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Harnessing Beneficial Plant-Microbe Interactions for Enhanced Plant Adaptation to Abiotic Stresses

William Makaza and Casper Nyaradzai Kamutando

Abstract

Boosting crop production is a vital venture for enhancement of humanity. However, it remains a dream, especially in developing countries. To attain food security at household level, productivity is constrained by a several biotic and abiotic stresses. Yield losses are usually influenced by abiotic stresses, particularly drought and heat stress, and poor soil fertility. Optimal crop production under these stress factors requires substantial inputs, including irrigation and heavy fertilization, strategies which majority of farmers in poor countries lack capacity to exploit. Therefore, much more sustainable and accessible alternatives need to be developed in order to address the problem of food insecurity. Recently, research has proven that plant adaptation to abiotic stresses can be promoted by beneficial microbial species, especially those that reside in the rhizosphere. For instance, mycorrhizal fungi have been found to expand the root system of plants to access more water and nutrients. In-depth understanding of the mechanisms underlying beneficial plant-microbe interactions is key in development of holistic programs for boosting yields under abiotic stress conditions. This chapter seeks to unravel the mechanisms underlying beneficial plant-microbe interactions and the importance of these interactions in stress-adaptation.

Keywords: abiotic stress management, climate change impact, crop production and food-security, ecosystem, plant growth promoting microbes, role of plant-microbial interaction

1. Introduction

Food security is a basic human requirement that is being jeopardized by a rapidly booming demography, unsustainable agricultural practices, and a changing global environment. This puzzling divergence is drastically reducing agricultural productivity and is exacerbated by abiotic stresses, contributing to more than 70% global food losses [1, 2]. Nonetheless, the implications of the Green Revolution which intensified the use of high yielding varieties, synthetic pesticides, inorganic fertilizers and mechanization (eg., irrigation), significantly contributed to the reduction in microbial diversity within arable farmlands; and this phenomenon had a negative bearing on overall soil health [3, 4].

Abiotic stresses (including, high and low temperatures, salinity, flooding, drought, nutrient limitation, toxic metals and organic contaminants) contribute to unsustainable agriculture [5–7]. The potential costs of these abiotic stresses are significant, implying the need for sound, economical, and ecologically friendly measures to reduce their negative effects on plant growth and development [1].

Plants, unlike animals, cannot use avoidance and escape as stress-relieving tactics and as a survival strategy, their evolution has been defined by development of very advantageous relationships with their more mobile companions, microorganisms. Some of these relationships entail complex symbioses that provide stress tolerance, such as mycorrhizae and rhizobia, which aid in alleviation of nutritional and water deficiency [6, 8–10]. Beneficial microorganisms are increasingly being used in agriculture, with several research programs assessing microbial strains for their capacity to provide protection against a specific stress (eg., nitrogen and phosphorus deficiency) as well as cross-protection against numerous stresses [11–13]. Understanding the underlying physiological mechanisms by which the beneficial microbial taxa mediate stress tolerance is crucial to ensuring sustainable agricultural production under the current and predicted climatic conditions.

Plant growth and soil fertility are all aided by the beneficial microbes-interactions [14–16]. It has been now commonly recognized that certain unique and efficient microbial strains, known as plant growth promoting (PGP) microorganisms, improve plant growth, fitness, guard against pathogenic organisms, and aid to maintain soil health under diverse environmental conditions [4, 17, 18]. In addition, some microbial taxa are known to contribute to the biological processes of the soil formation [11, 19]. For instance, rhizosphere microorganisms contribute to the biogeochemical cycling of nitrogen (N), phosphorus (P), potassium (K) and sulfur (S) [10, 17, 20]. For the past 3 decades, knowledge on beneficial microorganism has dramatically increased and in some cases, PGP microbes were used as inoculants for enhancement of sustainable crop productivity [13, 21–23]. In this chapter, we provide a synthesis on the rhizospheric microbiome interactions; the influence of abiotic stresses on plant-microbe associations; as well as, describe roles performed by PGP bacteria in aiding plant adaptation to abiotic stresses.

2. Beneficial and harmful plant-microbe interactions

Plant-microbe interaction is a complex, dynamic, and ongoing process that dates back to Earth's first plant colonization. Plants and bacteria have been associated for millions of years, resulting in an assemblage of host and non-host species forming a holobiont [24–26]. A metagenomic study by Xu et al. [20] revealed over-representation of KEGG Orthology (KOs) involved in known plant-microbe and microbe-microbe interactions, such as bacterial secretion systems, flagella assembly, bacterial chemotaxis, bacterial toxins, bacterial motility, two-component system and biofilm formation. These KOs were responsible for transporting plant-derived nutrients such as; amino acids, peptides, urea, oligosaccharides and monosaccharides, into microbial cells [11, 13, 20].

Plants are regularly approached by both the beneficial and the harmful microorganisms (especially, fungi and bacteria) in both, the natural and cultivated lands. The phenomenon results in formation of beneficial partnerships between the plants and the microbes. These partnerships enhance both direct and indirect stimulation mechanisms. Indirect stimulation mechanisms such as those performed by mycorrhizal fungi and rhizobia, results in optimal availability of mineral nutrients and fixed nitrogen to plants [8, 27, 28]. The direct stimulation mechanisms can be attained through phytohormones, antagonism towards pathogenic microorganisms

and mitigation of stresses [4, 11, 29]. On contrary, the harmful interactions have detrimental effects on plant growth and development [12, 30]. Therefore, understanding the beneficial plant microbial interactions can recognize both positive and negative impacts of microbes on plants.

Beneficial microbial communities correlated with plant ecosystems can be classified as follows; phyllospheric, endophytic and rhizospheric [10, 31, 32]. Phyllospheric (above ground) microorganisms are known to significantly contribute to nitrogen fixation as well as phytoremediation [7, 24]. Most of the phyllospheric microbes have been encountered on plant surfaces in moss forests and were shown to tolerate abiotic stresses due to UV radiation and high temperature (35–50°C) [33]. Phyllospheric microbes belongs to different species of diverse genera including, *Achromobacter*, *Acinetobacter*, *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Bacillus*, *Delftia*, *Erwinia*, *Methylobacterium*, *Pantoea*, *Pseudomonas*, *Pseudobacterium*, *Phytomonas*, *Sarcina* and *Xanthomonas* [1, 3, 24, 25]. Furthermore, in blue green algae (BGA), species like *Anabaena*, *Calothrix*, *Nostic*, *Scytonema* and *Tolypothrix* were observed very beneficial for plant adaptation under low N conditions [34].

Endophytic microbiomes characterize another useful plant growth microbes that infiltrate vertically or horizontally into the internal plant tissue (eg., root, stem, flower, fruits and seeds) [4, 25]. As for bacteria, they are from a diversity of taxa that include; *Azoarcus*, *Achromobacter*, *Burkholderia*, *Nocardioides*, *Herbaspirillum*, *Pantoea*, *Klebsiella*, *Gluconoacetobacter*, and *Enterobacter* [26, 35–37].

Above all, the most superior plant-microbe interaction is of soil microbes with the root ecosystems (i.e., rhizosphere microbiome) (see, **Figure 1**). Historically, Morgan et al. [31] cited Hiltner (1904) as the first person to discover and introduce the term rhizosphere. This term was derived from ‘*rhiza*’ and ‘*sphere*’, the Greek names which means root and field of influence, respectively. The rhizosphere is ‘home’ to a wide range of microorganisms, many of which are unquestionably

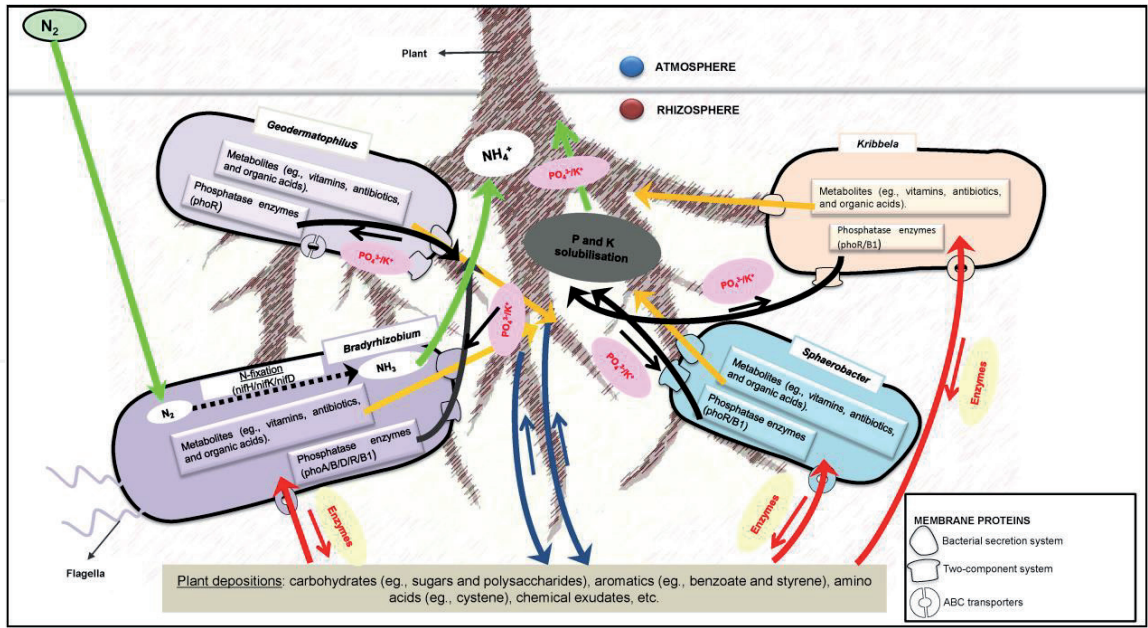


Figure 1. Summary of putative PGP roles of the genomes reconstructed from *A. dealbata* rhizosphere metagenomes. Results are based on RAST and KAAS annotations of genome bins ($\geq 70\%$ completeness). Black arrows illustrate transference of phosphorus solubilizing enzymes from bacteria to the soil and the uptake of phosphate and potassium by the bacteria. Orange arrows denote conveyance of bacterial metabolites into the soil. Dark blue arrows depict plant depositions into the rhizosphere and re-uptake of organic nutrients by plant roots. Red arrows illustrate secretion of various enzymes involved in decomposition of plant deposits and uptake of organic nutrients by the bacteria. Light green arrows elucidate assimilation of nitrogen, phosphorus and potassium into the plant host (adapted from Kamutando et al. [38]).

beneficial to plants through preventing pathogenic infection and assisting in the acquisition of nutrients from the soil [31, 39, 40]. The taxonomic, genetic, and functional components of the rhizosphere microbiome must be understood in order to manage them for long-term crop productivity and agricultural sustainability under abiotic stress conditions [4, 6, 41]. Furthermore, the characterization of rhizosphere microbes as well as the determination of functional mechanisms mediating plant-microbe interactions has progressed in certain models, plant and non-plant species for sustainable agriculture [26, 29, 38, 42]. Considering the mobility and activity of the microbes in the rhizosphere, which is mediated by the rhizodeposits occurring around soil-root zone; *Methylobacterium*, *Pseudomonas*, *Serratia*, *Rhizobium*, *Paenibacillus*, *Erwinia*, *Enterobacter*, *Flavobacterium*, *Bacillus*, *Azospirillum*, *Burkholderia*, *Arthrobacter*, *Alcaligenes*, and *Acinetobacter*, have all been characterized and identified as rhizospheric microorganisms with plant growth promoting ability [6, 11, 29, 31]. These rhizodeposits include lost root cap, border cells, dead and lysed root cells, lost gases, passively and actively released solutes, gelatinous material from the mucigel; all stimulate microbial activity and enzyme production [9, 19, 43].

In establishment of the plant-microbe partnerships, both plants and microbe communicate through signals, such as volatile chemical chemicals, hormones and hormone mimics, as well as carbohydrate and protein-based signals [12, 40, 44]. For example, microbe and/or pathogen-associated molecular patterns (MAMPs or PAMPs) are carbohydrate-based and protein-based signals that are required for microbial survival [2, 30, 31].

3. Effect of abiotic stresses on plant-microbe interactions

Abiotic stress conditions are one of the most critical limiting factors for agricultural crops worldwide ([45], **Figure 2**). These harsh conditions include, low water availability due to salinity or drought, flooding, high or low temperatures, high or low soil pH, soil nutrient deficiency, and exposure to harmful chemicals including, toxic metals and organic pollutants [1, 4, 15, 26, 40, 47]. Impact of these stresses on food security is being studied more and more around the world and its effects were observed to be more on the disruption of metabolic homeostasis and pathways of the plant [5]. The habitats affected by these stresses may potentially generate a plethora of adapted PGP microbial strains that might be used as inoculants to alleviate the stress conditions [45].

For example, when exposed to abiotic stresses (e.g., heat stress), plant accumulate high levels of reactive oxygen species (ROS) in their tissues [9]. The ROS include hydrogen peroxide (H_2O_2), hydroxyl radicals ($OH^{\cdot-}$), singlet oxygen (1O_2) and superoxide radicles (O^{2-}), and these interact with the plant cell proteins, DNA as well as lipids, posing oxidative damage and cell malfunctioning [3, 48]. In addition, drought-induced moisture stress in the rhizosphere induces an increased plant respiration and carbon alterations assimilation [3, 47], which results in decreased ATP synthesis and an increase in ROS production; which have serious consequences on cellular metabolism [9, 12, 26, 49]. Under these circumstances, beneficial microorganisms can respond through synthesizing antioxidants and osmoprotectants [2, 19, 35].

Arid and semi-arid regions of the globe are more prone to salinity and drought stress conditions. Arid conditions are responsible for higher reductions of; crop productivity as well as arable land, especially in areas where sea levels are arising into agricultural lands [19, 29, 48, 50]. Plant growth is harmed by salinity in different ways [19]. From cereals to horticultural species, salinity can affect germination, plant vigor and crop productivity [21, 51, 52]. Nevertheless, it can lower nodulation,

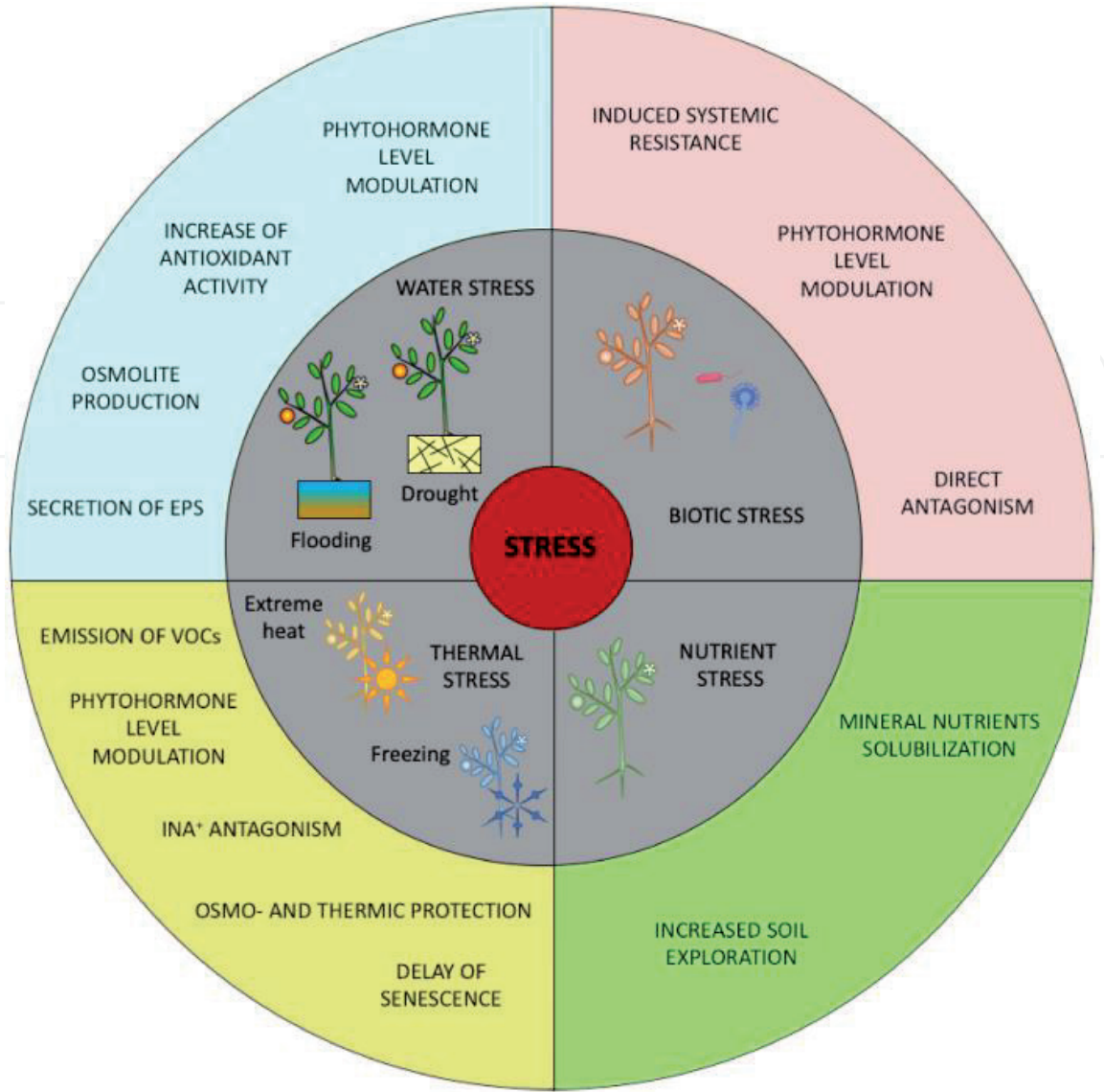


Figure 2.
 Protective mechanism of plant microbial interactions under different levels of abiotic stress conditions.
 Exopolysaccharides (EPS), volatile organic compounds (VOCs), ice-nucleating activity (INA+). Sourced from Sangiorgio et al. [46].

nitrogen fixation and total nitrogen content in legumes, which has a negative impact on biological nitrogen fixation [1, 6, 9, 53]. Previous studies highlighted the sensitivity of symbiotic nitrogen fixation with global impact of salinity and drought stress, which occurs during both the development of symbiotic nodules and the succeeding period of nitrogen fixation and plant nitrogen intake [15, 29, 54].

In addition, presence of large levels of Na⁺ and Cl⁻ on the roots modifies the functioning of uptake systems and changes the competitive interactions between ions for binding and transport into root cells thus limiting nutrient and water uptake [1, 45, 47]. In terms of nutrient uptake deficiency, this can be induced by saline conditions as Na and P uptake and accumulation is inhibited due to the formation of calcium phosphate precipitates which deter beneficial microbes away from its interaction with the plant roots [21, 51, 55]. Nonetheless, the performance of soil microbial enzymes such as nitrogenase, ureases or phosphatases can be inhibited, thus in turn, lowering biogeochemical cycling process [17, 53]. Also, non-calcareous soils of tropics were reported to harbor less beneficial bacterial taxa compared to neutral and calcareous soils of the deserts [45, 48]. A denaturing gradient gel electrophoresis profiling study of 16S rRNA by de Los Rios et al. [56] ascertained high microbial activity in desert conditions with high ability to survive hypersaline

conditions. However, in general, abiotic stressors contribute to the visual appearance of sterile environment for the plant and microbial association [19, 40].

4. Beneficial plant-microbe interactions and sustainable agriculture

The principal factors that influence agricultural production by disrupting rhizosphere functioning are environmental pressures and their unpredictability [3, 20, 57]. A healthy plant rhizosphere not only aids in the provision of nutrients and water to plants, but it also gives long-term advantages to microbial diversity, which in turn aids plant health [22, 50]. The composition of root exudates, which account for microbial recruitment in the rhizosphere is mostly determined by plant genotypes [6, 29, 31]. These exudates, promote the multiplication of beneficial microbes of the plants at nanomolar concentration. Rhizobacteria, mycorrhizal fungi and other microbes are among the beneficial microbial diversity associated with the root zones that contribute to increased plant growth [4, 24, 48]. These beneficial microbes interact symbiotically or asymbiotically in promoting plant and soil health through a myriad of techniques including pathogen control, secondary metabolite synthesis and increased stress resistance [43, 45, 56, 58]. Also, many commercial products based on beneficial microorganisms or microbial consortiums, such as Subtilexfi (BeckerUnderWood, Inc., Ames, IA, USA), Kodiakfi (Gustafson, Inc., Plano, TX, USA), Biota Maxfi (CustomBio, Inc., Deerfield Beach, FL, USA), Triatum-Pfi (Koppert, Srl, Verona, Italy), express multiple functions and synergistic and additive effects on plant growth and development [46]. The various mechanisms in-with beneficial microorganism promote sustainable agriculture are detailed below.

5. Root-zone soil nutrient availability

Many of the nutrients required by plants are present in soil, but they are in insoluble precipitates or are bonded to inorganic and/or organic soil elements, making them unavailable to plants [7, 36]. Nutrient deficiency in plants is not only stressful, but can also increase the impact of other abiotic stresses. With the aid of plant-microbe associations, plant growth and development can be enhanced to sustain food production [6, 11]. Nutrient uptake activities facilitate this phenomenon [18, 59]. For instance, mycorrhizae interactions with plant roots increase the root surface area thus in turn improving efficient water and nutrient absorption from the bulk soil [9, 12, 57]. More than 80% of plant species form associations with glomeromycotan fungi which penetrate the root cortex and grow intercellularly before forming arbuscules [1, 45, 48].

Mycorrhizal fungi (AMF) are the main source for N, P and other mineral exchange (e.g., K, Mg, Cu, Zn and Fe) as initiated by the fungal hyphae in the soil [9, 15, 40, 60]. They enhance growth activities through symbiotic interaction with the host plants. Arbuscular mycorrhizae, ectomycorrhizae, ectendomycorrhizae, arbutoid mycorrhizae, ericoid mycorrhizae, monotropoid mycorrhizae, and orchid mycorrhizae are the main mycorrhizal classes studied which form symbiotic relationships with plants [6, 12, 33, 36, 43, 61, 62]. Their symbiotic relationship makes the host plants supply fixed C to AMF where in turn, greater nutrient uptake, drought and salinity tolerance, metal stress alleviation as well as resistance to pathogens and biotic stresses can be enhanced [45, 48, 57, 60, 61]. AMF such as *Glomus intraradices*, *Glomus mosseae*, and *Glomus caledonium* generally improve crop performance under drought conditions, alleviate salt and heavy metal-induced oxidative stress [45, 48, 59, 61].

Symbiotic microbes (e.g., rhizobia bacteria) migrate to the end of the absorbent hairs of the roots where they will attach, aggregate and respond to flavonoid signals excreted by the host root plant *via* the synthesis and excretion of lipochito-oligosaccharides (LCOs), called “Nod” factors [53, 61, 62]. Genetically, biological nitrogen fixation is controlled by three main genes; *nod*, *fix* and *nif* genes, and these are responsible for infection and nodulation as well as governing specificity for nodulation of specific species and specific genotypes, respectively [63–65]. *Fix* genes are specifically involved in the binding of N₂ and they include, *fixABCX*, *fixGHIS* and *fixKNR* [66]. Also, *nif* genes have three gene components (i.e., *nifH*, *nifD*, and *nifK*) code for polypeptide precursors of the two components of nitrogenase enzymes and facilitate N₂-binding process during BNF [53, 65].

Studies ascertained that about 60% copper (Cu), 25% nitrogen (N), 25% Zinc (Zn), and 10% potassium (K), were converted by microorganisms from their insoluble and/or organic forms into soluble and/or inorganic forms, available for plant uptake [1, 47]. The free-living nitrogen fixing PGP bacteria of the following genera; *Cyanobacteria*, *Azotobacter*, *Azospirillum* and *Beijerinckia* were reported to improve soluble sugars and electrolyte concentration in maize for its adaptation under drought stress [4, 45, 51, 57]. Considering N as the major nutrient required for plant growth and yield development, Morgan et al. [31] and Gupta and Sharma [57] revealed the implementation of 4R nutrient Stewardship for sustainable agriculture by exploiting biological nitrogen fixing microbes. Following the negative impacts of Green Revolution, anthropogenic N is drastically increasing and posing a cascade of large-scale problems on terrestrial and aquatic ecosystem [24, 33, 67, 68]. Biological nitrogen fixation (BNF) microbes were shown to be capable of contributing 180 x 10⁶ t annually of in the world N, worthy approximately US\$160-180 billion dollars [11, 15, 53, 61]. This finding justified the need of integrating BNF microbes for use as biofertilizers.

The intracellular PGP microbes (iPGP) form several nodule structures to improve N₂ fixation. For example, the endophytes like *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium* and *Rhizobium* of the family Rhizobiaceae, generally invade the root systems of crop plants to form nodules and all these contribute to N₂ fixation [13, 36, 37, 69]. In addition, extracellular PGP microbes (ePGP) including, *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, and *Serratia*, were also observed in close association with different plant species of leguminous species and a few cereals crop plants [4, 19, 45].

Globally, more than 90% of P in soil is unavailable for plant uptake [39, 70]. On contrary, P is being depleted in soils in spite of high chemical fertilizer uses [71]. The impact is brought by high weathering, prolonged warm and moist climatic conditions which deplete P sources, forming complexes with geochemical sinks like Calcium (Ca²⁺), Aluminum (Al³⁺) and iron (Fe²⁺) ([60, 72, 73]. This immobilized P is metabolized by plants and microbial communities through the secretion of enzymes with high biological relevance, which are still almost exclusively recovered from cultured organisms [26, 56, 71]. More specifically, phosphate solubilizing microorganisms (PSMs) release phosphatase enzymes and organic acids and these activate innumerable biogeochemical processes which contribute to lowering of soil pH and in increasing chelation activities with additional P adsorption sites [74, 75]. Phosphatase enzymes are the central to the processing and stabilization of nutrients as well as P nutrient cycling in terrestrial ecosystems [57, 70]. They dephosphorylate phosphoester or phosphoanhydride bonds of both phosphoric acid (H₃PO₄) and organic matter [75, 76], thus producing soluble phosphate (mainly, PO₄³⁻, HPO₄²⁻, and H₂PO₄⁻) which can be taken up by the plants and microbes. Increased activity of phosphatases occurs in response to P deficiency as part of P starvation responses

[39, 77, 78]. PSMs belong to various bacterial genera such as; *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* and these are highly associated with plants for P solubilization and mineralization [2, 19, 26, 61].

Apart from N and P, PGP microbes interact beneficially with plants in making K, Fe, Zn and sulfur (S) available for plant uptake. Studies revealed that more than 90% of K in the soil exists in insoluble forms (i.e., micas, illite, and orthoclases) [13, 79]. *Pseudomonas*, *Burkholderia*, *Acidithiobacillus*, *Bacillus* and *Paenibacillus* are known to use organic acids to solubilize K for plant uptake [13, 47, 50]. A strong correlation was observed between K solubilizing bacteria and eggplant grown under limited K soils [80]. Sattar et al. [22] and Verma et al. [69] postulated that K-solubilizing bacteria caused high productivity of food and/or feed crop production by enhancing nutrient uptake efficiency.

As for iron (Fe), soil pH changes towards alkaline conditions contributes to the conversion of Fe^{++} to Fe^{+++} , thus making it difficult for the plant uptake [11, 15, 18]. Plant-microbe associations that initiate efficient siderophore molecule synthesis for Fe chelation include *Pseudomonas*, *Burkholderia*, *Enterobacter* and *Grimontella* [45, 47, 80]. On the other hand, *Klebsiella*, *Stenotrophomonas*, *Rhizobium*, *Herbaspirillum* and *Citrobacter* are also known to generate siderophores in small quantities [6, 13]. A study by Wang et al. [81] and Fan et al. [37] ascertained that inoculating *Arabidopsis thaliana* plants with *Bacillus amyloliquefaciens* results in increased iron absorption.

In terms of Zn nutrient availability and its uptake, *Bacillus*, *Pseudomonas*, *Rhizobium*, *Burkholderia*, *Acinetobacter*, *Mycobacterium*, *Stenotrophomonas*, *Enterobacter* and *Xanthomonas* are among the bacteria identified as Zn solubilizers under Zn limited soils [82, 83]. In a wheat study by Shaikh and Saraf [84], inoculation of the crop with *Exiguobacterium aurantiacum* strain revealed 6-fold increase in Zn and Fe to 18.2 ppm and 24.67 ppm in grain, respectively which signifies its potential use as biofortification. For S, PGP oxidizing microbes convert unavailable S to available form for plant uptake through the synthesis of arylsulphatase enzymes [4, 15, 85].

6. Withstanding climate-induced abiotic stresses

Yadav [25] and Song et al. [68] revealed that extremophilic bacteria (e.g., psychrotrophiles and thermophiles) are linked to crop growth in harsh agro-ecosystems. For example, beneficial microbes that interacts with roots of calcareous and/or non-calcareous-growing plants were identified and these include; *Azotobacter*, *Flavobacterium*, *Bacillus*, *Bifidobacterium*, *Burkholderia*, *Methylobacterium*, *Pseudomonas*, *Proteobacteria* and *Serratia* [12, 26, 30]. In terms of soil salinity, adaptation of plants flourishing under hypersaline settings was shown to be aided by halophilic bacteria and haloarchaea [21, 51, 55]. These halophilic or halotolerant microbiomes aid PGP and adaptability to hypersalinity's abiotic stress [25, 40, 43, 48]. Additionally, *Paenibacillus yonginensis* DCY84^T strain was identified to efficiently protect ginseng plants of China under salinity stress conditions [86]. In the same study, high proline production was shown to be strongly associated with high transcription levels of *PgP5CS* gene that codes for salinity tolerance [87].

7. Phytohormone production as a stress-adaptation mechanism

Hormones like auxins, cytokinins (CK) and gibberellic acid (GA3) have a pivotal role in plant microbial signaling and plant growth [48, 68, 88]. These hormones contribute to BNF of rhizobia-plant interaction. For instance, cytokinins facilitate

nodule organogenesis which has been exploited in diverse legume crops [14, 89]. In previous studies, exogenous cytokinin successfully stimulated amyloplast accumulation, cortical cell division and expression of early nodulation markers [4, 86].

Auxin producing PGP microbes like *Azospirillum*, *Acetobacter*, *Alcaligenes*, *Bradyrhizobium*, *Enterobacter*, *Pseudomonas*, *Rhizobium* and *Xanthomonas* synthesize indole-3-acetic acid (IAA) for sustained plant development [14, 32, 90]. In addition, *Pantoea* sp., *Marinobacterium* sp., *Acinetobacter* sp., and *Sinorhizobium* sp., with potential to synthesize IAA, have been found to have a considerable impact on wheat germination and seedling growth in saline conditions [19, 21, 33, 87]. In salinity-stressed barley and oats, *Pseudomonas* sp. and *Acinetobacter* sp. have also been reported to boost IAA production [4, 6, 48, 86]. A strong association between IAA and GA3 producing microbes has been revealed, where both induce the proliferation of root architecture under abiotic stress conditions [45, 47, 69, 87, 88].

Nevertheless, increased quantities of endogenous GA3 in PGPR *Burkholderia cepacia* SE4-, *Promicromonospora* spp. SE188- and *Acinetobacter calcoaceticus* SE37-treated cucumber plants, increased plant growth under drought and salinity stress ([87, 88]. Also, drought tolerance in soybean plants was improved by *Pseudomonas putida* H-2-3 which secretes GA3 (Kang et al., 2014; Goswami and Deka, 2020). Transgenic canola plants were assessed for their response to submergence tolerance [91]. The findings showed that the plants expressed the *acdS* gene from *P. putida* UW4 under the control of the root-specific *rolD* promoter from *Agrobacterium rhizogenes*.

Cohen et al. [92] investigated the effects of *Azospirillum brasilense* Sp 245, an abscisic acid (ABA)-producing bacteria, on *A. thaliana* Col-0 and *aba2-1* mutants. Results showed improved tolerance which was linked to increased IAA production in *Azospirillum* cells due to overexpression of the indole-3-pyruvate decarboxylase gene [14, 37, 93]. The study discovered that priming the two mutant plants with Sp 245 boosted the amounts of endogenous ABA under drought stress. Apart from increased chlorophyll content and water potential in drought-stricken plants, ABA was also involved in root growth, increased plant biomass and other required plant adaptations under drought stress conditions [94]. By inoculating soybean roots under drought stress circumstances in South Korea, Park et al. [95] investigated the efficacy of inoculating *Bacillus aryabhattai* SRB02 in producing gibberellin and other associated phytohormones associated with improved plant growth and development. Also, Ghosh et al. [96] ascertained that inoculating *A. thaliana* seedlings with GA3-auxin-CK-producing *Pseudomonas aeruginosa* PM389, *P. aeruginosa* ZNP1, *Bacillus endophyticus* J13 and *Bacillus tequilensis* J12 strains individually, resulted in a significant increase in plant performance under drought conditions.

Similar to IAA, bacterial 1-aminocyclopropane (ACC) deaminase aids in the relief of drought stress and the development of drought tolerance in plants [45]. The hormone lowers ethylene production levels which has negative effects on plant metabolic activities [88]. ACC deaminase enzymes cleave plant ethylene precursor thus promoting adaptability of plants to both biotic and abiotic environmental stresses [45, 47, 48]. Rice rhizobacteria which were found to harbor ACC deaminase were also found to be efficient in increasing salt tolerance and, as a result, promoting the growth and development of rice plants under salt stress [97]. ACC deaminase-producing rhizosphere-colonizing bacteria like *Achromobacter xylosoxidans* Cm4, *Pseudomonas oryzae* Ep4 and *Variovorax paradoxus* C2, improve potato plant development and yield by reducing amino acid levels in the root zone [98].

Furthermore, using exopolysaccharides (EPS)-rich *Azospirillum* strain AbV5 in combination with polyhydroxybutyrate (PHB) increased maize output by 80% in nutrient stressed field trials, revealing a method for bio-inoculating non-legume crops with diazotrophic bacterial species [3]. The water holding capacity (WHC) of microbial EPS makes them even more important in water-stressed environments,

where its presence can efficiently provide enough moisture supply in the rhizosphere [4, 9, 45]. With reference to Sandhya et al. [99], Sandhya and Ali [16] and Ghosh et al. [96], the *P. putida* strain GAP-P45, produced more EPS thereby indicating thermo-tolerance of the strain when exposed to abiotic stresses such as heat stress ($\geq 50^{\circ}\text{C}$), drought stress (-0.73 MPa) and salt (1.4 M). The composition of polysaccharide chains varies by species; however, recurring monomers in polysaccharide chains include units of glucose, galactose, mannose, rhamnose, uronic acids (glucuronic and galacturonic acids), amino-sugars (N-acetyl amino sugars), organic ester-linked substituents and pyruvate ketals [100–102]. EPS producing microbes are important because these strains can be used as biofertilizers in soil conditions that are under abiotic stress.

8. Functional roles of microbes in bio-control, phytoremediation soil renovations

The use of biocontrol agents in management of phytopathogens can contribute to an increased food yield and quality [44, 103]. These phytopathogens include nematodes, insects, bacteria, fungi, protozoa and viruses [41]. Some of the studied PGPR genera which act as biocontrol agents include; *Agrobacterium*, *Arthrobacter*, *Azoarcus*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Klebsiella*, *Micrococcus*, *Rhizobium*, *Pantoea*, *Pseudomonas* and *Serratia*. *Pseudomonas* and *Bacillus* are highly preferred among them, because of their aggressiveness as invaders of the rhizosphere and have broad-spectrum antagonistic actions [41, 104]. *Bacillus sp.* had an antagonistic capacity against *Botrytis cinerea*; thus, minimizing nutrient competition [105]. The synthesis of salicylic acid, pyochelin and pyoverdine from siderophore-producing microbes suppresses illness by limiting pathogens' access to critical trace minerals in the rhizosphere [11]. *Bacillus subtilis* CAS15, has a biocontrol effect on *Fusarium wilt* of pepper and watermelon under controlled conditions, thus enhancing plant growth and development [11, 52, 106, 107].

Nevertheless, there are essential volatile and non-volatile organic compounds which have antagonistic effects against pests and pathogens [105, 107]. The volatile compounds include hydrogen cyanide, aldehydes, alcohols, ketones and sulfides whilst non-volatile ones have polyketides such as diacetylphloroglucinol (DAPG) and mupirocin [4, 8]. In addition, there are heterocyclic nitrogenous compounds such as phenazine-1-carboxylic acid (PCA), phenazine-1-carboxamide (PCN) and hydroxy phenazines; all these compounds contribute to sustainable biotic stress management [4]. As previously highlighted, the EPS-producing *Pseudomonas* strains were further reported as bio-control agents which increased sunflower crop productivity by defending it against the disease, *Macrophomina phaseolina* [108]. In the same study, the efficacy of salicylic acid (SA) which is produced by fluorescent pseudomonads in fungal phytopathogen biocontrol was also exhibited.

In other studies, potential of enzymes produced by PGP microbes with antagonistic mechanisms was assessed [24, 31]. Some studies showed that synthesis of enzymes guard against phytopathogens *via* induced lysis of their cell walls, which is accomplished by secreting hydrolytic enzymes like chitinases, glucanases, proteases, and lipases [4, 48].

Kamle et al. [109] reported the effect of induced systemic resistance (ISR) and systemic acquired resistance (SAR) on stress management by plants. These mechanisms can be initiated by microorganisms or chemical stimulants. For instance, lipopolysaccharides (LPS), siderophores, cyclic lipopeptides, DAPG, homoserine lactones and volatiles such as acetoin and 2, 3-butanediol, are some of the chemical

elicitors produced by PGPR strains to trigger ISR and SAR [52, 107]. Bacterial species including; *Pseudomonas*, *Bacillus*, *Serratia* and *Azospirillum* have been reported as ISR inducers [45, 47, 48]. Conversely, SAR is triggered by the pathogenesis-related proteins like SA where it acts directly on invading cells to lyse them, reinforce cell wall borders to prevent infections, or cause localized cell death [4, 109].

Presently, more than 30% of arable land has been projected to be degraded by the year 2025 [49]. This is widely attributed to the negative effects of the Green Revolution [50]. The puzzling divergence of decreased fertile soil in relation to booming demography, pollution and perturbation of natural resources contribute to the drastic narrow range of soil microbial diversity and its activity [110]. EPS-producing microbes highlighted by Sandhya and Ali [16] and Ghosh et al. [96] were also reported to have contributed significantly to phytoremediation and/or land restoration. For example, these microbes react with cations like Na⁺, and due to the quorum sensing technique, rapid multiplication of EPS producing microbes occurs within the rhizosphere with the ability to decrease Na⁺ availability [3]. This reaction was based on high sensitivity, tolerance, and the sequestration ability of the microbes against pollutants, as well as biotic and abiotic stress conditions [4]. With reference to Mishra and Arora [41], heavy metal pollutants in soils, with concentrations ranging from 1 to 100,000 mg/kg can be eliminated mostly *via* soil bacteria geoactive behavior [111]. *Bacillus* strain reported by Dary et al. [112] proved to have remediation power against copper (Cu), cadmium (Cd), and lead (Pb), and was also proven to contribute significantly to increased biomass of the *Lupinus* plant.

9. Climate change impacts on plant-microbe interactions

Climate challenges like increased CO₂ levels in the atmosphere, rising global temperatures and drought have had a global impact on plant and microbial ecology and physiology [90]. Since plants transfer some of the assimilated carbon to feed related microbial populations, a disruption in the C assimilation pathway as a result of climate change would have a significant impact on plant microbial interactions [45, 46]. Climate change has impacted on the interactions and dynamics of the plant-microbe responses, as well as, on the microbial communities associated with plants, thereby affecting their establishment and performance in regulating soil N and C dynamics [9, 29].

Under rising and/or elevated temperatures, species are migrating to higher elevations (altitudes) and latitudes [110]. As a result, early leafing and flowering time in the growing season have been discovered to modify the reproductive physiology of the host plant under the warming effect; thus altering plant phenological trait performances as well as multiple properties of the ecosystem [90, 110]. In terms of elevated CO₂ concentration, maximum biomass accumulated on both C₃ (45%) and C₄ (12%) plants has been observed as influenced by the changing climatic conditions, which initiate variations in C partitioning and distribution [29]. The differences in biomass accumulation levels reported between C₃ and C₄ plants could be attributed to the host's connection with beneficial microorganisms, especially arbuscular mycorrhiza (AM) fungi [94].

To profit from AMF, C₄ plants transfer more C to these fungi, and hence the selection force favors AM fungal growth over biomass accumulation by C₃ species in the case of C₄ plants [90, 113]. In another study, drought conditions impacted on plant growth and development such that photoassimilates partitioning were more biased towards rhizospheric microbes and AMF in the soil [110].

The relative abundances and diversity of microbial communities in soil can be used to infer the direct impact of climate change on microbial activities, response

mechanisms and functional profiles [46, 110]. Furthermore, the disparity in behavior could be attributed by their differing growth rates and temperature sensitivity. As evidenced by microbial respiration, decomposition processes and C release from the soil, the influx of carbon to the soil has an impact on the activity and dynamics of microbial communities [90]. Explicitly, enhanced decomposition would produce a substantial amount of greenhouse gasses (GHGs), resulting in increased CO₂ efflux in the atmosphere and dissolved organic C export via the hydrologic leaching process as well as other physiological characteristics [114].

10. Future outlooks

Climate change impacts on plant-microbe, microbe-microbe interactions, as well as ecosystem functions are still poorly understood. One of the key limitations in this context is that the impact of global climate change has not been exploited further in plant-microbe interactions, yet this knowledge is key for harnessing beneficial plant-microbe interactions in promotion of crop productivity under climate change-induced abiotic stresses. For instance, understanding of cycles and doses of radiation exposure may impact the range of gene functional strategies viable in the soil. The functional potential of the electromagnetic radiation which could be strongly related to soil pH, total nitrogen, and organic matter can explain the effects of radiation on the phenological and genetic diversity of microbial populations as well as its interaction mechanisms (e.g., co-occurrence networks).

11. Conclusion

Climate change is expected to continue posing abiotic stresses globally, and if current trends continue, many parts of the planet will become hostile to agriculture. Investments in exploring and harnessing beneficial plant-microbial interactions for enhanced plant production under abiotic stresses as well as efficient agricultural production systems are required to ensure future food and nutrition security in the face of climate change. Stable and/or well adapting soil microbes and their mechanisms can thrive in challenging situations. This is associated to plant-microbial interactions ability which can contribute positively to root-zone soil nutrient availability as it can withstand climate-induced abiotic stresses. Also, plant-microbial interactions towards phyto-hormone production as a stress-adaptation mechanism as well as bio-control and phytoremediation soil renovations attributes can counterbalance any climate-related challenges. Therefore, plant-associated microorganisms have a principal important role in aiding productivity of plants under abiotically-constrained environments. For sustainable agriculture, developing microbial tools and technologies to exploit the beneficial plant-microbe-soil interactions is paramount.

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