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Beneficial Plant-Microbe Interactions and Stress Tolerance in Maize

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Abstract: Beneficial microbes are crucial for improving crop adaptation and growth under various stresses. They enhance nutrient uptake, improve plant immune responses, and help plants tolerate stresses like drought, salinity, and heat. The yield potential of any crop is significantly influenced by its associated microbiomes and their potential to improve growth under different stressful environments. Therefore, it's crucial and exciting to understand the mechanisms of plant-microbe interactions. Maize (*Zea mays* L.) is one of the primary staple foods worldwide, in addition to wheat and rice. Maize is also an industrial crop globally, contributing 83% of its production for use in feed, starch, and biofuel industries. Maize requires significant nitrogen fertilization to achieve optimal growth and yield. Maize plants are highly susceptible to heat, salinity, and drought stresses and require innovative methods to mitigate the harmful effects of environmental stresses and reduce the use of chemical fertilizers. This review summarizes our current understanding of the beneficial interactions between maize plants and specific microbes. These beneficial microbes improve plant resilience to stress and increase productivity. For example, they regulate electron transport, downregulate catalase, and upregulate antioxidants. We also review the roles of plant growth promoting rhizobacteria (PGPR) enhancing stress tolerance in maize. Additionally, we explore the application of these microbes in maize production and identify major knowledge gaps that need to be addressed to utilize the potential of beneficial microbes fully.

Keywords: abiotic and biotic stress; beneficial microbes; stress tolerance; maize; plant growth-promoting rhizobacteria (PGPR); AMF; mycorrhiza

1. Introduction

Maize (*Zea mays* L.), alongside wheat and rice, stands as one of the primary staple foods worldwide, boasting a global production of 1147.7 million metric tons in 2020 [1]. Maize has risen to prominence as an industrial crop on a global scale, with 83% of its production allocated for use in feed, starch, and biofuel industries. Among the 125 developing countries, approximately 75 consider maize a staple crop, contributing to 70% of the world's maize production originating from these nations [2]. Maize is a nitrogen-hungry crop requiring a significant amount of nitrogen fertilization to achieve optimal growth and yield, particularly during its vegetative and early reproductive stages, which are more sensitive to nitrogen requirements. Inadequate nitrogen supply during these phases limits plant development, reduces photosynthetic efficiency, and ultimately decreases the grain yield [3,4]. Moreover, maize crops are extremely susceptible to heat, salinity, and drought stresses. Global maize yield is projected to decline by 20-40% under a 2°C warming scenario and by 40-60% under a 4°C warming scenario [5]. The variability in global maize production between 1980 and 2013 can be attributed to heat stress and drought [5]. Salinity stress further exacerbates challenges by decreasing the germination rate in maize. It causes osmotic stress, inhibiting water uptake by seeds delaying germination [6]. In salinity stress, the accumulation of Na^+ competes with K^+, leading to inhibition of protein synthesis [7]. This stress causes ionic toxicity, reactive oxygen species (ROS) generation, and

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osmotic stress [8]. In addition to abiotic stresses, between 6% to 19% of maize production worldwide is lost annually due to damage caused by insects and other herbivores. The primary pests of maize are Leaf aphids (*Rhopalosiphum maidis),* thrips (*Frankliniella williamsi)* [9], fall armyworm (*Spodoptera frugiperda),* black cutworms *(Agrotis ípsilon),* cotton bollworm *(Helicoverpa armígera),* corn earworm *(Helicoverpa zea)* [10] stalk borer (*Elasmopalpus lignosellus) and* armyworm (*Spodoptera spp.).*

Plant microbiomes are microorganisms that live in and around plant, forming a complex microbial ecosystem and can play a significant role in plant growth and development. These microbiomes includes bacteria, fungi, nematodes, archaea and viruses that inhabits at different parts of plants. These parts include rhizosphere (soil surrounding roots), phyllosphere (above-ground parts like leaves and stems), endosphere (internal tissue) and spermosphere (seed surfaces) [11,12]. Beneficial plant-microbial interactions significantly affect plant's growth and development and mitigate environmental stresses [13,14]. Plants are intimately associated with microbes for their growth and survival; they play a significant role in plant nutrient availability and uptake and plant stress tolerance [15]. Studies reported the presence of plant growth-promoting rhizobacteria from the native plant *Ceanothus velutinus, which contains several rhizobacteria possessing plant growth-promoting traits such as the production of IAA, siderophore, protease, catalase, ability to fix nitrogen, and phosphate solubilization [16]*. Moreover, inoculating native soil from the *Ceanothus velutinus* to the propagation mix enhanced the cutting propagation, and IAA-producing isolates from the rhizosphere promote Arabidopsis growth [17]. Thus, exploring plant microbiomes to improve the maize yield and help it withstand different biotic and abiotic stresses is crucial. This review focuses on the beneficial plant-microbe interactions in maize to enhance yield and mitigate environmental stresses.

2. Abiotic Stresses and Their Impact on Crop Productivity

To meet high consumptive demand of maize they are often grown in arid locations where maize may experience drought-related stress. Maize life cycle has various distinct growth stages, including seedling emergence and development, vegetative growth, flowering and pollination, grain filling, and maturation. Drought and high temperatures can negatively impact maize crops throughout these growth stages, with the most significant effects at vegetative and during grain filling stage and when plants reach the 8th leaf stage [18]. In regions where water is scarce during the growing season, maize production may decline by up to 15% [19]. In China's key maize-producing areas, approximately 60% of crops face water and heat stress, leading to a 30% reduction in annual yield [20]. However, the most alarming prospect is the future. With the ongoing climate change and global shifting weather patterns, water, and heat stress are projected to diminish the global maize supply by 15-20%, annually [18]. Elevated temperatures exceeding 35°C can impede maize crop's reproductive and vegetative growth, from seed germination to grain filling, the final stage [21]. Concurrently, when maize faces water and heat stress during its reproductive phases, it becomes even more vulnerable [22]. The impact of drought stress on maize includes reduced leaf area, low water-use efficiency, lesser nutrient uptake, decreased photosynthetic efficiency, and reduced biomass accumulation and lower productivity. Studies have shown that water stress during vegetative growth can diminish growth rate, decrease root system development, prolong the vegetative phase, and affect CO_2 distribution. A brief period of water scarcity can lead to a 28-32% reduction in dry weight during vegetative growth and 66-93% during tasseling/ear formation [23]. Extended drought stress before flowering can decrease leaf size and internodal distance, delaying silk emergence and tasseling and resulting in a 15-25% overall yield decrease [24]. Additionally, even a few days of drought stress during pollination/fertilization can lead to abnormal embryo formation and fewer kernels per plant. Drought stress before and after pollination is associated with a significant decline in kernel set [24]. The primary photosynthetic activity of maize plants occurs in their five- or six-ear leaves, mainly contributing to plant biomass. However, drought stress can diminish the photosynthetic rate by reducing ear leaf size, and slowing crop growth [25].

Higher temperatures at reproductive stages, such as tasseling, pollination, and grain filling, can lower maize grain quality. A study by Izaurralde et al.,[26] suggests that increasing the mean seasonal temperature by 1°C can reduce the maize economic yield by 3-13%. The study by Hussain et al., [20]

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on two maize hybrids, Xida 319 and Xida 889, subjected to heat stress, observed reduced plant height, lowered biomass accumulation, and decreased yield. Increased heat stress reduces the efficiency of light utilization in maize plants leading to chlorophyll degradation. Additionally, the increased temperature during the anthesis stage of maize cultivation results in reduced growth [27]. Similarly, exposure of maize to heat stress during the 12-leaf stage reduces pollen production, germination rate, zeatin content, salicylic acid content, and tassel size [28].

Salt stress is among several abiotic stresses affecting maize growth and yield. Increased salt concentration reduces plant height and biomass due to high osmotic stress and ion toxicity [29]. This reduction in growth is followed by decreased stomatal conductance and photosynthetic pigments, disturbance in cytosolic enzyme activity, and impairment of carbon fixation enzymes [30,31]. In a research by Kaya et al., [32] applying a salt concentration of 100 mM NaCl during the reproductive phase of maize reduced kernel weight and yield by 8% and 25%, respectively. Similarly, a study by Katerji et al., [33] showed an 11.3% reduction in maize grain yield in clay soil subjected to salinity stress. The increase in salt concentration interferes with the maize plant's ability to absorb nitrate ions due to antagonistic action between chloride and nitrate ions [34]. The effect of abiotic stress has been described in Figure 1B)

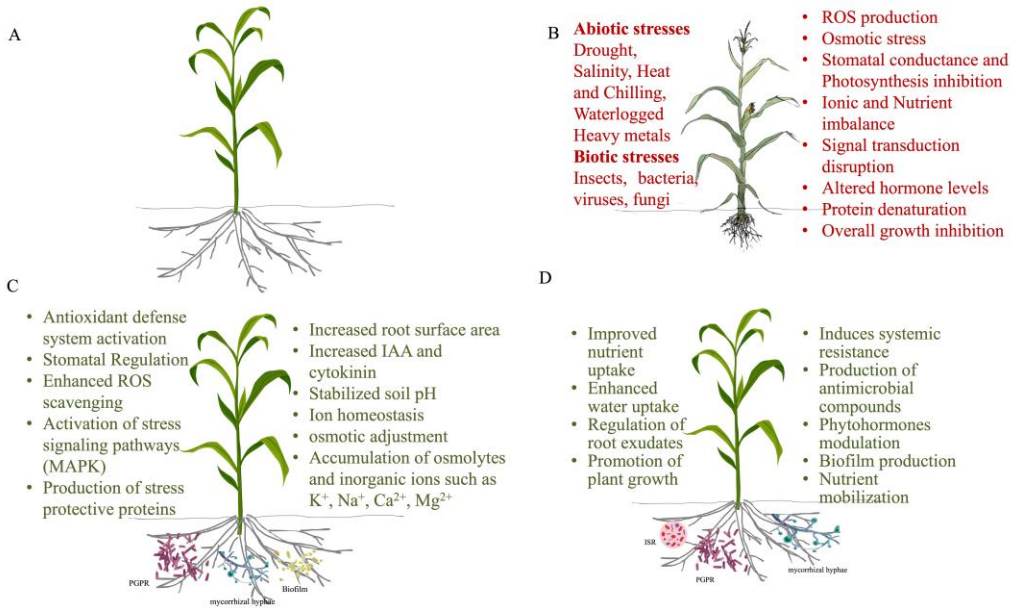

Figure 1. An overview of maize plants showing (A) a healthy maize plant, (B) a maize plant affected by abiotic and biotic stresses, (C) mechanisms of abiotic stress tolerance including osmotic adjustment, antioxidant activity, and stomatal regulation, and (D) mechanisms of biotic stress tolerance such as activation of pathogenesis-related proteins and structural barriers.

3. Biotic Stress and Crop Production

Abiotic stress is the major obstacle in attaining potential yield for maize production worldwide. In addition to abiotic stress biotic stress also threaten maize cultivation, often leading to substantial yield losses [35]. Diseases, insects and pests are the primary factors responsible for these losses, with pathogens such as fungi, bacteria, and viruses eliciting syndromes like ear/stalk/kernel rot, rough dwarf/wilt disease, and northern leaf blight/maize mosaic [36], which are the major diseases that reduce maize yield. The simultaneous occurrence of abiotic and biotic stresses exacerbates the situation, resulting in a remarkable reduction in global maize production. Studies indicate that over 50% reduction in yield occurs in major crops, including maize, due to abiotic stresses alone. In comparison, approximately 10% of maize productivity is lost annually to biotic stresses worldwide [37], and 22.5% of global maize loss is due to diseases and pests. The effect of abiotic stress has been described in Figure 1B.

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4. Mechanism of Abiotic Stress Tolerance in Maize

Plants developed various mechanisms to cope with various abiotic stresses, which are described below for three major abiotic stresses in maize.

4.1. Drought Stress

To cope with drought stress, maize plants have evolved various mechanisms broadly categorized into escape, avoidance, and tolerance strategies [38]. Drought escape refers to shortening a crop's life cycle to avoid drought stress, which is particularly crucial during reproductive growth stages. Traits like days to sowing, flowering, and maturity are genetically heritable, allowing for phenological adjustments in response to water availability [38]. Developing early maturing cultivars aids in evading terminal drought stress [39]. However, this strategy may reduce yields, as crop duration directly correlates with yield [40]. Through selection, crops adjust their growth period based on available moisture, completing their life cycle before drought onset. The maize plant tries to complete the reproductive stage before the drought becomes more prevalent. Maize, highly susceptible to drought, benefits significantly from this escape mechanism [41].

Drought avoidance in maize is assessed by measuring tissue water status, typically indicated by turgor water potential under drought stress conditions. Avoidance involves maintaining plant water status by reducing transpiration rates or increasing water uptake [42]. Various physiological and morphological traits are essential selection criteria for drought avoidance in maize, including leaf rolling, leaf firing, canopy temperature, stomatal closure, leaf attributes, and root traits [43]. Stomata regulate transpiration and gaseous exchange, governing photosynthesis and respiration. Plants reduce water loss by closing their stomata, preserving water status, and enhancing drought avoidance [40]. Drought tolerance for the combination of heat and drought stress involves maintaining growth and development through cellular and biochemical adaptations. Along with sustaining average physical growth, drought tolerance is also associated with yield stability under water-stressed conditions, a complex process in which crops have developed various natural mechanisms to adapt and tolerate drought stress [44]. These adaptations include accumulating compatible osmolytes like proline, glycine betaine, soluble sugars, and various inorganic ions (K^+, Na^+, Ca^{2+}, Mg^{2+}, Cl^-, and NO_3^-) to support plant water status via osmotic adjustment [44,45].

Additionally, the enzymatic and non-enzymatic antioxidant systems, including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX), are activated to mitigate oxidative damage. Growth regulators like abscisic acid (ABA) also play a role [20,25]. Moreover, transcription factors (TFs) are activated to regulate gene expression sensitive to drought and high temperatures, while stress proteins like heat shock proteins (HSP), late embryogenesis abundant (LEA) proteins, and aquaporins assist in water movement under stress [41].

4.2. Maintaining Ion Homeostasis in Salinity Stress

An imbalance in the cellular ion exchange process causes salinity stress in the plant. Due to this ionic imbalance, Na^+ influx and K^+ efflux through various ion transporters in the cell membrane [46]. The excess concentration of Na^+ increases oxidative stress by enhancing ROS (reactive oxygen species) production [47]. Consequently, cellular membranes become disrupted, leading to a breakdown in cell homeostasis. During salinity stress, genes and transcription factors regulating ion transports are activated which, helps alleviate ion toxicity in cells. These include plasma membrane protein (PMP), high sodium affinity transporter (HKT), Salt overly sensitive (SOS) pathway, and Na^+/H^+ exchangers (NHXs) [48]. ZmCIPK24a and ZmCBL4 plus ZmCBL8 act as SOS2 and SOS3 in maize [49]. During salinity stress, SOS3 senses the changes in the cytoplasmic Ca2+ level, which activates SOS2. The SOS2-SOS3 complex phosphorylates ZmSOS1, activating SOS1 and increasing root-to-soil Na^+ efflux, enhancing salt tolerance [50]. The study identified QTL for K^+ content (qKC3), which encodes ZmHKT2, a K^+ transporter localized in the xylem parenchyma [51]. ZmHKT2 reduces shoot K^+ content by retrieving K+ from xylem vessels. The mutants lacking ZmHKT2 have higher shoot K^+

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content and salt tolerance [52]. Decreasing the activity of ZmHKT2 is one viable strategy for developing salt tolerant maize varieties.

4.3. Osmotic Adjustment

Osmotic adjustment involves creating a water gradient to enhance water influx, thereby maintaining turgor by reducing osmotic potential. This adjustment aids in preserving tissue water status by minimizing the detrimental effects of drought through the accumulation of solutes in cellular cytoplasm and vacuoles. By sustaining turgor potential and supporting physiological processes, osmotic adjustment protects against drought-induced damage [53]. Relative water content is a crucial indicator for estimating drought tolerance in plants with closed stomata and reduced CO_2 accumulation resulting from decreased relative water content under drought stress [42]. The sustainable regulation of photosynthetic rate and turgor potential ensures the translocation of photosynthetic assimilates to developing kernels [54]. Osmoprotectants, including nitrogenous compounds like proline, polyols, polyamines, and glycine betaine, as well as hydroxy compounds like polyhydric alcohols, sucrose, and oligosaccharides, play crucial roles in osmotic adjustment [55]. These compounds protect cellular proteins and membranes against dehydration effects and help maintain cellular integrity [56]. Glycine betaine, for instance, acts as an important osmoprotectant, safeguarding plants against various stresses such as drought, salinity, cold, and heat by protecting the photosynthetic apparatus and stabilizing cellular proteins [57]. Proline, another osmoprotectant, helps maintain water status, protect cellular membranes, and prevent protein denaturation under osmotic stress [57,58]. Soluble sugars, accumulated in response to drought stress, serve multiple roles in plant metabolism and protection, including acting as substrates for biosynthesis processes and protecting cellular organelles through vitrification [59]. Polyols, such as sorbitol, glycerol, and mannitol, form hydration spheres around macromolecules, safeguarding them from dehydration [60]. These mechanisms collectively contribute to plants' ability to tolerate drought stress and maintain essential physiological processes.

Antioxidants and plant growth regulators

Antioxidants are molecules that protect plants by scavenging reactive oxygen species, thus preventing oxidative damage. They form a defense shield against oxidative stress. Antioxidants can be enzymatic or non-enzymatic. Enzymatic antioxidants include catalase (CAT), superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase (APX), peroxidase, and polyphenol oxidase. Non-enzymatic antioxidants include α-tocopherol, ascorbic acid, β-carotene, glutathione, and cysteine [61]. These components are essential in neutralizing reactive oxygen species and preserving plant health under oxidative stress conditions. Plant hormones, also known as plant growth regulators or phytohormones, play vital roles in governing the growth and development of plants, acting as signaling molecules that trigger cellular differentiation and function locally or are transported to distant targets.

In response to drought stress, plants undergo various adaptations, including maintaining endogenous hormonal balance [62]. Different plant growth regulators confer drought tolerance, including auxins, cytokinins, abscisic acid (ABA), gibberellins, salicylic acid, brassinosteroids, methyl jasmonate, polyamines, ethylene, and zeatin. These hormones interact to regulate plant responses, specific growth stages, tissues, and environmental conditions. For instance, auxins are involved in drought stress responses, with interactions observed between ethylene, cytokinins, and auxins affecting their biosynthesis [63,64]. The concentration of indole acetic acid (IAA) decreases in maize leaves under drought stress, while the accumulation of ABA increases, influencing hormonal balance. The IAA accumulation increases under moderate stress (13.4%) while decreases under severe drought stress (63.2%) in maize [25]. Salicylic acid helps maintain photosynthesis by retaining higher chlorophyll content under drought stress, contributing to drought tolerance [65]. ABA and ethylene regulate stomatal conductance, grain number, grain filling rate, and plant apex growth antagonistically, with cytokinin enhancing growth and development. ABA plays a crucial role as a stress hormone, modulating growth, development, and stress responses through a signaling pathway involving various components highly responsive to ABA. Average water availability does not induce

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ABA accumulation, and extremely severe drought reduces ABA accumulation due to the cessation of ABA precursors [66]. The antioxidant defense system detoxifies ROS and maintain redox homeostasis [67]. Overall plant hormonal balance is critical for various growth and development processes, with interactions between hormones playing a crucial role in plant adaptation to drought stress.

4.5. Polyamines and Their Roles in Biotic Stress in Maize

The detrimental effects of biotic stress on significant crop plants, maize, are not just a concern, but a pressing issue. The production of highly carcinogenic aflatoxins by Aspergillus flavus alone has led to a staggering loss of USD 686.6 million in maize cultivation in the U.S These statistics are not mere statistics but a stark reminder of the economic havoc wreaked by biotic stress. Other climate-dependent pathogens, such as Fusarium spp. and Ustilago maydis, further compound the issue [68,69].

Polyamines (PA) has emerged as a beacon of hope in reducing biotic stress caused by various pathogens in maize. PAs play a crucial role in the production of H_2O_2, acting as both a defensive tool and a signaling molecule in response to biotic stress [69]. For example, spermine (Spm), a form of PA, functions as a signaling molecule in pathogen defense and plays a critical role in resistance against viral infections [70]. In the case of Ustilago maydis, a dimorphic host-specific fungus, it induces 'huitlacoche' or common smut in maize plants. The accumulation of H_2O_2 derived from polyamine oxidase plays a significant role in tumor formation caused by U. maydis in maize plants. The maize polyamine oxidases (zMPAOs) transcription factor was found to be downregulated in tumors. The symptoms of the disease were observed to reduce upon application of 1,8-diamino octane (1,8-DO), a potent polyamine oxidase inhibitor[69].

5. Beneficial Plant-Microbe Interactions in Maize

5.1. Arbuscular Mycorrhizal Symbiosis

Maize forms symbiotic associations with Arbuscular mycorrhizal (AM) fungi. This partnership, established via the mycorrhizal and root pathway, allows plants to efficiently uptake nutrients from the soil. In this symbiosis, the fungi and plants engage in a mutual exchange where the fungi provide mineral nutrients while the plant supplies carbon (C). Maize roots, in addition to beneficial relationships with microbes such as mycorrhizal fungi, play a crucial role in uptake of nutrients like phosphorus (P) and nitrogen (N). Maize root residues, a significant byproduct of this symbiosis, provide N for other plants in crop rotation, thereby improving agricultural productivity [71,72]. This exchange occurs via arbuscules inside root cortex cells, where AM fungi acquire 4–20% of the total photosynthetic carbon fixed by the plant through symbiotic relationships. The AM fungal hyphae then utilize this carbon to generate specialized exudates, which attract and establish a hyphosphere microbiome. This microbiome plays a crucial role in compensating for the fungi's incapacity to utilize organic nutrients directly. By secreting enzymes and fostering the mineralization of organic nutrient sources, the hyphosphere microbiome significantly increases nitrogen and phosphorus availability. This collaborative functionality within the holobiont substantially enhances nutrient accessibility for all interacting organisms, including plants, AM fungi, and hyphosphere bacteria (Figure 1C and D).

In maize, the colonization of maize roots by AM fungi begins early in the plant development phase, which peaks at the vegetative growth stages. Maize roots produce strigolactones (5-deoxy-strigol and Sorghumol), essential for establishing AM symbiosis [73,74]. These compounds act as chemoattractants and guide the fungal hyphae toward the root system [75]. Upon contact with strigolactones, AM fungi initiate signaling cascades that activate genes such as SYM and RAM1 involved in colonization. Like other plants such as carrots, maize roots form pre-penetration apparatuses (PPAs) at the root surface to facilitate penetration of fungal hyphae into root tissue. Upon penetration, the fungal hyphae initiate a series of molecular events, such as the production of chitin and lipochitooligosaccharides for recognition and signaling between plant and fungus [76]. The signal transduction also leads to activation of transcription factors and arbuscule formation. Fungal-

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derived proteins, such as Small Secreted Effector Proteins (SSEPs), are transported into the plant cell and are believed to play roles in arbuscule formation and function [77]. The nutrient exchange between fungus and maize plants occurs within the arbuscules. In addition to arbuscules, vesicles are formed within root cells, which act as storage structures for lipids, glycogen, and other metabolites.

Once the symbiosis between AM fungi and maize plants is established, AM fungi can increase the root volume, increasing the surface area for water absorption. D-myo-inositol-3-phosphate synthase (IPS) and the 14-3-3-like protein GF14 (14-3GF) are pivotal in facilitating signal communication between maize and AMF during drought stress. Co-expression of these two genes has been shown to enhance maize drought tolerance significantly [78]. Similarly, the AM fungi infection upregulates the expression level of NPF4.5 homologs, indicating higher nitrate uptake during symbiosis [78]. The ammonium transporter ZmAMT3;1 expressed in cortical cells of maize during AM fungi infection absorbs 68-70% of the transported nitrogen AM fungi to maize plants [79].

5.2. Nitrogen-Fixing Symbiosis with Rhizobia

Rhizobia, the widely distributed Gram-negative bacteria in soil, can enhance maize cultivation. Despite being primarily associated with legumes, these beneficial bacteria can promote growth and yield in maize through various mechanisms. While their efficiency with maize is generally lower than with legumes, the potential for improvement is promising [80].

The inoculation of the Azospirillum strain in maize roots increased the GA_3 levels, thereby boosting root growth [81]. Similarly, the strains of Rhizobium (such as R. etli bv. Phaseoli and R. leguminosarum bv. trifolii) and Sinorhizobium sp. Have shown promising results in enhancing growth, increasing plant height, and improving grain yield in maize [82]. Numerous studies have reported on the nitrogen-fixing ability of Herbaspirillum seopedicae and Azospirillum spp. in maize. A study on two maize genotypes, Morgan 318 and Dekalb 4D-70, demonstrated a significant increase in grain yield and higher N accumulation with the inoculation of a mixture of Azospirillum spp. strains, a result comparable to the application of 100 Kg N ha^{-}[83]. Another study unveiled the identification of a nitrogen-fixing association with the native variety of maize grown in nitrogen-depleted soils in Mexico. The microoxic environment for better nitrogen fixation is created by the mucilage tube surrounding the roots, which had a high abundance of proteobacteria. [84]. These symbiotic relationships are crucial in enhancing plant growth, higher nutrient acquisition, and crop yield, offering a hopeful outlook for the future of maize cultivation.

5.3. Agricultural Application of Stress-Tolerant Microbes

The use of stress-tolerant microbes shows a significant increase in the yield of maize plants. Maize plants inoculated with Piriformospora indica, an endophytic fungus grown under drought stress conditions, resulted in increased leaf area, SPAD value, higher root fresh and dry weight, and upregulation of antioxidants catalase and superoxide dismutase. Upregulating drought-related genes DREB2A, CBL1, ANAC072, and RD29A increased resistance to drought stress [85]. The Bacillus spp. PM31 also improved maize growth under salinity stress [86]. The microbes can be applied to enhance plant yield and improve soil health. Stress-tolerant microbes can replace 20-40% of chemical fertilizers while alleviating drought stress impact. Integrating stress-tolerant bacteria with other beneficial microbes, such as AM fungi, can increase stress tolerance in maize and other plants, offering more significant agricultural benefits. These microbes can be integrated into agronomic practices through various application strategies that contribute to sustainable agriculture (Table 1).

5.4. Microbe Mediated Induced Systemic Resistance (ISR) in Maize

Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR) are different mechanisms by which plants can develop systemic resistance against pathogens and diseases. SAR is a plant defense mechanism that protects plants against a broad spectrum of pathogens following an initial infection. SAR is induced by recognizing pathogen-associated molecular patterns (PAMPs)

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or effector molecules released by the pathogen [87]. ISR is a plant defense mechanism in which exposure to certain beneficial microorganisms, pathogens, or chemical compounds primes the plant's immune system to enhance its resistance against subsequent pathogen attacks. Unlike SAR, which is induced by direct pathogen infection, ISR is triggered by beneficial microbes or certain chemical compounds in the plant's environment [88].

ISR is a complex process that involves the activation of various defense responses within the plant, including the production of antimicrobial compounds, reinforcement of cell walls, and the activation of defense-related genes. ISR is triggered by non-pathogenic rhizobacteria, which colonizes the rhizosphere. The microbes prime the plant's innate immune system, enhancing its defense response against subsequent pathogen and insect attacks [89]. Specific microorganisms, such as beneficial rhizobacteria, B. velezensis SQR9, and the fungus Trichoderma harzianum, play crucial roles in inducing ISR in maize against pathogens. B. velezensis SQR9 colonizes maize roots and activates defense signaling pathways. This colonization leads to the enrichment of phenylpropanoid biosynthesis, amino acid metabolism, and plant-pathogen interaction pathways in maize roots. The calcium signaling pathway is pivotal in SQR9-induced ISR, as inhibiting calcium signaling weakens the induced resistance [51]. Similarly, Trichoderma harzianum triggers ISR in maize against Curvularia leaf spot by releasing cellulases and cellobiose from roots. The cellobiose released from T. harzianum-colonized roots prompts the expression of defense-related genes (Opr7, Pr4, Aoc1, Erf1) in maize, thereby enhancing ISR against the pathogen [90]. ISR in maize involves jasmonic acid and ethylene signaling pathways mediated by the NPR1 protein.

Table 1. The Plant Growth Promoting Rhizobacteria (PGPR) enhancing stress tolerance in Maize.

Host associated microbial strains	Effect/Mechanism of Stress tolerance	References
Microbial mediated beneficial drought stress tolerance		
Rhizobium (*R. etli* bv. *Phaseoli*, *R. leguminosarum* bv. *Trifolii*, *Sinorhizobium* sp	Enhanced growth, increased plant height, improved grain yield	[82]
Herbaspirillum seopedicae *Azospirillum* sp	Increased grain yield Higher N accumulation Increased leaf area and SPAD value Increased root fresh and dry weight	[83]
Piriformospora indica	Decreased Malondialdehyde (MDA) accumulation Upregulation of antioxidants and drought related genes	[85]
Pseudomonas putida	Forms viable biofilms around roots Increase soil holding capacity Improve soil structure Increase soil moisture content	[91]
Pseudomonas aeruginosa *Alcaligenes faecalis* *Proteus peneri*	Enhances plant growth traits such as leaf area, shoot length, root length Downregulation of catalase, ascorbate peroxidase and glutathione peroxidase	[92]
Klebsiella variicola *Pseudomonas fluorescens* *Raoultella planticola*	Increased levels of betaine, glycine and choline Improved plant growth	[93]
Burkholderia sp. *Mitsuaria* sp.	Increased proline and phytohormone accumulation Higher antioxidant activity Decreased MDA content	[94]
Megathyrsus maximus	Increased proline accumulation Decrease in MDA content Reduced glutathione reductase activity	[95]

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Azospirillum brasilense *Pseudomonas putida* *Sphingomonas*	Symcoms containing these microbes increases shoot dry weight, root dry weight and plant height	[96]
Azospirillum lipoferum	Increased proline, soluble sugar and amino acids accumulation Enhances shoot and root weight, root length	[97,98]
Bacillus sp.	Increased proline accumulation Reduction in electrolyte leakage Decreased activity of antioxidants	[99]
Burkholderia phytofirmans Strain PsJN *Enterobacter* sp. FD17	Increased root and shoot biomass Higher chlorophyll content Increased leaf area and photosynthetic rate	[100]
Rhizophagus irregularis	Increased hydraulic conductivity and water permeability coefficient Increased phosphorylation of Plasma membrane intrinsic proteins (PIPs) Increased photosynthetic activity	[101]
B pumilus	Increased relative water content and osmotic potential Higher photosynthetic activity Increased ABA production	[102]
Azospirillum brasilense SP-7 *Herbaspirillum seropedicae Z-152*	Decreased expression of ZmVP14	[103]
Microbial mediated beneficial saline stress tolerance		
Bacillus sp. PM31	Improved maize growth under salinity stress	[86]
Co-inoculation of *Rhizophagus intraradices* *Massilia* sp. RK4	Increased nutrient uptake Increased AMF root colonization Decreased leaf proline levels	[104]
Rhizobium sp. *Pseudomonas* sp.	Enhanced proline production Decrease in electrolyte leakage Reduction in osmotic potential Selective K ions uptake	[105]
Pseudomonas fluorescens, *P. syringae*, *P. chlororaphis Enterobacter aerogenes*	ACC-deaminase for increasing plant height, biomass, and cob yield Higher grain mass and straw yield Increased P and K uptake Higher K^+/Na^+ ratio	[106]
Glomus mosseae	Enhanced soluble sugars accumulation Increased total organic acids, acetic acid, malic acid, oxalic acid, fumaric acid and citric acid accumulation Increased upregulation of osmoregulation process	[107]
B. amyloliquefaciens SQR9	Increased chlorophyll content Enhanced soluble sugar content Decreased level of Na^+ Upregulation of RBCS, RBCL, *H^+-PPase*, *HKT1*, *NHX1*, *NHX2* and *NHX3*	[108]

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Kocuria rhizophila Y1	Increased photosynthetic capacity and relative water content Increased antioxidant levels Decreased level of Na^+	[109]
Azotobacter chroococcum	Increased K^+/Na^+ ratio Higher chlorophyll content Increased proline concentration	[91]
Microbial mediated beneficial heat stress tolerance		
Bacillus sp. AH-08, AH-67, AH-16 *Pseudomonas* sp. SH-29	Upregulation of heat shock proteins (HSP) Increased total chlorophyll, catalase, and peroxidase Enhances plant height, leaf area, root & shoot fresh and dry weight Decreased concentration of MDA	[110]
Rhizophagus intraradices *Funneliformis mosseae* *F. geosporum*	Increased quantum efficiency of PSII Higher photosynthetic rate Increased plant height, leaf width and cob number	[111]
Glomus etunicatum	Increased water content and leaf water potential Increased photosynthetic activity Higher stomatal conductance	[112]
Glomus sp.	Regulation of electron transport through PSII Increased plant height and leaf width	[113]

6. Challenges and Future Perspectives

Abiotic and biotic stresses significantly influence the growth and development of maize plants. Salt stress disrupts water uptake and nutrient acquisition, while drought stress hinders photosynthetic activity, decreasing in maize yield. Despite their heat tolerance, prolonged exposure to temperatures exceeding 35°C is detrimental to crop growth and development, and exceeding 40°C during flowering and grain-filling season will reduce grain productivity.

Despite the known benefits of plant-microbe interactions such as arbuscular mycorrhizal (AM) fungi, rhizobia, as well as bacterial and fungal endophytes, there is still much to learn about the diversity of beneficial microbes present in maize rhizosphere and their specific functions. Understanding which microbes are most helpful under different growing conditions and soil types is crucial for optimizing microbial inoculants. The interactions between introduced beneficial microbes and native soil microbiota are complex and poorly understood. Competition, cooperation, and antagonistic interactions among microbes can influence their effectiveness in promoting plant growth. More research is needed to assess the long-term effects of microbial inoculation on soil health, microbial community dynamics, and crop productivity. We are responsible for developing sustainable management practices that integrate microbial interactions into existing agricultural systems.

7. Conclusions

The positive interactions between maize plants and beneficial microbes offer a promising solution for enhancing plant growth and nutrient absorption under challenging conditions. These interactions not only have the potential to bolster the environmental resilience of maize agriculture but also to promote sustainability. using microbes for defense against various stresses can significantly increase crop yield and productivity, leading to economic benefits for farmers and potentially reducing the need for chemical inputs, thus benefiting the environment.

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