscular mycorrhizal fungi (AMF), such as Glomus spp., create symbiotic relationships with roots and extend the root network by extramatrical hyphae. This increases water and nutrient intake, particularly phosphorus, and improves the plant’s drought resistance [31].

2.1.6 Modulating gene expression

PGPM can activate drought-responsive genes such as DREB2A (Dehydration-Responsive Element Binding Protein) and LEA (Late Embryogenesis Abundant). These genes participate in protective biological responses such as osmolyte production and stress signal transmission [22].

2.2 Salinity Stress

Plants exposed to salinity stress produce damaging reactive oxygen species (ROS) such as superoxide radicals, hydrogen peroxide, and hydroxyl radicals, which induce antioxidant enzymes. These chemicals harm lipids, proteins, and nucleic acids, thereby affecting normal cellular processes [33]. Plant Growth-Promoting Microorganisms (PGPM) boost the plant’s antioxidant defense by producing enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). SOD transforms harmful superoxide radicals to hydrogen peroxide, which is then broken down into water and oxygen by CAT and APX [34]. This enzymatic function lowers oxidative stress, allowing plants to maintain metabolic balance under saline conditions [35].

2.2.1 Phytohormone Production

PGPM also produce phytohormones such as indole-3-acetic acid (IAA) and gibberellins, which aid in root elongation, shoot growth, and nutrient absorption [36]. Enhanced root systems improve water and nutrient uptake while boosting salt tolerance. Furthermore, several PGPM exhibit ACC deaminase activity, which degrades 1-aminocyclopropane-1-carboxylate (ACC), an immediate precursor of ethylene. Plants overproduce ethylene under stress, which inhibits development and causes premature senescence. PGPM lower ethylene levels, reducing stress-induced growth inhibition and helping plants maintain productivity under salinity stress [27, 37].

2.2.2 Nutrient Solubilization

PGPM increase nutrient availability (e.g., phosphorus, nitrogen) under saline conditions, compensating for nutrient deficits caused by ion competition. Pseudomonas fluorescens has been reported to improve salinity tolerance in wheat by boosting SOD and CAT activities, thereby reducing oxidative damage [38]. These bacteria enhance plant growth and biomass by promoting K^+ absorption and producing EPS in high-salt environments. By upregulating stress-responsive genes (e.g., SOS1, NHX1), halotolerant PGPM such as Bacillus subtilis and Streptomyces spp. Produce volatile organic compounds (VOCs) that initiate systemic salt tolerance. Rhizophagus irregularis and other arbuscular mycorrhizal fungi (AMF) increase plant vigor by improving nutrient uptake (particularly P and K^+) in saline soils. Additionally, certain PGPM release organic acids that chelate Na^+, thereby reducing ion toxicity in the rhizosphere.

2.3 Temperature stress

High temperatures impair photosynthesis, membrane integrity, and protein activity, leading to ROS accumulation. PGPM mitigate heat and cold stress by strengthening stress-response pathways and maintaining cellular structures. They produce heat shock proteins (HSPs) under high temperatures and cold-responsive proteins (e.g., COR genes) under low temperatures, which help stabilize cellular proteins [39]. Additionally, modifications in membrane lipid composition induced by PGPM maintain fluidity and functionality under temperature extremes. PGPM also enhance antioxidant systems to counteract temperature-induced oxidative stress, improving overall plant tolerance.

2.3.1 Protein stabilization

High or low temperatures can denature plant proteins, disrupting enzyme function and metabolism. Plant growth-promoting microorganisms (PGPM) promote protein stability by increasing the production of heat shock proteins (HSPs) under high-temperature stress. HSPs function as molecular chaperones, promoting normal protein folding, preventing aggregation, and mending damaged proteins [40]. Under low-temperature stress, PGPM can activate cold-responsive (COR) genes, which express protective proteins that assist in sustaining enzyme performance and structural integrity at lower temperatures [41]. This joint response allows plants to maintain functional proteins, ensuring normal physiological functions under temperature stress.

2.3.2 Membrane modification

Temperature stress can impact the fluidity and stability of plant cell membranes. High temperatures can make membranes overly fluid, while low temperatures can cause them to stiffen, both of which hinder transport activities and cell signaling. PGPM aids membrane adaptability by changing the lipid composition, for example, increasing the amount of unsaturated fatty acids. Unsaturated lipids stay more fluid at low temperatures and contribute to membrane integrity at high temperatures [42]. By changing membrane lipid profiles, PGPM allows plants to maintain optimal membrane function even in severe temperatures.

2.3.3 Regulation of Phytohormones

To control stress signaling and encourage growth, PGPM generate hormones such as gibberellins and IAA. Ethylene-mediated stress reactions are lessened by ACC deaminase.

2.3.4 Osmolyte accumulation

To sustain cellular structures under temperature stress, PGPM synthesize osmolytes, such as trehalose. For instance, Bacillus subtilis and Pseudomonas species increase thermotolerance in crops by raising osmolyte levels (such as proline) and antioxidant enzyme activity (SOD, CAT), according to Chowdhury *et al.* [43]. Additionally, these microorganisms produce HSPs, which enhance plant life by shielding proteins from heat stress. Under heat stress, PGPM such as Trichoderma spp. Increase plant aquaporins, which enhances water transport and cellular hydration. During cold stress, antifreeze proteins produced by cold-tolerant PGPM, including Pseudomonas fluorescens, prevent ice crystal formation in plant tissues. Systemic acquired resistance (SAR), which increases a plant's resistance to temperature changes, can be triggered by VOCs from PGPM.

2.3.5 Heavy metal stress

Heavy metals, such as Cd, Pb, and As, interfere with enzyme activity, produce reactive oxygen species, and hinder nutrient absorption. Through a variety of mechanisms, PGPM improves plant tolerance and detoxifies metals.

2.3.5 Biosorption and bioaccumulation

PGPM reduces the bioavailability of heavy metals to plants by binding or sequestering them on their cell walls or inside cells. Production of Siderophore: Siderophore enhance iron availability by chelating harmful elements (such as Cd and Pb) and limiting their uptake by roots. Metallothioneins and Glutathione: To counteract metal-induced ROS and detoxify metals within cells, PGPM produces metallothioneins and glutathione. In order to immobilize harmful metals in the soil and decrease their uptake by plants, PGPM solubilizes phosphates and forms insoluble metal-phosphate complexes.

Antioxidant Defences: To lessen oxidative stress brought on by heavy metals, PGPM increases plant antioxidant enzymes. For instance, Pseudomonas and Bacillus species sequester Cd and Pb in contaminated soils, decreasing metal uptake and increasing plant biomass [44]. These microorganisms bind metals and promote plant growth by producing EPS and siderophores. Rhizobium and Azotobacter are examples of PGPM that create organic acids (such as citric and oxalic acid) that chelate metals and lessen their toxicity. Glomus mosseae and other mycorrhizal fungus envelop roots in a protective layer that prevents metals from moving to the shoots. Certain PGPM improve internal metal detoxification by inducing the genes of plant metallothioneins (e.g., MT1, MT2).

3. Microbial mixtures and bioinoculants for stress control

To improve plant stress tolerance, microbial consortiums — combinations of two or more suitable microorganisms — have significantly replaced single-strain microbial inoculants in the last ten years. These consortia aim to enhance plant growth, nutrient availability, and resistance to abiotic stressors such as heat, salt, drought, and heavy metal toxicity. Arbuscular mycorrhizal fungi (AMF), nitrogen-fixing bacteria, endophytes, and plant growth-promoting rhizobacteria (PGPR) are frequently found in these consortia. According to Malusá and Vassilev [45], the rationale behind this strategy is that a consortium can deliver multiple benefits simultaneously more effectively than individual strains, including hormone modulation, antioxidant stimulation, osmolyte synthesis, and enhanced soil structure. Recent studies have demonstrated the effectiveness of microbial consortia across various crops and stress conditions. For example, Ortiz *et al.* [46] reported that a combination of Glomus intraradices and Bacillus subtilis significantly improved drought tolerance and nutrient uptake in wheat. Similarly, a consortium of Azospirillum, Pseudomonas, and Rhizobium enhanced maize salt tolerance by regulating osmotic balance and activating antioxidant enzymes [47]. These results highlight the potential of consortium-based bioinoculants to simultaneously combat multiple stresses, a key advantage amid climate change.

The development of bioinoculants—commercial formulations of beneficial microbes—has rapidly progressed. These formulations are applied as foliar sprays, seed coatings, or soil amendments and are often delivered via liquid suspensions, peat, or lignite. Bioinoculants containing stress-tolerant strains such as heat- or salt-resistant Bacillus spp. Are increasingly developed for specific agro-ecological conditions [48]. Examples include products like BioSalinity and Rhizogold that utilize PGPR strains to confer drought and salinity tolerance. However, environmental variability, plant genotype, and soil heterogeneity often influence bioinoculant efficacy in the field. Therefore, current research emphasizes the need for environmentally compatible, functionally complementary multi-strain formulations alongside omics-based strain selection and formulation design [49].

4. Using multi-omics to understand plant-microbe stress responses

Advanced scientific techniques transcriptomic, proteomics, metabolomics, and genomics — collectively termed multi-omics approaches, have emerged as powerful tools to elucidate how microbes and plants cooperate to withstand abiotic stresses such as drought, salinity, temperature extremes, and heavy metal toxicity. These tools enable comprehensive analysis of genes (genomics), gene expression (transcriptomic), proteins (proteomics), and metabolites (metabolomics) involved in stress responses.

For instance: Genomics helps identify microbial genes responsible for producing exopolysaccharides (EPS) and enzymes like ACC deaminase that facilitate plant stress tolerance [50]. Transcriptomic reveals stress-activated genes in both plants and microbes, including drought-responsive element-binding proteins (DREB), heat shock proteins (HSPs), and aquaporins that protect plants from damage [51]. Proteomics analyzes proteins synthesized under stress conditions, such as antioxidant enzymes and molecular chaperones, aiding cellular protection [52]. Metabolomics studies small molecules like proline, glycine betaine, and glutathione that accumulate during stress to maintain cellular homeostasis [53]. By integrating multi-omics data, researchers gain a holistic understanding of plant-microbe interactions under stress, which aids in selecting or engineering microbial strains with enhanced functional traits for bioinoculant development. This integrative approach also facilitates identification of beneficial microbial partners and stress-related genes for crop breeding or biotechnological interventions, making multi-omics indispensable for modern sustainable agriculture.

5. Researcher gaps and limitations

Despite numerous studies confirming microbial assistance in plant stress tolerance, several gaps and practical limitations remain. Most successful results have been reported from controlled laboratory or greenhouse experiments that do not fully represent complex field environments. The efficacy of microbial inoculants is often inconsistent due to variability in soil types, climatic conditions, moisture, and crop species in real agricultural settings [45]. Another critical gap is the limited understanding of interactions among diverse microorganisms within consortia and with host plants. Microbial competition or antagonism can reduce overall effectiveness. Additionally, the colonization potential and long-term survival of beneficial microbes in the rhizosphere, especially under severe stress, remain poorly understood. Some bioinoculants fail to persist long enough to benefit plants meaningfully. Most omics research focuses on model crops like rice and Arabidopsis, leaving molecular stress pathways in non-model or underutilized crops largely unexplored. Finally, farmers often lack awareness and training regarding optimal timing, methods, and management of microbial inoculants, limiting adoption [48]. Bridging these gaps requires more extensive field trials, refined strain selection using omics, and stronger collaboration between researchers, industry, and farmers.

6. Future scope and research directions

Microbial approaches hold substantial promise to sustainably improve plant resistance against abiotic stresses. To realize this potential, future research must prioritize several key areas Expanding extensive field-based trials is essential to evaluate bioinoculant consistency and effectiveness across diverse agro-climatic zones, considering soil heterogeneity, climate change, and crop genotypes [47]. Development of crop- and region-specific microbial consortia tailored to local soil, plant, and environmental conditions should be emphasized. Advanced multi-omics techniques will continue to deepen understanding of plant-microbe interactions and enable identification of elite microbial strains and key stress-responsive genes [49]. Bioinoculant formulation improvements are crucial. Many current products have limited shelf life and stability, especially under high temperature or prolonged storage. Innovations in encapsulation, liquid carriers, and biofilm-based delivery systems can enhance microbial viability and efficacy [45]. Integrating artificial intelligence (AI), machine learning, and bioinformatics in microbiome research is an exciting frontier. These tools can analyze large omics datasets, predict optimal microbe-plant-environment combinations, and guide precise microbial applications [50]. Overall, advances in biotechnology, omics, and digital agriculture will enable next-generation bioinoculants that are cost-effective, robust, and customized for specific farming systems, promoting climate-smart and sustainable agriculture globally.

7. Conclusion

Drought, salinity, extreme temperatures, and heavy metal toxicity impose significant challenges to modern agriculture by affecting plant growth, physiology, and yield. Plant growth-promoting microorganisms (PGPM), including rhizobacteria, endophytes, actinomycetes, and mycorrhizal fungi, have emerged as effective, eco-friendly solutions to enhance plant tolerance against these stresses. PGPM mitigate stress by producing key enzymes like ACC deaminase to lower ethylene levels, synthesizing osmoprotectants such as proline and glycine betaine, enhancing antioxidant defense, and releasing exopolysaccharides to improve soil structure and water retention. They also promote nutrient uptake, stimulate root development, and activate stress-responsive genes (e.g., DREB, LEA), enabling plants to adjust molecularly to adverse conditions. Continued research integrating microbial consortia, bioinoculant formulation, multi-omics approaches, and advanced computational tools holds great promise to develop sustainable strategies for stress-resilient agriculture

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