REVIEW ARTICLE

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Enhancing Agricultural Sustainability through Microbial-Mediated Abiotic Stress Tolerance

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Abstract

Global environmental problems lead to plants life extremely stressful. Plants are exposed to more prevalent incidences of abiotic stresses like salinity, drought, high temperature, etc. The most significant factors that reduce agricultural productivity are abiotic stresses. Plants are part of ecosystem entities, and the future of sustainable agriculture will be based on the exploitation of the potential of plant-associated microbial communities. Microorganisms produce significant amounts of metabolites that help plants to cope with these stresses. Plants interactions with microorganisms create a diverse ecosystem in which both partners occasionally share a cooperative relationship. This review emphasizes the plant-microbe interactions and provides a roadmap that how microorganisms such as Arbuscular Mycorrhizal Fungi, Plant Growth Promoting Rhizobacteria and endophytes are used to mitigate the negative effects of various stresses to improve crop productivity. This review also elaborates molecular and biochemical mechanisms in plants and microbes to tolerate abiotic stress. Furthermore, the most recent developments in the study of plant-microbe intermodulation with a novel approach will allow us to use a multifaceted tool "biostimulants" against abiotic stress. The important challenges of commercializing biostimulants for improving crop yield under several plant growth environmental constraints are also included in this review. As a result, the purpose of this review is to illustrate the effects of different abiotic stressors on plants, as well as the role of beneficial plant microbes in helping to overcome the negative impact of abiotic stresses.

Keywords: Abiotic stress, Biostimulants, Microbe, Mycorrhiza, PGPR, Sustainable Agriculture

1. Introduction

The most important threat to modern civilization is climate change. Worldwide, as the food demand is increasing global warming is becoming more severe. As climate change accelerates, there is a significant rise in Earth's temperature. This rise has adverse effects on crop yields and cultivable land worldwide[1,2]. Abiotic stresses act in synergy with biotic stresses to minimize the crop yield. Plant-microbe relations are critical components of our biosphere as they ensure agricultural sustainability. Plants are associated with a huge number of microbes including mutualists to pathogens. Positive interaction is demonstrated by mutualistic and symbiotic interactions

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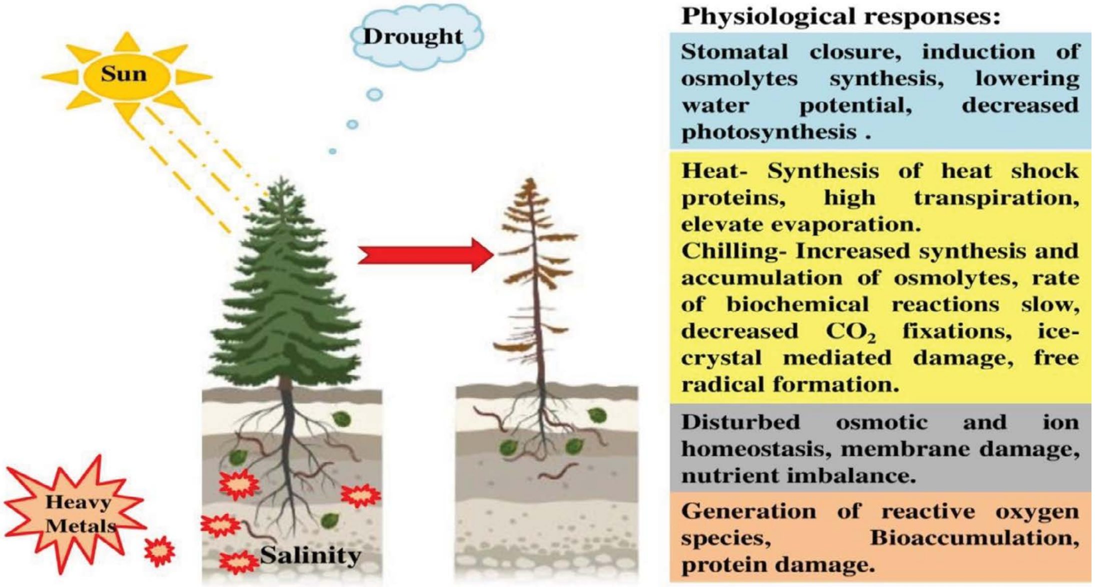
with beneficial microbes while negative interaction is demonstrated by interactions with pathogenic microbes[3,4]. Plant symbiotic microbes have been isolated from plants cultivated in both natural and harsh environmental conditions. Plant-microbial populations from extreme conditions provide hints for understanding how microbes and plants survive in extreme conditions. Beneficial microbe-plant interaction promotes plant development, crop production, and soil fertility. Endophytes (microbes that live within plant tissues without harming the plant), Plant Growth Promoting Rhizobacteria (PGPR) (microbes that colonize in the rhizosphere), and Arbuscular Mycorrhizal Fungi (AMF) can all cause changes in the host plant[5-8]. Currently, it is well known that certain potent microbial isolates plant microbial diversity, known as Plant Growth Promoting (PGP) microorganisms that improve plant fitness protect against harmful organisms, and help to maintain soil health[9]. Microbes, for example, are utilized to develop a powerful, low cost and eco-friendly tool to minimize the negative effects of extreme environmental conditions[10,11]. Plant Growth Promoting Rhizobacteria (PGPRs) and Plant Growth-Promoting Fungi (PGPFs) are the two different microbial populations that help to remove abiotic stress[12]. Bacteria in the rhizosphere typically secrete plant hormones that repress the abiotic stresses[13]. Furthermore, there is a growing interest in biostimulants to mitigate the negative effects of climate change on agriculture. This review provides existing knowledge based on plant reactions to abiotic stresses and signalling actions.

2. Major Abiotic Stressors in Plants

Plants are constantly subjected to environmental challenges that affect their growth and yield, including both biotic (pests and viruses) and abiotic[14]. There are several types of abiotic stresses including salinity, drought, heavy metals, and temperature (Figure 1) that decrease crop production[15,16]. Stress leads to changes in various physiological, biochemical, and molecular processes[17,18].

2.1 Salinity

Currently, saline land is rapidly increasing for a variety of reasons, including the melting of glaciers, heat stress-mediated accumulating of salt in soils[19], and vigorous use of chemical fertilizers[20,21]. These processes are predominant in coastal areas, where coastal erosion into groundwater increases soil salinization[22]. Furthermore, the overuse of pesticides and chemical fertilizers takes part in soil salinity, reducing both the diversity of soil microbes and plant growth and productivity[23,24]. Several salts are required by the plants for their growth and development but, they can be toxic if consumed in high concentrations[25]. In salt-prone soils, a suitable amount of NaCl enhances



Physiological responses:

Stomatal closure, induction of osmolytes synthesis, lowering water potential, decreased photosynthesis .

Heat- Synthesis of heat shock proteins, high transpiration, elevate evaporation.
Chilling- Increased synthesis and accumulation of osmolytes, rate of biochemical reactions slow, decreased CO_2 fixations, ice-crystal mediated damage, free radical formation.

Disturbed osmotic and ion homeostasis, membrane damage, nutrient imbalance.

Generation of reactive oxygen species, Bioaccumulation, protein damage.

Figure 1. Various abiotic stresses and their physiological responses by the plants.

plant growth, whereas at higher concentrations inhibits seed germination and development[26,27]. In the context of agricultural yield, moderate salinity can reduce crop yield by 50-80 per cent depending on the plant species[28,29], posing a serious threat to food security. It begins with stress detection by sensors, in which molecules or structures change form or lose function, triggering a signaling cascade (Figure 2) that causes a response[30]. These sensors detect reversible physical changes (for example, changes in membrane fluidity and protein shape, as well as partial separation or melting of DNA and RNA strands), resulting in differential transcription control and stress-sensitive gene regulation[17]. The initial location of stress sensing is represented by the cell surface or cell membrane, and this generates changes in the cytosolic calcium (Ca^{2+}) level. Ca^{2+} is a secondary stress messenger that transmits stress signals from cell surface/membranes to effector proteins, activating other messengers/sensors like Calcineurin B-Like proteins (CBLs), Calmodulin (CaMs), Calmodulin-Like proteins (CMLs), and Calcium-Dependent Protein Kinases (CDPKs/CPKs)[17].

Salinity affects plants by damaging the cell through disruption of membrane and by inhibiting the plant's physiological processes such as photosynthesis, osmoregulation, respiration, and transpiration resulting in necrosis or chlorosis[31,32]. The disruption of ROS homeostasis, resulting in an overabundance of singlet oxygen, superoxide anion radical, hydrogen peroxide, and hydroxyl radical, is a biological response[33]. Plants can cope with oxidative stress by employing a scavenging system that includes both enzymes and a non-enzymatic antioxidant including low molecular weight compounds like amino acids, phenolic compounds, Glutathione (GSH), ascorbic acid, carotenoids and α-tocopherol[34].

2.2 Drought

Climate change induces water scarcity and causes an agricultural threat, limiting crop productivity and thus food security. Alizadeh *et al.*,[35] and Lesk *et al.*,[36] estimated that physical dryness and ultra-high temperatures minimised worldwide cereal production by 9-10 % over the last few years. Like salt stress, drought also affects crop growth and productivity. Changes in rhizosphere physicochemical and biological properties due to drought stress hurt soil microbes and crop yield[37]. Temperature increases above optimum cause membrane disruption, protein denaturation, DNA damage and the accumulation of Reactive Oxygen Species (ROS), resulting in oxidative stress and ultimately plant cell death[38,39]. Stomatal closure is the first response of plants to control water loss which disrupts respiration and photosynthtic activity[40]. The stomatal closure leads to an increase in solar radiation causing a reactive oxygen species to burst provoked by water deficit, disrupting the rate of electron production[41]. Plants can use phytohormones to magnify the early stress signals during stress exposure. These phytohormone-related signaling events may either initiate new signaling pathways including early signals or induce new signaling pathways with diverse components[42,43].

2.3 Heavy Metals

Heavy metals accumulate in soil due to industrial and agricultural activities. Because of their higher density, heavy metals are lethal to plants at low concentrations[44]. The composition and nature of the bedrock determine the heavy metal content in the soil. Many heavy metals (As, Cu, Cd, Cr, Pb, Hg, Ni and Zn) are now hazardous and hurt human health worldwide[45]. Plants have developed a wide array of metabolic, physiologic, and genetic defence mechanisms to deal with heavy metal toxicity. The primary goal of these mechanisms is to limit the metal uptake from soil to stop heavy metal entrance into plant roots[46,47]. Low molecular weight organic acids, such as those found in root exudates, may act as chelating agents, limiting heavy metal entry into plants[48]. Furthermore, heavy metals activate detoxification and antioxidant defence mechanisms in plant tissues[49].

2.4 Temperature

In plants, temperature-driven stress is of three types: High, chilling and freezing. Global climate change affects current and future mean temperatures, as well as the risk of extreme weather events. Heat and cold are physical stresses that affect plant growth and productivity by directly influencing molecular and supramolecular structures[50]. One of the most serious results of heat and cold stress is an increase in ROS production, which causes oxidative stress[51,52], causing damage to biomembranes, proteins, pigments and nucleic acids causing impairment of plant growth and development[53]. Heat and cold stress also affect chlorophyll biosynthesis and photosynthesis because both have a large impact on chloroplast metabolism and structure. Heat shock, for example, disrupts the thylakoid membrane and supports grana stacking and swelling[54], whereas low temperature causes the development of a huge thylakoid protein complex[55]. Furthermore, heat and cold stresses can diminish plant water absorption which leads to dehydration[56]. Plant-associated bacteria, such as PGPR, may be able to improve these responses by allowing plants more time to adapt to heat and cold stresses.

Plants also activate their response to heat stress through enzyme biosynthesis and osmolyte accumulation. Furthermore, the synthesis of Heat Shock Proteins (HSP-20, HSP-60, HSP-70, HSP-90, and HSP-100) as well as ROS scavenging enzymes allows plants to survive during brief periods of heat stress. During heat and cold stress, different signal transduction molecules are involved in stress-responsive gene activation[57]. Together with transcription factors, these molecules activate stress-responsive genes. Once the stress-responsive genes are activated, they aid in the detoxification of ROS as well as the reactivation of essential enzymes and structural proteins[58].

3. Plant-Microbe Interaction Under Abiotic Stress

Several microbes are found in the rhizosphere region of plants, on leaf surfaces and other plant parts. Collectively, these microbial populations are considered plant microbiomes. These plant-linked microorganisms have a beneficial result on the plant they support plant growth and development. These microbes help the plants by increasing nutrient acquirement, granting resistance to pathogens, and increasing tolerance towards abiotic stresses including drought, heat soil salinity etc. The function and composition of the plant microbiome are regulated by environmental factors[59].

3.1 Beneficial Microbes

About ecosystem practices, plant-microbe interactions are crucial as the plant root system contains several microbial populations[60]. Microbes around the roots form the niche where the microbial populations thrive

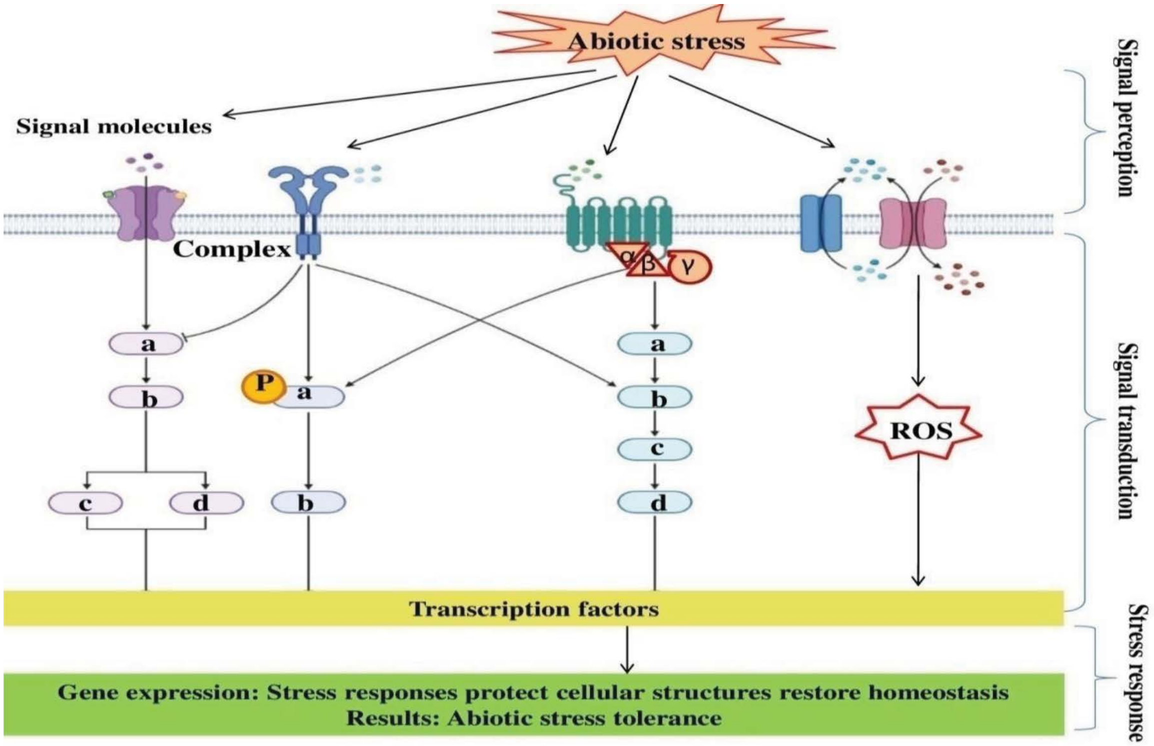


Figure 2. General abiotic stress signalling pathways in plants, starting from signal perception to stress responses. ROS-PKs (ROS-modulated protein kinase), PPs (Protein Phosphatases), MAPKs (Mitogen-Activated Protein Kinase), and CDPKs (Ca^+-Dependent Protein Kinase) are represented as a, b, c, d.

whereas microbes are present on the leaves for example Plant Growth Promoting Microbes (PGPM) promote the nutritional condition, growth, and wellness of plants[61].

PGPM is a helpful microbe that includes Arbuscular Mycorrhizal Fungi (AMF), PGPB (Plant Growth-Promoting Bacteria) and Rhizobia (PGPR)[62,63]. Drought state, inoculation of both AMF and PGPB was used to speed up water deficit tolerance by enhancing the Glutathione Peroxidase (GPX) and Ascorbate Peroxidase (APX) accumulation in plants. The dual inoculation has proved its beneficial effect on plant metabolism[64,65]. PGPM is supposed to offer a crucial role in controlling the genetic machinery which controls root-shoot formation during germination of seed. These microbial populations may colonize the area near the root and help to withstand the plants during various abiotic stresses like drought, salinity and ultra-high temperatures[66,67].

PGPR includes various groups of soil bacteria, for example, *Bacillus, Azobacter, Alcaligenes, Arthrobacter, Azospirillum, Bradyrhizobium, Burkholderia, Enterobacter, Flavobacterium, Klebsiella, Mesorhizobium, Pseudomonas, Streptomyces, Variovorax, Rhodococcus* and *Serratia* etc., that are an important part of soil-plant systems and thus affect the plant growth and development and yield. PGPR supports plant growth directly and indirectly by releasing plant hormones or other bioactive compounds, changing internal levels of plant hormones, increasing nutrient uptake, and reducing the harmful effects of pathogens on plants. PGPR are grouped into two main categories: (a) symbiotic rhizobacteria that exist in the interior of the cell (intracellular PGPR like nodule forming bacteria) and (b) free-living rhizobacteria, that are present outside of the plant cells (extracellular PGPR like Azotobacter)[68].

Endophytes reside inside healthy plants without causing any negative action on the host plant. Several fungal endophytes supports plant growth even with environmental limitations[69]. They play a key role by providing the host plant with increased phosphorus, nitrogen, iron etc. by which the host plant defends itself from environmental stresses[70,71].

Similarly, AMF also assists the host plants in defeating many environmental stresses such as acidity, pathogens, desiccation and heavy metal toxicity by improved photosynthesis, nutrient uptake and gaseous exchange[72,73]. AMF are mainly used as biofertilizers and plants make a symbiotic connection with AMF particularly under water deficit conditions by osmotic regulation[74,75]. AMF association can increase nutrient withdrawal by plants and thus increase the rate of photosynthesis and biomass accumulation[76,77].

3.2 Tolerance Mechanism by Microbes to Abiotic Stresses

Microbial association with the plant is the key adaptation, required for plant survival under extreme conditions. Microbial-mediated resistance against abiotic stresses is known as Induced Systemic Tolerance (IST). The microbiome supports vegetation to overcome such stress by utilizing its inherent metabolic properties[78]. It was found that the crucial rhizospheric inhabitants that help in the removal of many plant-related abiotic stresses are from genera *Azotobacter*[79], *Azospirillium*[80], *Bacillus, Enterobacter, Rhizobium, Pantoea*[81], *Burkholderia* and *Trichoderma*[82], *Methylobacterium*[83] and the group Cyanobacteria[84]. PGPRs employed both direct and indirect modes of action for plant growth and development under stress conditions. In the direct mode of action, PGPRs facilitate N_2-fixation and the production of plant regulators and organic catalysts in plants. The indirect mode of action involves antibiotics production, siderophores production and enzyme release[85].

3.2.1 Direct Mechanism of Tolerance

Nitrogen Fixation

The plant growth and yield directly rely on the presence of important nutritional elements such as nitrogen, phosphorus iron etc. N_2-fixing microorganisms are grouped into symbiotic and non-symbiotic nitrogen-fixing bacteria. Symbiotic nitrogen-fixing bacteria include leguminous (pulses) and non-leguminous plants such as *Rhizobia* and *Frankia* etc. The non-nitrogen fixing bacterium includes *cyanobacteria* like *Azotobacter, Azocarus* and *Nostoc*[86]. The symbiotic association leads to the formation of root nodules in which N_2-fixation occurs efficiently[87].

Phosphate Solubilization

Plants usually face a scarcity of phosphorous under stress conditions. Both organic and inorganic form of phosphorous is naturally present in the soil[88]. The deficiency of phosphorous occurs in plants because it can only be absorbed in its monobasic and diabasic ionic form[86]. Phosphate-solubilizing bacteria supply the phosphorous in the form of biofertilizers to enhance plant growth and yield. Phosphate solubilizer includes *Azotobacter, Burkholderia, Enterobacter, Microbacterium, Bacillus, Flavbacterium, Rhizobium, Erwinia* and *Serratia*[89].

Siderophore Production

Typically, iron is present in ferric form (Fe^{3+}) in soil. PGPRs make it soluble by the secretion of siderophores, which promotes the chelation of ferric iron (Fe^{3+}). Microbial siderophores are metal chelating agent, which ensures the iron presence in the rhizosphere of plants[90].

Phytohormone Production

Several microbes help in the biosynthesis of phytohormone auxin. Several microbes isolated from many crop plants show the potential to synthesize auxin as a secondary metabolite[91]. Auxin mediates an important role in the communication between rhizobacteria and plants[92].

3.2.2 Indirect Mechanisms of Tolerance

The eco-friendly way to control plant diseases is the appliance of microorganisms. Mostly PGPRs biocontrol activity controls the onset of systemic tolerance, nutrient accessibility, and the liberation of antifungal compounds. It was reported that many rhizobacteria generate antifungal molecules or compounds like hydrogen cyanide, 2,4-diacetyl phloroglucinol, viscosinamide, pyoluteorin and pyrrolnitrin. Rhizobacteria act together with plant roots and provide resistance against pathogenic microorganisms by Induced Systemic Resistance (ISR)[93]. The symbiotic relation of AMFs promotes the growth of plants and water availability under abiotic stress conditions[94]. Similarly, endophytes help in N2 fixation and produce plant hormones and nutrient uptake for better plant growth. During the initial phase of endophyte colonization, the bacterial cells produce exo-polysaccharides for attachment to the root surface and guard the bacterial cells against oxidative damage[95]. The common mycorrhizal networks involved in the phosphorus transport and nitrogen to plants and thus improve plant growth during tense environmental conditions[96]. The endophytes that promote superior growth of plants are *Bacillus pumilus* (Ps19), *Bacillus subtilis* (Ps8), *Bacillus licheniformis* (Ps14), *Lysinibacillus fusiformis* (Ps7), and *Pseudomonas putida* (Ps30), which produce plant phytohormones for example Indole Acetic Acid (IAA), Gibberellic Acid (GA3), Zeatin and Abscisic Acid (ABA)[97].

4. Microbe-Mediated Mitigation of Abiotic Stresses

Diagne *et al.*,[62] Liu *et al.*,[63] and Sangiorgio *et al.*,[98] defined that beneficial microorganisms include PGPB, AMF and rhizobia found in rhizospheres or free-living soils, or the interiors of plant tissues. Over the last few years, PGPM has been widely employed in numerous regions of the world for sustainable agriculture to limit the usage of chemical pesticides and fertilizers[99-101]. It is evident that beneficial microbes, including Plant Growth-Promoting Bacteria (PGPB), rhizobia, and fungi, play a promising role in sustainable agriculture and increasing plant tolerance to abiotic stresses[102] (Figure 3).

4.1 Rhizobacterial Based Mitigation

Plants have adapted in several ways to protect themselves in stressful environments and stimulate their growth and development[103,104]. One of the most peculiar adaptations for the survival of plants in a stressed environment is a microbial relationship with the plant. The microbiome aids plants in mitigating abiotic stress by utilizing metabolic and genetic mechanisms[78]. The application of useful microbes to increase tolerance for abiotic stress in plants is cheaper and more feasible[105-107]. Microbes on the roots create a niche for microbe populations to thrive, whereas microbes on the leaves, particularly PGPB, boost plant nutritional status, development, growth and fitness[61]. These soil microbes conduct abiotic stress regulation by several mechanisms simultaneously improving crop water relation and improving ion balance pathways[105]. It was found that the number of rhizospheric microbes that are used for mitigation of abiotic stresses in plants related to the genera *Pseudomonas*[105], *Azotobacter*[79], *Azospirillium*[80] and the group cyanobacteria[84]. PGPR helps to mitigate the negative impact of abiotic stress by the production of phytohormones, antioxidants and degradation of 1-Aminocyclopropane-1-Carboxylate (ACC) by bacterial ACC deaminase[108,109]. Plants inoculated with PGPR expressing the enzyme ACC deaminase can help to minimize abiotic stress by controlling ethylene[110]. Microbes can boost the production of low molecular

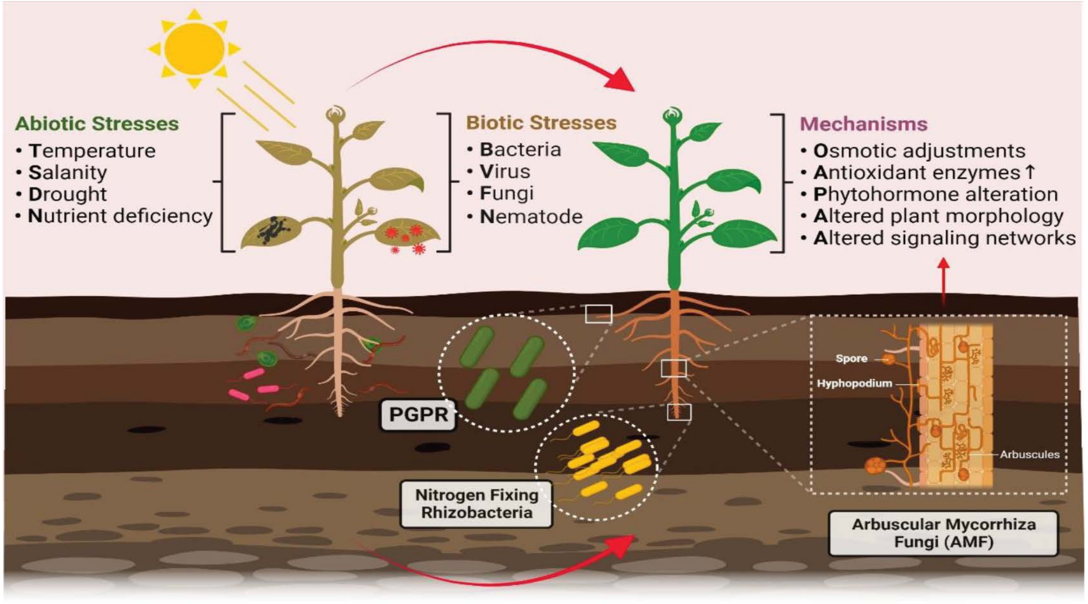


Figure 3. Mechanism of Plant Growth Promoting Rhizobacteria (PGPR) and *Arbuscular Mycorrhiza Fungi* (AMF) against abiotic stress tolerance in plants. Figure 3 is reprinted from Kamran *et al.,*[102] and is an open-access article (Copyright © 2022 by authors) distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license.

weight osmoprotectives, N_2-fixation, organic acids and mineral phosphate solubilization to face abiotic stress[111]. Microbes speed up heavy metal tolerance by transporting them across the plasma membrane[112].

4.2 Mycorrhizae Based Mitigation

Arbuscular Mycorrhizal Fungi (AMF) is a symbiotic fungus that can also play a role in plant development and health[113]. More than 70% of vascular plants form symbiotic associations with AMF, specifically during dryness for osmotic adjustment and increased antioxidant enzyme activity[74,75]. Crop yield is normally affected by drought and AMFs assist plants in retaining growth, increasing productivity and yield[114]. AMFs help in drought tolerance by ensuring continuous water intake to plants[115].

AMF has the potential to thrive in salty environments. AMF can improve nutrient intake, assimilate carbohydrates, and reduce Cl^- and Na^+ ions in plants. AMFs can also increase stomatal conductance and reduce oxidative damage in plants exposed to salt stress[111]. Al-Karaki *et al.,*[105] observed that when a tomato plant was inoculated with fungi *Funneliformis mosseae* under salty conditions, plant biomass increased. When wheat plants are infected with AMFs under salt conditions, oxidative damage is dramatically decreased[116].

5. Plant Biostimulants and their Role in Abiotic Stresses

Due to uncontrolled anthropogenic activities, plants are now facing several abiotic stresses that cause harmful effects on plant growth and thus reduce plant productivity[117]. These stresses may influence the biochemical as well as physiological processes of plants which make plants more prone to damage to pests and pathogens[118]. Currently, abiotic stresses are a major risk for food safety. Under abiotic stresses, the plant produces a variety of secondary metabolites for molecular, cellular, and physiological changes to produce resistance against abiotic stress. Diverse phytochemicals or agrochemicals are being used traditionally to mitigate adverse environmental conditions and their effects[119]. Biostimulants are the products obtained from plants and/or microbes and proven their role in enhancing resistance to many abiotic stresses and supporting various physiological processes for nutrient uptake, plant quality traits and translocation in plants. Biostimulants are non-nutrient entities, and they mediate the uptake of nutrients and have a beneficial role in stress resistance or plant growth promotion[120]. Currently, one of the most important and eco-friendly methods is to use biostimulants to counteract abiotic stress which have been proposed as agronomic tools. Various raw materials from algae extracts, plant hormones (auxins, gibberellins and cytokinins), humic acids and PGPB have been used as biostimulant compositions[121].

5.1 Plant Hormone as Biostimulant

Plant hormones auxins, gibberellins and cytokinins directly affect the life of plants. Auxin is the key regulator of apical dominance, cell differentiation, cell division, flowering, senescence, and abscission whereas cytokinins mainly regulate cell division, vascular development, apical dominance, and nutrient mobilization[122]. Gibberellic acid regulates the seed germination process, promotes the breakdown of seed dormancy, induction of hydrolytic enzymes α-amylase and protease and stem elongation and leaf expansion[123]. Experimental data showed that when a combination of Indole-Butyric Acid (IBA) cytokinin and gibberellic acid is used as a biostimulant on the seed of *Gossypium hirsutum* L. plant causes an increase in the seedling emergence percentage, leaf area, height, as well as the growth of seedlings[124]. Indole acetic acid and gibberellic acid are well-studied bacterial and fungal signalling molecules that are produced during plant-microbe interactions as Microbial Plant Biostimulants (MPB) to boost plant growth and tolerance to abiotic stresses[125,126]. It has been reported that IAA improves root development in wheat with the administration of MPB *Azospirillum brasilense*[127].

5.2 Algal Extract as Biostimulant

Algal extracts as biostimulants are promising preparations to apply as plant growth-promoting factors and have beneficial effects against abiotic stresses. It considerably improved the total chlorophyll content and antioxidant compound in plants[128]. Ghaderiardakani *et al.*,[129] reported that the application of algal extracts on Kentucky bluegrass (*Poapratensis* L.) showed more salinity stress tolerance from saline soil. de Vasconcelos *et al.*,[130] reported that when a leaf of *Glycine max* (L.) is exposed to algal extract causes higher seed yield. Currently, more than 47 companies are working on algal formulations in producing and marketing for agricultural use in which brown algae (*Ascophyllum nodosum*) and red algae (*Lithothamnium calcareum*), scientists are using various algal extract formulations[131,132]. Seaweed extracts from *A. nodosum* have been used for enhancing drought tolerance in ornamental plants (*Spiraea nipponica* and *Pittosporum eugenioides*) and results showed that plants treated with *A. nodosum* extract have higher phenolic content and improved physiology under mild drought stress conditions[133].

5.3 Plant Parts as Biostimulants

The application of natural bioactive compounds as plant biostimulants has a profound impact on plant physiology. They trigger metabolic pathways of plant and leads to diverse expression of plant genes that are engaged in plant defense[134]. It has been reported that leaf extract of *Moringa oleifera* is used as biostimulants under normal and salty conditions for plant growth. Mohamed De *et al.*[135] demonstrated that the biostimulants derived from ascorbate and *Moringa oleifera* leaf extract were shown to improve salt stress in pea plants by increasing antioxidant enzymes.

5.4 Microbes as Biostimulants

Currently, microbes as plant biostimulants are used for plant growth under stress conditions. Some microorganisms that show association with plants and increase abiotic stress tolerance have been identified and reported as *Rhizobium, Azospirillum, Bradyrhizobium, Azotobacter, Pseudomonas,* and *Bacillus*[136]. Members of these genera developed tolerant mechanisms by changing cell wall composition, forming protective biofilm and accumulating high concentrations of solutes which increases water-holding capacity. Inoculation of maize and wheat with the bacterium *Azotobacter* leads to increased biomass, nitrogen content and grain yield under salt stress[137]. Additionally, Bradacova *et al.*[138] revealed that zinc and manganese-containing seaweed extract applied to maize crops as biostimulants showed improved cold resistance by improved ROS scavenging systems.

There are some categories of biostimulants which may be food and industrial waste-derived extracts, manures, composts and vermicompost extracts[139]. Agro-industrial by-product-derived biostimulants were also reported to be effective in improving plant productivity, and secondary metabolites synthesis which supports several plant physiological responses. Juarez-Maldonado *et al.*[140] reported that nanoparticles and nanomaterials are considered a new source of biostimulants. It has been found that nanoparticles and nanomaterials positively interact with plant surfaces and modulate the transportation of ions and metabolites which increases the plant's tolerance against abiotic stresses. Raliya *et al.*,[141] reported that the application of zinc oxide nanoparticles as a biostimulant on tomatoes increased chlorophyll and total soluble protein content as well as plant height.

6. Conclusion and Future Directions

Abiotic stresses lead to economic and social difficulties for the global population. Changes in environmental scenarios have a lethal impact on plants, resulting in reduced growth and yields. PGPB is an excellent alternative to chemical fertilizers as they offer affordability, sustainability, and long-term effectiveness in increasing plant tolerance to many abiotic stresses. Future research is used to promote sustainable agriculture by using PGPBs that can offer plant resistance towards a variety of environmental stresses. For the effective use of beneficial microbes, researchers must conduct field trials and communicate results to farmers regarding the benefits of bacteria on plant growth, soil fertility and crop yield. Nano-encapsulation, a newly designed technology is ready for field testing to improve plant tolerance. This technology has the potential to save PGPRs from environmental disturbances, increase their distribution, and help in the regulation of microbial release in the soil. Furthermore, an investigation is required to search whether the "plant-fungal-bacterial" interactions can have cumulative effects on plants. Future research should also account for the ecological fear of the large-scale use of PGPRs. Thus, it should be wrapped up that PGPRs, by various mechanisms, tolerate abiotic stresses and provide a better environment for sustainable agriculture. There is also an important role of governments and the private sector in the promotion of PGPB, PGPR, biostimulants and AMF-formulated organic fertilizers for sustainable agriculture.

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