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Review

A Review on Practical Application and Potentials of Phytohormone-Producing Plant Growth-Promoting Rhizobacteria for Inducing Heavy Metal Tolerance in Crops

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Abstract: Water scarcity and high input costs have compelled farmers to use untreated wastewater and industrial effluents to increase profitability of their farms. Normally, these effluents improve crop productivity by serving as carbon source for microbes, providing nutrients to plants and microbes, and improving soil physicochemical and biological properties. They, however, may also contain significant concentrations of potential heavy metals, the main inorganic pollutants affecting plant systems, in addition to soil deterioration. The continuous use of untreated industrial wastes and agrochemicals may lead to accumulation of phytotoxic concentration of heavy metals in soils. Phytotoxic concentration of heavy metals in soils has been reported in Pakistan along the road sides and around metropolitan areas, which may cause its higher accumulation in edible plant parts. A number of bacterial that can induce heavy metal tolerance in plants due to their ability to produce phytohormones strains have been reported. Inoculation of crop plants with these microbes can help to improve their growth and productivity under normal, as well as stressed, conditions. This review reports the recent developments in heavy metal pollution as one of the major inorganic sources, the response of plants to these contaminants, and heavy metal stress mitigation strategies. We have also summarized the exogenous application of phytohormones and, more importantly, the use of phytohormone-producing, heavy metal-tolerant rhizobacteria as one of the recent tools to deal with heavy metal contamination and improvement in productivity of agricultural systems.

Keywords: environmental pollution; urbanization; industrialization; heavy metals; phytohormones; microbes

1. Introduction

Climate change is among the leading factors affecting water availability. Water scarcity for irrigation is a result of drought spells, depletion of surface and ground water resources, and shifting of fresh water for domestic and industrial use [1]. The use of untreated wastewater has been widely accepted by the farmers in Pakistan due to easy availability around metropolitan areas and in peri-urban areas. The use of industrial wastewater and sewage is gaining popularity due to the provision of dissolved plant nutrients and organic matter, which improves soil biological properties and its physical quality [2]. Urbanization and industrialization caused a significant reduction in productive lands for agriculture, which challenged scientists to develop strategies for meeting food requirements through existing sources. In the current scenario, the increase in cultivation area seems difficult, so strategies are required to improve the crop productivity per unit area. The use of agrochemicals and intensive cultivation may result in deterioration of land resources and environmental quality.

Environmental pollution is one of the major problems all over the globe, particularly in metropolitan areas and industrial cities. The problem is more severe in developing countries, including Pakistan, due to unplanned disposal of untreated sewage water, industrial effluents, farms wastes, and application of agrochemicals. Normally, these wastes and agrochemicals improve crop productivity by serving as a carbon source for microbes, providing nutrients to plants and microbes, and improving soil physicochemical and biological properties. They, however, may also contain significant concentrations of potential heavy metals, including nickel (Ni), lead (Pb), cadmium (Cd), arsenic (As), and chromium (Cr), etc., [3]. Globally, soil pollution with heavy metals is increasingly dominant along with agricultural and economic intensification, which, in return, poses serious damages to the soil health and productivity [4]. In Pakistan, the use of industrial effluents, untreated sewage water, agrochemicals, and farm wastes is the major source of organic and inorganic pollutants in soils.

Heavy metals are among the main inorganic pollutants that also affect plant systems, in addition to soil deterioration. These heavy metals may pose toxic or beneficial effects on soil microbes, depending upon bioavailability and nature [5], along with climatic factors. Some heavy metals, including Ni, Mn, and Zn, serve as micronutrients and are required for physiological processes in microbes. They are required in enzyme activity and stabilization of molecules [6]. Others, including Pb, As, mercury (Hg), silver (Ag), Cd, and gold (Au), are not required for body functioning [6]. A few heavy metals, such as Zn and Ni, can be toxic when present in heavy concentrations only. The continuous use of untreated industrial wastes and agrochemicals may lead to accumulation of phytotoxic concentration of heavy metals in soils [7]. These metals, when taken up by plants, become a part of food chain and affect humans and animals. The phytotoxic concentrations of these heavy metals may adversely affect the entire environment, including plants, soil, animals, and human beings [8].

Cadmium is one of the most toxic heavy metals for soil, plants, animals, and human beings [9]. The main source of Cd in soils is anthropogenic activities. Cadmium compounds are more soluble than other heavy metals, which favors its bioavailability, absorption, and accumulation in plant systems. Cadmium can easily be translocated to aerial parts so Cd-induced phytotoxicity has widely been reported in literature [10–12]. Cadmium-induced negative impacts on plants include physiological, morphological, biochemical, and molecular changes in plants [13]. It can also induce oxidative stress that can cause inhibition of seed germination, water and ionic imbalance, a decrease in photosynthesis, cellular organelles and cell membrane disintegration, and a decrease in protein synthesis that leads to decreased crop productivity [14]. Cadmium also affects soil biology and microbial activity, thus disturbing microbial community structure and functioning.

Phytotoxic concentration of Cd (5.8 to 6.11 mg kg^{-1}) in soils has been reported in Pakistan along the road sides [15], which may cause its higher accumulation in edible plant parts, as reported in paddies (0.116 to 0.370 mg ka^{-1}) by Nawaz et al. [16] in areas around Faisalabad. Lead and Cr are also widely spread in top layers of soils, as they are aerially deposited from smoke of vehicles [9]. Other sources include mining, industries, and agrochemicals. Variable soil lead concentration (10 to 293 mg kg^{-1}) has been reported in agricultural soils [17]. Potentially hazardous levels of Cr (VI) have also been reported in soil samples around residential colonies, industries, and recreational sites [18].

Cadmium is promptly absorbed and accumulated in plant tissues due to its high solubility, which makes it highly toxic to plants, leading to disruption of the entire plant's metabolic functions [19]. Plants responds to Cd stress by synthesizing stress-related proteins and signaling molecules. Plant roots release a number of chelating compounds, which include low molecular weight organic acids, nicotianamine, and phytosiderophores [20]. These compounds may affect the heavy metals uptake by plants. Studies on functional genomics report complex regulatory networks, which are associated with Cd stress in plants [19]. Nutrient management is also one of the possible responses of plants to Cd stress [21]. Similarly, chromium (Cr) is a toxic trace element for the plants growing in Cr-contaminated soils. Its higher concentration causes deterioration of certain metabolic, physiological, and biochemical attributes, resulting in stunted growth and development of plants [3]. Accumulation of Cr in higher quantities results in generation of reactive oxygen species that causes damages to the cell structure, and hence disturbs the normal metabolism of the plants [22]. Higher concentrations of Cr are found in areas having tanning industries and slaughter houses, where the effluent often contains Cr concentrations in toxic levels [3].

Lead (Pb), on the other hand, makes its way into the soil through industrial activities and is found in higher amounts in areas near public societies, industrial set-ups, roads, and highways [23]. Higher concentrations of Pb in plant bodies cause certain morpho-physiological damages and results in poor growth and development and hence limits crop production [24]. Intake of food contaminated with Pb is associated with development of chronic diseases in humans, leading to failure of human organs [25].

Heavy metal contamination of soils is a complex process and a number of conventional physicochemical methods are being used to remediate the metal-contaminated soils, which are costly, less efficient, and are not suitable for large-scale application [26]. Moreover, financial and technical implications have made soil remediation a difficult task to be achieved in the current era [27].

Use of phytohormone-producing heavy metal tolerant plant growth promoting rhizobacteria (PGPR) can be used as an alternate strategy to decontaminate heavy metal-polluted soils, which is a more efficient, inexpensive, sustainable, and ecofriendly approach [28]. The PGPR produce phytohormones, in addition to several other growth-promoting traits, can reduce the heavy metal toxicity and improve crop growth under heavy metal polluted soil conditions [29–31]. Phytohormone-producing Cd-tolerant PGPR can be effective to induce resistance against heavy metal toxicity in crop plants. Scientists have reported a number of Cd, Pb, Ni, As, Zn, Cu, Fe, and Cr-tolerant PGPR strains belonging to different genera such as *Ochrobactrum* [32], *Bradyrhizobium* [33], *Chryseobacterium* [34], *Klebsiella* [35], *Serratia* [36], *Bacillus* spp. [37], *Ralstonia* [38], *Exiguobacterium* [39], *Stenotrophomonas*, *Morganella* and *Providencia* [40], *Enterobacter* [11,41], *Leifsonia* [42], *Burkholderia phytofirmans* PsJn [31], *Burkholderia cepacia* [43] *Pseudomonas fluorescens* [44], and *Pseudomonas aeruginosa* [45]. These strains have been well documented to have multifarious plant growth-promoting traits, in additions to phytohormone producing ability, and thus can be used to develop biofertilizer for inducing heavy metal stress tolerance in crop plants. This review provides an overview on the current status of application of plant growth-promoting rhizobacteria to confer resistance against heavy metals in plants as a most feasible alternate strategy. Special attention has been given to the potentials of exogenous application of phytohormones, especially the phytohormones producing plant growth and promoting rhizobacteria in remediation of metal polluted soils and healthier crop production.

2. Heavy Metals as Inorganic Pollutants

Environmental pollution is one of the most serious problems faced by mankind over the globe. It is more severe around big cities and metropolitan areas, particularly in developing countries like Pakistan. The agricultural use of untreated wastewater and sewage sludge from industries, use of agrochemicals, and automobiles are among the main sources of environmental pollution. These effluents may contain a number of organic and inorganic pollutants, including heavy metals. The toxicity or beneficial effect of heavy metals on plants and microbes be beneficial or harmful for microbes, depending upon the nature and bioavailability of metals. For example, heavy metals like Mg, Zn, Co, Mn, Cr, Cu, Fe, and Ni are considered to be the essential elements for microorganisms due to their involvement in a number of physiological processes [46]. These may be part of enzyme complexes, act as stabilizing molecules, or play direct role in redox reactions [7]. Some others, such as Ag, Al, Hg, Au, Pb, Sb, and As, do not have a biological role in microbial metabolic processes [7]. The higher concentrations of these heavy metals can be toxic to microbes due to complexation with body parts. Moreover, some of the essential heavy metals, such as Ni and Zn, can be toxic to microbial bodies when present in higher concentrations.

Untreated wastewater contains a number of organic and inorganic pollutants, including heavy metals such as Pb and Cd [47]. Long-term use of wastewater incorporates contaminants such as heavy metals and salts in agricultural soils, making them unfit for crops and microorganisms [3,48] Previous studies have reported that sewage water application resulted in increased accumulation of Cr, Pb, and Cd, which caused a deterioration in the quality of vegetables [49]. The phytotoxic concentration of heavy metals in soils may result in accumulation of these metals in crops and vegetables to thus enter into food web [7,50]. It has been reported that irrigation of vegetables with untreated industrial effluents caused the higher accumulation of Ar, Ni, Co, Pb, and Cd in the edible portions of vegetables, which may pose potential health problems.

Heavy metals have been recognized by the environmentalists as the major inorganic pollutants due to their toxic nature. Heavy metal contamination of foods has been reported as a major threat to human health, as these metals have more potential to transfer into food chains [51]. Heavy metals are naturally occurring in normal water and soils, however, many of them are toxic even in very lower concentrations [52]. For example, metals such as As, Co, Cr, Hg, Ni, Pb, and Cd are highly toxic, even in very minute quantities. Anthropogenic activities, such as mining, automobiles, agrochemicals, and discharge of untreated industrial effluents, are the major cause of heavy metal accumulation in our environmental compartments [50,53].

The accumulation of heavy metals in soft tissues of the body make them more toxic as they cannot be metabolized by the normal physiological processes. Soils have been considered as the major sink for heavy metal accumulation as a result of the aforementioned anthropogenic activities. Mostly, heavy metals are nondegradable and do not undergo any chemical or microbial degradation so they can persist in the environment for longer periods once being released into the environment [54,55]. The presence of heavy metals in the environment as pollutants is a serious issue that is destroying the environment. They are more harmful than organic pollutants, as most of the organic pollutants are biodegradable. The degradation rate of organic pollutants can, however, be decreased due to the presence of heavy metals, thus they in fact double the environmental pollution problems [56].

3. Plant Response to Heavy Metal Stress

The bioaccumulation of higher concentrations of heavy metals as pollutants in the environment has become one of the major threats for living organisms. The toxic levels of heavy metals may interact with important biomolecules in the cell, including DNA and protein, leading to excessive production of reactive oxygen species (ROS). Serious physiological, metabolic, and morphological anomalies thus occur in plants, ranging from chlorosis of leaves, to protein degradation and lipid peroxidation [57].

In response to heavy metal stress, plants have developed a number of defensive mechanisms at physical and molecular levels. The morphological structures, such as formation of trichomes, thick cuticles, and cell walls are among the physiological barriers that have been studied to be evolved in plants in response to heavy metal stress [58]. For example, trichomes either have the ability to secrete secondary metabolites that cope with harmful effects of metals or serve as primary storage sites for heavy metals to detoxify them [59]. In some cases, however, heavy metals overcome the biophysical barriers to enter into plant tissues and cells. Once these metal ions enter into plant tissues and cells, several defensive mechanisms are initiated in plants to attenuate and nullify the heavy metal toxicity.

Plants, for instance, produce several biomolecules at the cellular level to cope with heavy metal toxicity. A number of organic compounds, such as metallothioneins, phytochelatins, glutathione, mugineic acids, and putrescine, or protons, phenolic compounds, heat shock proteins, and flavonoids are produced as defensive mechanisms. Some specific amino acids and hormones, like jasmonic acid, salicylic acid, and ethylene, are also produced in response to metal stress [60–62].

A failure of the above-mentioned strategies results in the imbalance of the cellular redox systems that induces the production of ROS. In such situations, plants develop antioxidant defense mechanisms to cope with free radicals' toxicity. Thus, enzymatic antioxidants like catalase, (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), glutathione reductase (GR), and superoxide dismutase (SOD), and nonenzymatic antioxidants, like tocopherols, proline, alkaloids, carotenoids, glutathione (GSH), and ascorbate (AsA), along with phenolic compounds, such as lignin, tannins, and flavonoids, are produced that have the ability to act as scavengers of free radicals in crop plants that suffer different stresses [63–67].

Metal complexation and removal at intra and intercellular level by formation of metallothioneins (MTs) or phytochelatins (PCs) and production of polysaccharides and organic acids have also been studied in plants [61,68,69]. Plants detoxify heavy metals by producing low molecular weight PCs using the enzyme phytochelatin synthase (PCS). These PCs have high affinity to heavy metals when present at toxic concentrations [70]. Different species of microorganisms and animals produce PCs as a pathway for heavy metal detoxification and homeostasis [71]. Literature has reported that plants produce PCs in response to different abiotic stresses, including heavy metal stress, herbicides, and excess of UV-B, heat stress, and salinity stress [72]. Thus, production of PCs can be used as biomarkers for early detection of heavy metal stress in crop plants [73]. The Cd2+ ions have been identified as strong inducers of PCs in red spruce [74]. The PCs can be produced and accumulated both in roots and aerial parts, however, studies suggest that they are first produced in roots. For example, in sunflowers, Cd stress induced two times more PCs in roots than leaves [75]. In another study, Heiss et al. [76] reported that prolonged Cd stress in *Brassica juncea* produced three times more PCs in leaves than roots. The study thus led to the identification of PCS genes in *Brassica juncea*. Metallothioneins are small cysteine-rich, low molecular weight metal-binding proteins or polypeptides that are produced in a number of organisms, including microorganisms and plants [77]. The MTs show strong affinity with heavy metals such as As, Cd, Zn, and Cu [78]. In plants, the MTs nullify the toxicity of heavy metals through metal transport adjustment, homeostasis of intracellular metal ions, and cellular sequestration of heavy metals [79].

Certain plant species have developed mechanisms for nonenzymatic synthesis of organic compounds such as proline (Pro). These metabolites help plants to detoxify metals, thus strengthening mechanisms of intracellular antioxidant enzymes. For example, Gohari et al. [80] reported increased accumulation of Pro in roots of *Brassica napus* L. in response to Pb2 + stress. The production of plant hormones in response to external stimuli such as heavy metal stress is also a well-established mechanism in plants. These hormones, also called phytohormones, are organic compounds that coordinate plant physiological processes, thus regulating their growth and development. These phytohormones perform functions at the site of production or work at some other place after their transport [81,82].

Among phytohormones, abscisic acid (ABA), indole acetic acid (IAA), ethylene, salicylic acid (SA), gibberellins (GA), jasmonates, and brassinosteroids (BRs) have been well studied to be produced under different abiotic stresses, including heavy metal stress. Ethylene, for instance, is a stress hormone that regulates the senescence in plants, and thus modifies/limits the plant growth under abiotic stress. It has been well documented as a stress tolerance inducer in plants [83]. It is a well-established fact that SA alleviates heavy metal toxicity in plants [84]. The BRs modulate antioxidative defense systems in plants against abiotic stresses [85]. Jasmonates, the multifunctional hormones, have also been reported to be produced in plants under abiotic stresses [86]. Boron is an essential metal but its higher concentration can be toxic for crop plants. For instance, boron application at the rate of 5 mmol L^{-1} and 12.5 mmol L^{-1} negatively affected the growth and photosynthetic activity of potato cultivars. The ABA and

IAA contents were also significantly increased in both potato cultivars grown under boron stress [87]. Zinc (Zn) application at lower levels increased GA3 contents, while its higher concentration decreased the GA3 level in germinating chickpea seeds [88]. Cytokinins (CKs) modulate plant development and stress conditions altered the endogenous level of CKs, which shows the involvement of CKs in stress tolerance induction in crop plants [89]. The CK production and transport from roots to upper parts decreases through heavy metal stress. The CKs have antagonistic interactions with ABA, therefore the increased production of ABA under heavy metal stress decreases the production of CKs [90].

Abscisic acid has a direct role in abiotic stress tolerance in crop plants. Brien and Benkova [89], for example, observed a rapid increase in endogenous level of ABA in response to environmental stresses. The higher levels of ABA, in turn, activated the specific signaling pathways and modulated the gene expression level in plants. Exposure to heavy metals such as As, Cu, Hg, and Cd induced the overexpression of ABA biosynthetic genes, leading to an increase in endogenous ABA levels in crop plants [91,92].

Indole acetic acid is a multifunctional hormone that is equally effective under normal, as well as stressed, conditions [93]. Increased production of IAA under heavy metal stress has been observed. It was noted that heavy metal stress increased the level of IAA and decreased plant growth that might be due to heavy metal-induced hormonal imbalance [94].

The symbiotic association between higher plants and arbuscular fungi can also effectively immobilize heavy metals, thus reducing their uptake by host plants [95,96]. During such associations, the fungal counterparts bind the metals to the cell wall of their hyphae and also excrete molecules, thus inducing antioxidant defense mechanisms in crop plants. Exploitation of these mechanisms and production of aforementioned biomolecules in response to heavy metal stress depends on plant species, the genotype, and the level of metal tolerance of these crop plants [97]. Although plants have developed mechanisms to deal with heavy metal toxicity, the production of these metabolites divert the normal metabolic processes to defensive ones, thus compromising the yield potentials. It is, therefore, the need of the hour to find ways and means for mitigating the negative impacts of heavy metal stress on crop plants, thus improving the productivity of cropping systems.

4. Heavy Metal Stress Mitigation Strategies

Heavy metals are among the most dangerous pollutants for environment and human population over the globe. These have become more dangerous than pesticides and other well-known inorganic pollutants such as sulfur dioxide and carbon dioxide [98]. According to recent opinion, heavy metals may surpass solid and nuclear wastes in terms of their toxicity to the environment [99]. Heavy metals also impart indirect cell toxicity by producing excess reactive oxygen species (ROS), which can inhibit antioxidative systems by inducing oxidative stress. To withstand metal stress and metal toxicity, plants use certain defense mechanisms, such as activation of various antioxidant enzyme systems, binding of heavy metals to phytochelatins/metallothioneins, metal sequestration into vacuoles, and reduction in heavy metal uptake [100]. Certain plants have developed strong antioxidative systems, and thus can better adapt to heavy metal stress [101].

Different physicochemical strategies are being used to decontaminate the heavy metal-contaminated sites. These techniques include physicochemical extraction (washing of soil), in situ fixation by changing the metal structure through chemicals, metal stabilization, and excavation [91]. Physicochemical techniques adversely affect soil physicochemical and biological properties, leading to secondary pollution in soils as reported by Ali et al. [102]. Due to these hazards, as well as high cost and less efficiency of these strategies [103], scientists are trying to find out cost-effective, eco-friendly, and reproducible solutions to remediate heavy metal contaminated soils.

Environmentalists and biological scientists are working together to develop potential alternative strategies to deal with heavy metal toxicity. Heavy metal contamination of agricultural soils is a serious environmental issue. Plants cope with heavy metal stress by modulating their metabolic processes through production of phytohormones. In recent years, the exogenous application has been well recognized as an alternative technology to deal with heavy metal toxicity in agricultural soils. Certain soil microbes can tolerate higher concentrations of heavy metals and also have the ability to produce phytohormones, so application of phytohormone-producing heavy metal-tolerant PGPR can be a promising approach to tackle the serious issue of heavy metal toxicity in agricultural systems.

4.1. Exogenous Application of Phytohormones

Exogenous application of phytohormones is considered as an eco-friendly and cost-effective approach to deal with heavy metal toxicity in crop plants. Phytohormones regulate plant metabolic processes, thus helping them survive under biotic and abiotic stresses [104]. Exogenously applied phytohormones can mitigate heavy metal toxicity by enhancing the efficacy of antioxidative enzyme systems through reduction in lipid peroxidation and ROS levels in plants. For instance, salicylic acid, ethylene, and brassinosteroids have been reported to enhance photosynthesis in plants grown under heavy metal stress by reducing the ROS level and lipid peroxidation through improvement in antioxidative enzyme systems [105].

Brassinosteroids, a comparatively new class of hormones, have been recognized to induce Cu stress tolerance in mustard by Sharma and Bhardwaj [106]. They exogenously applied brassinosteroids to seven-day old seedlings of *Brassica juncea* under Cu stress and reported significant improvement in emergence of shoots as compared to control. The brassinosteroid application also reduced the uptake and accumulation of Cu in plants grown under Cu stress. In another study, Choudhary et al. [107] reported the improvement in shoot and root growth, and a decrease in Cu toxicity to *Raphanus raphanistrum* subsp. *Sativus* plants by application of epibrassinolide under Cu stress. They also observed the change in ABA, IAA, and polyamine concentration in radish plants and improvement in antioxidative enzyme systems of radish seedlings subjected to copper stress. Recently, Yadav et al. [108] reported that exogenously applied castasterone helped to improve the antioxidative defense system of *Brassica juncea* L. plants under Cu stress by modifying the amino acid metabolism and ascorbate glutathione cycle.

Similarly, Alam et al. [109] studied the effectiveness of 28-homobrassinolide application under nickel stress in *Brassica juncea*. They analyzed leaves of 40-day old mustard plants and reported the improvement in plant growth, chlorophyll contents, and photosynthesis in mustard plants grown under Ni stress. The phytohormone application also improved the activities of the antioxidative enzyme system, which is evident by the increase in activities of glutathione reductase, superoxide dismutase, peroxidase, catalase, carbonic anhydrase, and nitrate reductase. Thus, exogenous application of phytohormones reduced the Ni toxicity in mustard plants.

Cadmium is also one of the most toxic heavy metal pollutants in soils that enters into soil systems through anthropogenic activities. Janeczko et al. [110] studied the effect of 24-epibrassinolide on 14-day old seedlings of rapeseed under Cd stress. The results showed that phytohormone application decreased the Cd toxicity by recovering damage to photosystem two and improving efficiency of photosynthetic electron transport. In another study, Rady, [111] reported the improvement in growth, yield, Cd content, and antioxidative defense system of *Phaseolus vulgaris* L. plants by 24-epibrassinolide application under Cd stress. Similarly, improvement in plant growth, the antioxidant system, and photosynthesis of *Cicer arietinum* was observed by exogenous application of 28-homobrassinolide under Cd stress by Hassan et al. [112].

Recently, Jan et al. [113] studied the combined effect of silicon and 24-epibrassinolide on *Pisum sativum* L. under Cd stress. They reported that combined application of silicon and 24-epibrassinolide modulated the negative effect of Cd by stabilizing the leaf RWC, photosynthetic efficiency, and gas exchange parameters of plants grown under Cd toxicity. They also observed that combined application of phytohormone and silicon was effective in glyoxalase I (GlyI) accumulation and maintenance of the antioxidative defense system. Similarly, Kaur et al. [114] reported that combined application of citric acid and castasterone restored the photosynthetic parameters in *Brassica juncea* L. under Cd stress. They observed significant improvement in anthocyanin and flavonoid content in leaves of 30-day old mustard plants. The combined use of citric acid and castasterone also increased the activity of chalcone synthase and phytoene synthase genes of mustard plants under Cd stress.

The combined use of salicylic acid and 24-epibrassinolide reduced the Pb toxicity in 10-day old seedlings of *Brassica juncea* L. plants [115]. They reported that the use of salicylic acid and 24-epibrassinolide in combination improved the growth and photosynthetic pigments of mustard seedlings under Pb stress by regulating the antioxidative defense system. A significant improvement in tocopherol, ascorbic acid glutathione content was also observed. In another study, improvement in growth and pigment contents in root, shoot, and leaves of 30, 60, and 90 old Pb-stressed mustard plants was observed by the combined application of salicylic acid and 24-epibrassinolide [116]. They also reported the improvement in phenolic compounds in *Brassica juncea* L. under Pb stress.

Cytokinins (CKs) are a group of plant hormones that have a major role in plant growth and development, however, they are also involved in plant stress responses [117]. Tassi et al. [118], for example, studied the effect of CK-based plant growth regulators on assisted phytoextraction of Zn and Pb in heavy metal-contaminated soil of a gas plant site. They analyzed the roots, stem, and leaves of 49-day old *Helianthus annuus* L. plants and reported that CKs stimulated the cell division and root initiation, and thus improved biomass production and positively assisted in phytoextraction of heavy metals. The CKs also increased the transpiration of plants growing under Pb and Zn-stressed conditions. In another study, Piotrowska-Niczyporuk et al. [119] studied the effect of exogenous application of CKs on the growth and metabolism of green microalga under Cu, Pb, and Cd stress. They reported that phytohormones inhibited the heavy metal absorption and increased the primary metabolite level in Chlorella vulgaris L. under multimetal stressed conditions. They also reported the positive role of CKs on the algal growth, antioxidant enzyme systems, and ability of algae to adapt to metal-contaminated conditions in aquatic environments. Similarly, Cassina et al. [120] reported the increased transpiration rate and plant biomass of Alyssum murale Waldst. & Kit by cytokinin application under Ni stress.

Auxins play a role in plant developmental processes, as well as environmental stress responses. They have been well documented to be involved in heavy metal stress tolerance induction in crop plants [92,121,122]. Auxins have been reported to improve Pb and Zn phytoextraction ability, and root and shoot growth of *Helianthus annuus* L. [123]. Similarly, Hadi et al. [124] reported that combined use of IAA and GA3 increased the plant growth and Pb uptake and translocation ability of Zea mays L. In another study, improvement in phytoextraction ability and plant growth of Panicum virgatum L. has been reported by combined application of auxin and citric acid under Pb toxicity [125]. Similarly, Bashri and Prasad (2015) [126] reported the improved antioxidant activity and ascorbate-glutathione cycle in *Trigonella foenumgraecum* L. plants under Cd stress. They also observed that IAA improved the growth and chlorophyll a content of *Trigonella foenumgraecum* L. under Cd stress. Exogenous application of IAA increased the growth of *Brassica juncea* plants under As stress. This can be attributed to hormonally induced miRNAs expression that regulated the As response under exogenous application of IAA. It was shown to improve growth of plants under HM (As) stress [127].

Gibberellins play an important role in plant developmental processes and positively influence heavy metal stress responses [106]. Gangwar et al. [128], for example, reported that exogenous gibberellic acid application improved antioxidative enzyme systems and upregulated the nitrogen assimilation enzymes in *Pisum sativum* (L.) seedlings under Cr toxicity. In another study, Zhu et al. [129] reported that gibberellic acid alleviated the Cd toxicity by decreasing nitric oxide and Cd content accumulation, as well as stimulating the expression of Cd2+ uptake-related gene-IRT1 in Arabidopsis thaliana. Hadi et al. [130] reported that GA3, in combination with synthetic chelator, improved phytoremediation of Cd-contaminated soil and increased the growth and biomass of *Parthenium hysterophorus* under Cd stress. In another study, upregulation of Fe translocation and transport was observed in rice by gibberellins application under Fe deficiency [131].

The exogenously applied methyl jasmonate effectively reduced the negative effect of Cd stress in seedlings of *Capsicum frutescens* [132]. They reported the activation of antioxidative defense mechanisms in plants in response to exogenous application of methyl jasmonate. Exogenous application of MeJA modulated the GR, SOD, and CAT activity, along with improvement in glutathione pools in O. sativa under Cd toxicity [133]. The exogenously applied MeJA also reduced transpiration and photosynthetic damage, controlled stomatal aperture, and maintained endogenous levels of JA by reducing the Cd uptake.

Salicylic acid has been well documented to alleviate metal toxicity in crop plants. For example, Belkhadi et al. [134] studied the effects of exogenously applied salicylic acid on leaf lipid contents *Linum usitatissimum* L. under Cd toxicity. They reported that SA application raised the MDA level, total lipids and linoleic content, and chlorophyll contents in *Linum usitatissimum* L., thus improving tolerance to Cd toxicity. In another study, Kazemi et al. [135] reported the improvement in antioxidative enzyme system along with decrease in H_2O_2, lipid peroxidation level, and proline contents in *Brassica napus* L. through exogenously applied SA in combination with nitric oxide. Similarly, Xu et al. [136,137] reported the Cd-tolerance induction in peanut plants (*Arachis hypogaea*) through combined application of SA and nitric oxide. They reported the improvement in plant growth, photosynthetic activity, chlorophyll contents, and mineral nutrition in peanut plants under cd stress. The SA application also stimulated antioxidant enzyme activities and increased the nonenzymatic antioxidants contents.

Recently, Kohli et al. [138,139] reported that combined application of SA and 24-epibrassinolide mitigated the Pb toxicity in *Brassica juncea* L. by changing the level of various metabolites. They observed improvement in relative water content and the heavy metal tolerance index by combined application of SA and 24-epibrassinolide. A significant decrease in polyphenol contents, thiol level, and metal uptake was also observed. They also reported the upregulation of GR, CAT, POD, SOD, and GST 1 genes by combined application of SA and 24-epibrassinolide. Similarly, improvement in antioxidative defense system and nonenzymatic osmolytes content was also observed [140].

Salicylic acid alleviated the cadmium-induced oxidative damage in *Brassica juncea* L. plants [86]. The researchers reported that Cd stress reduced the growth, physiology, photosynthesis rate, and relative water contents in mustard plants. They also observed significant increase in electrolyte leakage, lipid peroxidation, and proline contents due to Cd-induced oxidative stress. The SA application, however, showed a marked decrease in these parameters under Cd stress. Salicylic acid also mitigated the Cd-induced growth inhibition of *Brassica juncea* L. plants. The Cd stress also increased the activities of antioxidant enzymes such as GR, CAT, APX, and SOD, however activities of these enzymes were reduced by exogenous application of SA. Similarly, alleviation of mercury toxicity in roots of *Medicago sativa* has been reported by the exogenous application of SA [141]. These researchers reported a significant improvement in plant growth parameters due to application of SA under mercury stress and correlated this improvement with prevention of oxidative stress *Medicago sativa* plants. The alleviation of Cd toxicity in soybean seedlings has also been reported due to application of SA [142].

Ethylene is a stress hormone and is produced in plants in response to biotic and abiotic stresses. Khan and Khan [143] observed that exogenous application of ethylene can improve photosynthetic activity of crop plants by reducing the negative effects of Ni and Zn in mustard. They reported the improvement in antioxidant metabolic processes, nitrogen use efficiency, and PS II activity. In another study, Khan et al. [144] reported the alleviation of Cd stress in mustard plants by ethylene in the presence of sulfur. They reported the decrease in superoxide and H_2O_2 accumulation and improvement in glutathione, cysteine, and methionine contents in mustard plants by ethylene application under Cd toxicity.

4.2. Phytohormone Producing Microbes

Rhizosphere serves as a niche for diverse groups or microorganisms due to the presence of root exudates, which serve as a nutrient source for proliferating microorganisms [145,146]. Rhizosphere microbes serve as a natural source of phytohormones. These microbes have the ability to produce compatible solutes, antifungal compounds, and soil enzymes, along with production of auxins, CKs, gibberellins, and ABA. Although very small amounts of phytohormones are produced by soil microbes, they are very crucial for plant metabolic processes [20,147,148]. Phytohormone-producing soil microbes can stimulate developmental processes in plants and can induce tolerance in plants against a number of biotic and abiotic stresses [148,149], which is one of the several plant growth-promoting mechanisms of microbes residing in the rhizosphere and plant tissues [150]. Phytohormone-producing microbes alter the endogenous production of plant hormones [151], thus changing the root morphology and inducing tolerance in plants against heavy metal stress [152].

Heavy metals can affect the microbial phytohormone production ability positively or negatively. For instance, Carlos et al. [153] studied the effect of Mn, Ni, Pb, As, Cu, and Cd on the IAA-producing ability of ten bacterial strains belonging to the genera *Escherichia*, *Klebsiella*, *Serratia*, and *Enterobacter*. They reported that Cu, Pb, and As positively affected the IAA-producing ability of bacterial strains *Serratia* K120, *Enterobacter* K131, *Enterobacter* N9, and *Escherichia* N16. The IAA production ability of all tested bacterial strains, except *Klebsiella* Mc173, was negatively affected by Mn, Ni, and Cd. Interestingly, positive correlation was observed between IAA production ability and ACC deaminase ability of *Serratia* K120 under heavy metal stress, which in turn helped bacterium to improve growth of *Helianthus annuus*, thus regarded as a potential candidate for use in phytoremediation purposes. Similarly, Seneviratne et al. [154] reported that Pb and Ni application in pure culture reduced the bacterial growth and IAA production ability of *Bradyrhizobium japonicum*, while Cu stress caused a nonsignificant decrease in bacterial growth with a slight increase in IAA production. In another study, phytohormone-producing bacterial strains have been reported to accumulate more heavy metals and showed more growth under metal-contaminated liquid media [155].

Diversity of microorganisms can produce phytohormones [156]. For example, Egamberdieva et al. [157] reported phytohormone-producing bacteria belonging to the genera *Arthrobacter*, *Brevibacillus*, *Bacillus*, *Enterobacter*, *Mycobacterium*, *Cellulosimicrobium*, *Ochrobactrum*, *Paenibacillus*, *Pseudomonas*, *Pseudoxanthomonas*, and *Rhizobium*. Similarly, Sorty et al. [151] isolated phytohormone-producing stress tolerant microorganisms from *Psoralea corylifolia* L. These microbes were identified as members of the genera *Enterobacter*, *Pseudomonas*, *Pantoea*, *Bacillus*, *Rhizobium*, *Sinorhizobium*, and *Acinetobacter*. Mishra et al. [158] reported that *Pseudomonas* spp. and *Ochrobactrum* spp. can produce IAA and have great potential for plant growth promotion. Similarly, GA and ABA production by rhizosphere microflora have been well documented in previous studies [159,160].

Seed inoculation with phytohormone-producing microorganisms can induce stress tolerance in plants [161]. For example, Singh et al. [162] presented a comprehensive study on role of microbial inoculation and phytohormones in modulating defense systems in plants. They reported that the number of microorganisms viz. *Acinetobacter calcoaceticus*, *Bacillus cereus*, *Rhizobium phaseoli*, *Pseudomonas putida*, *Trichoderma* spp., *Paenibacillus polymyxa*, *Pseudomonas fluorescens*, *Bacillus subtilis* *Rhizobium* spp., *Rhodospirillum rubrum*, *Pantoea agglomerans*, and *Azotobacter* spp. have the ability to synthesize phytohormones.

5. Applications of Phytohormone-Producing Bacteria for Inducing Heavy Metal Stress Tolerance in Plants

Inoculation with beneficial soil microorganisms is emerging as one of the most promising approaches for crop production in modern agrosystems. Studies suggest that plant–soil–microbe interactions can be harnessed to acclimatize plants with metal-polluted environments, and thus can be explored to induce metal tolerance in crop plants [28]. Soil microorganisms can be effective to improve plant growth under heavy metal stress as they have developed different mechanisms (Figure 1) to survive in the presence of heavy metals [163]. They can consume waste by converting complex waste materials into simple/nontoxic compounds and can transform heavy metals into less toxic forms. Soil microbes can also change heavy metal bioavailability by acidification, precipitation, and chelation by producing phytohormones or lowering the soil pH through production of organic acids [164].

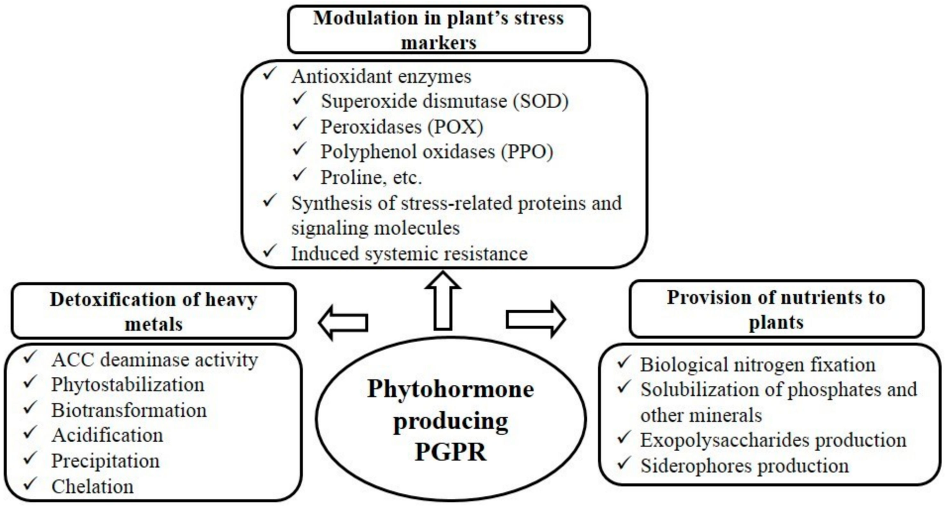

Figure 1. Mechanisms used by phytohormone-producing plant growth-promoting rhizobacteria (PGPR) to improve crop productivity under heavy metal toxicity.

Use of plant growth-promoting rhizobacteria (PGPR) for improving crop productivity under heavy metal stress is an emerging technology that performs dual functions. For example, Román-Ponce et al. [165] isolated and screened 60 bacterial strains from the rhizospheres of two plant species, *Spharealcea angustifolia* and *Prosopis laevigata*, growing in heavy metal-contaminated soil. They tested selected PGPR strains and reported that *Curtobacterium* sp. NM1R1 and *Microbacterium* sp. CE3R2 were able to tolerate high levels of Cu, Zn, Pb, and As, and were positive for IAA production. They observed that these strains significantly improved the germination and root growth of *Brassica nigra* under heavy metal stress, and hence, regarded these as potential candidates for bioremediation purposes and improving plant growth under heavy metal stress.

Inoculation with phytohormone-producing bacterial strains viz. *Variovorax* sp. (Va), *Pseudomonas fluorescens* (Pf) and Bacteroidetes bacterium (Ba), separately and in combination, improved the growth of *B. napus* in alluvial soil contaminated with Zn and Cd [166]. The single inoculation of bacterial strains significantly improved the potassium concentration in leaves and chlorophyll contents of *B. napus* plants under metal stress. The combined inoculation with *Variovorax* sp. (Va), *Pseudomonas fluorescens* (Pf), and Bacteroidetes bacterium (Ba), however, was most promising in improving the physiological parameters of *B. napus* plants and decreased the concentration of metals in plant roots, possibly through extraction and stabilization of metals. They reported that the tested strains can effectively be used to improve growth of *B. napus* under metal-contaminated soils that can also help to remediate metal-contaminated soils [166]. Similarly, Sheng et al. [167] reported the improvement in germination and reduction in toxic effects of heavy metals following the growth of *Brassica* in metal-contaminated/degraded land under the application of metal-tolerant bacteria. In another study, *Bacillus* sp. RJ16 and *Pseudomonas* sp. RJ10 promoted the root growth of rapeseed plants growing under toxic concentrations of Cd [168]. Inoculation with rhizobacterial strains, however, also reported to decrease the phytoextraction efficiency of *Salix* spp. growing under Cd-contaminated soil conditions [169]. Siderophore-producing, heavy metal-tolerant rhizobacterial strain *Pseudomonas aeruginosa* has been reported to improve plant growth with reduced uptake of Cd in pumpkin and mustard plants under Cd toxicity [170].

Siderophore-producing, heavy metal-tolerant PGPR can accelerate bioavailability and accumulation of nutrients in plants, thus helping to reduce the deleterious effects of heavy metals on plants as shown in (Table 1). It has been reported that IAA-producing, heavy metal-tolerant rhizobacterial strains *Microbacterium* sp. 3ZP2, *Achromobacter* sp. 1AP2 and *Rhodococcus erythropolis* EC 34 enhanced the biomass of *Trifolium repens* in the soil spiked with Zn and Cd [171]. They attributed this improvement with the IAA producing ability of bacterial strains, along with their characteristics to produce siderophore and ACC deaminase activity. The strains *Arthrobacter* sp. EC 10 and *Microbacterium* sp. 3ZP2 also improved the bioavailable metal concentration in clover rhizosphere, which have thus have been reported as potential phytoremediation agents.

Seneviratne et al. [154] studied the effect of Ni, Pb, and Cu on bacterial growth, IAA production ability, and growth promotion of lettuce seedlings. They reported that IAA-producing bacterial strain *B. japonicum* was effective in improving the root and shoot growth of lettuce seedlings under heavy metal stress. In another study, inoculation with phytohormone-producing, metal-tolerant bacterial strains *Bacillus cereus* and *Pseudomonas moraviensis* decreased the toxic effects of heavy metals on wheat growth under saline sodic soil conditions [172–174].

Table 1. Application and potentials of phytohormone producing bacterial strains for improving plant growth under heavy metal stress.

Bacterial Strains	Plant Growth Promoting Traits	Plants	Heavy Metals	Effects on Plants and Metal Uptake	Reference
Enterobacter sp.	IAA production, Cd tolerance, siderophore production	*Pea*	Cd	Inoculation retrieved metal-induced growth disturbance by minimizing metal uptake in mung bean	[13]
				Increase in growth parameters and xanthophyll, carotenoid, and chlorophyll content	
Bacillus sp.	Auxins production, phosphate solubilization	*Lens culinaris*	Cr	Inoculation reduced the negative effects of Cr on plants, improved plant growth parameters	[175]
Bacillus megaterium MCR−8	IAA production, siderophore production, ACC deaminase activity, phosphate solubilization, Cd tolerance ability	*Vinca rosea* L.	Ni	Inoculation improved plant growth, proline contents and total soluble protein under Ni amended media	[176]
				Enhanced the activity of antioxidant enzymes, i.e., APX, CAT, SOD, and POD under Ni stress	
				Increased the Ni phytoextraction from soil	
Kocuria sp. CRB15	IAA production, NH_3 production, phosphate solubilization, tolerance to Cu stress	*Brassica nigra*	Cu	Improved root and shoot growth of *Brassica nigra*	[177]
				Decrease in toxic effect of Cu on plants	
Klebsiella pneumoniae MCC 3091	IAA production, siderophore production, ACC deaminase activity, phosphate solubilization, Cd tolerance ability	*Oryza sativa*	Cd	Significant improvement in seed germination and root and shoot growth under Cd stress	[29]
				Improved the antioxidant SOD, MDA, and CAT activity	
				Significantly improved the chlorophyll contents, total protein, total sugar, proline, α-amylase, and protease activity	
				Reduced the ethylene production Cd uptake in rice seedlings	
Klebsiella pneumoniae (HG 3);	IAA production, siderophore production, NH_3 production, exopolysaccharides secretion, ACC deaminase activity, phosphate solubilization, K and Zn solubilization, Hg-stress tolerance	*Triticum aestivum*	Hg	Inoculation significantly improved the relative water contents and root and shoot growth of wheat plants	[178]
Enterobacter ludwigii (HG 2)				Malondialdehyde content, electrolyte leakage, and proline contents were also improved under mercury stress	
Azospirillum	IAA production, tolerance to Pb and Cd, phosphate solubilization	*Panicum virgatum*	Cd, Pb	Inoculation increased the surface area, number of branches, root length, and root and shoot biomass	[179]
				Neutralized the soil pH	
				Prevented the Pb and Cd translocation to aerial parts	
Bacillus, *Klebsiella*, *Leifsonia* and *Enterobacter*	Auxin production, Cd-stress tolerance, phosphate solubilization, oxidase and catalase activity, EPS-production	*Zea mays*	Cd	Significant increase in shoot and root growth, dry biomass under Cd-stress	[42]
				Inoculation significantly increased the membrane permeability and relative water contents in maize leaves	
				Helped in Cd extraction and stabilization	
Pseudomonas putida (ATCC 39213)	IAA production, ACC deaminase activity	*Eruca sativa*	Cd	Inoculation was more effective in improving root and shoot growth and chlorophyll contents at lower levels, while efficiency decreased at higher	[7]
				level, also lowered the proline contents in leaves	
				Inoculation increased the Cd uptake by *E. sativa* plants	

Table 1. *Cont.*

Bacterial Strains	Plant Growth Promoting Traits	Plants	Heavy Metals	Effects on Plants and Metal Uptake	Reference
Achromobacter sp. E4L5, *Bacillus* sp. E4S1, *Bacillus* sp. E1S2, *Bacillus pumilus* E2S2 and *Stenotrophomonas* sp. E1L	IAA production, ACC deaminase activity, siderophore production, phosphorus solubilization, tolerance to heavy metals	*Sedum plumbizincicola*	Zn, Cd, Pb	Heavy metal-tolerant bacterial strains effectively colonized the roots of *S. plumbizincicola* plants in multimetal contaminated soils.	[180]
				Inoculation effectively improved the root and shoot growth and dry biomass of plants.	
				Increase in water-extractable Cd and Zn concentration in soil.	
				Enhanced the phytoextraction ability of *S. plumbizincicola* plants.	
Rhizobium leguminosarum	IAA production, siderophore production, phosphorus solubilization	*Brassica juncea*	Zn	Inoculation improved plant growth and Zn accumulation in *Brassica juncea*	[181]
				Zinc stored in the roots as Zn cysteine and Zn phytate	
				Induced metal resistance in plants through chelation of Zn	
Pseudomonas sp. LK9	Ability to produce low molecular weight organic acids, siderophore and biosurfactants	*Solanum nigrum*	Cu, Zn, Cd	Inoculation improved the root and shoot growth and plant biomass of *Solanum nigrum* L.	[182]
				Significantly improved the Cu, Zn, and Cd uptake in aerial parts	
				Enhanced the P and Fe bioavailability in soil	
				Inoculation improved the bioavailability of Cu, Zn, and Cd in soil	
Rahnella sp. JN6	IAA production, ACC deaminase activity, phosphorus solubilization, tolerance to heavy metals	*Brassica napus*	Zn, Pb, Cd	Inoculation significantly improved the plant growth and dry weights of roots and shoots	[183]
				Improved the uptake and accumulation of Zn, Pb, and Cd in roots and shoots	
				Effectively colonized the tissue interior of rape plants	
Staphylococcus arlettae	IAA production, ACC deaminase activity, siderophore production	*Brassica juncea*	As	Inoculation with *S. arlettae* improved the growth and As uptake of *Brassica juncea* (L.)	[184]
				Significantly improved the plant biomass, chlorophyll, and protein contents in plants	
				Helped in phytostabilization of As by accumulating metal in roots	
Achromobacter xylosoxidans strain Ax10	IAA production, ACC deaminase activity, phosphorus solubilization, tolerance to heavy metals	*Brassica juncea*	Cu	Inoculation with *A. xylosoxidans* significantly improved the root and shoot growth and fresh and dry weight of *B. juncea* plants under Cu stress	[184]
				Improved the Cu uptake by plants and effectively sequestered the metal from soil	

6. Conclusions and Future Prospects

Heavy metals are among the most dangerous potential inorganic pollutants, which can enter into food chain through contamination of soil water and air. The problem is more severe around the metropolitan areas and big cities with heavy industries. Production of phytohormones by plants has been reported as a tool to cope with abiotic stresses. However, all plants do not have equal potential to produce phytohormones. Exogenous application of phytohormones to crop plants with low indigenous potential to produce these metabolites has been well documented to reduce the effect of stresses especially heavy metal stress. Literature has reported the potential of exogenous application of microbially produced phytohormones as an efficient tool to increase the stress tolerance of plants. The approach has also been reported as a potential practical approach to induce stress tolerance in crop plants under extreme environments. In addition to producing phytohormones such as cytokinins, auxins, SA, gibberellins, and ABA, these microbes can also improve plant growth by different direct and indirect mechanisms. Thus, microbes have the potential to modify the endogenous hormone production of plants, leading to changes in metabolic processes in plant tissues. These microbes have the potential to be used as preventers of damaging effects of heavy metal stress. The use of phytohormone-producing microbes under heavy metal stress is among the sustainable approaches for crop production under changing environments.

Further studies are needed to characterize the beneficial soil microbes with potential to produce phytohormones for inducing heavy metal stress tolerance in specific crop plants. Soil–plant–microbe interactions should also be studied to evaluate the effectiveness of these microbes with varying physico-chemical properties under different environments. Specific studies are also required to explore the mechanisms associated with production of different metabolites, and their synergistic and antagonistic interactions with host plants. Genetic studies are also needed to investigate the best time to identify the receptors for expression of specific genes of host plants after microbial inoculation, as well as changes in the genetics of associated microbes. Strategies should be devised to improve the plant–microbe interactions using molecular genetics, bioinformatics, and modeling tools to improve crop productivity as well as soil and environmental health.

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