agronomy

Review

Mechanisms and Strategies of Plant Microbiome Interactions to Mitigate Abiotic Stresses

Neelma Munir [1], Maria Hanif [1], Zainul Abideen [2,*], Muhammed Sohail [3], Ali El-Keblawy [4], Emanuele Radicetti [5,*], Roberto Mancinelli [6] and Ghulam Haider [7,*]

[1] Department of Biotechnology, Lahore College for Women University, Lahore 54000, Pakistan
[2] Dr. Muhammed Ajmal Khan Institute of Sustainable Halophyte Utilization, University of Karachi, Karachi 75270, Pakistan
[3] Department of Microbiology, University of Karachi, Karachi 75270, Pakistan
[4] Department of Applied Biology, College of Sciences, University of Sharjah, Sharjah P.O. Box 27272, United Arab Emirates
[5] Department of Chemical, Pharmaceutical and Agricultural Sciences (DOCPAS), University of Ferrara, Via Luigi Borsari, 46, 44121 Ferrara, Italy
[6] Department of Agricultural and Forestry Sciences (DAFNE), University of Tuscia, Via S. Camillo de Lellis snc, 01100 Viterbo, Italy
[7] Department of Plant Biotechnology, Atta-ur-Rahman School of Applied Biosciences, National University of Sciences and Technology, Islamabad 44000, Pakistan
* Correspondence: zuabideen@uok.edu.pk (Z.A.); emanuele.radicetti@unife.it (E.R.); ghulam.haider@asab.nust.edu.pk (G.H.)

Abstract: Abiotic stresses are the most significant factors reducing agricultural productivity. Plants face extreme environmental conditions that may affect their biological mechanisms, thereby influencing their growth and development. Microorganisms possess substantial metabolites that aid in helping plants mitigate abiotic stresses. Plants' interaction with microbes constitutes a diversified ecosystem, as sometimes both the partners share a mutualistic relationship. Endophytes, plant-growth-promoting rhizobacteria (PGPRs), and arbuscular mycorrhizal fungi (AMFs) are examples of microorganisms that play an essential role in alleviating abiotic stresses and, hence, improving plant growth. The plant–microbe interaction leads to the modulation of complex mechanisms in the plant cellular system. Moreover, the residing microbial flora also inhibits the phytopathogens, therefore, it becomes part of plants' innate defense system. Keeping in view the growing environmental concerns, it is important to identify the role of the plant microbiome in the transportation of nutrients to maintain sustainable production. Furthermore, it is important to identify the factors enabling plants to recruit beneficial microbial species and how to deal with the potential pathogens. Therefore, this review aims to summarize the impacts of various abiotic stressors on agricultural productivity and the role of beneficial microorganisms in mitigating the negative effects of abiotic stresses. The literature review also shows that the beneficial microbes, including PGPRs, AMFs, and endophytes, adopt various mechanisms for ameliorating the negative effects of various stresses. It has been observed that biochar and microbes, either individually or in combination, can play a significant role in maintaining plant growth under stress conditions. Although conventional inoculation of beneficial microbes mitigates abiotic stresses and enhances productivity, the advancement in genetic engineering would help transfer specific genes from the microbes to plants to aid in abiotic stress mitigation.

Keywords: arbuscular mycorrhizal fungi (AMFs); abiotic stresses; endophytes; microbiomes; mutualistic relationship; plant cellular system; plant-growth-promoting rhizobacteria (PGPRs); plant–microbe interaction; biochar

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1. Introduction

In the current century, the availability of sufficient food is a major problem due to the growing population and fewer food-production resources [1]. Decreased area of arable farmlands is one of the major reasons for the food shortage. Various human activities; degradation of soil; deforestation; and multiple environmental factors, such as flooding, salinity, extreme temperature, and heavy metal stress, are the main reasons for decreased fertile lands [2]. Somehow, plants have adapted various traits according to their surrounding environment, while some plants increased the production of osmolytes and scavenging of ROS [3]. In the last few decades, some modern plant biotechnology techniques have been used extensively to modify plants with desired adaptations such as resistance to phytopathogens, tolerance against stressful conditions, and enhanced nutritional values. These techniques include conventional breeding and genetic engineering, which are used to transfer desirable traits from one plant to another [4].

It is estimated that by the year 2050, crop productivity should be increased from 60 to 100% to meet the anticipated global population (9.7 billion). The current agricultural practices and climate-change situation do not favor the achievement of this target [5]. Particularly, the use of infertile land is a major challenge. The increase of crop productivity by using infertile lands is challenging. To enhance crop yield, some farmers apply chemical fertilizers which are not suitable for soil health or for the food chain. Another disadvantage of using chemical fertilizers is that they are more expensive and damage plant health, as well [6].

Soil salinity incurs a decrease in the plants' growth and yield. Usually, the soil salinity is increased by using saline water and different manures [7]. The lower productivity in agricultural lands also affects agribusinesses. According to the FAO, more than 20% of the lands are affected by salinity [8]. Soil salinity causes sodium aggregation, which promotes chlorosis and changes in ion stability, which ultimately results in yield loss, as well as a reduction in the nitrogen content in plants. The salinity in the roots' area may decrease the weight of plant parts [9]. The rhizosphere is the root zone of a plant where rhizobacteria reside. These rhizobacteria are vital for the maintenance of soil health [10]. The inoculation of plants with 3–5% rhizobacteria enhances plant growth. Thus, they are named plant-growth-promoting rhizobacteria. These rhizobacteria include a diversity of microbes that have the potential to increase plant growth and yield [11].

Although some microorganisms are considered harmful to plants due to their disease-causing properties [12], most soil microorganisms help plants to survive stressful conditions. These microorganisms are now being used in agriculture to produce food crops. Several microorganisms play a significant role in the fixation of atmospheric nitrogen; organic wastes; pesticide detoxification; mitigation of plant disease; and production of bioactive compounds, such as vitamins, hormones, and enzymes [13].

Plant-growth-promoting rhizobacteria (PGPRs) and plant-growth-promoting fungi (PGPFs) are examples of some microorganisms that help to mitigate abiotic stress [14]. Beneficial microorganisms mitigate abiotic stress by adapting various strategies such as phytohormone production, lowering ethylene oxide levels, upregulation of dehydration response, and the induction of genes encoding antioxidant genes. Bacteria that reside in the plant's root usually secrete phytohormones that mitigate the salinity and decrease seedling growth [15]. It has been observed that plant-growth-promoting bacteria such as *Pseudomonas* sp. and *Bacillus* promote plant growth under stressed conditions by the secretion of indole acetic acid and siderophores. The lowered ethylene level helps plant roots grow, ultimately leading to a healthy plant [16].

Some studies revealed that the enhanced growth of plants under abiotic stress by microorganisms is due to the activation of primary metabolisms, leading to increased plant growth, improved photosynthesis, better uptake of nutrients, and higher antioxidant enzymes activity. Moreover, some secondary metabolites also help in tolerating abiotic stress, such as flavonoids, phytoalexins, phenyl-propranoids, and carotenoids [17]. Both fungal and bacterial species help to enhance the production of secondary metabolites under abiotic stress [18].

The use of PGPRs from manures is also a promising approach to decrease the negative effects of abiotic stress. PGPRs aid in the growth of the plant and the removal of heavy metals and to overcome the negative effects of pesticides. Thus, they lead to the bioremediation of polluted soils [19].

It is assumed that crop productivity can be enhanced by using various modern strategies, including the use of beneficial microorganisms. These microorganisms have the potential to increase crop productivity through the stimulation of phytohormones, nitrogen fixation, and resistance against abiotic and biotic stress. By the detailed study and research on these microorganisms, one can make suitable microbial formulation or consortia that can help a plant to increase its productivity at a low cost [20].

In the last few years, several reports reviewed the role of beneficial microbes, especially PGPRs, AMFs, and endophytes, in mitigating stressful effects of salinity [21], drought [22,23], and both drought and salinity [24]; environmental decontamination [25,26]; and climate change and high temperatures [27,28]. However, no recent reviews extensively covered the ameliorating effects of all of these stressors on plants. Importantly, the possible mechanisms behind the ameliorating effects of beneficial microbes are rarely covered in the extensive reviews covering many environmental stressors. This review aims to summarize the important studies in which various abiotic stressors led to losses in agricultural productivity and the role of using beneficial microorganisms to mitigate the negative effects of the stresses to enhance crop productivity. It also discusses various mechanisms behind the ameliorating effects of PGPRs, AMFs, and endophytes to different stresses

2. Climate Change and Loss of Soil Fertility

Climate change has been recognized globally, and its impacts have been witnessed in different ways. Its effect on the global environment can be assessed by considering various parameters [29]. A steep increase in the level of carbon dioxide [30] and temperature has been associated with it. It is estimated that by the year 2100, the atmospheric temperature may raise by 1.8 and 3.6 °C. The increased temperature will conceivably cause a decrease in soil water content in some areas, leading to drought conditions. In addition to crops, the rise in temperature and drought will have an impact on terrestrial microorganism and wild plants [31]. It is considered important to understand how biotic and abiotic factors affect plant morphological traits to predict the responses of species, the community, and the ecosystem toward global climate change. One of the complex traits in temperate deciduous trees is bud break phenology; mostly it is triggered by the interaction of extreme temperature, photoperiod, and plant genetic architecture. The impact of global climate change on soil microbial communities influences their interactions with the plant and indirectly affects the physiological traits of the plants [32]. This indicates the complexity of biotic interaction in soil. A number of human-induced activities have caused the loss of soil fertility and production. Various alternative nutrient management techniques can be applied to reinstate the soil fertility. A significant alternative to treat soil fertility is to use microbial inocula and organic fertilizers. Various techniques are useful to restore the fertility of soil by using many bacterial and fungi [33]. The soil fertility can be improved by using multiple species of microbes, i.e., bacteria and fungi. These microbes help to increase organic matter content, which, in return, enhances the availability of nutrients in the soil such as N, P, K, and Fe. Some microbes also help in the mobilization of nutrients to plants from the rhizosphere. The application of microbial inoculum also helps with the recovery of soil fertility. For the recovery of soil fertility, several microbes use direct or indirect mechanisms [34].

The soil microbes may affect the circadian clock by affecting the timings of plant phonological traits such as flowering and leaf-growth timings, as well as nutrient acquisition [35]. The biotic regulation of plant performance, plant development, and plant fitness is also affected by the soil–microbe relation. For instance, in *Boechera stricta*, the flowering time depends on the soil microbes and biotic factors. It was proved experimentally that the delayed flowering in *Arabidopsis thaliana* may be triggered by the microbially derived Indole acetic acid (IAA), which downregulates the gene responsible for flowering [36].

The soil microbial community as a whole confers tolerance to various environmental stress. In one study, the application of ectomycorrhizal fungi (EMF) inoculum on the sterile *Pinus edulis* seedlings showed that the growth rate in drought conditions was the same as obtained under normal conditions. Meanwhile, under dry conditions, the seedlings' growth rate was 25% higher in drought-tolerant seedlings. The study affirmed the hypothesis that soil microbial communities play an essential role in determining plant phenotypes and their responses to abiotic stress. Somehow, the effect of the soil microbiome on plant physiology and in plant genetics remains unknown [37].

Climate change has also affected the root exudates, as the higher rate of CO_2 leads to the increased carbon concentration to the root zone, and the composition of the root exudates becomes altered. The ratio of plant chemoattractants and the C/N ratio has also been affected due to climate changes. Moreover, it can also lead to the alteration in composition and activity of the plant microbial community. Thus, researchers have studied how climate change may affect the relationship of plant and microbial communities, as they have a mutualistic association. Under certain climatic conditions, plants exhibit sufficient properties and colonization capacity, as some microbiomes are known to be beneficial for plant growth. It was observed that the plant microbial community is affected by the altered environmental conditions or by plant physiology [38]. Figure 1 shows the effects of elevated CO_2 concentrations on plants.

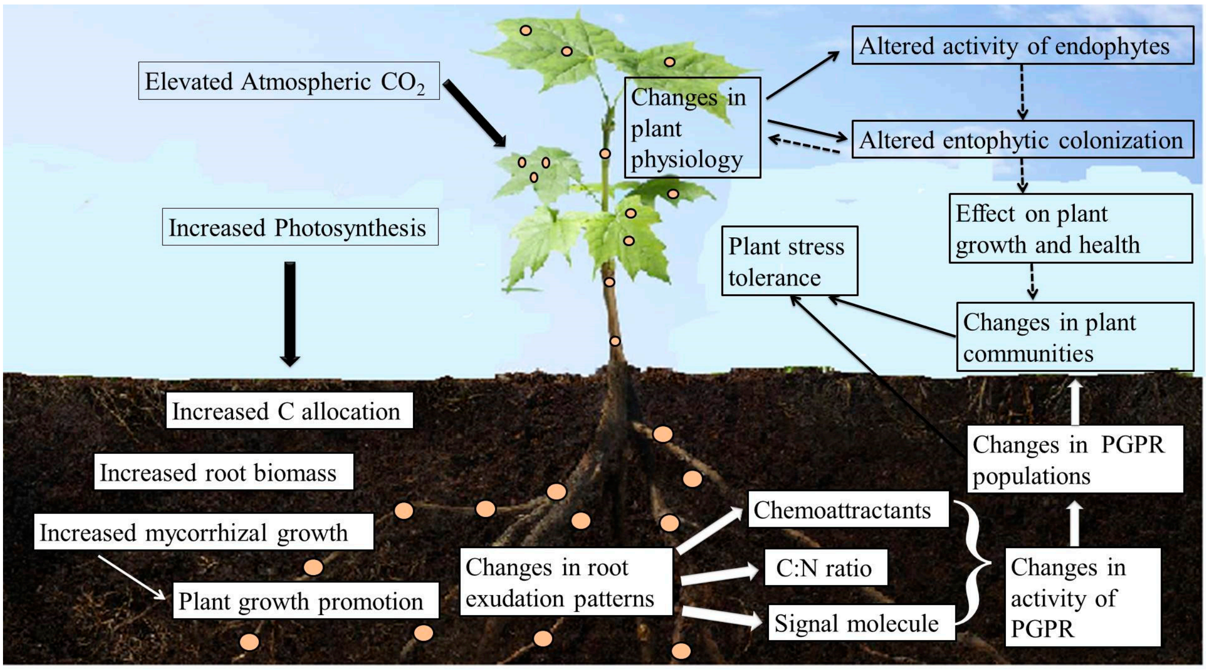

Figure 1. Effects of elevated CO_2 concentration on plants.

It has been observed that the rhizosphere is impacted by the soil microbiome. Many rhizospheric microbial species exhibit an affinity for the plant tissues and can invade the root, where they adopt an endophytic lifestyle. This mechanism was observed in plant-growth-promoting fungi (PGPF), for instance, arbuscular mycorrhizae, ectomycorrhizae, and other endophytic bacteria. The well-characterized plant-growth-promoting rhizobacteria were also proved to be beneficial for their host [39].

3. Plant-Associated Microorganisms

Many microbes are allowed to reside in the plant rhizosphere, surfaces of leaves, and other plant tissue. These microbes are collectively known as plant microbiomes. These plant-associated microbes have a positive effect on plant health, influencing plant physiology and development. The composition and function of the plant microbial community are managed by environmental factors [40]. A symbiotic relationship between fungi and vascular plants is considered as mycorrhiza. Some obligate mycorrhizal fungi have a symbiotic association with terrestrial plants, including halophytes, which are known as arbuscular mycorrhizal fungi (AMFs). AMFs can form vesicles and hyphae in roots and can also sporulate in the rhizosphere. The hyphal network created by AMFs provides excellent access to the soil surface area, thus causing an increase in plant growth. AMFs aid in the improvement of plant nutrition through the efficient translocation of nutrients. They also also help in the improvement of soil quality and plant health [3]. Various mechanisms have been employed by AMFs for the amelioration of abiotic stresses. These include increased mineral acquisition, improved water uptake, ionic homeostasis, synthesis of phytohormones, enhanced photosynthesis activity, and improved production of antioxidant enzymes [41]. For increased mineral nutrition, the higher ratio of Na^+ and Cl^- in soil usually competes with the translocation of important ions such as Ca^{2+}, P, K^+, and Mg^{2+}. These ions change the ratio of salt in the soil solution, and this may cause an alteration in the plant nutrition ratio, ultimately leading to declined plant growth and biomass. The salinity tolerance in host plants such as wheat, alfalfa, tomato, and maize has been found to be ameliorated by AMF–plant symbiosis [42].

AMFs also help plants increase their water uptake. Due to the extended network of hyphae in the soil, plants improve their water-absorption capacity. AMFs cause the accumulation of osmolytes in plants such as proline, glycine, and betaine. These fungi also help to improve the working of water-channel proteins and aquaporins. This may enhance the transport of water inside plant cells to maintain cellular osmoregulation [43]. Ionic homeostasis can also be controlled by AMFs. The salinity stress causes higher Na^+ concentration in plants, and this, in return, may interfere with the transporters in the root plasma membrane. Ionic homeostasis may cause the reduction of nutrient uptake in plants. The higher ratio of Na^+ and K^+ in plants may interrupt multiple enzymatic processes and the synthesis of protein. Therefore, AMFs help the plants under salinity stress to reduce the absorption of Na^+ and K^+ and enhance the uptake of essential soil nutrients [44]. Under salt stress, AMFs produce auxins and cytokinins in plants that help in plant growth and also initiate hormone synthesis. The synthesis of abscisic acid, jasmonic acid, and salicylic acid takes place more in plants with AMFs [45]. Salinity stress in plants causes the excessive production of ROS, which ultimately reduces the activities of antioxidant enzymes. Plants that have a strong association with AMFs may have a lower amount of ROS, thus helping plants to alleviate salinity stress by increasing enzymes such as catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX), superoxide dismutase (SOD), and monodehydroascorbate reductase (MDHAR). All of these enzymes protect plants from oxidative damage [45].

4. Salinity, Drought, and Waterlogging

To survive under suboptimum conditions, plants develop various mechanisms to alleviate negative impacts. The plants' survival rate depends on how they react to biotic and abiotic stress. These mechanisms include the significant association with plant roots and soil microbes. Microbes in the soil can easily move into and inhabit their surrounding environment [46]. The root microbiome, archaea, oomycetes, fungi, and bacteria are all considered to be colonizers of plant roots [47]. Plants mostly engage microbes in their roots from the soil microbial community. The composition of the root bacterial and fungal community can be determined by the pool of soil microbes and root compartments. These are the rhizosphere, rhizoplane, and root endosphere [48]. The composition of the soil bacterial and fungal community depends on soil factors such as the pH. Many nutrients, such as phosphorus (P), carbon (C), and nitrogen (N), play a significant role in the soil microbial community [49]. The composition of the plant rhizosphere community is affected by the excretion of organic compounds, mucilage, and microbe-signaling hormones, as well as sloughed root border cells. All of these components, together, provide better nutrient-rich growth conditions for microbes. It works for the selection of soil microbes toward the rhizosphere. The microbe-signaling compounds and plant immune response are activated by the host-plant's genetic factors. This phenomenon allows the soil microbiome to bind with the rhizoplane. Subsequently, the microbiome enters into the root endosphere [50]. Figure 2 shows how abiotic stress factors affect plant microbiomes and their morphology.

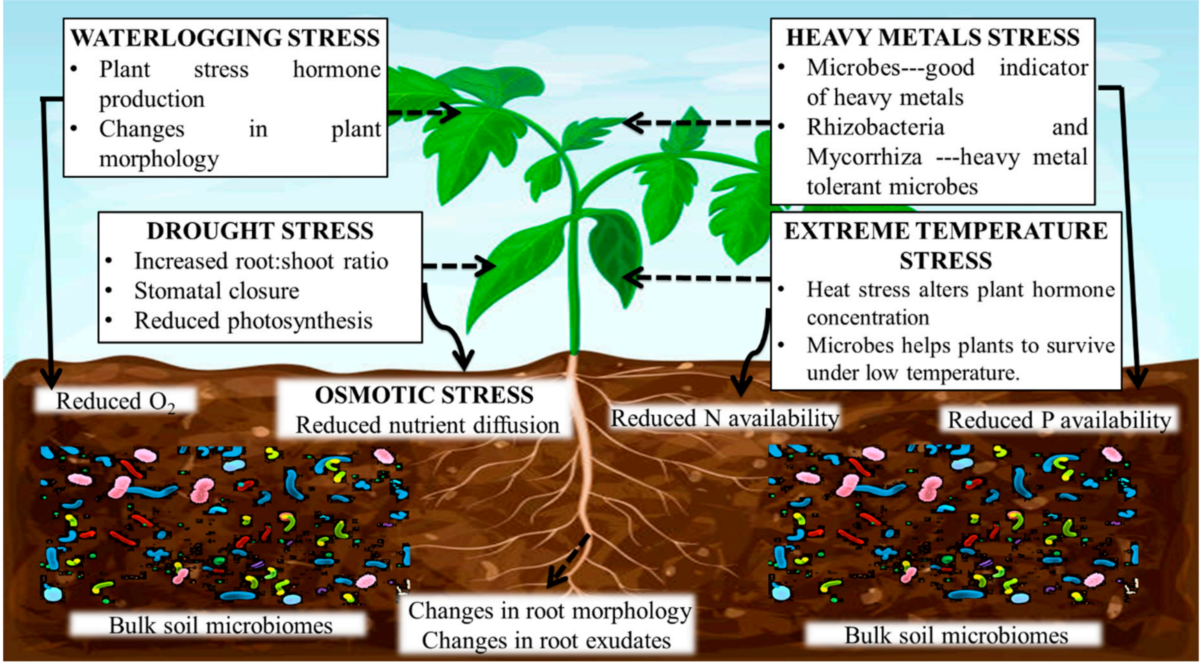

Figure 2. Abiotic stress factors affect the plant microbiomes and their morphology.

4.1. Salinity

Salinity is one of the global soil-degradation problems. There are multiple factors governing soil salinity, for instance, agriculture inputs and the use of sewage sludge, municipal garden waste, and manure. Soil salinity may lead to suboptimal plant development and can reduce the activity of soil microbes. It has also been reported that soil salinity may cause changes in water in relation to plant tissue, nutrition, and ion imbalance [51]. Salinity causes toxicity in plant tissues via the accumulation of Cl^- and Na^+ ions [52]. The presence of soluble salt in soil may lead to the shortage of water in plant cells, thus leading to plasmolysis. Plasmolysis may kill soil microbes and plant roots [53]. An increase in the levels of salinity leads to the condition known as the "rapid osmotic phase", while osmotic stress may remove water from soil, ensuing "slower ion toxicity phase" [54]. Salinity-tolerant microbes are of two types: halophiles and halotolerant. Halophilic microbes necessarily require salt for their better growth, while halotolerant microbes are those that can adapt to a saline environment but do not necessarily require a high salt concentration for their growth. Halophilic bacteria are characterized based on their salt-tolerance level into weak halophiles, moderate halophiles, and extreme halophiles. Weak halophiles need (1–3%) of NaCl concentration, moderate halophiles require (3–15%) of NaCl concentration, and extreme halophiles can grow in 15–30% of NaCl. These bacteria secrete novel enzymes with polyextremophilic features, including cellulases, xylanases, proteases, amylases, lipase, and gelatinase [55]. These enzymes are conceivably haloenzymes (or halozymes), having salt-tolerance or salt-tolerant catalytic properties. Haloenzymes and non-halophilic predecessors exhibit the same enzymatic properties. Somehow, their structural properties differ which allows them to survive under extreme conditions [56]. Enzymes excreted by the halophile play a major role in plant–microbiome interactions and also help with the maintenance of soil structures [57]. Salt-tolerant plants have a beneficial microbiome in their rhizosphere. The microbiome plays a significant role in plant growth and resistance against to soil salinity [58]. It was reported in many studies that salinity may lower microbial activity, as well as alter the composition of the microbial community [59]. Andronov et al. [60] observed that salinity levels may cause variation in the composition of bacterial and fungal communities. Fungi are more susceptible to salt stress than bacteria. Thus, the fungi–bacteria ratio may vary in saline soils. It may lead to an altered composition of the soil microbiome, indicating that salinity can be critical for microbial communities. Primary organic osmolytes are proline and glycine betaine, while other inorganic osmolytes that are present in salt-tolerant bacteria include potassium ions. The formation of osmolytes from inorganic salts proved to be hazardous; thus, only those halophilic microorganisms that have salt-tolerant enzymes survive under saline conditions [60].

4.2. Drought

It was observed that a shortage of water may lead to stress in plants. Many studies have been carried out to study the effect of drought as a water stress. Under drought stress, the root colonization levels decrease by arbuscular mycorrhizal fungi (AMFs). AMFs could enhance plant efficiency under drought stress. The plant's drought fitness has been maintained by increasing the nutritional content and stomatal conductance, and as a result, the water utilization efficiency is enhanced [61]. Few studies have been carried out regarding drought-induced changes in non-mycorrhizal and root-associated fungal communities [62]. The profiling of those bacterial communities that are responsive to drought has been carried out. Under drought stress, it was observed that the root microbiome of rice (*Oryza sativa*) and sorghum (*Sorghum bicolor*) contains more bacteria belonging to Actinobacteria. In a study, 30 plant species were subjected to drought stress, and it was revealed that *Streptomyces* species dominated the root endosphere community. Indeed, the plant species became resistant to drought stress by the increase of the *Streptomyces* species [63]. In sorghum seedlings, the root growth increases due to the plant-growth-promoting activities of *Streptomyces* [64]. Under drought stress, Actinobacteria may dominate the soil bacterial community [65]. In dried soil, the diffusion pathways become reduced, leading to nutrient deficiency. To lower the internal solute potential, microbes must accumulate osmolytes inside their cells and avoid losing water to their environment [66]. Figure 3 represents changes caused by the environmental factors on soil microbial composition.

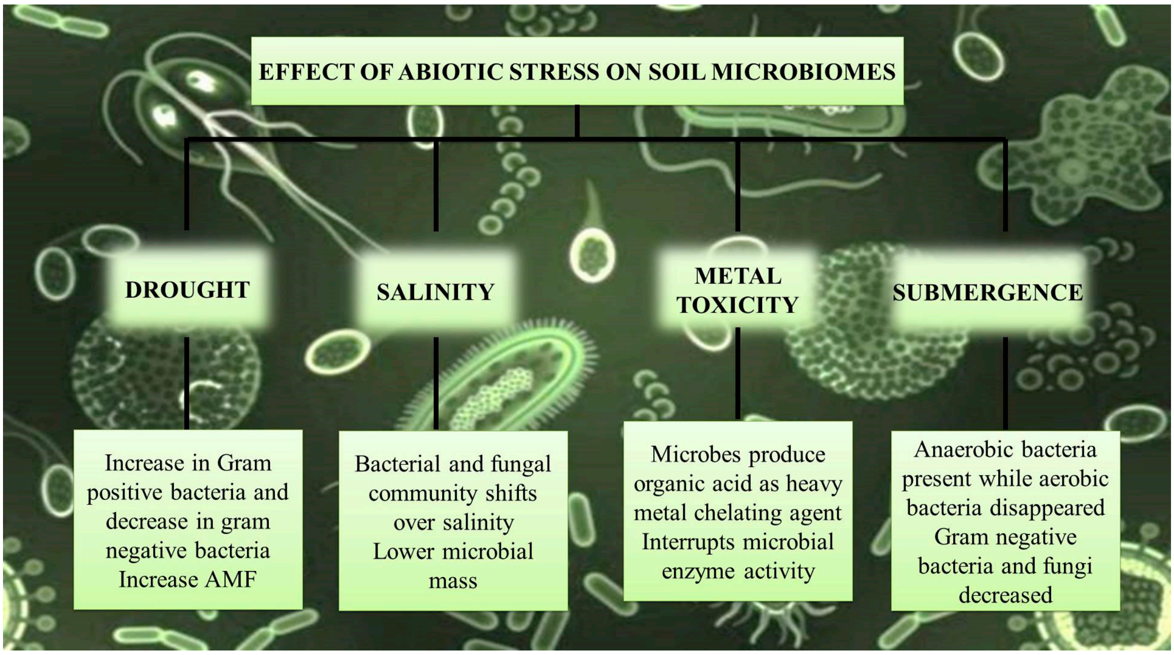

Figure 3. Changes caused by the environmental conditions on soil microbial composition.

4.3. Waterlogging

Water is one of the main factors for plant growth, but excessive water irrigation may cause plant death. The change in global climate may also increase the chances of floods. The increase in water level may cause damage to the non-photosynthetic parts of the plants, such as the roots. It may lead to decreased oxygen (O_2) levels; one of the major stresses faced by the plants during waterlogging is the inhibition of cellular respiration. Waterlogging can cause many biochemical, as well as physiological, changes in plants, such as a higher production rate in the plant stress-signaling hormone ethylene. This production has an adverse effect on plant shoot and leaf morphology [67]. The exploration of plant-growth-promoting bacteria and fungi, with a particular emphasis on their role in protecting plants during floods, can broaden our understanding of plant–microbiome interaction. It is speculated that the microbiome may help in conferring stress tolerance to plants under no oxygen supply. Indeed, many bacteria activate ethylene levels by producing 1-aminocyclopropana-1-carboxylate (ACC) deaminase. ACC is the natural precursor of ethylene in plants. The plant damage rate under stress can be reduced by the cleavage of ACC, using the enzyme ACC-deaminase produced by bacteria. The cleavage of ACC results in a decreased amount of ethylene [68]. For instance, the basil (*Ocimum sanctum*) plant was inoculated with ACC-deaminase producing bacteria, and enhanced growth and a decreased ethylene level were observed in plants under waterlogged soil conditions [69]. An ACC-deaminase produced by *Pseudomonas putida* UW4 was inoculated in cucumber (*Cucumis sativus*) grown under anoxic conditions. This enzyme shifted the protein sequence toward the protein profile that plays a significant role in nutrient metabolism, defense stress, and antioxidant activity [70]. In few studies, root-associated microbial-community responses in non-wetland plants species which are exposed to waterlogging have been reported. For instance, in the terminal restriction fragment length polymorphism profiling of root-free bulk soil, rhizosphere and whole-root samples from poplar seedlings (*Populus species*) were subjected to waterlogging experiments, revealing a bacterial community composition in both the rhizosphere and roots [69]. In another study, it was observed that the concentration of denitrifying bacteria decreases in wheat (*Triticum aestivum*) due to waterlogging and nitrogen limitation. These abiotic stresses also affect the rhizosphere community structure [71]. The overflow of waterlogging may cause many physicochemical changes in the soil where plants grow. Soil pores allow gas exchange between the atmosphere, the soil, and microbes. Due to waterlogging, these soil pores filled with water and gaseous exchange are reduced [72]. During waterlogging, microbiomes can cause the depletion of oxygen in soil, leading to anoxia in the upper layer of the soil [73]. These kinds of changes in the soil such as oxygen deficiency can cause shifts in soil microbiomes such as they may change from aerobic microorganisms to facultative anaerobes and to strict anaerobes. It was observed that during waterlogging, *Aquaspirillum* increases in the rhizosphere and roots of poplars [74].

4.4. Heavy Metals Stress

Multiple industrial and agricultural activities accumulate heavy metals in soil. Heavy metals are not suitable for plants, as they are of a higher density and poisonous at lower concentrations [75]. To protect plants from tissue damage, various sustainable approaches have been used. One of them is phytoremediation, which uses microbes to eliminate heavy metals from soil. Microbes are also a good indicator of heavy metals; microbes (rhizobacteria and mycorrhiza) have the potential to enhance plant growth and development under heavy-metal stress [76]. These microbes can reduce the heavy-metal stress by using various mechanisms, such as efflux, volatilization, metal complexation, and enzymatic detoxification. These microbes help to improve plant growth by the release of plant-growth regulators such as IAA, deaminase, and ACC. The plant-associated microbes also aid in the decrease of ethylene concentration for the better development of plants under metal stress. The heavy metals in plants can be removed both by using living and non-living microbial biomass. The bacterial and fungal cell wall plays a significant role in plants under metal stress [77]. It has been observed that various microbes, such as Proteobacteria, Firmicutes, and Actinobacteria, play a significant role in the removal of Pb, As, and Mn from soil [78]. For instance, the reduced growth of *Vicia faba* was observed when copper was accumulated, but the negative impact of copper is reversed by inoculation with rhizobia and PGPRs [79].

4.5. Temperature Stress

The climate change may alter the intensity of temperature stress in plants. Plants tolerate extreme temperature conditions such as heat and cold stress. The temperature stress causes the alteration of the plasma membrane, photosynthesis activity, cell division, and plant growth. Under heat stress, fluidity increases in plants, while in cold stress, it is reduced [80]. One of the major abiotic stresses include the heat stress, which alters the plant hormone concentration. To overcome heat stress, plants use multiple mechanisms such as the release of enzymes and osmolytes accumulation. Multiple microbes help plants to survive under low temperatures [81]. It was reported by Yadav et al. [82] that *Pseudomonas cedrina*, *Brevundimonas terrae*, and *Arthrobacter nicotianae* have the potential to maintain plant health under low temperatures.

5. How Do Abiotic Stresses Cause Loss of Plants Productivity?

For optimal growth, development, and production, plants need light for photosynthesis, and they need water and minerals for their growth. Extreme environmental conditions can limit plant growth. Undesirable environmental stresses such as salinity and drought stresses render stressful conditions [83]. Plants have "a memory" about the past exposure to abiotic stresses and, hence, can develop a defensive mechanism to bear such extreme conditions for any future exposure [84]. Initially, in response to unfavorable conditions, plants develop symptoms at the cellular level. Plants' physiological appearance and photosynthetic ability are highly affected by the drought stress [85]. Prolonged water stress may cause various changes in plants, such as lower leaf-water potential, decreased stomatal opening, reduction in leaf size and root growth, and delay in flowering and fruiting [86]. The intensity of light above or below the optimum concentration may alter or diminish the physiological process and affect plant growth and development. A bulk amount of reactive oxygen species has been produced in response to excessive light and influences photo-oxidation, which also has an impact on enzymes and other biomolecules. The loss of plant productivity ratio also increases under extreme conditions [87]. Most of the crop loss occurs due to the extreme cold or an increase in temperature.

Pollutant contamination and anthropogenic disturbance also affect crop production [88]. Acidic soil becomes nutrient deficient, and in response, this affects plant physiology and growth. Exposure of plants to salinity at the initial stage may cause ion toxicity within a cell. The prolonged duration of salinity leads to the disruption of osmotic balance. Ionic, as well as osmotic, shock may alter the plant growth and development [89]. For the salinity-stress tolerance, plants need to maintain osmotic and ionic homeostasis within their cells. Under extreme cold temperatures, plants avoid cold injury of tissues through freezing tolerance. Plants tolerate freezing temperature by the activation of their anti-freezing response within a short photoperiod. This phenomenon is known as cold acclimation [90]. Plants release a stress-specific signaling cascade in response to stress stimuli. In response to the defense system, the expression of stress-specific genes in plants initiates the synthesis of phytohormones such as abscisic acid, jasmonic acid, salicylic acid, and ethylene. The accumulation of phenolic acid and flavonoids and activation of transcription factors and antioxidants also help to mount the defensive system [91].

To deal with the mitigation of plants abiotic stress, it is important to understand the molecular machinery, as well as metabolic pathways and regulatory genes. To understand stress mitigation strategies, the identification of stress-responsive multigenic traits and exploration of linked markers for stress related genes are the current focus [92].

6. Microbiome and Stresses

Plant metabolism is highly affected by biotic, as well as abiotic, stresses. These stresses also have a significant effect on the composition of root exudates. Field-grown plants are highly exposed to environmental stresses. Biotic stress factors are extremely harmful to plant growth and development. These factors include pathogenic fungi, bacteria, viruses, nematodes, and insects, while abiotic stress factors include temperature, drought, waterlogging, salinity, toxic organic compounds, and metal salts. These abiotic stresses also have negative effects on plant growth. There is a high chance that plants may encounter various environmental stresses at the same time. Contrarily, much rhizospheric microbiota protect plants from massive environmental stresses. The selection of plant-growth-promoting bacteria (PGPBs) depends on the range of environmental stresses. It has been observed that PGPBs play a significant role in the growth and development of plants. Under biotic and abiotic stresses, the synthesis of phytohormones such as ethylene can vary under moderate environmental stresses. In response to ethylene production, plant defensive genes are expressed to protect plants from environmental stresses. A high concentration of ethylene in plants may lead to plant senescence, chlorosis, and abscission [93]. Biotic stresses often alter the composition of microbial communities associated with the stress plants. It has been reported that, in the diseased cotton plant of *Verticillium*, the number of beneficial bacteria and arbuscular mycorrhizal fungi decreased, while plant pathogenic fungi increased. The relationship between the soil microbiome and the strawberry plant's resistance against *Verticillium dahlia* and *Macrophomina phaseolina* has been observed. In another experiment, an alteration in the root exudate was observed due to the aphid infestation in the pepper plant. This phenomenon leads to the decreased resistance of pepper plants to aphids due to plant-recruiting rhizobacteria [94]. In another study, it has been observed that compost has a significant effect on tomato plant growth and can also aid in fighting the diseases caused by *Fusarium oxysporium* and *Verticillium dahlia*. The added compost also helped to decrease the disease intensity caused by these pathogens. Thus, it was concluded that fungal pathogens may alter the composition of plant microbiomes, and added compost may overcome the negative effects [95].

Many abiotic factors, such as drought and salinity, inhibit the crop yield and have negative effects on the crop microbiome. In yet another study, a significant difference was observed between dry-wheat land and irrigated crops. Later, it was noted that the density of the rhizosphere microbiome increases in irrigated crops [96]. Thus, it can be concluded that, for the maintenance of a healthy rhizosphere microbiome, an adequate amount of water is necessary. An improvement in a drought-ridden cotton plant through a beneficial microbiome has also been observed. It was observed that the development of the sorghum root microbiome has been delayed due to drought stress. The drought stress leads to the abundance of bacteria within the microbiome. Climate change, including extreme temperatures, may affect the phyllosphere and rhizosphere microbiome of many plants. The soil microbiome is also affected by the low nitrogen and carbon levels. Devastating changes in soil pH and C:N ratios can alter the composition of the microbiome [97].

7. Plant Microbiome

To understand the defense mechanism in plants, one needs to study the plant–pathogen interaction. Many microbial communities and microbes have beneficial effects on their host plant. These microbes benefit the plants by improving nutrient acquisition and growth; providing resistance against pathogens; and y enhancing resistance against abiotic stresses, such as heat, drought, soil salinity, and many others. Somehow, beneficial microbes are often specific to a species cultivar. It was observed that few plant signals that trigger plant immune response can distinguish between pathogenic and beneficial microbes. However, it is still unclear which factors help a plant distinguish between beneficial and pathogenic microbes [98]. Naturally, a plant's habitat is a conducive environment for several microbes, including bacteria, oomycetes, fungi, archaea, and even pathogenic microbes. Plant microbiota composition is shaped by the complex multilateral interaction among microbes.

Microbes exhibit commensal, pathogenic, and mutualistic relations with their host plants. The microbiome profiling of plants and looking at root-associated soils revealed the dynamic and diverse range of microbiomes. Many environmental factors (soil type, daylight, and season) and host factors (species and developmental stage) may affect the shape of bacterial communities. Soil and air act as physical barriers for plant-associated microbiomes [99]. The phyllosphere is the aerial part of the plant and is a suitable habitat for microbes. The phyllospheric microbiome greatly affects the performance of the plant. These microbes also help to remove contaminants from plants. They also help to maintain plant health and suppress the growth of plant pathogens. The microbiota of plant parts that are far from the soil or in other aerial parts of plants are highly affected by the long-distance transport process. Highly beneficial and functionally significant microbes are found belowground. At the early stages of growth, microbial communities above the ground are highly influenced by the soil. Microbial communities are found abundantly in soil, with lower amounts in the rhizosphere portion and a more decreased proportion in the endophytic compartment. Four bacterial phyla were found to dominate around the rhizosphere and endosphere of plants: Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria [100]. Members of bacterial communities have a strong influence on each other, as they can have antagonistic, mutualistic, and competitive interactions. Mostly, microbes interact by engaging in nutritional competition, exchange, and interdependence relations. The endosphere compartment of the plant has lower microbial diversity than rhizosphere. The microbial community of the root endosphere is more abundant than in the leaves. However, it is also known that entophytic microbes also play a significant role in plant development [101]. The effect of the root bacterial microbiome on maize, barley, and *Arabidopsis thaliana* in soil has been studied [102]. Peiffer et al. [103] observed that approximately 5–7% of the microbiome genotypes differ from the host genotype. These differences were mostly related to the quantitative nature, at a large scale, when maize rhizosphere microbiomes were studied. The microbiome was sampled during the growing season and then replicated after 5 years, showing that the root-associated microbiota was not changed. Only 143 operational taxonomic units (OTUs) were identified that correlated to the plant genotype [104]. About 200 naturally occurring *Arabidopsis thaliana* accessions have been screened in a single member of the rhizosphere community. Those accessions that were selected have been planted in natural soils; two of them could inhibit the growth of *Pseudomonadaceae*. Thus, it can be concluded that even a single cultivar is enough to affect the structure of microbial communities. The rhizosphere is a significant zone between the plant's root and soil microbiomes. The rhizosphere provides a suitable environment for both plant and microbial growth. The assemblage of microbiomes in the rhizosphere mostly depends on plant-derived metabolites [105].

8. Microbe-Mediated Mitigation of Abiotic Stresses

For the survival of a plant in an environment with abiotic stress, one of the key adaptations is microbial interaction with the plant. Microbe-mediated induction of abiotic stress response is termed Induced Systemic Tolerance (IST). The microbiome helps plants mitigate abiotic stress by using their metabolic and genetic capabilities [106]. It was observed that the most significant rhizospheric occupants that aid in the mitigation of various abiotic stresses in plants belong to the genera *Pseudomonas* [107], *Azotobacter* [108], *Azospirillium* [109], *Rhizobium*, *Pantoea*, *Bacillus*, *Enterobacter* [107], *Bradyrhizobium* [110], *Methylobacterium* [111], *Burkholderia* [112], and *Trichoderma* [112] and the group cyanobacteria [113]. To overcome crop productivity limitations, one of the viable methods is the selection, screening, and application of stress-tolerant microorganisms. *Trichoderma* species have been thoroughly investigated in this regard. In one of the studies, *Trichoderma harzianum* was used for the alleviation of stress in rice by upregulating aquaporin, dehydrin, and malonialdehyde [114]. *T. harzianum* was also employed for the enhanced production of oil from NaCl-affected Indian mustard (*Brassica juncea*). This, as shown in the results, also improved the nutrient uptake, enhanced the accumulation of antioxidants, and lowered the Na^+ uptake [115].

Brotman et al. [116] demonstrated that mutant *Trichoderma* can mitigate salinity stress by the production of ACC-deaminase. In barley and oats, the production of IAA and ACC-deaminase seemed to be enhanced by the use of *Pseudomonas* sp. and *Acinetobacter* sp. [117]. Simmons et al. [118] used *Streptomyces* sp. for the alleviation of salt stress and growth enhancement in the Micro-Tom tomato plant. Meanwhile, in maize and wheat, drought stress was ameliorated by using the strain *Burkholderia phytofirmans* PsJN [119]. Alteration in the levels of phytohormones, defense-related protein, enzymes, antioxidants, and epoxy-polysaccharides is identified as Rhizobacteria-induced drought endurance and resilience (RIDER). These alterations make plants more resistant toward abiotic stresses [120].

The soil microenvironment of the root region contains many microbes, as it harbors a diversity of nutrients, minerals, and metabolites. Substances secreted by a plant root significantly affect microbial colonization within the rhizosphere. Microorganisms move toward the root exudates by chemotactic movement. This movement acts as a dragging force for the colonization of microbial communities around the roots. PGPRs function as biofertilizers, phytostimulators, and biocontrol agents while harnessing the benefits of the rhizosphere/microenvironment. PGPRs depend upon their capabilities, interaction mode, and surrounding conditions. Plant growth is stimulated by bacteria through direct, as well as indirect, actions [121]. Synthesis of bacterial compounds through the direct method is beneficial for the uptake of essential nutrients and micronutrients from the soil. These bacteria also help produce plant-growth regulators such as IAA, deaminase, and ACC, which help improve plant growth. These growth-promoting compounds enhance the growth and prevent stress ethylene from becoming overly inhibitory to plant growth [122,123]. Moreover, the microbes help sequestrate iron and zinc, phosphorous and potassium solubilize, atmospheric nitrogen fixation, and plant hormone synthesis. However, on the other hand, the indirect mechanism shows antagonistic activity toward plant pathogenic organisms and the production of antifungal compounds [64]. Bacterial metabolites act as extracellular signals to induce systemic resistance. This initiates a series of internal processes. The activation of plant defense mechanisms is triggered by the translocated signal received by distant plant cells. Another significant microbiome that acts as a plant-growth promoter is fungi, particularly mycorrhiza, either mycorrhizal fungi or vesicular-arbuscular mycorrhizal (VAM) fungi. These fungi form endosymbiotic associations with plants. Their hyphae form complex networking; thus, nutrient uptake by roots increases.

Salt tolerance in barley and drought tolerance in Chinese cabbage were found to be induced by the root fungal endophyte identified as *Piriformospora indica* [124]. Microbes help plants maintain their growth and development, even under abiotic stress, and they also aid in the production of nutrients, hormones, and organic phytostimulant compounds. These actions of microbiomes make them strong and viable to fight against abiotic stress for plants. Various studies were carried out that elaborate on the role of microbiomes in the mitigation of abiotic stress for crop plants. Some soil-inhabiting microbes, such as *Achromobacter*, *Azospirillum*, *Variovorax*, *Bacillus*, *Enterobacter*, *Azotobacter*, *Aeromonas*, *Klebsiella*, and *Pseudomonas*, help to enhance plant growth even under undesirable environmental conditions [120]. Such soil bacteria that help plants to grow under abiotic stress have been classified as plant-growth promoters (PGP). Indole acetic acid (IAA) synthesized in plant shoots acts as plant-growth-regulating molecules. Auxins and IAA perform as a growth-stimulating effect, resulting in root-growth initiation, while a higher concentration of auxin negatively affects plant root growth [107]. Table 1 presents a list of microbes and tolerance strategies used to control abiotic stress in plants. It was observed from recent studies that PGPRs not only help in the alleviation of abiotic stresses but also increase the plant crop yield of several crops, including rice, maize, barley, and soybean [125].

Table 1. Various tolerance strategies used to control abiotic stress in plants.

Plants	Abiotic Stress	Microbial Inoculation	Tolerance Method	References
Arabidopsis thaliana	Salt	*Bacillus subtilis* GB03	Tissue-specific regulation of sodium transporter *HKT1*.	[126]
Glycine max	Salt	*Pseudomonas simiae*	4-nitroguaiacol and quinolone promote soybean-seed germination.	[61]
Oryza sativa	Salt	Root-associated growth-promoting rhizobacteria	Expression of salt-stress-related *RAB18* plant gene.	[127]
Oryza sativa, *Triticum aestivum*, *Zea mays*, *Gossypium hirsutum*	Salt	Cyanobacteria and cyanobacterial extracts	Phytohormones as elicitor molecule.	[128]
Zea mays	Osmotic stress	*Bacillus megaterium*	High hydraulic conductance and increased root expression and ZmPIP isoforms.	[129]
Vitis vinifera, *Capsicum annuum*	Salt	*Burkholderia*, *Arthrobacter Bacillus*	Increased accumulation of proline.	[130]
Capsicum annuum	Salinity	*Azospirillum brasilense* and *Pantoea dispersa* (Co-inoculation)	High stomatal conductance and Photosynthesis.	[131]
Arabidopsis	Salinity	*Bacillus subtilis*	Decreased root transcriptional expression of a high-affinity K^+ transporter (*AtHKT1*) decreasing root Na^+ import.	[126]
Phaseolus vulgaris	Salinity	*Azospirillum brasilense* strain Cd	Stimulation of persistent exudation of flavonoids.	[132]
Zea mays	Drought	*Burkholderia phytofirmans Enterobacter* sp. FD17	Increased photosynthesis, root and shoot biomass under drought conditions.	[133]
Arabidopsis thaliana	Drought	*Pseudomonas chlororaphis* O6	Production of 2R,3R butanediol-a volatile compound.	[134]
Triticum aestivum	Heat	*Bacillus amyloliquefaciens*, *Azospirillum brasilence*	Reduced regeneration of reactive oxygen species, pre-activation of heat shock transcription factors, and changes in metabolome.	[135]
Brassica juncea	Arsenic toxicity	*Staphylococcus arlettae*	Increased dehydrogenase, phosphatase, and available phosphorus in soil.	[136]
Triticum aestivum	Zn toxicity	*Pseudomonas aeruginosa*	Improved biomass, N and P uptake, and soluble protein.	[137]
Phragmites australis	Hg toxicity	*Photobacterium* spp.	IAA and mercury reductase activity.	[138]
Miscanthus sinensis	Cd, AS, Cu, Pb and Zn toxicity	*Pseudomonas koreensis* AGB-1	ACC deaminase and IAA production.	[139]

8.1. Mechanisms of PGPRs

The changes in the rhizosphere microbial community may cause plant-growth promotion by PGPRs [140]. PGPRs use both direct and indirect modes of action for plant growth. Some PGPRs are strains of *Bacillus*, *Rhizobium*, *Acinetobacter*, *Alcaligenes*, *Azotobacter*, *Arthrobacter*, *Enterobacter*, *Pseudomonas*, *Serratia*, and Burkholderia. In the direct mode of action, PGPRs include atmospheric nitrogen fixation, the production of phytohormones and enzymes in plants. Meanwhile, siderophores' production, antibiotics' production, and enzymes' release (e.g., chitinase) are among the mechanisms of the indirect mode of action [141].

8.2. Direct Mechanisms

In direct mechanisms, PGPRs help to promote plant growth in the absence of the pathogen. Rhizospheric microbial activity also affects the rooting and nutrient-availability pattern. Some direct mechanisms of PGPRs for plant growth are discussed hereunder.

Nitrogen fixation—The plant growth and productivity depend on the availability of vital nutrients such as nitrogen (N_2). Nitrogen-fixing microorganisms play an important role in biological nitrogen fixation under mild temperatures [142]. Nitrogen-fixing organisms are classified into symbiotic and non-symbiotic N_2-fixing bacteria. Symbiotic N_2-fixing bacteria include leguminous and non-leguminous plants such as *rhizobia* and *Frankia.* Meanwhile, non-N_2-fixing bacteria refer to cyanobacteria such as *Nostoc*, *Azotobacter*, and *Azocarus* [143]. The symbiosis connection may lead to the production of nodules [144]. The nitrogen-fixation mechanism is carried out by an enzyme nitrogenase complex. For nitrogen fixation and the regulation of the enzyme, genetic control is present in such bacteria and nitrogenase genes are required. Meanwhile, for the synthesis and regulation of enzymes, regulatory genes are required; nitrogenase genes are also required. Moreover, regulatory genes are required to synthesize and regulate the enzymes. Structural genes are involved in activating Fe protein, iron–molybdenum cofactor biosynthesis, and electron donation [145].

Phosphate Solubilization—Under stress conditions, plants usually face a shortage of nutrients such as phosphorous. It is mostly present in the soil in both forms, i.e., organic and inorganic [146]. The shortage of phosphorous in plants occurs due to the presence of insoluble P in plants, but plants can only absorb it as monobasic and diabasic ions [143]. Phosphate-solubilizing bacteria can work as a source of phosphorous in the form of biofertilizers. Some phosphate-solubilizing bacteria are *Azotobacter*, *Microbacterium*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Flavbacterium*, *Erwinia*, *Rhizobium*, and *Serratia* [147]. As plants cannot absorb inorganic P, Rhizobacteria have the potential to solubilize it, thus enhancing plant growth and yield. However, another cause of P solubilization could be due to the synthesis of organic acids by rhizospheric microorganisms [148]. In plants such as the potato, tomato, wheat, and radish, phosphorous was solubilized by microbial species such as *Azotobacter chroococcum*, *Enterobacter agglomerans*, *P. putida*, *Bradyrhizobium japonicum*, *Cladosporium herbarum*, and *Rhizobium leguminosarum* [149].

Siderophore production—Iron is present abundantly in nature, but it is still unavailable for plants. Mostly, iron is found in the form of Fe^{3+}. PGPRs help to solubilize it by the secretion of siderophores, which are low-molecular-weight iron-binding proteins that help in the chelation of ferric iron (Fe^{3+}). The bacterial cell membrane dissolves siderophores and Fe^{3+} in a 1:1 complex. This Fe^{3+} is reduced to Fe^{2+} and then released from siderophores to the cell. PGPRs enhance plant growth by releasing siderophores, which also help mitigate various plant diseases. Microbial siderophores act as a metal-chelating agent, which helps to control the iron availability in the rhizosphere [150].

Phytohormone production—It is well-known that microbes help in the synthesis of phytohormone auxin, also known as indole-3-acetic acid (IAA). Many microorganisms that are isolated from multiple crops have the ability to synthesize IAA as a secondary metabolite [151]. IAA plays a significant role in the interaction of rhizobacteria and plants [152]. The synthesis of IAA affects plat cell division and helps to stimulate seed and tuber germination and the formation of adventitious roots. The secretion of bacterial IAA provides higher access for plants to nutrients by increasing their root surface area and length [153]. Mostly, *Rhizobium* species produce IAA, which upregulates cell division and the formation of vascular bundles. Several environmental stress factors, such as an acidic pH, osmotic stress, and carbon limitation, cause the modification of IAA synthesis in bacteria [154].

9. Indirect Mechanisms

The environmentally friendly method to control diseases is the application of microorganisms [155]. In PGPRs, biocontrol activities mostly influence nutrient availability, induction of systemic resistance, and the release of antifungal metabolites. It was observed that various rhizobacteria produce antifungal metabolites such as HCN, pyoluteorin, pyrrolnitrin, viscosinamide, 2,4-diacetylphloroglucinol, and tensin. Rhizobacteria interact with the plant roots, leading to the resistance against pathogenic bacteria, fungi, and viruses. This is known as induced systemic resistance (ISR) [148]. Various bacterial components can induce ISR, such as lipopolysaccharides; cyclic lipopeptides; homoserine lactones; flagella; siderophores; and volatile compounds, e.g., acetoin and 2,3-butanediol [155].

9.1. Mechanisms of AMFs

Usually, AMFs work by developing symbiosis with plant roots to obtain essential nutrients, such as N, P, K, Ca, Zn, and many other trace elements, from the host plant. This shows that AMFs provide nutritional support to the plant under abiotic stresses. Meanwhile, in the case of fungal structures, they produces arbuscules, which cause the exchange of inorganic minerals and compounds to host plants [127]. Under abiotic stress such as drought, heavy metals, flooding, salinity, and extreme temperatures, AMFs respond differently. The symbiosis of AMFs improves plant growth, hydration, and physiology under environmental stress conditions [156].

AMFs and drought tolerance—Mostly, plant productivity is reduced by drought stress, under which AMFs help plants retain growth and increase yield [157]. Mycorrhizal plants have the potential to cope with water stress through drought mitigation and drought tolerance. In the drought-mitigation mechanism, AMFs help increase water uptake, helping plants cope with stresses [158]. Other mechanisms include the synthesis of phytohormones under drought stress by AMFs. Plant tolerance under abiotic stress is regulated by hormone homeostasis. Abscisic acid has the potential to modulate transpiration rate and aquaporin expression, as it works as a hormonal stress signal [159]. Osmotic adjustment under drought tolerance by AMFs is another mechanism that helps plants maintain their health. Osmotic adjustment accumulates soluble compounds such as sugar, glycine, betaine, proline, polyamines, and organic acids to maintain turgor pressure [160].

AMFs and plant flooding tolerance—Few AMFs can tolerate abiotic stresses such as flooding. Under such conditions, AMFs help the plant to enhance its nutrient uptake [161]. It has been observed that P was translocated to the rice plants through the mycorrhizal pathway under drought stress; it probably works through osmotic adjustment [162].

AMFs and salinity tolerance—AMF species have the potential to survive under saline conditions. AMF-inoculated plants have the capacity to the enhance water and nutrient uptake; assimilation of osmoregulators, such as proline and sugars; and reduction of Na^+ and Cl^- ions. AMFs can also improve stomatal conductance and decreases oxidative damage in plants under salinity stress [163]. Al-Karaki [164] observed that when a tomato plant was inoculated with *F. mosseae* under saline conditions, the plant biomass was increased, along with the fruit yield and shoot content of P, K, Cu, Fe, and Zn. The oxidative damage in the wheat plants is reduced significantly when inoculated with AMFs under salt stress [100].

9.2. Mechanisms of Endophytes

As discussed in detail, microorganisms enhance the plant tolerance to abiotic stress such as drought, salinity, and metal stress [165]. Along with rhizospheric and root-zone bacterial communities, entophytic bacteria interact with the host-plant tissue to mitigate abiotic stresses [166]. Endophytes release siderophores and lytic enzymes, which, in turn, reduce the bacterial, fungal, and viral diseases in plants. They also promote plant growth by producing indole acetic acid and phosphate-solubilization activity [165]. Table 2 shows the mechanism of endophytes for plant growth under abiotic stress. *B. phytofirmans* PsJN and *Enterobacter* sp. FD17 is known as an efficient plant-growth-promoting endophytes. These endophytes promote growth and enhance the biotic and abiotic tolerance in plants [167]. An entophytic bacterium, *Prosopis strombulifera*, promoted plant growth under saline conditions. The endophytic strains that help plants have better growth are *Lysinibacillus fusiformis* (Ps7), *Bacillus subtilis* (Ps8), *Bacillus licheniformis* (Ps14), *Bacillus pumilus* (Ps19), *Achromobacter xylosoxidans* (Ps27), and *Pseudomonas putida* (Ps30), which produce phytohormones such as IAA, Zeatin, GA3, and ABA [168].

Table 2. Endophyte mechanism for plant-growth promotion under abiotic stress.

Endophyte	Mechanism	Plant	Stress	References
Piriformospora indica	Mutualism mechanism, drought-related genes regulation	Barley	Salinity	[169]
B. phytofirmans PsJN	Initiation of host stress responses	Vegetables	Abiotic stress	[167]
Curvularia protuberate	Metabolite synthesis and improves plant physiology	Tomato and rice	Heat and drought	[170]
C. protuberata	Entophytic colonization	Wheat	Heat and salinity	[171]
P. indica	Increased ascorbate concentration	Barley	Salt stress	[172]
Chaetomium globosum LK4	Increased plat biomass	*Capsicum annum*	Drought	[170]
Trichoderma	Enhanced growth of roots	Cacao	Drought	[173]
Trichoderma harzianum strain T22	Low synthesis of lipid peroxides	Cacao		[174]

There is a possibility that, under abiotic stress, plant growth is stimulated due to the synthesis of antistress biochemicals by endophytes. These biochemical are phytohormones (ABA, Gibberellic acid, cytokinins, and IAA), production of ACC deaminase for ethylene reduction, induced systemic tolerance, and osmolyte accumulation [170]. For example, under osmotic stress, the proline content in *Capsicum annum* was increased due to the inoculation with entophytic bacteria *Arthrobacter* strains EZB4, EZB18, and EZB20 [170].

10. Tolerance Mechanism by Plant Microbiome Interaction

Endophytes live within plants throughout their lifecycle and exhibit symbiotic relationships with plants. Endophytes usually enter the seeds, roots, leaves, and stems of their host plant and make colonies in plant tissues. They could promote plant growth by improving nitrogen fixation, phytohormones secretion, and nutrition acquisition. Root exudates secreted by plants act as an energy source for entophytic microbes [175]. At the initial stages of colonization, exopolysaccharides are synthesized by bacterial cells, and this aids in the protection of bacterial cells from oxidative damage [176]. Plant nutrient acquisition has been increased significantly by arbuscular mycorrhizal fungi; it also can resist abiotic stresses. Plant growth and development are regulated through the symbiotic association of AMFs with their host plants. Nutrient uptake has also been increased due to the complex AMF mycelial network around the roots. The translocation of phosphorus (P) and nitrogen (N) has been positively affected by a common mycorrhizal network (CMN), which, in turn, supports plant growth under extreme environmental conditions [177]. Plants have used biochemical and molecular mechanisms through plant–microbe interactions, which help mitigate the negative effects of abiotic stresses on plant growth. Root morphology has been altered by many phytohormones, such as auxins, gibberellins, and cytokinins, that ultimately enable the plant to tolerate serious environmental conditions (salt stress, drought, heavy-metal accumulation, and nutrient deficiency).

Induced systemic tolerance (IST) plays a significant role in mitigating the negative effects of abiotic stresses. For example, the production of phytohormones, such as IAA, cytokinins, and abscisic acid (ABA), helps plants survive environmental stresses. Moreover, the synthesis of antioxidants such as superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), catalase (CAT), and glutathione reductase (GR) also helps to alleviate the negative effects of abiotic stresses, as well as the deterioration of ethylene precursor, ACC, by bacterial ACC deaminase [178]. One other method to mitigate the negative effect of abiotic stresses is the inoculation of plants with PGPRs that can produce the 1-aminoacylcyclopropane-1-carboxylate (ACC) deaminase enzyme, which catalyzes ACC into alpha-ketobutyrate and ammonia [179]. The increment of low-molecular-weight osmolytes such as glycine betaine, proline, amino acids, organic compounds, and many other enzymes (e.g., ACC-deaminase, chitinase, and glucanase) also helps in the growth and development of plants under abiotic stress [180]. Multiple mechanisms, such as the increased osmotic adjustment, proline accumulation, downregulation of stress-related genes, high glutathione level, jasmonic acid, and increased synthesis and expression of stress resistance genes to enhance the defense system, have been used by AMFs to alleviate the abiotic stress in plants [181]. Figure 4 shows plant stress-tolerance mechanisms mediated by microbial phytohormones.

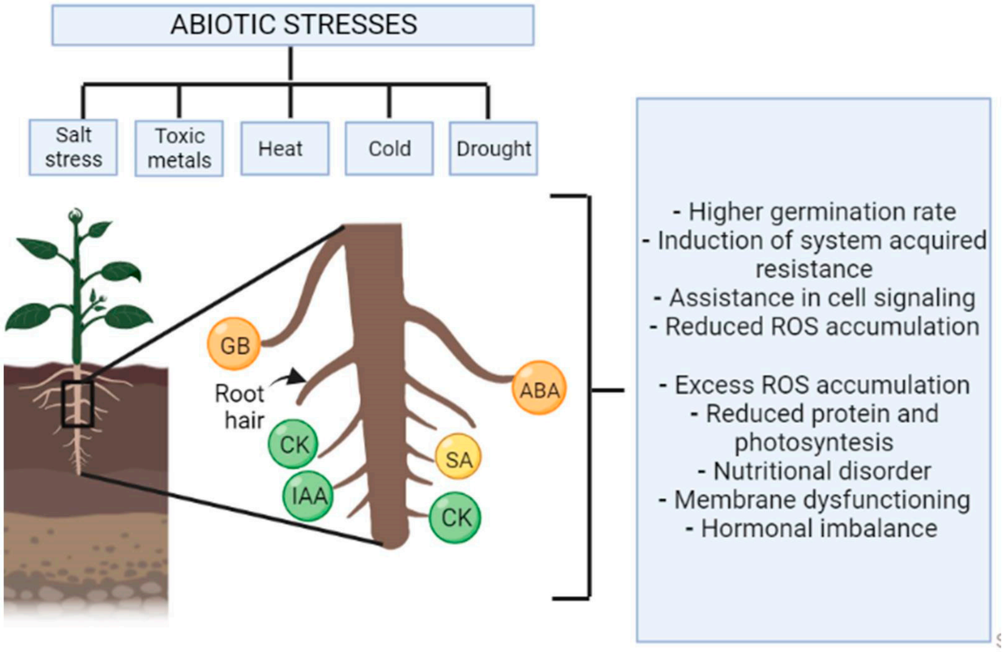

Figure 4. Plant stress-tolerance mechanisms mediated by microbial phytohormones.

11. Role of Microbes in Growth Improvement

For many decades, soil bacteria have been applied for crop production. Some of the vital functions of these bacteria include improved nutrient assimilation to crops and enhanced plant growth by synthesizing plant hormones or growth regulators. Soil bacteria also help plants to control and inhibit plant pathogens' activity, amelioration of soil structure, and bioaccumulation of inorganic matter [182]. Bacteria also play an important role in the mineralization of organic pollutants present in the soil. Rhizospheric microorganisms have the ability to secrete substances that help to promote plant growth and yield. Phytohormones (auxin and cytokinins) produced by the bacteria and fungi may affect the cell division in the shoot, leading to tumorous growths in the plant. This tumorous growth may occur due to the presence of *Agrobacterium tumefaciens*. However, it may improve the root and shoot structure with the subsequent uptake of water and nutrients. Thus, it can be stated that a stable relation between auxin and cytokinins may determine whether the microbial interaction is beneficial or harmful for plant growth [183]. For sustainable crop production, the strong interaction of plants and microbes in the rhizosphere plays a significant role in the transformation, mobilization, and solubilization of nutrients from the soil. Soil bacteria also help in the decomposition and transformation of essential nutrients in soils. PGPRs show a vital role in the development of sustainable crop production [184]. In the current era, various symbiotic and non-symbiotic bacteria are used to enhance plant growth and yield. *Rhizobium* sp. is an example of symbiotic bacteria, while non-symbiotic bacteria include *Azotobacter*, *Azosiprillum*, *Bacillus*, and *Klebsiella* sp. [185]. Some PGPRs, such as free-living bacteria, are beneficial for plant growth and can potentially promote plant growth by colonizing plant roots. Table 3 shows the production of various plant-growth regulators in response to PGPR inoculation in different crops. PGPRs have also been known as plant-health-promoting rhizobacteria (PHPRs) or nodule-promoting rhizobacteria (NPRs). PGPRs are linked with the rhizosphere, which provides a better soil environment for plant–microbe interaction. PGPRs are classified into two groups based on their interaction with plants. These groups are symbiotic bacteria and free-living bacteria. Based on their residing places, they can also be further divided into two groups that are iPGPRs and ePGPRs. The iPGPRs are symbiotic bacteria that reside inside the plant cells and produce nodules, while the ePGPRs are free-living bacteria that are often found outside the plant and promote plant growth [186]. One of the best examples of iPGPRs is *Rhizobia*, which produce nodules in leguminous plants. To enhance nutrient supply to plants, various bacteria are used as soil inoculants. Numerous *Rhizobium* species, including *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium*, and *Sinorhizobium*, have been used for the establishment of nitrogen-fixing symbiosis with plants. Menawhile, non-symbiotic nitrogen-fixing bacteria, including *Azotobacter*, *Azospirillum*, *Bacillus*, and *Klebsiella* sp., have also been used for enhancing plant production. *Bacillus* and *Paeninacillus* species are phosphate-solubilizing bacteria that have been used to improve the phosphorous level in plants. PGPRs contribute to the development of sustainable agriculture systems by performing various functions, such as facilitating the synthesis of particular compounds in plants, the transportation of nutrients from soil to plants, and mitigating plant diseases [187]. However, the mechanisms have not been fully understood [188]. Presumably, PGPRs manifest this action through the expression of an enzyme (1-aminocyclopropane-1-carboxylate deaminase) that reduces ethylene in the roots of plants, leading to increased root length and growth. PGPRs also produce plant hormones such as auxin, IAA, abscisic acid (ABA), gibberellic acid (GA), and cytokinins. They also show antagonism against phytopathogenic bacteria by producing siderophores, β-1, 3-glucanase, chitinases, antibiotic, fluorescent pigment, and cyanide. PGPRs aid in the solubilization and mineralization of nutrients, specifically mineral phosphates. Their role in increasing resistance to drought, salinity, and oxidative stress has been established. PGPRs also trigger the production of water-soluble vitamins such as niacin, pantothenic acid, thiamine, riboflavin, and biotin. Thus, the use of PGPRs has significant importance for the sustainable production of plants [189]. ABA helps in the production of other hormones, such as ethylene, which persists for the better growth of shoots and roots in *Zea mays*. Meanwhile, in the case of IAA, plant growth is usually enhanced due to the expansion of cell division. IAA is a growth hormone, while ABA is a stress hormone; both play a vital role in regulating biotic and abiotic stress [190].

Table 3. Production of various plant-growth regulators (PGRs) in response to PGPR inoculation in different crops.

Crops	**PGPR**	**PGR**	**Responses**	**References**
Maize	*Azotobacter* sp.	Indole-3-acetic acid	Inoculation with strain enhances IAA and growth-promoting effects on maize.	[191]
Canola, tomato	*Kluyvera ascorbate* SUD 165	Siderophores, indole-3-acetic acid	Both strains decreased plant-growth inhibition by heavy metals (nickel, lead, and zinc).	[192]
Groundnut	*Pseudomonas fluorescens*	Siderophores, indole-3-acetic acid	Involvement of ACC deaminase and siderophore production promoted nodulation and yield of groundnut.	[193]

Table 3. *Cont.*

Crops	PGPR	PGR	Responses	References
Rice	*Rhizobium leguminosarum*	Indole-3-acetic acid	Growth-promoting effects upon inoculation on axenically grown rice seedlings were observed.	[93]
Rice	*Azospirillum brasilense* A3, A4, A7, A10, CDJA	Indole-3-acetic acid,	Bacterial strains increased rice grain yield.	[194]
Brassica	*Mesorhizobium loti* MP6	Chrom-azurol, siderophore (CAS), hydrocyanic acid (HCN), indole-3-acetic acid	*Mesorhizobium loti* MP6–coated seeds enhanced seed germination, early vegetative growth, and grain yield.	[195]
Wheat	*Azospirillum lipoferum* strains 15		Promoted development of wheat root system, even under crude-oil contamination.	[196]
Sesbenia, Mung bean	*Azotobacter* sp. and *Pseudomonas* sp.	Indole-3-acetic acid	Increasing concentration of tryptophane from 1 to 5 mg mL^{-1} resulted in decreased growth.	[66]
Rice	*Bacillus* sp. and *Paenibacillus* sp.	Indole-3-acetic acid	The isolate SVPR 30, i.e., strain of *Bacillus* sp., proved to be efficient in promoting a significant increase in the root and shoot parts of rice plants.	[197]
Wheat	*Pseudomonas* sp.	Indole-3-acetic acid	A combined bio-inoculation of diacetyl-phloreglucinol-producing PGPRs and AMFs and improved the nutritional quality of wheat grain.	[198]
Cowpea	*Streptomyces acidiscabies* E13	Hydroxamate siderophores	*S. acidiscabies* promoted cowpea growth under nickel stress.	[199]

Fungal and bacterial species can enhance plant growth and development, and these species are known as plant-growth-promoting microbes (PGPMs). PGPMs help in the mitigation of biotic, as well as abiotic, factors and, in response, increase plant production. Some of the microbes that help in plant growth are *Burkholderia*, *Eneterobacter*, *Flavobacterium*, *Pseudomonas*, *Rhizobium*, *Frankia*, *Clostridium*, *Trichoderma*, *Beauveria*, *Serratia*, and *Streptomyces*. PGPMs act as biofertilizers, helping in the uptake of nutrients to plants by the solubilization of soil minerals such as phosphorous and potassium. PGPMs also work as biopesticide and biocontrol agents, thus increasing resistance against phytopathogens [200]. Table 4 shows the effect of abiotic factors on plant-microbiome interactions.

Table 4. Effect of microbes on plant ecophysiological parameters under abiotic stresses.

Plants	Abiotic Factor	PGPM	Inoculation	Effect	Reference
Cajanus cajan, *Eleusine coracana*	Soil	*Pseudomonas*	Seed	Increase growth and improve nutrient-deficient soil.	[201]
Glycine max	Soil	*Trichoderma* sp.	Seed	Improve germination, growth, and K uptake under drought and salts tress.	[202]
Brassica juncea, *aeruginosa*, *Alcaligenes feacalis*	Soil	*Pseudomonas*	Seed	Increase growth, metal tolerance, and phytoextraction efficiency.	[203]

Table 4. *Cont.*

Plants	Abiotic Factor	PGPM	Inoculation	Effect	Reference
Glycine max	Water	*Klebsiella variicola*	Soil	Improve plant growth and flood tolerance by inducing adventitious root.	[204]
Mentha pulegium L.	Water	*Azotobacter Chroococcm* *Azospirillum brasilense*	Seed	Improve physiological and phytochemical parameters and drought tolerance.	[205]
Vigna radiata	Water	*Pseudomonas fluorescens*	Seed	Increase vigor, biomass, activity of catalase and peroxidase, accumulation of proline, and water-stress tolerance.	[206]
Capsicum annuum	Soil	*Pseudomonas* sp.	Seed	Increase growth by increasing ACC deaminase and reduce ethylene under salinity stress.	[207]
Brachiaria brizantha	Light	*Burkholderia* *Pseudomonass*	Soil	Increase plant growth and shade tolerance.	[208]
Zea mays	Water	*Azospirillum* sp.	Seed	Increase growth and drought and flood tolerance.	[209]
Ophiopogon japonicus	Light	*Kaistobacter* sp. *Pseudomonas*	Soil	Increase growth and shade tolerance.	[210]

12. Role of Microbes in Minerals Improvements in Plants

Nutrient acquisition by plants through soil is affected by the microbial species residing in that habitat [211]. Soil microbes have better significant interaction with plants. Many studies reported the alleviation effects of pathogens on plants and mitigation of abiotic stresses [212]. Through the characterization of ecological parameters, it has been observed that microbes promote plant growth. For instance, in the 19th century mycorrhizal fungi and nodulated legumes, both were identified as a root symbionts [213]. Few bacterial cultures, such as *Azotobacter chroococcum* and *Bacillus megaterium*, have been used to coat crop seeds for the improvement in growth and development [214]. Various other bacterial strains, such as *Pseudomonas* and *Azospirillum*, help in promoting plant growth [215]. Three mechanisms have been analyzed to explain how microbes can enhance the nutrient content of plant. Soil microbes help in the metabolism of soilborne nutrients and excrete essential elements for plant nutrition. In the natural environment, many essential nutrients, such as N, P, and S, are present only in organic molecules; therefore, the availability of such nutrients becomes minimal for plants. Soil microbes contain metabolic machinery which mineralizes organic forms of N, P, and S. Cell lysis also causes the release of these essential nutrients [216]. This leads to the release of inorganic forms of N, P, and S into soil having an ionic content of ammonium, nitrate, phosphate, and sulfate, which are essential nutrients for plant. These essential nutrients are the key drivers for plant growth and development [217]. In agricultural practices, growth-promoting microbial strains can be re-inoculated on plants. Many plant-beneficial microbial strains have been tested for their ability to promote plant growth and nutrient acquisition. Nitrogenase genes present in bacterial taxa also provide benefits to the plant [218]. Non-leguminous plants usually have nitrogen-fixing bacteria as a host, while, on the other hand, other plant microbes, except legumes and *Rhizobia*, also promote nitrogen fixation [219]. It has been observed that the microbial mobilization of nitrogen sources may promote plant growth. Plants inoculated with bacterial strains show a higher yield [220]. In one of the experiments, it was observed that N has been sourced from ammonium sulfate fertilizer rather than organically bound soil N [221]. It was observed that unsterilized grass seeds have better access to protein-N as compared to sterilized seeds. However, microbes that showed this activity have not been identified yet [222]. A fungus known as *Glomus intraradices* has the ability to transfer organic nitrogen to plants. In the case of phosphorous compounds, many bacterial, as well as fungal, strains help in the solubilization of inorganic P and mineralization of organic P. P-mobilizing strains are also identified as a growth-promoting strains [223]. For sulfur, *Pseudomonas* strains are used as growth-promoting strains. These strains use sulfonate monooxygenase enzymes for the mineralization of organic-S [224]. In a study by Xia et al. [225], it was reported that bacterial strains boost tomato plant growth in a greenhouse environment. These bacterial strains were isolated from plants that were grown under organic management. Thus, it has been observed that plant-associated bacteria have the potential to promote plant growth, but still there is a need to explore the interactions of these microbial communities that affect plants' growth and their nutritional content [215]. Table 5 shows the inoculation of phosphorus-solubilizing bacteria (PSB) on crop plants from different mineral sources.

Table 5. Inoculation of phosphorus-solubilizing bacteria (PSB) on crop plants from different mineral sources.

Plants	Mineral Source	Bacterial Species	Outcomes	References
Stevia rebaudiana	Mussoorie rock phosphate	*Burkholderia gladioli* MTCC 10216; *B. gladioli* MTCC10217, *Enterobacter aerogenes* MTCC 10208, and *Serratia marcescens* MTCC 10238	Enhanced growth and stevioside and rebaudioside-A metabolites. Increased amount of P in soil.	[226]
Rice	Bayóvar rock phosphate	*Burkholderia* sp. UFLA 04-21; *Paenibacillus kribbensis* UFLA 03-10; *Enterobacter* sp. UFPI B5-6; and *Pseudomonas* sp. UFPI B5-8A	Increased biomass, tillers and nutrients accumulation	[227]
Vicia faba	Rock phosphate	*Serratia plymuthica* BMA1	Increased plant growth and P uptake	[228]
Lentil (*Lens culinaris Medik.* cv. VL Masoor 507)	Udaipur rock phosphate	*Pseudomonas* sp. RT5RP2 and *Pseudomonas* sp. RT6RP	Increased P uptake by plants	[229]
Medicago truncatula Gaertn.	Tunisian rock phosphate	*Pseudomonas corrugata* SP77, *Pseudomonas koreensis* LT62 and *Pseudomonas*	Enhanced shoot dry weight and nodule fresh weigh	[230]

13. Microbial Plant Biostimulants

Over the past few decades, high-quality agricultural lands have been decreasing due to the drastic climate change and demands to maintain the production of crops under stressful conditions. To fulfill this purpose, microbial plant biostimulants play a vital role in increasing the yield of the plant under abiotic stresses and alleviating the adverse climate impacts [231]. Promising microbial plant biostimulants consist of *Azotobacter* spp., Mycorrhizal fungi, *Rhizobium* spp., and *Azospirillum* spp. genera. Till now, probably 20 commercially available microbial plant biostimulants have been derived from PGPRs [26]. Plant biostimulants can be associated with the accumulation of naturally occurring bioactive compounds that potentially improve plant performance. Microbial plant stimulants enhance hormone production and nutrient uptake, which helps improve the photosynthesis of plants and their growth rate.

Synthetic microbial community (SynCom) is one of the emerging fields that deals with the synthetic-biology-derived microbial-community analysis, bioinformatics approaches, and metagenomic study to augment plant fitness and productivity [232]. SynCom can be synthesized by the co-culturing various taxa under desired conditions. The principle of SynCom is the complexity reduction of the original microbial community [233]. Various studies have shown that the application of SynCom enhances plant growth and yield under greenhouse conditions, as well in the field [234]. The SynCom technique is one of the promising techniques, as it also includes the concept of microbial ecology. This technique is formed by the isolation of microbial cultures from natural sources, leading to the manipulation of specific microbes [235].

Biofertilizers are a composition of multiple microorganisms that can promote plant growth even under abiotic and biotic stresses. They are composed of PGPRs, AMFs, and a mixture of other beneficial microbes. They have the potential to maintain plant growth, photosynthesis, and water and nutrient retention even under undesirable conditions. Biofertilizers can have direct, as well indirect, mechanisms. The direct mechanisms include phytostimulation and nutrient mobility, while indirect mechanism includes biocontrol activity. The impact of biofertilizers on plants depends on the soil fertility, type of crop, and environmental conditions [236]. Biofertilizers are a combination of microbial inoculants containing cells that are effective for N-fixing and P-solubilizing [237]. The application of biofertilizers improves the function and structure of soil microorganisms. It also enhances the physiochemical properties of the soil. PGPRs are also considered an organic fertilizer. Biofertilizers are applied to the soil directly, or they can also be used for the treatment of seeds. The application of biofertilizers to the soil also helps in nourishing the plant by the indirect supply of essential nutrients. Biofertilizers help to increase the yield of crops both by direct and indirect mechanisms [238]. The direct mechanisms include nitrogen fixation, production of phytohormones, and solubilization of phosphate, while the indirect mechanism includes biocontrol activity. The indirect mechanism does not enhance the plant growth directly. This mechanism protects plants from the harmful effects of plant pathogens. The synthesis of antibiotics, siderophores, and lytic enzymes are the indirect mechanisms of biofertilizers that help in the lyses of the cell wall of pathogenic fungi [239].

14. Synergic Effects of Biochar and Microbes in Ecophysiological Parameters

Biochar (BC) can be produced by following the pyrolysis of organic compounds by having no or limited oxygen. BC is rich in organic compounds, mineral elements, and inorganic carbonates [240]. It is a manmade form of black carbon. BC is composed of mainly aromatic hydrocarbons, alkyl groups, and many other inert substances. These compounds are difficult to be oxidized or decomposed by microorganisms [241]. BC has some prominent characteristics; for instance, it contains various functional groups on its surface, as it has a porous structure. These characteristics help to improve the pH and ion-exchange capacity of the soil [242]. BC helps to enhance the nutrient uptake and reduces the loss of nutrients [243]. To prepare BC-based compound fertilizers, the synergic effect can be achieved by loading organic fertilizer into the pores of BC. This BC compound fertilizer helps to release nutrient elements into the soil. Carbon-based fertilizers are of three types, organic, inorganic, and organic–inorganic fertilizers. These fertilizers are environmentally friendly and help to improve nutrient efficiency in plants. Glaser et al. [244] reported that the addition of BC to compost increased the corn yield as compared to pure compost. In another irrigation treatment, it was observed that both BC and inorganic fertilizers enhance the maize grain yield, as well its growth and productivity [245]. Thus, it is clear that the combination of organic fertilizers and BC is more significant as compared to the individual components [246]. In many studies, microbes are abundantly used to enhance plant growth and to improve soil properties. Plant waste has been utilized by methylotrophic bacteria to synthesize methanol as a source of carbon and energy. Methylotrophic bacteria are plant-growth-promoting bacteria that enhance plant growth by the production of growth hormones such as indole-3-acetic acid and cytokinins [247]. These bacteria also secrete other beneficial metabolites and improve plant growth through antagonism, competition, and induction [248]. In one of the studies reported by Juan et al. [249], the weight and plant height of tomato plants increased with *T. afroharzianum* TM2-4 treatment as compared to the control. Many studies have been carried out on the synergic effect of microorganism- and BC-based organic fertilizers on plant growth and quality. Somehow, microbial agents also promote nutrient transformation in BC-based organic fertilizer [250].

15. Customized Adjustment of Plant Microbiome: A Revolution in Progress

Many studies reported the benefits of microbial communities for plant growth and development. These microbes help to attain resistance against biotic, as well abiotic, stresses [251]. The microbiome related to plants highly affects plant health and productivity. A lot of research work has been carried out on the plant microbiome. The utilization of plant microbiomes aids to enhance tolerance for biotic and abiotic stresses and, in turn, increases agricultural production and reduces chemical usage [252]. Utilization of the plant microbiome in the agricultural sector may help to reduce greenhouse gas emissions [253]. Indigenous microbes are still used for better crop performance and maintenance [254]. Most of the plant microbiomes that help in developing a model plant are still unknown. The rhizobiome also plays a significant role in enhanced plant productivity. Various conventional and modern breeding methods have been used to make changes in the root exudates for reshaping rhizobiome and microbial activity. Still, many researchers are trying to produce PGPBs to reconstruct plant microbiomes [255]. A research work reported by Adesemoye and Egamberdieva [256] observed that the inoculation of tomato plants with PGP consortium (*Bacillus amyloliquefaciens* IN937a, *Bacillus pumilus* T4, and AMF *Glomus intaradices*) leads to an increased yield by up to 30%. In another case study, the soybean biomass of two cultivars was found to be increased by the inoculation of *B. japonicum* 532C, RCR3407, and *B. subtilis* MIB600. This also led to the improved soybean nodulation efficiency [257]. Thus, it can be stated that the microbiome plays a significant role in the maintenance of crop yields. The genetic diversity of the microbiome also aids in the improvement and stabilization of the effects of microbial inoculants.

16. Conclusions and Future Perspective

In the current era, various microbiomes have been used for the better production of crops. Plant microbiomes are significant for plant health, growth, and productivity. Still, intensive research is required to reveal various other mechanisms of plant microbiome interactions. For developing numerous and diverse varieties of crops, plant microbiomes are used widely. Microbiomes associated with the relevant plants may help to control abiotic stress. In another study, it was reported that transgenic plants could be developed by transferring beneficial genes from microbes into the desired plant. Likewise, the ACC deaminase gene from bacteria was transferred to transgenic plants. There are various other environmental issues regarding the development of transgenic plants, so it would be more beneficial to introduce such techniques that can easily handle microbial inoculants in order to mitigate abiotic stress. The use of PGPMs leads to the improvement in stress tolerance in crops; however, some crops have shown negative results or no effects by PGPMs. The microbial consortium has also been used in field to tailor the rhizobiome for both biotic- and abiotic-stress management. Thus, more work is needed to be carried out for the better performance of ready-to-use microbial formulations for the alleviation of environmental stresses.

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