



Resilience of Beneficial Plant-Microbe Interactions in a Changing Global Climate: Emerging Concepts and Future Prospects

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Abstract

Climate change is intensifying both abiotic stresses such as drought, salinity, and heat and biotic stresses from pathogens and pests, collectively threatening global food production. These environmental pressures disrupt plant physiology, impair nutrient uptake, and weaken defence systems, while also altering soil microbial communities and their beneficial functions. Plant-associated beneficial microorganisms, including rhizobacteria, endophytes and mycorrhizal fungi, have emerged as key allies in bolstering crop resilience. These microbes enhance plant tolerance through multiple mechanisms: they improve nutrient acquisition, modulate phytohormone signalling, produce stress-alleviating metabolites (including siderophores, osmolytes and antimicrobial compounds), strengthen antioxidant defences and activate systemic resistance pathways such as induced systemic resistance (ISR) and systemic acquired resistance (SAR). Recent advances in microbial consortia and stress-responsive signalling networks highlight the potential of multifunctional microbes to sustain crop productivity under changing climatic conditions. Nevertheless, translating these promising laboratory findings into reliable field applications faces substantial hurdles, including inconsistent performance, limited shelf life and inadequate formulation stability. This review synthesizes current understanding of beneficial plant–microbe interactions under climate-induced stresses, compares the effectiveness of diverse microbial strains and consortia, and identifies critical knowledge gaps. We propose strategic priorities for future research and agricultural implementation, including strain banking, long-term field validation, formulation standardization and integration with precision agriculture. Harnessing beneficial microbes as climate-smart solutions offers an effective pathway towards improving crop productivity, restoring soil health and strengthening global food security in an era of environmental change.

Keywords: Climate Change; Plant Microbe Interaction; Acquired Systemic Resistance; Induced Systemic Resistance

Introduction

Climate change represents one of the most pressing challenges to global food security in the twenty-first century. Ecological stressors driven by rising temperatures, altered precipitation patterns, increasing atmospheric CO₂ concentrations, and soil degradation collectively contribute to substantial declines in agricultural productivity worldwide (Battisti & Naylor, 2009; Mirzabaev et al., 2023). With the global population projected to reach approximately 8.9 billion by 2050 (Singh et al., 2011), the demand for food production intensifies, while traditional

farming systems become increasingly unsustainable due to environmental degradation and intensive agricultural practices (Wassmann et al., 2009; Masciarelli et al., 2014). Furthermore, the excessive application of agrochemicals—including fertilizers, pesticides, and herbicides—has led to a significant decline in beneficial microbial diversity within agroecosystems, exacerbating soil health deterioration and reducing ecosystem resilience. Agroecosystems are continuously subjected to both abiotic and biotic stressors, which are amplified by climate change. Abiotic stressors, including extreme temperatures, drought, salinity, heavy metal pollution, and elevated CO₂ levels, account for approximately 50% of global agricultural production losses, while biotic stressors contribute around 30% (Chodak et al., 2015; Prasad, 2021a; Sinha et al., 2022). These stressors disrupt plant physiological, biochemical, and molecular processes, impair nutrient uptake, increase oxidative damage, and weaken plant defense systems, ultimately leading to reduced crop yields and food quality. A critical consequence of these stresses is the decline in soil microbial diversity, which disrupts nutrient cycling, reduces soil fertility, and compromises ecosystem stability. In response to these challenges, plant-associated beneficial microbes, including rhizobacteria, endophytes, and mycorrhizal fungi—have emerged as promising sustainable tools for enhancing plant resilience under adverse environmental conditions. These microorganisms enhance nutrient acquisition, regulate phytohormone balance, produce stress-alleviating metabolites (e.g., siderophores, osmolytes, exopolysaccharides, and antimicrobial compounds), strengthen antioxidant defense systems, and activate plant immune responses, including systemic acquired resistance (SAR) and induced systemic resistance (ISR) (Finkel et al., 2017; Vimal et al., 2017; Santoyo et al., 2021). Notable plant growth-promoting bacterial genera includes *Pseudomonas*, *Enterobacter*, *Bacillus*, *Variovorax*, *Klebsiella*, *Burkholderia*, *Azospirillum*, *Serratia*, and *Azotobacter* (Prasad, 2021b).

Despite substantial progress in understanding plant–microbe interactions under controlled conditions, several critical knowledge gaps remain unresolved. These include inconsistent field performance of microbial inoculants, limited understanding of molecular signaling under combined stress scenarios, insufficient characterization of microbial community dynamics, and challenges related to formulation stability, shelf life, and delivery methods. Addressing these gaps is essential for translating laboratory findings into reliable, field-ready agricultural solutions. Therefore, this review aims to comprehensively synthesize the role of beneficial plant–microbe interactions in mitigating climate change-induced abiotic and biotic stresses, while identifying emerging concepts, knowledge gaps, and future research priorities for sustainable agriculture. The scope encompasses an elucidation of mechanisms by which plant growth-promoting microorganisms—including rhizobacteria, endophytes, and mycorrhizal fungi—enhance stress tolerance; a comparative evaluation of microbial strains and consortia across diverse environmental conditions; an examination of molecular signaling pathways (SAR, ISR, and phytohormone crosstalk); identification of practical challenges limiting commercial application (formulation stability, shelf life, delivery methods); and the proposal of strategic priorities for future research, policy development, and climate-smart agricultural implementation.

Beneficial Plant-microbe interactions assisting climate change

Bacterial and fungal species form beneficial relations with plants, significantly enhancing plant growth and development under adverse climatic conditions (Nadeem et al., 2014; Santoyo et al., 2021; Prasad, 2023a, 2023b). These microbes pay both direct and indirect mechanisms to support PH during stress, involving a wide range of biochemical and molecular processes. They contribute to plant growth through the production of plant growth regulators (PGRs), modulation of hormonal and nutrient balances, and induction of resistance against phytopathogens (Spence and Bais, 2015; Dhawi, 2023). Many valuable microbes produce specific metabolites that suppress pathogenic organisms in the rhizosphere. Such as siderophores produced by rhizospheric microbes chelate

iron, thereby reducing its availability to plant pathogens and limiting their growth (Zloch et al., 2016). In addition to biocontrol, these microbes improve plant productivity by fixing atmospheric nitrogen (FAN), solubilizing phosphate (P), and producing plant hormones like auxins, cytokinins, and gibberellins (Ahmad et al., 2011; Prasad, 2022a). Other beneficial mechanisms include nutrient mobilization, exopolysaccharide production, and the synthesis of Rhizobitoxine—an ethylene inhibitor that promotes root development and plant growth under stress (Vardharajula et al., 2011; Prasad, 2022b). Rhizobitoxine suppresses ethylene biosynthesis, which is commonly elevated under stress and can inhibit plant growth (Kumar et al., 2009). Furthermore, microbial enzymes such as 1-Aminocyclopropane-1-carboxylic acid (ACC) deaminase, chitinase, and glucanase have been shown to improve plant tolerance to abiotic and biotic stresses by reducing ethylene levels and degrading pathogen cell walls (Farooq et al., 2009; Shahid et al., 2023). Certain bacteria also possess sigma factors—regulatory proteins that help modify gene expression in response to environmental stress, thereby improving plant survival under adverse conditions (Gupta et al., 2013). Fungi, mostly ecto and endomycorrhizae, form symbiotic associations with plant roots in agricultural soils. These fungal interactions play a key role in nutrient cycling, improving nutrient absorption, translocation, and ultimately contributing to improved plant growth and development (Prasad, 2022c). Collectively, the interactions between plants and useful microbes offer a promising and sustainable approach to mitigating the effects of climate change, improving crop resilience, and ensuring future global food security.

Microbial Interactions in a Changing Global Climate

Microbial interactions play a central role in maintaining agricultural productivity and soil ecosystem stability under changing climatic conditions. Soil microorganisms, including bacteria, fungi, archaea, and actinomycetes, are essential for nutrient cycling, organic matter decomposition, soil aggregation, and plant health. However, climate change-associated factors such as rising temperatures, irregular rainfall patterns, prolonged drought, flooding, salinity, and elevated atmospheric CO₂ significantly influence the structure and function of soil microbial communities. These environmental stresses can alter microbial diversity, disrupt beneficial plant–microbe associations, and ultimately reduce soil fertility and crop performance. Since microorganisms respond rapidly to environmental fluctuations, shifts in microbial communities are often among the earliest indicators of climate-induced changes in agroecosystems. Plant-associated microbes are particularly important in helping crops adapt to abiotic and biotic stresses caused by climate change. Beneficial rhizobacteria and mycorrhizal fungi enhance nutrient availability, improve water uptake, stimulate root growth, and regulate stress-responsive mechanisms in plants. Symbiotic microorganisms such as nitrogen-fixing bacteria contribute to maintaining soil nitrogen balance and sustaining crop productivity under nutrient-limited conditions. However, climatic disturbances may negatively affect these beneficial interactions by reducing microbial survival, colonization efficiency, and functional activity in the rhizosphere. For example, drought conditions often decrease microbial biomass and enzymatic activity, while excessive soil moisture can create anaerobic environments that suppress beneficial microbes and promote pathogenic populations.

Climate-driven changes in microbial activity also influence greenhouse gas emissions and carbon cycling in agricultural soils. Increased soil temperatures may accelerate microbial decomposition of organic matter, leading to higher emissions of carbon dioxide and methane, which further contribute to global warming. At the same time, certain microbial groups can support climate change mitigation by promoting soil carbon sequestration and improving soil structure. Understanding these microbial processes is therefore essential for developing sustainable agricultural practices aimed at enhancing soil resilience and maintaining long-term food security. Studying microbial interactions under climate stress provides valuable opportunities for improving climate-resilient agriculture. Manipulation of beneficial microbial communities through biofertilizers, microbial consortia, and

rhizosphere engineering has emerged as an environmentally sustainable strategy to reduce dependence on chemical fertilizers and pesticides. Such approaches can improve crop tolerance to environmental stress, enhance nutrient use efficiency, and restore degraded soils. Therefore, integrating knowledge of plant–microbe interactions into climate-smart agricultural systems is crucial for sustaining crop productivity, preserving soil health, and mitigating the adverse effects of climate change on global food systems

Molecular Signaling Pathways and Genes in Plant–Microbe Biotic Stress Responses

Beneficial microbes trigger complex molecular signaling networks in plants to enhance resistance against pathogens. Two major systemic defense pathways are Induced Systemic Resistance (ISR) and Systemic Acquired Resistance (SAR): ISR is typically induced by *PGPR* (*Pseudomonas*, *Bacillus*) through jasmonic acid (JA) and ethylene (ET) signaling activation of these pathways leads to transcription of defense-related genes and enhanced resistance, especially to necrotrophic pathogens. Microbe-associated molecular patterns (MAMPs) such as flagellin or chitin trigger IF-like responses through pattern recognition receptors (PRRs) on plant cell membranes. Beneficial microbes also produce elicitors like siderophores and volatile organic compounds (VOCs) that modulate plant defense signaling. SAR is often linked to salicylic acid (SA) accumulation, leading to activation of NPR1 (Non-Expressor of PR genes 1) and increased expression of PR genes (PR1, PR2, PR5), strengthening structural defenses and enhancing systemic protection. SA signaling also integrates with local pathogen recognition to establish long-term immunity (Figure 1).

Key plant genes and regulatory factors: Key plant genes and regulatory factors involved in biotic stress responses include NPR1, a central regulator that links salicylic acid (SA) signaling to the activation of pathogenesis-related (PR) gene expression. Among the PR proteins, PR1, PR2, and PR5 are widely recognized as molecular markers of systemic acquired resistance (SAR) and are consistently upregulated during pathogen attack. In addition, WRKY transcription factors play a crucial role in modulating defense-related gene networks by regulating the expression of downstream target genes associated with immune responses. Furthermore, jasmonic acid (JA) and ethylene (ET)-responsive genes are activated during induced systemic resistance (ISR), particularly in response to beneficial rhizobacteria. Other important regulatory components include mitogen-activated protein kinase (MAPK) cascades, which transduce extracellular stress signals into intracellular responses, and calcium-dependent protein kinases (CDPKs), which mediate calcium signaling during early defense activation. Transcription factor families such as MYB and bZIP also contribute to the fine-tuning of defense pathways by coordinating hormonal crosstalk between SA, JA, and ET signaling networks. Additionally, genes involved in the production of reactive oxygen species (ROS), such as respiratory burst oxidase homologs (RBOHs), play a vital role in the oxidative burst that restricts pathogen spread. Together, these genes and regulatory elements form a complex and integrated network that enables plants to perceive, respond to, and adapt to biotic stress conditions.

Comparative Effectiveness of Microbial Strains: Comparative studies on microbial inoculants have demonstrated significant variation in effectiveness among different strains and their combinations. These differences are often attributed to variations in colonization ability, metabolite production, and compatibility with host plants. For instance, certain strains of plant growth promoting rhizobacteria (PGPR) exhibit superior performance due to their enhanced capacity to produce phytohormones, solubilize nutrients, and induce systemic resistance. Moreover, synergistic interactions observed in microbial consortia frequently result in greater efficacy compared to single-strain applications. Such consortia can improve nutrient acquisition, suppress phytopathogens, and enhance plant tolerance to environmental stress through complementary functional traits. However, the effectiveness of these combinations is highly context-dependent and influenced by factors such as soil type,

environmental conditions, and plant genotype. Recent research also highlights that not all strain combinations produce additive or beneficial effects; in some cases, antagonistic interactions may reduce overall performance. Therefore, careful selection and evaluation of compatible microbial partners are essential for optimizing their application in sustainable agriculture. Overall, these findings underscore the importance of strain-specific and environment-specific assessments when developing microbial-based strategies for crop improvement.

Bacterial Strains: *Bacillus* and *Pseudomonas*: Comparative evaluations of bacterial biocontrol agents, particularly *Bacillus* and *Pseudomonas* species, reveal notable differences in their effectiveness against plant pathogens. Strains of *Bacillus subtilis* are frequently reported to exhibit strong biocontrol potential, contributing to reduced disease severity and enhanced activity of defense-related enzymes in crops such as wheat affected by powdery mildew. In one study, the *B. subtilis* strain DTBS-5 demonstrated greater efficacy at the seed treatment stage compared to *Bacillus amyloliquefaciens* and *Pseudomonas fluorescens*. Meta-analytical evidence further suggests that *Pseudomonas* spp. may, in some cases, provide greater overall disease suppression, particularly against bacterial wilt caused by *Ralstonia solanacearum*, indicating taxon-specific functional advantages. These differences are often linked to distinct mechanisms of action. For example, *Pseudomonas* species are well known for the production of siderophores, antibiotics, and hydrogen cyanide, which contribute to pathogen inhibition and competitive exclusion in the rhizosphere. In contrast, *Bacillus* species are recognized for their ability to form endospores, produce lipopeptide antibiotics (such as surfactin, iturin, and fengycin), and maintain stability under adverse environmental conditions. In addition, quorum sensing (QS) and quorum quenching (QQ) mechanisms play a critical role in microbial interactions. Genes such as *aiiA* in *Bacillus* spp. are involved in the degradation of signaling molecules (e.g., N-acyl homoserine lactones), thereby disrupting pathogen communication and reducing virulence. Beyond QS interference, both genera are also capable of inducing systemic resistance in plants, modulating host defense pathways associated with salicylic acid, jasmonic acid, and ethylene signaling. Overall, the effectiveness of these bacterial strains depends on their ecological fitness, compatibility with the host plant, and adaptability to environmental conditions. These findings emphasize the importance of targeted strain selection and context-specific application strategies in the development of microbial biocontrol systems.

Fungal Agents: *Trichoderma*: *Trichoderma* spp. are widely recognized as effective fungal biocontrol agents that suppress plant pathogens through both direct and indirect mechanisms. Direct antagonistic effects include antibiosis, competition for nutrients and space, and mycoparasitism, in which *Trichoderma* species degrade pathogen cell walls using hydrolytic enzymes such as chitinases and glucanases. Indirectly, these fungi enhance plant defense responses by activating induced systemic resistance (ISR), primarily through jasmonic acid (JA) and ethylene (ET) signaling pathways. This activation is commonly associated with increased activity of defense-related enzymes, including polyphenol oxidase (PPO), peroxidases (POD), and β -1,3-glucanase. In addition, *Trichoderma* spp. is known to promote plant growth by improving nutrient uptake and producing secondary metabolites that function as plant growth regulators. Combined inoculations of *Trichoderma* with plant growth-promoting rhizobacteria (PGPR) often result in synergistic effects, leading to enhanced systemic resistance compared to single inoculations. Such interactions have been shown to increase the accumulation of pathogenesis-related (PR) proteins, phenolic compounds, and other defense metabolites. Recent studies also indicate that *Trichoderma* can modulate the structure and function of the rhizosphere microbiome, thereby contributing to long-term suppression of soil-borne pathogens. This microbiome-mediated effect enhances ecological stability and resilience against pathogen invasion across a range of crops. Furthermore, strain-specific variability within *Trichoderma* influences its efficacy, highlighting the importance of selecting well-adapted isolates for specific agroecological conditions. Collectively, these findings support the role of *Trichoderma* spp. as versatile and sustainable agents in integrated disease management strategies.

Molecular Elicitors and Secondary Metabolites: Microbial-derived molecular elicitors and secondary metabolites play central roles in the regulation of plant defense responses under biotic stress conditions. Among these, volatile organic compounds (VOCs), such as acetoin and 2,3-butanediol produced by *Bacillus* spp. and other PGPR, are known to prime plant immunity and promote growth by enhancing systemic signaling pathways. These VOCs function as signaling molecules that trigger induced systemic resistance (ISR), often without direct physical contact between the microbe and the plant. In addition to VOCs, a wide range of secondary metabolites including lipopeptides, antibiotics, and hydrolytic enzymes such as chitinases and proteases are produced by both bacterial and fungal biocontrol agents. These compounds contribute to pathogen suppression through direct inhibition of growth and by disrupting cell wall integrity. At the same time, many of these metabolites act as elicitors that stimulate plant defense mechanisms, leading to the activation of key molecular pathways. Typically, ISR is mediated through jasmonic acid (JA) and ethylene (ET) signaling, whereas systemic acquired resistance (SAR) is associated with salicylic acid (SA)-dependent pathways. At the transcriptional level, microbial interactions result in the upregulation of defense-related genes, including pathogenesis-related (PR) proteins and transcription factors such as WRKY, which coordinate downstream immune responses. This transcriptional reprogramming is often accompanied by increased production of phenolic compounds, phytoalexins, and reactive oxygen species, all of which contribute to enhanced resistance against invading pathogens. Comparative analyses further indicate that microbial efficacy varies among strains of *Bacillus* and *Pseudomonas*, reflecting differences in metabolite profiles, colonization efficiency, and signaling capacity. Particularly, microbial consortia frequently outperform individual strains due to synergistic interactions that amplify defense enzyme activity, secondary metabolite accumulation, and overall plant resilience. Recent advances in molecular and genomic approaches have provided deeper insight into these processes, revealing gene-level interactions between plants and beneficial microbes. Such findings highlight the complexity of plant–microbe communication and underscore the potential of microbial-based strategies for sustainable management of biotic stress in agricultural systems.

Climatic Changes Impact

Biotic stress: Pathogenesis and its importance of crop production

In natural environments, soil and plant roots serve as habitats for a diverse community of both useful and pathogenic microbes. Plants release various chemical compounds, including root exudates, which attract and shape these microbial communities. However, pathogenic microbes like bacteria, fungi, viruses, and pests can severely reduce crop productivity, causing substantial economic losses internationally (Ramegowda & Senthil-Kumar, 2015). Evaluations indicate that global crop production losses due to pathogen and pest infestations amount to roughly \$220 billion annually (Chakraborty & Newton, 2011; Rohr et al., 2019; Ristaino et al., 2021; van Dijk et al., 2021). These losses not only threaten food security but also impact local economies and socio-economic stability. Beyond pre harvest damage caused by environmental stressors, post-harvest losses due to microbial pathogens such as *Penicillium* spp. and *Xanthomonas euvesicatoria* further jeopardize crop quality and yield (Tripathi et al., 2022). Such biotic stresses disrupt hormone balance, nutrient uptake, and overall plant physiology, leading to diminished yield. Climate change exacerbates these challenges by increasing the incidence and severity of plant diseases, thereby threatening global food security (GFS) and biodiversity (Velasquez et al., 2018; Burdon et al., 2020; Muluneh, 2021). Forecasts suggest that anticipated gains in crop yields over the next five decades may be negated by heightened disease pressures from existing and emerging pathogens (Chaloner et al., 2021). Forest ecosystems are similarly vulnerable, with climate induced pathogen spread recognized as a major threat to global forest health (GFH) (Trumbore et al., 2015). Consequently, there is an imperative need to improve understanding

of plant-pathogen interactions through integrated epidemiological and molecular ecological research to develop resilient agricultural and natural systems capable of withstanding climate change impacts (Rohr et al., 2019; van Dijk et al., 2019). Climate change can simplify plant infections by altering pathogen populations, modifying host pathogen vector interactions, and enabling the evolution of new pathogenic strains that compromise plant defenses (Velásquez et al., 2018; Newbery et al., 2016; Cohen & Leach, 2020). Furthermore, shifts in the geographic distribution of pathogens and their hosts are expected, promoting the emergence of plant diseases in previously unaffected areas (Burdon & Zhan, 2020; Chaloner et al., 2021; Delgado-Baquerizo et al., 2020; Dudney et al., 2021). Although substantial progress has been made in understanding how climatic factors like temperature and precipitation interact with anthropogenic activities to influence pathogen dynamics, additional research is essential. Notably, fungal soil-borne pathogens are predicted to increase in abundance across numerous natural ecosystems under future climate scenarios, potentially causing profound and unpredictable impacts on global primary productivity (Delgado-Baquerizo et al., 2020). Changes in relative humidity have also been shown to affect pathogen prevalence and virulence (Romero et al., 2022). Reassuringly, recent studies highlight the promising role of useful microbes as sustainable alternatives or complements to conventional pest control strategies, such as chemical pesticides and fertilizers (Figure 2 & 3).

Mechanism of biotic stress tolerance

Microorganisms have increasingly been recognized as environmentally sustainable and economically viable agents for controlling plant diseases. These microbes enhance plant defense mechanisms (PDMs) by activating various cellular responses, including cell wall strengthening, cellular rupture, and the accumulation of secondary metabolites. Crucial signaling hormones involved in these defense processes include Jasmonic acid, ethylene, and salicylic acid (SA), which play a vital role in signaling and triggering plant immune responses (PIRs) (Verhage et al., 2010; Bari & Jones, 2009). Moreover, reactive oxygen species and oxidative bursts serve as important components of plant tolerance to biotic stress (Miller et al., 2010). Microbial induction of plant defenses typically involves two distinct pathways: induced systemic resistance (ISR) and systemic acquired resistance (SAR). Induced systemic resistance is commonly activated by non-pathogenic root-associated growth-promoting microbes (PGPMs), whereas systemic acquired resistance is associated with changes in gene expression and the accumulation of pathogenesis-related (PR) proteins. The gene activation mechanisms differ between induced systemic resistance and systemic acquired resistance, reflecting their reliance on different signaling pathways (Nawrocka & Malolepsza, 2013; Al Raish et al., 2025). Explicitly, PGPMs (Figure 1) can induce systemic acquired resistance, which involves SA accumulation and pathogenesis-related protein synthesis, while ISR is primarily regulated by jasmonate and ethylene signaling pathways under biotic stress conditions (Salas-Marina et al., 2011; Bari & Jones, 2009). Furthermore, Reactive Oxygen Species (ROS) and reactive nitrogen species (RNS) influence the synthesis of specialized defense compounds such as ethylene, JA, and salicylic acid, forming a complex network that modulates pathogen populations (Bari & Jones, 2009; Choudhary & Johri, 2009). Ethylene and transcription factors also play a vital role in regulating pathogenesis-related gene expression during plant disease resistance proteins (PDRs). Activation of defense-related genes by elicitors released from non-pathogenic microbes can enhance plant resistance to pathogens. Compant et al. (2005) demonstrated that the induction of defense mechanisms against *Fusarium* wilt disease in carnation and cucumber was mediated through pathogenesis-related gene activation. Certain bacterial genera, such as *Pseudomonas* and *Bacillus*, have been widely documented to induce systemic resistance and suppress plant diseases across diverse crop systems. *Paenibacillus* strain P16 showed effective biocontrol against black rot caused by *Xanthomonas campestris* in cabbage (Ghazalibigla et al., 2016). Moreover, *Bacillus* spp. and *Arthrobacter* spp. isolated from tomato plants exhibit multiple plant growth

promoting (PGP) traits, including phosphate solubilization, indole-3-acetic acid (IAA) production, and biocontrol activities (Banerjee et al., 2010).

Microbial Biofertilizers

Mycorrhizal fungi
Azotobacter spp.
Azospirillum spp.
Acetobacter spp.
Rhizobium spp.
Fraturia spp.

Non -Microbial Biofertilizers

Algae biofertilizers
Botanical extracts
Humic/fulvic substances
Protein hydrolysates
Seaweeds extracts
Chitosan base
Amino acid-based

Inorganic fertilizers

Cobalt and silicon

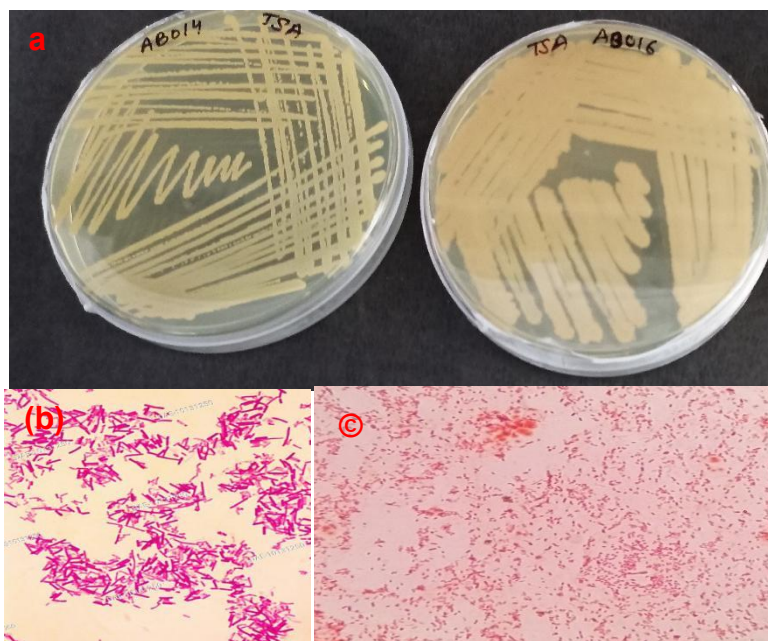


Figure 1: Different types of microbials, nonmicrobial and inorganic PGPR and their function in plant growth, biotic and abiotic stress tolerance (Figure a, b, c is microbial PGPR)

Abiotic stress

Drought and its impact on crop production

Drought is one of the most extensively studied environmental stresses and remains a major concern for scientists focused on agriculture (Table 1). It is recognized as a critical global agricultural challenge, as it severely limits plant growth and productivity. Drought stress affects vast agricultural lands globally, leading to far-reaching social and economic consequences (Disante et al., 2011; Mishra & Singh, 2010). Underneath drought stress, plant development is meaningfully impaired, as multiple growth parameters and stress-responsive genes are negatively impacted. Reduced water availability leads to diminished cell turgor, loss of membrane integrity, elevated production of reactive oxygen species (ROS), and accelerated leaf senescence—all of which contribute to decreased crop yields (Tiwari et al., 2016). During periods of water deficit (WD), plants undergo a series of physiological and molecular modifications, such as increased ethylene synthesis, degradation of chlorophyll, damage to the photosynthetic machinery, and suppression of photosynthetic movement (Lata & Prasad, 2011; Seleiman et al., 2021). Moreover, drought stress intensifies the generation of reactive oxygen species, which disrupt protein structures, impair membrane functionality, trigger lipid peroxidation, and can ultimately lead to programmed cell death (Tiwari et al., 2016). With continuing climate change, the frequency, intensity, and duration of drought events are expected to rise, posing an even greater threat to global food security (GFS) and sustainable agriculture in the forthcoming decades.

Mechanism of drought stress tolerance

Drought tolerant microbes play a critical role in supporting plant overall performance under water-shortage conditions. These microbes have evolved numerous resistance strategies to survive in environments with low water potential, including the formation of thick cell walls, entry into dormancy, accumulation of osmolytes, and the secretion of exopolysaccharides (EPS) (Chithrashree et al., 2011; Costa et al., 2018). These adaptations not only aid microbial survival but also enhance soil structure and moisture retention, indirectly benefiting plant growth during drought conditions. Plant associated microbes (PAM) mitigate the negative effects of drought through both direct and indirect mechanisms. In the rhizosphere, valuable microbes facilitate nutrient availability and produce a more favorable microenvironment for plant survival, regardless of water availability. These microbes improve plant resilience through the production of plant growth regulators (PGR) such as indole-3-acetic acid (IAA), cytokinins, and abscisic acid (ABA), which are critical for stress response and physiological adaptation (Farooq et al., 2009; Porcel et al., 2014). Furthermore, they contribute to drought tolerance through other mechanisms, including exopolysaccharides production, aminocyclopropane-1-carboxylate deaminase activity, and induced systemic tolerance. indole-3-acetic acid, one of the most active auxins, promotes vascular tissue differentiation, adventitious root formation, cell division, and shoot elongation, all of which are vital during water-limited conditions (Goswami et al., 2015). Abscisic Acid functions as a central regulator of drought stress response, modulating the expression of stress-responsive genes and improving root hydraulic conductivity (Jiang et al., 2013). Inoculation with plant growth-promoting rhizobacteria (PGPR) has been shown to elevate abscisic acid levels, thereby helping plants adjust their physiological functions to cope with drought. Such as, *Azospirillum brasilense* enhances drought tolerance in *Arabidopsis thaliana* by increasing endogenous abscisic acid levels (Cohen et al., 2015). Another important mechanism involves the microbial enzyme aminocyclopropane-1-carboxylate deaminase, which breaks down the ethylene precursor 1-aminocyclopropane-1-carboxylate into ammonia and α -ketobutyrate. This reduces ethylene levels, a stress hormone that can inhibit root growth under drought conditions (Bal et al., 2013; Sarawaneeyaruk et al., 2023). Moreover, inoculation with drought tolerant PGPR such as *Pseudomonas putida* H2-3 has been found to mitigate drought-induced growth inhibition by enhancing chlorophyll content, shoot length, and biomass (Kang et al., 2014). It also increases proline and sugar accumulation, while reducing oxidative damage (Vardharajula et al., 2011). Combining endophytic bacteria with PGPR can further boost drought resistance. For instance, exopolysaccharides producing bacteria like *Proteus penneri* (Pp1), *Pseudomonas aeruginosa* (Pa2), and *Alcaligenes faecalis* (AF3) have demonstrated improved nutrient cycling and improved protein and sugar levels when inoculated into maize (Naseem & Bano, 2014). exopolysaccharides not only protect bacterial cells from desiccation but also improves plant drought tolerance by enhancing water retention and soil aggregation (Sandhya et al., 2009). In addition to exopolysaccharides, certain compatible solutes such as glycine, proline, betaine, and trehalose accumulate within microbes, helping preserve cellular membranes, enzymes, and proteins during drought (Costa et al., 2018). The co-inoculation of mycorrhizal fungi with drought-tolerant bacteria significantly enhances nutrient uptake and plant growth while reducing the adverse effects of drought (Prasad, 2022b). For example, the combination of *P. putida* and *Bacillus thuringiensis* has been shown to reduce stomatal conductance and electrolyte leakage under drought conditions (Ortiz et al., 2015). Communally, these findings highlight the significant role of drought-tolerant microbial communities in promoting plant resilience, ensuring growth and survival under water-limited environments. A summary of main studies and microbial strategies is presented in Table 1. The studies summarized in table 1 demonstrate that beneficial microorganisms enhance plant tolerance to drought and other environmental stresses through multiple physiological, biochemical, and molecular mechanisms. Among the reported microbial groups, *Bacillus* species appear consistently effective in improving drought tolerance across different crops by regulating osmolyte

accumulation, antioxidant activity, hormone signaling, and root development. For example, *Bacillus* strains in maize, ryegrass, lavender, and pepper enhanced proline accumulation, improved nutrient uptake, and activated stress-responsive pathways, indicating broad adaptability under water-limited conditions. In comparison, *Pseudomonas* strains showed stronger effects on maintaining leaf water status, chlorophyll stability, and oxidative stress reduction, particularly in *Brassica*, chickpea, and chili. However, some studies reported contrasting physiological responses between microbial strains. While *Bacillus* and *Azospirillum* frequently increased proline accumulation as a drought-protective mechanism, *Pseudomonas libanensis* and *Pantoea alhagi* reduced proline and malondialdehyde levels, suggesting that these microbes may alleviate stress damage sufficiently to minimize the need for osmotic adjustment. Similarly, *Trichoderma* species mainly promoted root growth and nutrient acquisition rather than directly influencing antioxidant metabolism, highlighting functional differences among fungal and bacterial inoculants. Symbiotic rhizobia such as *Sinorhizobium* and *S. meliloti* were particularly effective in legumes by improving nodulation, nutrient acquisition, and carbon metabolism during drought stress, whereas diazotrophic bacteria such as *Glucoacetobacter diazotrophicus* and *Azotobacter* contributed primarily through nitrogen fixation and phytohormone production. Overall, the findings indicate that microbial performance is highly strain-specific and depends on plant genotype, stress intensity, and environmental conditions. Although *Bacillus* strains generally exhibit broader drought tolerance mechanisms, *Pseudomonas* and rhizobial species may provide superior benefits in maintaining physiological stability and nutrient balance in specific host plants. These variations emphasize the importance of selecting crop-specific and stress-specific microbial inoculants for sustainable agricultural applications under climate change

Salinity and its impact on crop productivity

Salinity is one of the most widespread and severe environmental stresses affecting agricultural soils globally (Table 2). It poses a significant threat to crop yield and soil health. Both natural processes—such as low precipitation, high evaporation rates, and soil erosion and anthropogenic activities such as the excessive use of saline irrigation water and poor drainage management contribute to the accumulation of salts in arable lands (Shrivastava & Kumar, 2015). Salinity stress interferes with a plant's ability to absorb essential water and nutrients by lowering the soil's osmotic potential. High concentrations of ions such as sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), chloride (Cl^-), and nitrate (NO_3^-) in saline soils can disrupt ionic balance, damage plant cell membranes, and reduce the activity and diversity of useful soil microbes. These ions exert toxic effects on plant cells by disturbing key physiological processes and altering enzyme functions, ultimately reducing plant vigor and productivity. The osmotic stress imposed by salinity makes it increasingly difficult for plant roots to extract water from the soil, resulting in cellular dehydration and metabolic imbalances. Furthermore, excessive salt accumulation alters the soil's physical and chemical properties, affecting structure, permeability, and microbial interactions, which negatively impacts overall soil fertility and ecosystem function. The studies presented in table 2 demonstrate that salt-tolerant microorganisms improve plant performance under saline conditions through diverse but interconnected mechanisms, with ACC deaminase activity emerging as one of the most consistent traits among effective strains. Several genera, particularly *Pseudomonas*, *Bacillus*, *Acinetobacter*, and *Variovorax*, reduced ethylene-mediated stress responses by metabolizing ACC, thereby improving root growth, biomass accumulation, nutrient uptake, and overall plant vigor under salt stress. Among these, *Pseudomonas* species were the most frequently reported and showed broad functional versatility, including regulation of antioxidant enzymes, maintenance of ion homeostasis, enhanced uptake of nitrogen, phosphorus, and potassium, and reduction of oxidative damage. In contrast, *Bacillus* strains appeared more effective in stimulating osmolyte accumulation, catalase activity, and membrane stability, particularly in wheat, rice, and halophytic plants. Comparative

observations also reveal differences in microbial strategies for salinity tolerance. For example, *Brachybacterium*, *Brevibacterium*, and *Haererohalobacter* improved salinity resistance mainly through maintaining higher K^+/Na^+ ratios and nutrient balance, whereas cyanobacterial inoculation in tomato primarily enhanced ion homeostasis by reducing sodium accumulation in leaves. Some strains, such as *Bipolaris* sp. CSL-1, influenced hormonal and defense signaling by lowering stress-responsive gene expression and increasing salicylic acid levels rather than directly affecting ion regulation. Similarly, *Serratia*, *Stenotrophomonas*, and fluorescent *Pseudomonas* promoted growth through production of auxins and hydrolytic enzymes, highlighting that not all beneficial effects are linked exclusively to ACC deaminase activity. Contradictions among studies were also evident, particularly regarding antioxidant responses. While some microbial inoculants increased antioxidant enzyme activity to counter oxidative stress, others reduced lipid peroxidation and superoxide dismutase activity, suggesting reduced cellular stress levels after microbial treatment. Overall, the findings indicate that microbial responses to salinity are highly strain-specific and depend on plant species, soil conditions, and stress severity. Although *Pseudomonas* strains consistently demonstrate broad-spectrum salinity tolerance mechanisms, *Bacillus* and halotolerant bacterial consortia may provide superior ion regulation and Osmo protection under severe saline environments. These differences highlight the importance of selecting compatible microbial strains according to crop type and environmental stress conditions for effective application in saline agriculture.

Salinity stress (SSs) leads to a reduction in seed germination rates, stunted plant growth, decreased nutrient uptake, and impaired water absorption. It also significantly affects symbiotic interactions such as root nodulation, thereby reducing biological nitrogen fixation (BNF). Among the various physiological processes impacted by salinity, nitrogen fixation is particularly sensitive. The activity of nitrogenase, the important enzyme in NF, is greatly inhibited under saline conditions, diminishing the plant's nitrogen acquisition capacity and overall yield (Shrivastava & Kumar, 2015). Furthermore, salt stress induces ionic toxicity and osmotic imbalances that not only hinder PG but also affect the survival and efficiency of associated microbial communities. While some halotolerant bacteria can survive and function under moderate saline conditions, fungi tend to be more sensitive to salt-induced osmotic pressure. Even small changes in osmotic potential can restrict microbial metabolism and water uptake, with extreme salinity further exacerbating these constraints. In summary, salinity presents a multifaceted challenge to crop productivity by affecting water relations, nutrient balance, plant physiology, microbial dynamics, and soil structure. Thoughtful these effects are essential for developing effective strategies to mitigate the impact of salt stress and improve agricultural sustainability under saline conditions.

Mechanism of salinity stress tolerance

Salinity stress is a critical constraint to crop productivity (CP), but diverse salt tolerant microbes (STMs) play a vital role in enhancing PG under these adverse conditions (Table 2 and Figure 1 - 4). These valuable microbes employ multiple direct and indirect mechanisms to confer salinity tolerance (ST). Directly, STMs secrete numerous plant hormones such as auxins, cytokinins, ethylene, and gibberellins, which regulate important physiological processes in plants (Hayat et al., 2010; Singh et al., 2022). They also fix atmospheric nitrogen, mobilize nutrients, and produce siderophores that facilitate nutrient uptake and utilization. Collectively, these actions promote root elongation, increased root surface area, and a greater number of roots, thereby improving nutrient absorption and overall plant growth and improve soil health. Indirect mechanisms include the suppression of phytopathogens through the production of enzymes like 1-aminocyclopropane-1-carboxylate deaminase, which converts the ethylene precursor 1-aminocyclopropane-1-carboxylate into ammonia and alpha-ketobutyrate, lowering ethylene levels that inhibit root growth under stress (Vardharajula et al., 2011). PGPR also mitigate salt stress by accumulating salts in their cytoplasm to maintain osmotic balance and cell turgor. Additionally, bacterial exudates

can chelate harmful cations, reducing their availability to plants under saline conditions and refining growth outcomes. The synergistic use of valuable bacteria such as *Rhizobium* and *Pseudomonas* species has shown efficacy in alleviating salinity stress in crops by promoting nutrient uptake and enhancing plant vigor (Bano & Fatima, 2009). For instance, *Bacillus pumilus* and *Bacillus subtilis* produce indole-3-acetic acid (IAA), solubilize phosphate, generate ammonia and hydrogen cyanide (HCN), and exhibit salt stress tolerance, contributing to improved plant resilience under saline environments (Damodaran et al., 2013). Research indicates that inoculation of maize with *Rhizobium* and *Pseudomonas* reduces electrolyte leakage, modulates osmotic potential, increases proline synthesis, and promotes selective potassium ion uptake, thus enhancing salt tolerance (Bano & Fatima, 2009, Mano et al., 2026). Similarly, rice plants inoculated with *Pseudomonas pseudoalcaligenes*, and *Bacillus pumilus* show increased glycine betaine accumulation, a key osmoprotectant under salt stress (Jha et al., 2011). Other strains such as *Acinetobacter* and *Pseudomonas* produce 1-aminocyclopropane-1-carboxylate deaminase and indole-3-acetic acid in barley and oats, improving plant health under saline conditions (Chang et al., 2014; Shahid et al., 2023). Additionally, *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* reduce oxidative damage in salt-sensitive rice by lowering superoxide dismutase activity and lipid peroxidation (Jha & Subramanian, 2014; Mnotla et al., 2025; Smith & Lee, 2025). The application of PGPR induces systemic tolerance (IST) in plants, enhancing resistance to salinity stress and even fungal pathogens such as *Fusarium solani* in cotton (Egamberdieva et al., 2015). This effect extends to crops like wheat, where salt tolerance *Azospirillum* strains improve growth parameters under SS (Nia et al., 2012). Plant hormones (PHs) play a vital role in SS adaptation. Abscisic acid (ABA), for instance, regulates stomatal closure and apoplastic acidification in maize under salinity, aiding stress resistance. Lettuce seeds inoculated with *Azospirillum* exhibited enhanced yield and storage longevity under saline conditions (Fasciglione et al., 2015). Similarly, *Hartmannibacter diazotrophicus* strain E19 improved barley growth under salinity stress (Suarez et al., 2015). Other PGPR isolates such as *Bacillus polymyxa*, *Mycobacterium phlei*, and *Pseudomonas alcaligenes* have demonstrated survival and function in saline calcisol soils (Egamberdieva, 2007). Co-inoculation of *Rhizobium* and *Pseudomonas* has shown to enhance maize tolerance to salinity by promoting proline accumulation, reducing ionic leakage, maintaining water balance, and facilitating selective potassium uptake (Bano & Fatima, 2009). Furthermore, *P. fluorescens*, *P. aeruginosa*, and *P. stutzeri* isolated from saline tomato rhizospheres secrete plant hormones and 1-aminocyclopropane-1-carboxylate deaminase, aiding in salt stress resistance (Bal et al., 2013; Tank & Saraf, 2010). A study on *Bacillus amyloliquefaciens* NBRISN13 (SN13) revealed that this bacterium enhances ST in rice by modulating the expression of fourteen stress-related genes, thereby improving plant growth under salinity (Nautiyal et al., 2013). Endophytic microbes producing phytohormones like abscisic acid and auxin have been shown to further promote ST in rice (*Oryza sativa*) (Shahzad et al., 2017). Moreover, valuable bacteria can synergize with exogenous jasmonates to mitigate SS effects in *Solanum pimpinellifolium* (Khan et al., 2017). Recent studies also indicate that salinity resistance involves metabolic adjustments such as changes in the tricarboxylic acid (TCA) cycle in tomato plants, which play a crucial role in counteracting salt-induced oxidative and osmotic stress (Torre Gonzalez et al., 2017). The induction of systemic resistance by PGPB involves regulation of hormone levels, antioxidant enzyme activity, and osmotic adjustment, including the production of compatible osmolytes like proline. These mechanisms collectively contribute to improved PG and resilience under saline conditions.

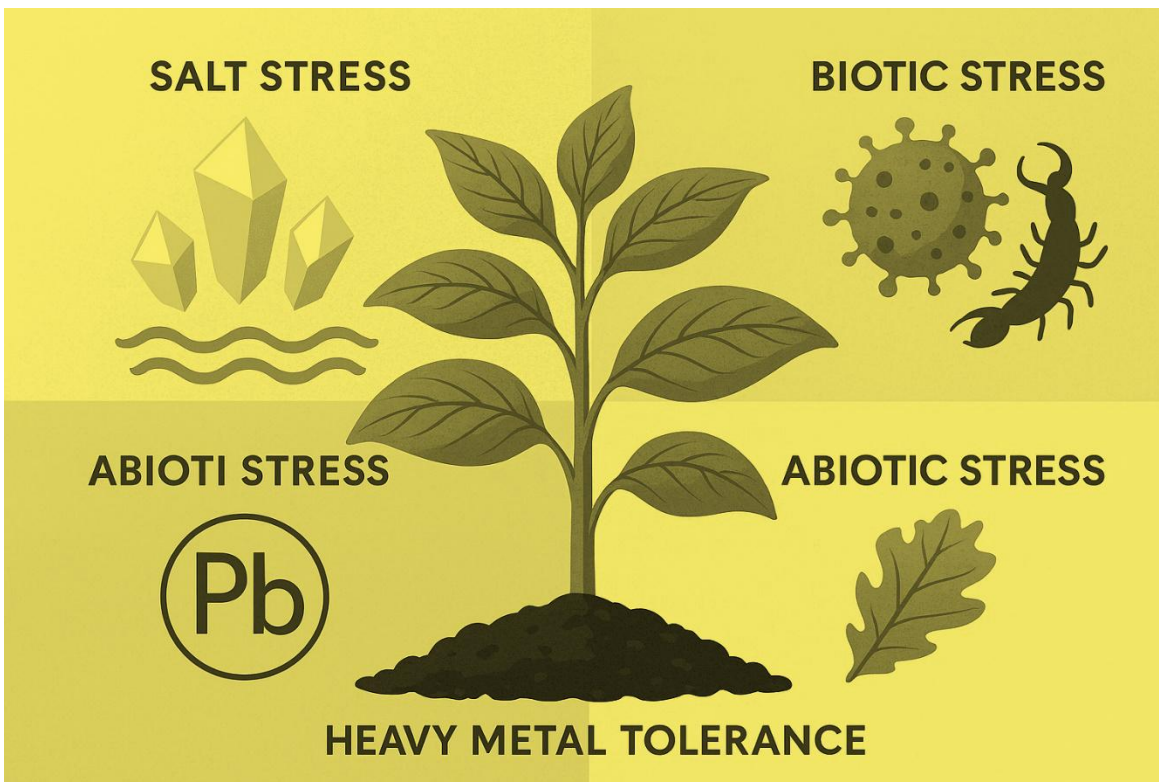


Figure 4: Microbial mechanism for salt stress and biotic stress and heavy metal tolerance

Heavy metals and their impact on crop productivity

The widespread use of modern technology and agricultural practices has led to the contamination of soils with destructive heavy metals (HMs) such as mercury, lead, and arsenic. These metals pose significant risks to both plant growth and human well-being. Dissimilar organic pollutants (OPs), HMs have a high density (greater than 4 g/cm^3), are not biodegradable, and can cause severe toxicity even at low concentrations (Duruibe et al., 2007; Ma et al., 2016a, 2016b). Accordingly, it is imperative to develop cost-effective and environmentally sustainable strategies to remediate heavy metal-contaminated soils and protect ecosystems. Traditional remediation techniques often involve high costs and may damage the soil's structural integrity, limiting their practical application (Glick, 2010). In contrast, phytoremediation a relatively recent approach leverages plants and their associated microbes to extract, stabilize, or detoxify heavy metals from contaminated soils. This method is both economical and eco-friendly (Ma et al., 2016a, 2016b; Chirakkara et al., 2016). Additionally, the involvement of soil microbes can improve the efficiency of phytoremediation by improving plant tolerance and responsiveness to heavy metal stress. Due to their high sensitivity to heavy metals, soil microbes serve as effective bioindicators of heavy metal contamination (Broos et al., 2004; Chen et al., 2014). A comprehensive summary of HM impacts on tolerance mechanisms is presented in Table 3. The studies summarized in the table 3 clearly demonstrate that beneficial microorganisms enhance plant tolerance to heavy metal stress through multiple physiological, biochemical, and phytoremediation-related mechanisms. Among the microbial groups, *Pseudomonas* and *Bacillus* species were the most frequently reported and exhibited broad-spectrum tolerance against metals such as Cd, Pb, Zn, Cr, Cu, Ni, and As. These bacteria consistently promoted plant growth through siderophore production, ACC deaminase

activity, phosphate solubilization, and phytohormone synthesis, while simultaneously improving metal uptake and reducing oxidative stress. In comparison, arbuscular mycorrhizal fungi such as *Claroideoglossum*, *Funneliformis*, *Glomus fasciculatum*, and *Glomus etunicatum* were particularly effective in enhancing nutrient acquisition, stabilizing cellular membranes, and reducing reactive oxygen species generation under metal stress. Fungal inoculants generally showed stronger effects on antioxidant defense and nutrient balance, whereas bacterial strains demonstrated greater efficiency in metal mobilization and phytoremediation processes. Several strain-specific differences were also evident across studies. For instance, *Pseudomonas brassicacearum* and *Rhizobium leguminosarum* promoted metal chelation and assisted phytoremediation in *Brassica juncea*, while *Burkholderia* species reduced cadmium toxicity primarily by limiting root metal absorption and minimizing chlorosis and peroxide accumulation. Similarly, *Bacillus megaterium* enhanced cadmium uptake and root-to-shoot translocation in *Sedum alfredii*, indicating its suitability for phytoextraction, whereas *Bacillus anthracis* PM21 mainly improved antioxidant defense and membrane stability rather than increasing heavy metal accumulation. Contrasting responses were also observed in terms of metal uptake strategies. Some microbes increased heavy metal accumulation in plant tissues to improve phytoremediation efficiency, while others reduced metal uptake to protect plants from toxicity. For example, *Cellulosimicrobium cellulans* and *Leifsonia* sp. promoted chromium and cadmium uptake, respectively, whereas plant growth-promoting bacteria in sorghum reduced chromium accumulation through Phyto stabilization mechanisms. The findings further suggest that combined microbial inoculations often perform better than single strains because of synergistic interactions between bacteria and fungi. Co-inoculation of *Glomus fasciculatum* with *Pseudomonas putida* and the combined use of *Thiobacillus thiooxidans* with *Pseudomonas putida* resulted in improved biomass production, enhanced metal accumulation, and greater stress tolerance compared with individual inoculants. Overall, microbial responses to heavy metal stress are highly strain-specific and depend on plant species, type of metal, contamination level, and environmental conditions. While *Pseudomonas* and *Bacillus* strains appear broadly effective across different metals, mycorrhizal fungi and specialized rhizobacteria may provide more targeted benefits in nutrient regulation, oxidative stress reduction, and Phyto stabilization. These differences emphasize the importance of selecting appropriate microbial consortia for efficient remediation of heavy metal-contaminated soils and sustainable crop production under stressed environments.

Mechanism of heavy metal stress tolerance

Heavy metal tolerant (HMT) microbes, including bacteria, Rhizobacteria and Firmicutes, as well as fungi like mycorrhizae, play a vigorous role in protecting plants from the detrimental effects of heavy metals by promoting plant growth and development under stress conditions. These microbes employ several mechanisms to mitigate heavy metal toxicity, including metal excretion, cell impermeability, volatilization, metal complexation, exopolysaccharide (EPS) sequestration, enzymatic detoxification, intra and extracellular accumulation, and biotransformation (Glick, 2010; Prasad, 2021b; Dhawi, 2023). Furthermore, they improve plant health by lowering ethylene levels through 1-aminocyclopropane-1-carboxylate deaminase production, synthesizing plant hormones (PHs) such as indole-3-acetic acid (IAA), and suppressing phytopathogens (Glick, 2010; Prasad, 2021b; Dhawi, 2023). Beyond these, microbial processes such as nutrient cycling, nitrogen fixation, and phosphate solubilization further support plant growth and Heavy metal tolerant (Verma et al., 2013; Ahmad et al., 2011). One key mechanism involves the secretion of siderophores small organic compounds secreted by microbes that chelate heavy metals, enhancing their availability for plant uptake in the rhizosphere. While siderophores primarily bind ferric iron, they exhibit high affinity for other HMs, forming complexes that can be transported into plant cells (Saha et al., 2016; Zloch et al., 2016; Pecoraro et al., 2022). This facilitates efficient uptake and utilization of HMs

by plants while reducing their toxic accumulation. Notably, siderophore iron complexes are translocated to the cytosol more frequently than other Heavy metals (Zloch et al., 2016). Microbial bioaccumulation of Heavy metals offers an effective approach for remediating contaminated soils. Several studies have shown that bacterial groups like Proteobacteria, Firmicutes, and Actinobacteria can efficiently remove metals like manganese (Mn) and arsenic (As) from polluted environments (Zhang et al., 2015; Fathollahi et al., 2021). Copper (Cu) concentrations exceeding 1 mM can inhibit growth in legume species such as *Vicia faba*, but inoculation with beneficial microbes can mitigate these adverse effects (Fatnassi et al., 2015). Arbuscular mycorrhizal fungi (AM fungi) have also been found to reduce cadmium (Cd) toxicity in plants by lowering malondialdehyde and hydrogen peroxide levels (Hashem et al., 2016). Furthermore, bacterial strains such as *Enterobacter* and *Klebsiella* demonstrate the ability to remove HMs like cadmium, lead (Pb), and zinc (Zn) from soils while producing plant growth promoting substances (Henaio & Ghneim-Herrera, 2021). Cadmium resistant bacteria including *Micrococcus* sp. MU1 and *Klebsiella* sp. *Bacillus amyloliquefaciens* Bam1 (BAM1) enhance Cd accumulation and stimulate PG (Prapagdee et al., 2013). Similarly, arsenic-resistant bacteria isolated from *Pteris vittata* produce siderophores that promote plant growth and nutrient uptake (Ghosh et al., 2015). Certain rhizobacteria such as *Bradyrhizobium japonicum* E109 and *Azospirillum brasilense* Az39 efficiently colonize and promote plant growth in arsenic-contaminated soils (Armendariz et al., 2015). These discoveries underscore the crucial role of such microbes in alleviating heavy metal stress (HMS) and enhancing plant resilience (Li et al., 2007). Additionally, biomethylation, the microbial transfer of methyl groups facilitates the mobilization and detoxification of HMs including lead, mercury, selenium, arsenic, and tin (Bolan et al., 2014). Lastly, phytochelatins (PCs), cysteine rich metal binding peptides produced by fungi and plants, serve as another important detoxification mechanism against HMS (Gadd, 2010) (Table 3).

Mechanisms of Salinity and Heavy Metal Stress Tolerance Mediated by Beneficial Microbes

Beneficial microorganisms play a crucial role in protecting plants against salinity and heavy metal stresses through a wide range of physiological, biochemical, and molecular mechanisms. Under salinity stress, plant growth-promoting rhizobacteria (PGPR), endophytes, and other salt-tolerant microbes enhance plant growth by improving nutrient uptake, regulating phytohormone production, maintaining ion balance, and reducing oxidative damage. These microbes produce important plant hormones such as auxins, cytokinins, gibberellins, and abscisic acid, which regulate root growth, stomatal activity, and stress adaptation. Many strains also synthesize 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an enzyme that lowers stress-induced ethylene levels and prevents inhibition of root growth under saline conditions. In addition, microbial inoculation promotes osmotic adjustment through the accumulation of osmoprotectants such as proline and glycine betaine, improves potassium uptake while reducing sodium toxicity, and enhances antioxidant defense systems to minimize lipid peroxidation and membrane damage. Numerous microbial genera including *Pseudomonas*, *Bacillus*, *Rhizobium*, *Azospirillum*, *Acinetobacter*, and *Hartmannibacter* have demonstrated significant effectiveness in improving salinity tolerance in crops such as maize, rice, wheat, barley, lettuce, and tomato. Co-inoculation of beneficial microbes often provides superior results compared with single strains because of synergistic interactions that improve nutrient mobilization, water balance, and stress-responsive gene expression. Some microbes also induce systemic tolerance in plants by regulating hormone signaling pathways and activating stress-related genes. Furthermore, microbial interactions influence important metabolic pathways, including the tricarboxylic acid cycle, helping plants cope with osmotic and oxidative stress under saline conditions. Collectively, these mechanisms contribute to improved crop productivity, soil fertility, and resilience in salt-affected agricultural systems. Heavy metal-tolerant microbes also play an important role in reducing toxicity and improving plant survival in contaminated soils. These microorganisms protect plants through mechanisms such as metal sequestration, bioaccumulation, biosorption,

volatilization, enzymatic detoxification, biotransformation, and exopolysaccharide production. Many bacteria and fungi produce siderophores that chelate heavy metals and regulate their mobility and uptake in the rhizosphere. In addition, microbial production of ACC deaminase, indole-3-acetic acid, and other growth-promoting substances enhances root development and reduces stress-induced ethylene accumulation. Beneficial microbes also improve nutrient cycling, phosphate solubilization, and nitrogen fixation, thereby supporting plant growth under toxic conditions. Bacterial groups such as *Proteobacteria*, *Firmicutes*, *Actinobacteria*, *Enterobacter*, *Klebsiella*, *Bacillus*, *Bradyrhizobium*, and *Azospirillum*, along with arbuscular mycorrhizal fungi, have shown strong potential for alleviating cadmium, arsenic, lead, zinc, copper, and other heavy metal stresses. Some strains increase heavy metal uptake and phytoremediation efficiency, while others reduce metal accumulation within plant tissues to minimize toxicity. Mycorrhizal fungi reduce oxidative damage by lowering hydrogen peroxide and malondialdehyde levels, whereas bacterial strains improve antioxidant defense and plant growth through hormone production and siderophore activity. Additional detoxification mechanisms such as biomethylation and phytochelatin production further contribute to heavy metal tolerance and remediation. Overall, beneficial microbes represent sustainable and eco-friendly tools for improving plant resilience, restoring contaminated soils, and supporting climate-resilient agricultural systems under multiple environmental stresses.

Temperature and its impact on crop productivity

Rising temperatures due to climate change are causing more frequent and intense heat stress (HS) in crops, posing a significant threat to global agricultural productivity (GAP) and food security. Elevated temperatures disrupt key physiological processes, including alterations in plasma membrane fluidity, reduced water content through increased transpiration, impaired photosynthetic efficiency, enzyme activity, cell division, and overall plant growth. The most severe impacts of heat stress are observed in tropical and subtropical regions, such as India, where these changes can have lasting effects on local agriculture and food systems (Alam et al., 2017; Rodell et al., 2009). Temperature fluctuations also affect various cellular structures and membranes, with heat increasing membrane fluidity, whereas cold causes rigidity, thereby enhancing vulnerability to damage. Inadequate management of thermal stress (TS) can lead to detrimental outcomes for plant survival and productivity. Heat stress is among the most critical environmental challenges for plants as it triggers significant changes in hormone levels and cellular responses. For example, stress conditions induce a progressive increase in jasmonic acid (JA) concentration within plant cells, which plays a vital role in stress signaling and adaptation. To manage with temperature extremes, many plant species have evolved complex physiological mechanisms, including the synthesis and accumulation of heat shock proteins (HSPs) such as HSP20, HSP60, HSP70, HSP90, and HSP100, along with reactive oxygen species (ROS) scavenging enzymes like ascorbate peroxidase and catalase that mitigate oxidative damage (Qu et al., 2013; Kotak et al., 2007). While some plants possess limited tolerance to extreme temperatures, continuing research emphasizes the need to develop strategies that enhance resilience to both HS and cold shock (Table 4). The studies presented in the table 4 indicate that beneficial microorganisms can significantly enhance plant tolerance to temperature-related stresses through diverse physiological and protective mechanisms. Among the reported microbes, *Burkholderia phytofirmans* strain PsJN showed broad-spectrum stress adaptation by improving both heat and cold tolerance in different host plants, including grapevine and tomato. Its ability to enhance plant defense responses, improve resource mobilization, and provide antifungal protection suggests that this strain possesses multifunctional traits that extend beyond temperature stress mitigation alone. In comparison, *Curvularia protuberata* demonstrated highly specialized thermotolerance effects in both *Dichanthelium lanuginosum* and tomato, indicating that certain fungal endophytes may confer direct heat adaptation through intimate symbiotic associations with host plants. These findings highlight that fungal symbionts

can be equally important as bacterial inoculants in protecting plants from extreme temperature stress. Distinct strain-specific differences were also evident in the mechanisms used to improve stress tolerance. *Pseudomonas cedrina*, *Brevundimonas terrae*, and *Arthrobacter nicotianae* primarily promoted plant growth through nutrient solubilization, phytohormone-like compound production, and pathogen suppression, suggesting indirect support for stress adaptation by improving overall plant vigor and nutrient status. In contrast, *Bacillus aryabhathi* appeared to contribute more specifically to heat stress tolerance in soybean, although the precise physiological pathways were less extensively described. Comparative observations suggest that bacterial strains generally support stress tolerance through enhanced nutrient acquisition, hormonal regulation, and defense activation, whereas fungal endophytes such as *Curvularia protuberata* may directly influence thermal adaptation at the cellular level. Although all reported microbes improved plant performance under temperature stress, variations were observed in host specificity and the range of stress responses induced. For example, *Burkholderia phytofirmans* strain PsJN demonstrated effectiveness across multiple crops and temperature extremes, indicating greater adaptability and broader application potential compared with strains showing crop-specific responses. Furthermore, some microbes mainly improved plant defense and growth under stress conditions, while others directly enhanced tolerance to heat or cold stress. These differences emphasize that microbial responses to temperature stress are highly strain-dependent and influenced by host plant compatibility and environmental conditions. Overall, the findings support the potential of beneficial microbes as sustainable tools for improving crop resilience under increasing temperature fluctuations associated with climate change.

Plant microbe interactions with biotic stress

The studies plant microbe interaction with biotic stress summarized in the table 5 demonstrate that beneficial microorganisms suppress plant diseases through diverse mechanisms, including induced systemic resistance (ISR), production of antimicrobial metabolites, activation of defense-related enzymes, competition for nutrients, and direct antagonism against pathogens. Among the reported microbial groups, *Bacillus*, *Pseudomonas*, and *Trichoderma* species were the most consistently effective across a wide range of crops and pathogens. *Bacillus* strains frequently enhanced host defense by stimulating pathogenesis-related proteins, phenylalanine ammonia lyase, peroxidase, polyphenol oxidase, and surfactin production, indicating a strong role in activating systemic plant immunity. In contrast, *Pseudomonas* species showed broader multifunctional activity, combining ISR induction with phosphate solubilization, siderophore production, volatile organic compound emission, hydrolytic enzyme activity, and direct pathogen suppression. Several studies also highlighted the superior performance of microbial consortia compared with single-strain inoculants. For example, combined applications of *Trichoderma*, *Pseudomonas*, and *Rhizobium* in chickpea and cucumber provided greater disease suppression and enhanced phenolic accumulation than individual treatments, suggesting synergistic interactions among beneficial microbes. Distinct strain-specific differences were evident in disease control strategies. *Trichoderma* species mainly acted through antagonism, secretion of antifungal secondary metabolites, and stimulation of systemic resistance, making them particularly effective against soil-borne fungal pathogens such as *Fusarium*, *Alternaria*, and *Botrytis*. In comparison, rhizobial strains such as *Rhizobium etli* and *Rhizobium tropicum* primarily enhanced host defense responses and reduced disease severity through improved plant vigor and systemic resistance rather than direct antagonism. Cyanobacteria and algal species, including *Anabaena*, *Oscillatoria*, *Ulva*, and *Cystoseira*, exhibited unique protective roles through production of extracellular hydrolytic enzymes and sulfated polysaccharides with antifungal properties, highlighting alternative biological approaches for disease management. Contradictions among studies were also observed regarding the dominant mode of action. While some microorganisms mainly inhibited pathogen growth directly through antimicrobial compounds, others depended largely on host-mediated defense activation. For instance, *Pseudomonas fluorescens* enhanced resistance through lipoxigenase, chitinase,

and polyphenol oxidase activity in rice, whereas *Bacillus subtilis* FB17 relied on root-secreted malic acid signaling to recruit beneficial rhizobacteria. The effectiveness of microbial inoculants also varied according to crop species, pathogen type, and environmental conditions. *Bacillus* strains appeared particularly efficient against bacterial and fungal foliar diseases, whereas *Trichoderma* species showed stronger suppression of soil-borne fungal pathogens. *Pseudomonas* species demonstrated broad-spectrum activity across bacterial, fungal, viral, and even insect-associated stresses, suggesting greater ecological versatility. Overall, the findings emphasize that disease suppression by beneficial microbes is highly strain-specific and dependent on the interaction between host plants, pathogens, and environmental conditions. These variations highlight the importance of selecting compatible microbial strains or microbial consortia for sustainable and crop-specific disease management strategies in agriculture.

Mode of action of temperature stress tolerance

A significant portion of the Earth's biosphere is inhabited by microbes capable of tolerating both high and low temperatures. These microbes possess unique enzymatic adaptations that enable them to survive extreme thermal conditions by protecting their proteins, cell membranes, and nucleic acids from heat or cold-induced damage. In reply to thermal stress, they express specialized genes encoding HSPs and enzymes that facilitate their survival. Under high temperature conditions, these microbes optimize nutrient and water uptake to maintain viability. Conversely, cold adapted microbes exhibit traits that promote plant growth for instance, species such as *Brevundimonas terrae*, *Arthrobacter nicotianae*, and *P. cedrina* have demonstrated multiple mechanisms to enhance plant development (Yadav et al., 2014). These microorganisms contribute significantly to soil fertility by solubilizing and mobilizing nutrients, releasing phytohormone like compounds that stimulate plant growth, and offering protection against pathogens, thus supporting optimal plant health (Kumar et al., 2021). Meena et al. (2015) reported that microorganisms isolated from roots of cold adapted pea plants could serve as effective bioinoculants for mitigating low temperature stress. Additionally, thermotolerant phosphate solubilizing microbes in agricultural soils act as multifunctional bioinoculants by promoting phosphorus biogeochemical cycling; they convert insoluble phosphorus compounds into soluble forms through acidification, thereby improving nutrient availability and enhancing plant growth (Chang & Yang, 2009). Rising temperatures also influence beneficial plant microbe interactions (PMI). Often, increased temperatures enhance the symbiotic association between plants and AM fungi, potentially due to faster carbon allocation from plants to the rhizosphere where AM fungi reside (Compant et al., 2010). However, environmental factors such as heat, humidity, and UV radiation can directly impact microbial survival and function (Fahimipour et al., 2018). A notable example is the symbiosis between the tropical panic grass *Dichanthelium lanuginosum* and the fungus *Curvularia protuberata*, which allows both organisms to survive at elevated soil temperatures that neither could withstand independently (Marquez et al., 2007) (Table 4).

CO₂ and its impact on crop productivity

Atmospheric carbon dioxide (CO₂) concentrations have steadily increased over time, primarily driven by rapid industrialization and human activities, with current levels exceeding 400 ppm, compared to a pre-industrial average of approximately 280 ppm (Canadell et al., 2007). Climate models mission that this upward trend will continue, potentially reaching around 700 ppm by the end of the 21st century (IPCC, 2014). This rise in atmospheric CO₂ is expected to have significant impacts on global agriculture and food security. Many studies have investigated the effects of elevated CO₂ on plant growth, biomass accumulation, and productivity parameters like nutrient content and milling quality (Singh et al., 2017; Rai et al., 2016; Saha et al., 2013; 2015a). It is well established that higher

CO₂ concentrations can stimulate photosynthesis and enhanced PG, leading to increased biomass and productivity (Rai et al., 2016; Ainsworth & Long, 2005). Early research highlighted the CO₂ fertilization effect, particularly in C₃ crop species, where elevated CO₂ was predicted to substantially increase biomass production (Drake et al., 1997; Ziska, 2022; Thornton et al., 2007). However, empirical evidence from over 227 free air CO₂ enrichment (FACE) experiments globally revealed that the actual biomass gains in C₃ plants often fall short of theoretical expectations, largely due to the downregulation of photosynthesis under prolonged high CO₂ exposure (Ainsworth & Long, 2005; Long et al., 2004; Moore et al., 1999; Long et al., 2006). This down regulation phenomenon has been observed in at least 25 different C₃ species and is thought to limit the sustained benefits of CO₂ fertilization. N availability plays a vital role in this process, with reduced photosynthetic capacity linked to limitations in N uptake and metabolism under elevated CO₂ conditions (Stitt & Krapp, 1999; Reich et al., 2006; Shimono & Bunce, 2009; Ruiz-Vera et al., 2017). Consequently, the impact of rising CO₂ on crop yields is closely tied to soil N acquisition and plant nitrogen use efficiency (Zhu et al., 2010; Ainsworth & Rogers, 2007). An increase in glucose production under elevated CO₂ acts as a signaling molecule that suppresses the activity and synthesis of Rubisco and other Calvin-Benson cycle enzymes, resulting in reduced photosynthetic capacity (Stitt & Krapp, 1999; Ainsworth & Rogers, 2007). This down regulation may also affect seed quality, with altered seed composition observed in some studies (Hampton et al., 2013). Research finding on the effects of elevated CO₂ on seed germination has produced mixed results: some studies report increased germination rates (Ziska & Bunce, 1993; Edwards et al., 2001), others find decreases (Lamichaney et al., 2019; Saha et al., 2015b), and some observe no significant changes (Thin et al., 2017; Thomas et al., 2009). These variations suggest that the effects of elevated CO₂ on seed quality are influenced by species specific traits and environmental conditions. Legumes, as a major protein source, along with cereals like rice and wheat, provide balanced nutrition when consumed together. However, rising CO₂ levels have been linked to nutrient imbalances, particularly reductions in N content in plants (Fernando et al., 2014; Hogy et al., 2013). A meta-analysis confirmed that elevated atmospheric CO₂ generally decreases protein concentrations across multiple food crops, regardless of experimental conditions (Taub et al., 2008; Ziska, 2022). This reduction is typically less pronounced in legumes such as soybean compared to non-legumes (barley, rice, and wheat). Nearly studies found negligible changes in N and protein content under elevated CO₂, such as in red kidney beans (Thomas et al., 2009). Overall, these results suggest that increased CO₂ may reduce the nutritional quality of C₃ grains and legumes, diminishing the bioavailability of essential micronutrients such as zinc, iron, and protein, with potential public health implications globally (Myers et al., 2014). Elevated atmospheric CO₂ also influences soil respiration, often increasing it due to enhanced microbial activity (Korner & Arnone, 1992; Hungate et al., 1997). Soil naturally contains higher CO₂ concentrations than the atmosphere, and microbial communities, including fungi, bacteria, and actinomycetes, respond differently to elevated CO₂ levels. For occurrence, AM fungi colonization in *Pisum sativum* cv. Solara increased at 700 ppm CO₂, while mycelial growth in barnyard grass soil also increased significantly at elevated CO₂ (Gavito, 2000). However, long term exposure to 550 ppm CO₂ reduced populations of *Claroideoglossum* and *Glomus* species in paddy soils under subhumid tropical conditions (Prasad, 2021; Gupta et al., 2025). Ectomycorrhizal fungal communities (EMC) are similarly affected; as exposure to 700 ppm CO₂ led to increased EMC mycelial biomass in *Boswellia pyrifera*, *Pinus strobus* (Godbold, 1997), and a threefold increase in *Pinus sylvestris* (Fransson, 2005). Additionally, several PGP bacteria including *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Erwinia*, *Proteus*, *Pseudomonas*, and *Rhizobium* play a crucial role in modulating plant responses under elevated CO₂ conditions.

Mechanism of CO₂ stress tolerance

Legumes often exhibit reduced photosynthetic activity when exposed to elevated CO₂ levels over prolonged periods (Rogers et al., 2009; Ainsworth & Rogers, 2007). However, these plants have evolved adaptive mechanisms to mitigate this effect by rebalancing their carbon (C) and N metabolism, thereby enhancing BNF, which supports their survival in nutrient poor environments (Rogers et al., 2009; Ainsworth & Rogers, 2007). Additionally, increased nitrogen availability through nodulation by rhizobial bacteria can further improve the carbon sequestration capacity of legumes under elevated CO₂ conditions, helping to alleviate photosynthetic limitations (Ainsworth & Rogers, 2007). With adequate N and the abundance of carbohydrates generated via enhanced photosynthesis, legumes can produce more organic matter (OM) and reduce carbohydrate concentrations in the phloem. This facilitates faster carbohydrate translocation from source tissues, allowing those tissues to maintain or boost photosynthetic activity (Ainsworth & Bush, 2011). Moreover, valuable bacterial communities act as biological sinks for carbon, utilizing around 14-25% of daily photosynthates (Ainsworth et al., 2004; Lambers et al., 2008; Kaschuk et al., 2010). In parallel, biological CO₂ capture methods mediated by cyanobacteria have gained interest under elevated CO₂ conditions, as they efficiently redirect excess carbon into soil biomass and valuable metabolites, offering potential for sustainable carbon management (Abinandan et al., 2019).

Practical Challenges of formulation stability, shelf life, and delivery methods of Beneficial Microbe

The resilience of beneficial plant–microbe interactions under a changing global climate is increasingly recognized as a key factor for sustaining agricultural productivity and ecosystem stability. However, for these microbial solutions to be effective beyond controlled environments, greater attention must be given to practical constraints that determine their real-world performance. Among these, formulation stability, shelf life, and delivery systems are critical determinants of whether beneficial microbes can successfully establish in the field and maintain their functional activity under variable environmental conditions.

Formulation stability is one of the most significant challenges in microbial technology. Beneficial microorganisms are living systems that are highly sensitive to temperature fluctuations, moisture loss, oxygen exposure, and UV radiation during storage and transport. In many cases, the loss of viability occurs even before field application, reducing their effectiveness. To address this, improved formulation strategies such as carrier-based formulations, encapsulation technologies, and protective additives are required. Materials like biochar, alginate beads, and organic carriers have shown promise in maintaining microbial viability and protecting cells from environmental stress. Closely linked to formulation stability is the issue of shelf life. Many commercial microbial products exhibit reduced effectiveness over time due to a decline in cell viability and metabolic activity. This limits their practical use, especially in regions where storage conditions are not well regulated. Extending shelf life requires not only improved formulation techniques but also better selection of stress-tolerant microbial strains that can withstand desiccation, temperature extremes, and nutrient limitation during storage. Developing standardized protocols for quality control and viability assessment is also essential to ensure consistent product performance.

Equally important is the development of efficient and farmer-friendly delivery methods. The success of plant–microbe applications depend on how effectively microbes are introduced into the soil–plant system and how well they colonize the rhizosphere or internal plant tissues. Conventional methods such as seed coating, soil drenching, and foliar sprays each have limitations in terms of uniformity and persistence. Emerging approaches, including controlled-release formulations, nano-carrier systems, and integration with irrigation technologies, offer improved targeting and efficiency. However, their adoption requires careful consideration of cost, scalability, and ease of use under diverse agricultural settings. Overall, strengthening the resilience of plant–microbe interactions require a

shift from purely biological optimization to a more application-oriented perspective. Ensuring formulation stability, extending shelf life, and improving delivery systems are essential steps to bridge the gap between laboratory success and field reliability. Addressing these practical challenges will significantly enhance the effectiveness of microbial technologies and support their integration into sustainable and climate-resilient agricultural systems.

Knowledge Gaps

Despite substantial progress in understanding plant–microbe interactions, several critical knowledge gaps remain that limit the effective deployment of beneficial microbes in climate-resilient agriculture. First, context dependency and inconsistency of microbial performance under field conditions remain poorly understood. Many PGPMs show promising results under controlled environments but exhibit variable efficacy across different soil types, climates, cropping systems, and native microbiomes. This variability highlights an incomplete understanding of microbe–soil–plant–environment interactions under dynamic climate conditions. Second, while individual mechanisms such as phytohormone modulation, nutrient solubilization, and induced systemic resistance (ISR) have been well documented, the integration and crosstalk among multiple stress-response pathways particularly under simultaneous abiotic and biotic stresses remain insufficiently explored. The molecular basis of how plants prioritize or balance salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and abscisic acid (ABA) signaling in the presence of beneficial microbes under combined stress scenarios is still unclear. Third, limited knowledge of microbial community dynamics and functional redundancy constrains the rational design of microbial consortia. Most studies focus on single microbial strains, whereas natural systems involve complex, multi-species interactions. The long-term ecological consequences of introducing non-native microbial inoculants, including their persistence, horizontal gene transfer, and interactions with indigenous microbiota, are not well characterized. Fourth, insufficient understanding of host specificity and genotype-dependent responses remains a major limitation. Plant genetic background strongly influences microbial colonization, signaling efficiency, and stress outcomes, yet crop-specific and genotype-specific microbial compatibility studies are scarce. Additionally, the regulatory roles of microbial metabolites, volatile organic compounds (VOCs), and small RNAs in plant stress adaptation remain underexplored. The studies summarized in the table 5 collectively demonstrate that plant–microbe interactions play a crucial role in mitigating biotic stresses through diverse and complementary mechanisms. Beneficial bacteria, fungi, and algae—including *Bacillus*, *Pseudomonas*, *Trichoderma*, *Rhizobium*, cyanobacteria, and marine algae—enhance plant resistance against fungal, bacterial, viral pathogens and insect pests across a wide range of crops. These microbes act through induced systemic resistance (ISR), activation of defense-related enzymes (such as peroxidase, polyphenol oxidase, chitinase, lipoxygenase, and phenylalanine ammonia lyase), production of pathogenesis-related (PR) proteins, secretion of antimicrobial metabolites (surfactin, VOCs, antibiotics), nutrient competition, and direct antagonism of pathogens. Several studies also highlight microbe-mediated signaling pathways involving jasmonic acid (JA) and ethylene (ET), root exudate-mediated recruitment of beneficial microbes, and the role of microbial elicitors and polysaccharides in triggering host defense responses. Overall, these findings emphasize the potential of microbial inoculants as sustainable and eco-friendly alternatives for managing biotic stresses in agriculture (Rudrappa et al., 2008; Son et al., 2014; Spence et al., 2014; Cawoy et al., 2014; Salas-Marina et al., 2015; Wu et al., 2017; Liu & Brettell, 2019; Pandey & Gupta, 2020; Smith & Lee, 2025). Numerous environmental pressures, including both biotic and abiotic factors, significantly influence plant growth and crop productivity. Plants have evolved diverse adaptive mechanisms to cope with stresses such as cold, heat, drought, salinity, and alkalinity, often mediated through the synthesis of stress-responsive proteins and close associations with beneficial microorganisms (Ansabayeva et al., 2025; Burlakoti, et al., 2024; Harikrishna et al.,

2024). However, prolonged or severe exposure to adverse environmental conditions disrupts plant physiological and biochemical processes, leading to reduced crop yield and quality, thereby posing a serious threat to global food security. Beneficial plant–microbe interactions modulate phytohormone balance, nutrient acquisition, and antioxidant defenses, alleviating stress effects at physiological and molecular levels (Ansabayeva *et al.*, 2025; Patel *et al.*, 2025; Gupta *et al.*, 2025; Zhang *et al.*, 2025; Mmotla *et al.*, 2025, Mano *et al.*, 2026). Stress-induced changes in root exudate composition can actively recruit specific beneficial microorganisms to the rhizosphere, enhancing plant resilience through a “cry for help” mechanism, whereby stressed plants modify exudate profiles to attract protective microbes (Al Raish *et al.*, 2025; Patra, *et al.*, 2025, Patel *et al.*, 2025). Beneficial microorganisms, particularly plant growth-promoting microorganisms (PGPMs) such as rhizobacteria, mycorrhizal fungi, and endophytes, enhance plant tolerance to both abiotic and biotic stressors by modulating plant hormone levels, improving nutrient uptake, producing siderophores and osmolytes, and stimulating antioxidant enzyme systems (Mmotla, *et al.*, 2025; Gupta *et al.*, 2025; Patel *et al.*, 2025). At the molecular level, PGPMs activate systemic acquired resistance (SAR) and induced systemic resistance (ISR) pathways, involving salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), which coordinate the transcriptional activation of defense-related genes including pathogenesis-related (PR) proteins and WRKY transcription factors (Ansabayeva *et al.*, 2025). These interactions also lead to enhanced expression of enzymes such as chitinases, glucanases, and peroxidases, which directly suppress pathogens and fortify plant defenses (MDPI, 2025). Comparative studies highlight that specific bacterial and fungal strains differ in their biocontrol efficacy for example, *Bacillus*, *Pseudomonas*, and *Trichoderma* species exhibit strain-specific abilities to induce host defense responses, stimulate secondary metabolite production, and improve plant stress tolerance. Mixed microbial consortia often outperform single-strain applications, providing synergistic and multifunctional protection by simultaneously targeting multiple stress pathways (Mmotla *et al.*, 2025; ScienceDirect, 2025). Moreover, omics-based analyses are expanding our understanding of PGPR interactions across transcriptomic, proteomic, and metabolomic levels, revealing complex networks of plant–microbe signaling that underlie stress resilience (Mmotla *et al.*, 2025). Maintaining microbial diversity and functional balance within agro ecosystems is therefore critical not only for crop productivity but also for long-term soil health and ecosystem stability. Leveraging beneficial microbes is central to developing climate-adaptive and sustainable agricultural practices. To address the growing challenges posed by climate change and intensifying agricultural demands, coordinated efforts among researchers, policymakers, and agricultural stakeholders are essential to integrate microbial solutions into sustainable farming systems (Patra *et al.*, 2025; Ansabayeva *et al.*, 2025).

Conclusion and Future Prospects

Beneficial plant growth-promoting microorganisms offer considerable potential for improving crop productivity, soil health, and stress resilience under changing climatic conditions. Their ability to enhance nutrient availability, regulate plant hormones, suppress pathogens, and improve tolerance to drought, salinity, heavy metals, and temperature stress makes them valuable tools for sustainable agriculture. However, inconsistent field performance due to variations in soil characteristics, environmental conditions, crop genotype, and interactions with native microbial communities remains a major limitation.

To strengthen practical application and commercialization, future research should focus on establishing national and international microbial strain banks for major food crops, conducting long-term field trials across multiple agro-climatic zones, and developing open-access genomic and metabolomic databases for plant growth-promoting microbes. Standardization of microbial formulation protocols, shelf-life testing procedures, and quality-control measures is essential to improve consistency among commercial bioinoculants. The development of multi-strain microbial consortia combining complementary traits such as nutrient solubilization, stress tolerance, pathogen

suppression, and phytohormone production should be prioritized, along with improved carrier technologies using biochar, alginate encapsulation, nanomaterials, and controlled-release formulations to enhance microbial survival and field persistence. Integration of microbial inoculants with precision agriculture tools—including soil sensors, remote monitoring systems, and climate-based advisory platforms—can optimize application timing and dosage. Farmer-participatory research programs, supportive regulatory guidelines for biosafety and environmental impact assessment, and public–private partnerships are needed to scale up production, reduce costs, and improve accessibility for smallholder farmers.

Future studies should emphasize molecular signaling under combined abiotic and biotic stresses using advanced omics approaches, while artificial intelligence and machine learning tools may help predict microbial compatibility and field performance under variable climatic conditions. Overall, successful integration of microbial technologies into climate-smart agriculture will require coordinated efforts among researchers, industry, policymakers, and farming communities to ensure long-term food security and environmental sustainability.

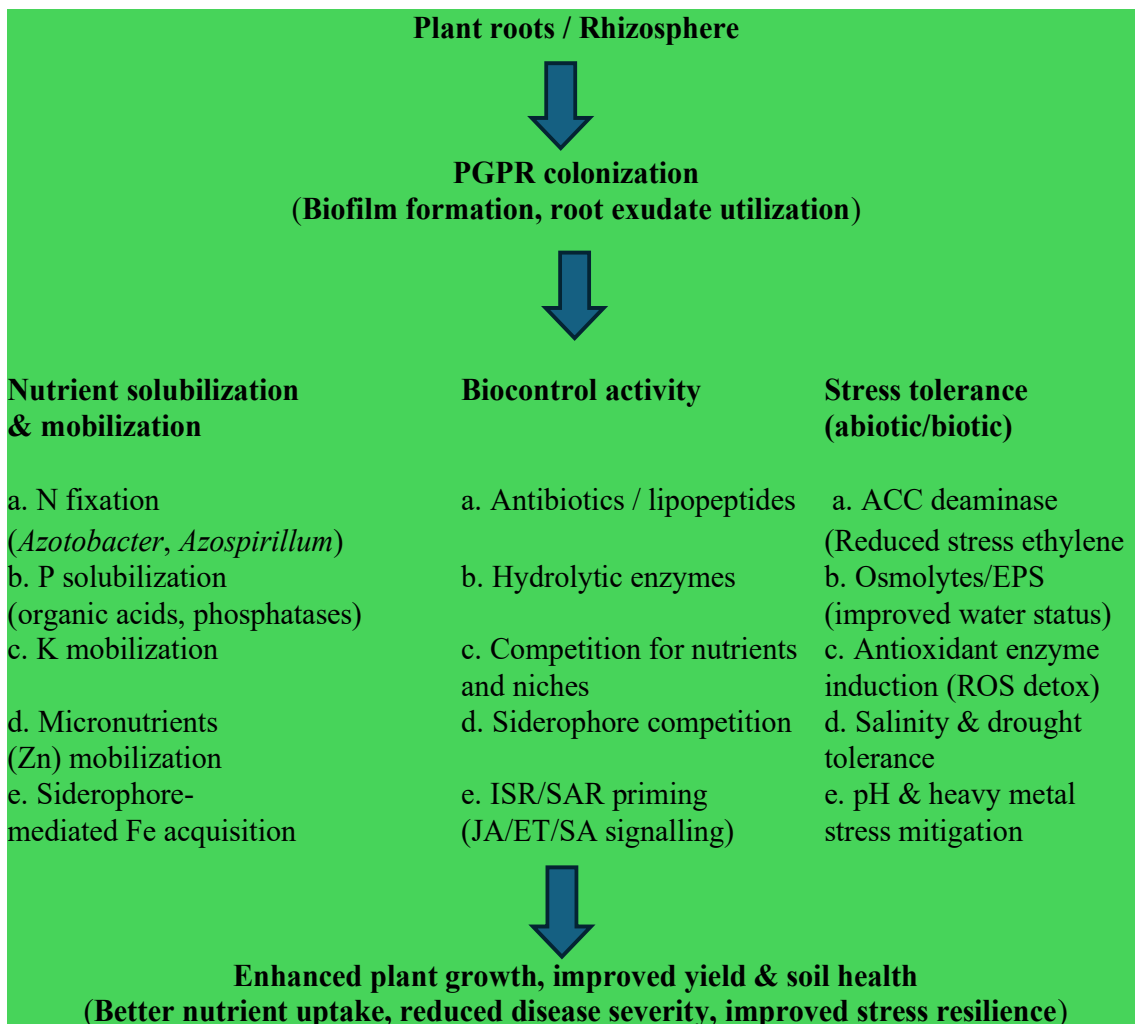


Figure 2: Conceptual diagram of PGPR mechanisms supporting plant growth and stress resilience

Arrows indicate the proposed sequence of processes from root colonization to outcomes. PGPR = plant growth promoting rhizobacteria; ISR = induced systemic resistance; SAR = systemic acquired resistance; JA = jasmonic acid; ET = ethylene; SA = salicylic acid; EPS = exopolysaccharides; ROS = reactive oxygen species.

Nutrient solubilization / mobilization	Biocontrol activity	Stress tolerance (Abiotic/Biotic)
N: biological N fixation; improved N uptake efficiency	Antibiosis: antibiotics, lipopeptides, VOCs	Drought: EPS-mediated soil aggregation and water retention; osmolytes (proline/trehalose)
P: solubilization (organic acids, phosphatases)	Enzymes: chitinase, β -1,3-glucanase, proteases	Salinity: ion homeostasis (higher K^+ / Na^+), compatible solutes
K: mobilization from minerals	Competition: nutrients/space, iron competition via siderophores	Heavy metals: immobilization/chelation; reduced uptake toxicity; improved phytoremediation
Zn/Fe: chelation and mobilization (siderophores)	Induced resistance: ISR (JA/ET) and SAR (SA) pathway activation	pH extremes: improved nutrient availability and rhizosphere buffering
Root growth: IAA and other phytohormones enhance rooting and absorption	Quorum interference: quorum quenching reduces pathogen virulence	Oxidative stress: enhanced antioxidant defenses (SOD, CAT, POD)

Figure 3: Systematic Summary of Key Functional Mechanisms of PGPR

(The Figure summarizes representative mechanisms commonly attributed to PGPR; specific effects depend on microbial strain, host plant, and environmental conditions. Abbreviations: IAA = indole-3-acetic acid; VOCs = volatile organic compounds; EPS = exopolysaccharides; SOD = superoxide dismutase; CAT = catalase; POD = peroxidase).

Table 1. Studies on plant microbe interaction and their adverse drought conditions

S. No.	Microbes	Plants	Stress Response	Reference
1	<i>Azospirillum lipoferum</i>	Maize (<i>Zea mays</i>)	Increase accumulation of soluble sugar, free amino acids, and proline. Affect the growth of root length, shoot fresh weight, shoot dry weight, root fresh weight and root dry weight	Bano et al., 2009
2	<i>Bacillus</i> Spp.	Maize (<i>Zea mays</i>)	Increased accumulation of proline, sugars, free amino acids and decreases electrolyte leakage. It also reduces the activity of antioxidants enzyme (catalase, glutathione peroxidase)	Vardharajula et al., 2011
3	<i>Azospirillum brasilense</i> Spp 245	<i>Arabidopsis</i>	Improved plants seed yield, plants survival, proline levels and relative leaf water content; it also decreased stomatal conductance, malondialdehyde and relative soil water content	Cohen et al., 2015

Table 1 Continued

4	<i>Sinorhizobium medicae</i>	<i>Medicago truncatula</i>	Root nodulation and nutrient acquisition of nutrients during drought stress	Staudinger et al., 2016
5	<i>Trichoderma harzianum</i>	Rice (<i>Oryza sativa</i> L.)	Promote root growth independent of water status and delay drought response	Shukla et al., 2012a
6	<i>Pseudomonas libanensis</i> TR1, <i>Pseudomonas reactans</i> Ph3R3	<i>Brassica oxyrrhina</i>	Increased plant growth, leaf relative water and pigment content and decreased concentrations of proline and malondialdehyde in leaves	Ma et al., n2016a; 2016b
7	<i>Azospirillum</i> sp.	Lettuce (<i>Lactuca sativa</i>)	Promote aerial biomass, chlorophyll and ascorbic acid content, better overall visual quality, hue, Chroma and antioxidant capacity, and a lower browning intensity	Fasciglione et al., 2015
8	<i>Pseudomonas putida</i> MTCC5279 (RA)	<i>Cicer arietinum</i> L.	Osmolyte accumulation, ROS scavenging ability and stress-responsive gene expressions	Tiwari et al., 2016
9	<i>Bacillus thuringiensis</i>	<i>Lavandula dentate</i>	IAA induced higher proline and K-content improved nutritional, physiological, and metabolic activities, and decreased glutathione reductase (GR) and ascorbate peroxidase (APX) activity.	Armada et al., 2014
10	<i>Bacillus</i> sp. WM13-24 and <i>Pseudomonas</i> sp. M30-35	Ryegrass (<i>Lolium perenne</i>)	Promoted growth and root development via regulating plant hormones and increased drought tolerance	He et al., 2021
11	Endophytic fungi LHL10 and LHL06	<i>Glycine max</i> L	Increased production of IAA	Bilal et al., 2020
12	<i>Trichoderma</i>	<i>Solanum lycopersicum</i>	Nutrient availability	Rawal et al., 2022
13	<i>S. meliloti</i>	<i>Medicago sativa</i>	Carbon Metabolism and Antioxidant Defenses	Naya et al., 2007
14	<i>Glucoacetobacter diazotrophicus</i>	Sugarcane	Drought tolerance	Vargas et al. 2022
15	<i>Pantoea alhagi</i>	wheat	Increased accumulation of soluble sugars, decreased accumulation of proline and malondialdehyde (MDA), and decreased degradation of chlorophyll	Chen et al., 2017
16	<i>Pseudomonas species S1</i>	Chili	water stress-induced promotion ability	Rolli et al., 2015
17	<i>Bacillus subtilis</i> and <i>Paenibacillus illinoensis</i>	Pepper	Overexpression of the plant root vacuolar proton pumps H ⁺ -ATPase (V-ATPase) and H ⁺ -PPase (V-PPase)	Vigani et al., 2019

Table 1 Continued

18	<i>Rhizobium</i> sp.	Sunflower	EPS production	Alami et al., 2000
19	<i>Azotobacter</i>	Maize	Enhance plant growth, production of siderophore and IAA, solubilization of phosphate and potassium and growth under drought stress	Shirinbayan et al., 2019

Table 2. Role of Plant-Microbe Interaction on soil salinity

S. No.	Microbes	Plants	Stress Response	Reference
1	<i>Brachybacterium saurashtrense</i> (JG-06), <i>Brevibacterium casei</i> (JG-08), and <i>Haererohalobacter</i> (JG-11)	Groundnut (<i>Arachis hypogaea</i> L.)	Higher K ⁺ /Na ⁺ ratio and higher Ca ²⁺ , phosphorus, and nitrogen content. Shoot and root have higher concentration of auxin.	Shukla et al., 2012; 2012b
2	<i>Pseudomonas putida</i> UW4	<i>Brassica napus</i> (canola) and Maize	Modulation of plant protein differential expression and ACC deaminase activity.	Cheng et al., 2017
3	<i>Rhizobium</i> and <i>Pseudomonas</i>	Mung bean (<i>Vigna radiate</i>)	ACC-deaminase for improving growth, nodulation and yield of mung beans under natural salt-affected conditions.	Ahmad et al., 2011
4	<i>Azospirillum</i>	Lettuce seeds	Promoted higher biomass, ascorbic acid content antioxidant capacity, and a lower browning intensity.	Fasciglione et al., 2015
5	<i>Hartmannibacter diazotrophicus</i> E19	Barley (<i>Hordeum vulgare</i> L.)	Increased root and shoot dry weight. ACC-deaminase activity of and lower ethylene content.	Suarez et al., 2015
6	<i>Acinetobacter</i> spp. and <i>Pseudomonas</i> Sp.	Barley and oats	Production of enzyme ACC deaminase lower ethylene and IAA promote plant growth	Chang et al., 2014
7	<i>Pseudomonas</i> and <i>Enterobacter</i>	Maize (<i>Zea Mays</i>)	Reduce triple response and more N, P, and K uptake and high K ⁺ -Na ⁺ ratios.	Nadeem et al., 2014
8	<i>Pseudomonas pseudoalcaligenes</i> and <i>Bacillus pumilus</i>	Rice GJ-17	Reduced the toxicity of reactive oxygen species (ROS) and reduced lipid peroxidation and superoxide dismutase activity. Reduce lipid peroxidation and superoxide dismutase activity.	Jha & Subramanian, 2014
9	<i>Pseudomonas</i> Sp. <i>Serratia</i> Sp.	Wheat	ACC deaminase activity, reduce ethylene level and enhance plant height, root length and yield.	Zahir et al., 2009

Table 2 Continued

10	<i>Bipolaris</i> sp. CSL-1	Glycine max	Lower stress response gene expression, antioxidant Increased salicylic acid	Khan et al. (2022)
11	<i>Bacillus pumilus</i> HR <i>Zhihengliuella halotolerans</i>	<i>Seidlitzia rosmarinus</i>	Catalase activity, anthocyanin and decreased malondialdehyde, Na ⁺ uptake	Zilaie et al., 2022
12	<i>Varivorax paradoxus</i> 5C-2	Pea	Enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (which metabolises ACC, the immediate precursor of the phytohormone ethylene, ion homeostasis and maintain plant water relations	Wang et al., 2016
13	<i>Bacillus subtilis</i> , <i>Arthrobacter</i> species	Wheat	Increase in dry biomass, total soluble sugars and proline content, Catalase activity	Upadhyay et al., 2012
14	<i>Serratia plymuthica</i> , <i>Stenotrophomonas rhizophia</i> and <i>Pseudomonas fluorescence</i>	Cucumis	growth-beneficial properties: production of auxin, HCN, lipase or protease and wheat growth promotion	Egamberdieva et al., 2008
15	<i>Pseudomonas fluorescence</i>	Groundnut	ACC deaminase	Saravanakumar & Samiyappan, 2007
16	<i>Pseudomonas</i> and <i>Acinetobacter</i> species	Barley and oats	Salt uptake	Chang et al., 2014
17	Microalgae cyanobacteria	Tomato	Enhanced K ⁺ uptake and reduced Na ⁺ /K ⁺ ratio in the leaves of treated plants indicate MEF's active role in reestablishing ion homeostasis	Mutale Joan et al., 2021
18	<i>Pseudomonas frederiksbergensis</i> OS261	Red pepper	Enhance plant, reducing the emission of ethylene and regulating antioxidant enzymes	Chatterjee et al., 2017

Table 3. Role of Plant-Microbe Interaction on heavy metals stress tolerance for Sustainable Agriculture

Sr. no.	Microbes	Plants	Heavy Metals	Mechanism	Reference
1	<i>Claroideoglomus claroideum</i> , <i>Funneliformis mosseae</i>	Marigold (<i>Calendula officinalis</i> L.)	Cd and Pb	Accumulation of secondary metabolites (phenols, flavonoids, carotenoids) and enhanced antioxidant capacity	Hristozkova et al., 2016
2	<i>Glomus fasciculatum</i> and <i>Pseudomonas putida</i>	<i>Helianthus annuus</i> L.	Cd and Zn	Promoted the dry biomass of the plant, accumulation of Zn and Cd in root and shoot.	Mani et al., 2016
3	<i>Glomus etunicatu</i>	<i>Calopogonium mucunoide</i>	Pb	Promoting plant nutrient (P, S and F) acquisition, attenuating the negative effects of Pb on membranes and contributing to the reduction of ROS generation.	De Souza et al., 2012
4	<i>Pseudomonas brassicacearum</i> and <i>Rhizobium leguminosarum</i>	<i>Brassica juncea</i>	Zn	Induced metal chelation, toxicity attenuation and microbial-assisted phytoremediation.	Adediran et al., 2015
5	<i>Bacillus thuringiensis GDB-1</i>	<i>Alnus firma</i>	Cd, Ni, As, Cu, Pb and Zn	Production of phytohormones, siderophore, (ACC) deaminase and solubilization of Phosphorus. Increased biomass, chlorophyll content, nodule number, and heavy metal (As, Cu, Pb, Ni, and Zn) accumulation	Babu et al., 2013
6	<i>Thiobacillus thiooxidans</i> and <i>Pseudomonas putida</i>	<i>Gladiolus grandiflorus</i> L.	Cd and Pb	Promote root length, plant height, dry biomass of the plant and enhanced accumulation of Cd and Pb	Mani et al., 2016
7	<i>Pseudomonas</i> spp. Lk9	<i>Solanum nigrum</i> L.	Cd, Zn and Cu	Improved soil Fe, P and heavy metal availability, shoots dry biomass and uptake of Cd, Zn and Cu biosurfactants. Production of siderophores and organic acids that induce growth and metal uptake by Cd hyperaccumulator <i>Solanum nigrum</i> L.	Chen et al., 2014
8	<i>Bacillus pumilus E2S2</i> ,	<i>Sedum</i>	Cd, Zn and Cu	Production of IAA, siderophores, ACC deaminase and solubilization of Phosphorus. Increased water extractable Cd	Ma et al., 2015a

Table 3 Continued . . .

10	<i>Bradyrhizobium japonicum</i>	Lettuce	Cd and Pb	and Zn contents in soil, Improved plant growth and metal uptake IAA production enhanced the growth and increased the shoot root lengths and dry biomass	Seneviratne et al., 2016
11	<i>Enterobacter</i> sp. JYX7 and <i>Klebsiella</i> sp. JYX10	<i>Polygonum pubescens</i>	Cd Pb, and Zn	Production of IAA, siderophores, ACC deaminase, solubilized inorganic phosphate improved phytoremediation efficiency	Jing et al., 2014
12	<i>Bacillus anthracis</i> PM21	<i>Sesbania sesban</i>	Cr and Cd	Improved antioxidant enzymes activity, decreased proline content, electrolyte leakage, malondialdehyde content	Ali et al., 2021
13	<i>Colletotrichum</i> sp.	<i>Oryza sativa</i>	Cd	IAA, gibberellic acid, bioaccumulation, phosphate solubilization, siderophore	Mukherjee et al., 2022
14	<i>Bacillus megaterium</i>	<i>Sedum alfredii</i>	Cd	Increased antioxidants, Cd ²⁺ uptake, root to shoot translocation	Tang et al., 2019
15	<i>Cellulosimicrobium cellulans</i>	Chili	Chromium toxicity tolerance	Cr uptake	Chatterjee et al., 2009
16	<i>Pseudomonas</i> sp. and <i>Bacillus</i> sp.	Spinach	Cd, Pb, Zn toxicity tolerance	Bioaugmentation	Shilov et al., 2019
17	<i>Leifsonia</i> sp. and <i>Bacillus</i> sp.	Maize	Cd toxicity tolerance	Cd uptake	Ahmad et al., 2016
18	<i>Trichoderma</i> species	Chickpea	As toxicity tolerance	Microbe mediated biotransformation	Tripathi et al., 2017
19	<i>Burkholderia</i> species	Tomato	Cd toxicity tolerance	the bacterium led to decreases in plant peroxide and chlorosis levels, promoted relative plant growth and decreased the root absorption of Cd, resulting in increased plant tolerance to this highly toxic	Dourado et al., 2013
20	<i>Achromobactin xylocopids'</i>	Mustard green	Cu toxicity tolerance	metal sequestering and growth promoting	Ma et al., 2008

21.	PGPB	Sorghum	Cr stress	Decrease the accumulation of Cr by improving Phyto stabilization process	Bruno et al., 2020
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Table 4. Role of Plant-Microbe Interaction on Temperature Mechanism for Sustainable Agriculture

S. No.	Microbes	Plants	Mechanism	Reference
1	<i>Pseudomonas cedrina</i> , <i>Brevundimonas terrae</i> , and <i>Arthrobacter nicotianae</i>	<i>Oryza sativa</i>	Absorption and solubilization of nutrients, releasing hormone-like compounds that stimulate plant growth, and protecting against pathogens	Yadav et al., 2014; Kumar et al., 2021
2	<i>Curvularia protuberate</i>	<i>Dichantheium lanuginosum</i> Tomato	Heat tolerance	Marquez et al., 2007
3	<i>Curvularia protuberate</i>	(<i>Solanum lycopersicum</i>)	Heat tolerance	Rodriguez et al., 2008
4	<i>Burkholderia phytofirmans strain PsJN</i>	Grapevine	Cold tolerance, antifungal effects, plant defense and makes better resource mobilization in plants	Miotto-Vilanova et al., 2016
5	<i>Burkholderia phytofirmans strain PsJN</i>	Tomato (<i>Solanum lycopersicum</i>)	Heat tolerance, antifungal effects, plant defense and makes better resource mobilization in plants	Issa et al. 2018
6	<i>Bacillus aryabhathi</i>	Soybean	Heat stress tolerance	Park et al. 2017

Table 5. Studies on plant microbe interaction biotic stresses Mechanism for Sustainable Agriculture

S. No.	Microbes	Plants	Diseases	Mechanism	Reference
1	<i>Brevibacterium iodinum</i> KUDC1716	Pepper	Gray leaf spot disease (<i>Stemphylium lycopersicum</i>)	Enhanced expression of pathogenesis-related (PR) protein genes	Son et al., 2014
2	<i>Bacillus</i> sp.	Rice	Bacterial leaf blight (<i>Xanthomonas oryzae</i>)	Increased accumulation of phenylalanine ammonia lyase, peroxidase and polyphenol oxidase.	Chithrashree et al., 2011
3	<i>Bacillus amyloliquefaciens</i> HK34	<i>Panax ginseng</i>	Root diseases (<i>Phytophthora cactorum</i>)	Induced systemic resistance	Lee & Ryu, 2021

Table 5 Continued . .

4	<i>Bacillus subtilis</i> , <i>Pseudomonas fluorescens</i> , <i>Azotobacter chroococcum</i>	Cucumber	<i>Cucumber mosaic cucumovirus</i> (CMV)	Higher peroxidase and b-1,3-glucanase enzyme activities Production of pathogen related (PR) protein Solubilized phosphate significantly and produced indole acetic acid (IAA) siderophores, <i>exo</i> -polysaccharides, hydrogen cyanide and ammonia.	El-Borollosy & Oraby, 2012
5	<i>Pseudomonas aeruginosa</i>	Greengram (<i>Vigna radiate</i> L.)	Fungicide-induced phytotoxicity		Ahmad et al., 2011
6	<i>Paenibacillus</i> sp.	Cabbage (<i>Brassica oleracea</i>)	Black rot (<i>Xanthomonas campestris</i>)	Induce systemic resistance	Ghazalibigla et al., 2016
7	<i>Bacillus subtilis</i> FB17	Tomato	<i>P. syringae</i> pv. <i>tomato</i>	Tricarboxylic acid cycle intermediate L-malic acid (MA) secreted from roots selectively signals and recruits the beneficial rhizobacterium	Rudrappa et al., 2008
8	Rhizospheres' microbes	Rice	<i>M. oryzae</i>	Direct antagonism, trigger ISR in rice plants through a mechanism that is dependent on JA and ET signaling	Spence et al. 2014
9	PGPR	Potato	<i>Fusarium</i> sp.	Inhibitory effects	Recep et al., 2009
10	PGPR and <i>Trichoderma koningiopsis</i>	Cape gooseberry	<i>Fusarium</i>	Antagonistic effect	Diaz et al., 2013
11	<i>Pseudomonas</i>	Potato	<i>Phytophthora infestans</i>	Protective effects	de Vrieze et al., 2018

12	<i>T. harzianum</i> Tr6 & <i>Pseudomonas</i> sp. Ps14	Cucumber	<i>Fusarium oxysporum</i> <i>f. sp. radicans</i> <i>cucumerinum</i>	Induce systemic resistance	Alizadeh et al., 2013
13	<i>Pseudomonas</i> <i>fluorescence</i>	Rice	Leaf folder pest	Resistance mechanisms, activities of polyphenol oxidase (PPO) and lipoxygenase (LOX)	Saravanakumar et al., 2008
14	<i>Stenotrophomonas</i> sp., <i>Xanthomonas</i> sp., <i>Microbacterium</i> sp	Arabidopsis	<i>Hyaloperonospora</i> <i>arabidopsis</i>	Active emission of volatile organic compounds (VOCs)	Liu & Brettell, 2019
15	<i>Bacillus subtilis</i> and <i>Bacillus</i> <i>amyloliquefaciens</i>	Tobacco	<i>Botrytis cinerea</i>	Surfactin production	Gupta et al., 2025
16	<i>Saccharothrix</i> <i>yanglingensis</i>	Arabidopsis	<i>P. syringae</i> pv. Tomato DC 3000	A novel protein elicitor BAR11 and its functions in plant defense responses	Zhang et al., 2018
16	<i>Rhizobium etli</i> strain G12	Glover Squash	<i>Aphis gossypii</i>	systemic resistance	Martinuz et al., 2012
18	<i>Trichoderma virens</i> , <i>T. atroviridae</i>	Tomato	<i>Alternaria solani</i> , <i>Botrytis cinerea</i> , <i>P.</i> <i>syringae</i>	Systemic disease resistance	Salas-Marina et al., 2015
19	<i>Pseudomonas</i> PHU094, <i>Trichoderma</i> THU 0816, <i>Rhizobium</i> R2091	Chickpea	<i>Sclerotium rolfsii</i>	Trigger the level of phenolic compound	Singh et al., 2013
20	<i>Anabaena variabilis</i> , <i>Anabaena torulosa</i> , <i>Anabaena laxa</i> , <i>Calothrix</i> sp.	Tomato, cotton	<i>Pythium debaryanum</i> , <i>Fusarium oxysporum</i> , <i>F. moniliforme</i> , <i>Rhizoctonia solani</i>	Extracellular hydrolytic enzymes, as antifungal activity i.e. FPase, chitosanase, xylanase activity, CMCase, cellobiase, protease	Prasanna et al. 2008; Chaudhary et al. 2012; Lee & Ryu, 2021
21	<i>Pseudomonas</i> sp.	Tomato	<i>Rhizoctonia solani</i>	Antagonistic	Pandey & Gupta, 2020

22	<i>Trichoderma</i> sp.	Tomato, canola	<i>Botrytis cinerea</i> and <i>Leptosphaeria maculans</i>	Antagonistic via secondary metabolite	Vinale et al., 2008a
23	<i>Pseudomonas fluorescense</i>	Rice	<i>Desmia funeralis</i>	Enzymes, lipoxygenase and chitinase activity	Karthiba et al., 2010
24	<i>P. fluorescense</i> Pfl, <i>B. subtilis</i> , <i>T. viridae</i>	Tuberose	<i>Lasiodiplodia michiganensis</i>	Systemic Resistance	Durgadevi et al., 2018
25	<i>B. subtilis</i> MB1600 & <i>R. tropicum</i> R1899	Common bean	<i>Fusarium solani</i> f. sp. <i>phaseoli</i>	Integrated reduce disease severity	Estevez de Jensen et al., 2002
26				compete with pathogens for nutrition, secrete antibacterial substances to inhibit the growth of pathogens, and induce plant defense systems to resist pathogen invasion	
	<i>B. amyloliquefaciens</i>	Litchi	<i>Peronophythora litchii</i>		Wu et al., 2017
27	<i>Ulva armoricana</i>	Bean, grapevine, and cucumber	<i>Erysiphepolygoni</i> , <i>Erysiphe necator</i> and <i>Sphareotheca fuliginea</i>	Algal polysaccharide polysaccharides that contain uronic acid and sulphated rhamnose	Jaulneau et al., 2011
28	<i>Cystoseira myriophylloides</i> and <i>Fucus spiralis</i>	Tomato	<i>Agrobacterium tumefaciens</i>	Induce the activity of defense enzymes polyphenol oxidase and peroxidase	Esserti et al., 2016
29	<i>Trichoderma</i> species	Vegetables and crops	<i>Alternaria</i> species and <i>Fusarium</i> species	Inhibited growth and spore production via antifungal, antimicrobial and antibiotic activities	Meena et al., 2017
30	<i>Spatoglossum variabile</i> , <i>Stokeyia indica</i> , and	Watermelon and egg plant	<i>Fusarium solani</i> , <i>Macrophomina phaseolina</i> and <i>Meloidogyne</i> spp.	Suppressive effect	Baloch et al. 2013

*Melanothamnus
afaqhusainii*

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|----|--|--------|--|---------------------|------------------------------------|
| 31 | <i>Oscillatoria,</i>
<i>Anabaena,</i> <i>Nostoc,</i>
<i>Nodularia,</i> and
<i>Calothrix</i> species | Pepper | <i>Alternaria alternate</i>
and <i>Botrytis cinerea</i> | Antifungal activity | Kim, 2006;
Khab et al.,
2022 |
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