Original Research Article

Journal of Biological Research

& Biotechnology

Bio-Research Vol. 20 No.1; pp. 1409-1425 (2022). ISSN (print):1596-7409; eISSN (online):2705-3822

Application of microbial synthesized phytohormones in the management of environmental impacts on soils

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Abstract

With the world's population growing at an exponential rate, pollution of the ecosystem by heavy metals from anthropogenic activities poses a major threat to agricultural and food security worldwide. Phytohormones are biochemical signal molecules that alter plant responses to different biotic and abiotic stresses. Exogenous use of microbially produced phytohormone in heavy metal remediation and stress tolerance induction, has gained popularity due to its environmental friendliness and sustainability. Microbially produced phytohormones have huge biotechnological potentials and have been exploited in phytoremediation assisted removal of heavy metals, and inducing stress tolerance to plants. This paper exhaustively discusses the remedial roles of microbial phytohormones in heavy metal removal and enhancing plant tolerance to stress. However, the exact mechanism of action and the genetic interplay during the process need to be further studied to better understand the specific key pathways involved in the process.

Keywords: Phytohormones; Microbial Synthesized Phytohormones, Heavy metal; Phytoremediation, Biotic and Abiotic stress

Received December 15, 2021**; Revised** February 7, 2022**; Accepted** February 11, 2022

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Journal Homepage: ***http://www.bioresearch.com.ng***.
Publisher***: Faculty of Biological Sciences, University of Nigeria, Nsukka, Nigeria*****.**

INTRODUCTION

Climate change, which is usually driven by abiotic stressors, poses global threat to the environment and agricultural systems. Nigeria, like many other developing countries, is unprepared for the effects of global warming and loss in biodiversity as evidenced by rising sea levels and erosion along the nation's coastline (Olaniyi *et al.,* 2013). Abiotic stress refers to environmental variables such as extremes in temperature, water, nutrients and any other environmental elements that affect plants and limit their development and output below optimal levels. One of such abiotic stresses is soil pollution by heavy metals, which is a major recurrent concern across the world, with negative consequences. These pollutants negatively affect available arable land, limiting the world food supply chain. The world's population is rapidly growing, and it is predicted to reach 9 to 10 billion people by 2050 (UN, 2019). This projected exponential increase in the global population poses serious challenge to the world food supply. Abiotic stressors, in general, have the potential to significantly limit agricultural plant development and production, resulting in significant yield reductions and presenting a threat to agricultural systems' long-term sustainability and global warming (Mahalingam, 2015). Besides the secondary consequences of climate change, rising Carbon dioxide (CO_2) levels and heat wave due to increased temperature have an immediate influence on plant growth, propagation, and tolerance.

Plants are rooted in the soil and must respond to abiotic stress using a variety of techniques, if they are to flourish. Their adaptation strategies against different stressors include morphological and biochemical changes as well as changes in physiological processes. These changes in morphological and biochemical processes are regulated by certain molecules known as phytohormones that work as chemical messengers and promote plant growth and development (Vob *et al.,* 2014). Phytohormones such as auxins, abscisic acid and gibberellins operate as growth regulators by promoting seed germination and initiating plant vegetative development in response to oxidative stress caused by heavy metals and other abiotic stressors (Li *et al.,* 2010; Adato and Gazit, 2014; Kang *et al*., 2015). Pirog *et al.* (2017) noted that these growth regulators are getting prominence in the agro-industrial sectors of advanced economies due to their capacity to improve crop yield and regulate plant metabolism.

Phytohormones, also known as secondary metabolites, have been discovered in algae, as well as bacteria and fungi associated with plants (Wang *et al.,* 2015; Egamberdieva *et al.,* 2017). Plant growth promoting rhizobacteria (PGPR) predominate the plant rhizosphere, which are capable of boosting plant development directly (via phytohormone synthesis) or indirectly (via the antimicrobial agents that can suppress the growth of pathogens). Greenberg *et al.* (2008) linked these PGPRs to the reduction of the deleterious effects of salinity stress on plant growth, while Arkhipova *et al.* (2019) noted that though the relative importance of specific bacterial trait was unclear, field experiments revealed that inoculation of wheat seeds with auxin-producing or phosphate-solubilizing strains raised crop yield by 10% to 36%.

In addition to promoting and modulating plant growth, microbial synthesized phytohormones also have unique remediation potentials by signaling the presence and stimulating the production of an endogenous defensive mechanism. This consists of different enzymatic (superoxide dismutase, catalase, dehydrogenases, glutathione reductase, etc.) and non-enzymatic (ascorbic acid, alkaloids, flavonoids, α-tocopherol, etc.) antioxidants (Gill and Tuteja, 2010; Hasanuzzaman *et al.,* 2020). Plant cells maintain steady-state homeostasis through an antioxidant defense mechanism and the buildup of reactive oxygen species (ROS) (Hasanuzzaman *et al.,* 2012). Plant hormone levels in plant tissue are modulated by microbial regulators, which have been discovered to have effects comparable to exogenous phytohormones (Shahzad *et al*., 2016; Egamberdieva *et al.,* 2017).

This review describes possible roles of microbial phytohormones in controlling plant growth and enhancing plant tolerance to stress. We highlighted the current status of the application of phytohormone-producing microbes in imparting tolerance against several environmental stressors whilst modulating plant growth.

PHYTOHORMONES

Since the discovery of phytohormones, plant biologists have been captivated by their regulatory ability. Researchers have been intrigued by the possibility that hormone levels or responses may be changed to enhance desired plant traits (Gray, 2004). It has long been known that their capacity to promote plant adaptation to continuously changing climates by influencing growth, development, and nutrient allocation is important. Phytohormones are "signal molecules" that influence plant growth and stress tolerance (Figure 1).

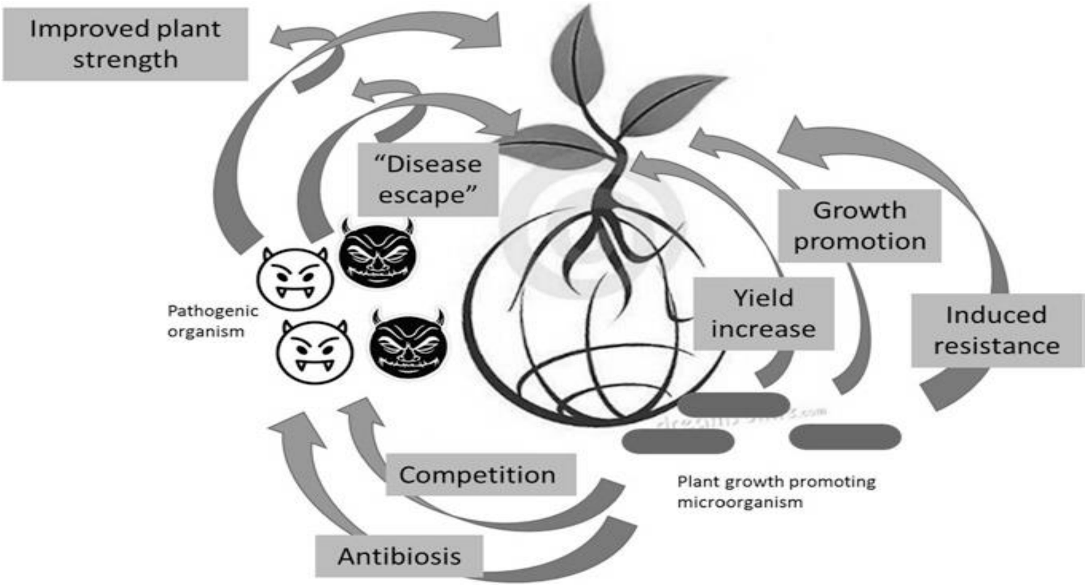

Figure 1: Microbial synthesized phytohormones modes of action (Source: Kilian *et al*., 2000).

Plant Synthesized Phytohormones

Among the five "classical phytohormones", auxins were the first to be discovered, followed by gibberellins, ethylene, cytokinins and abscisic acid. Other phytohormones discovered recently include strigolactones, salicylic acid, jasmonates and brassinosteroids, polyamines, and nitric oxide. Abscisic acid, salicylic acid, jasmonates, and ethylene have all been shown to play critical roles in controlling plant defense responses to pathogens and abiotic stresses (Bari and Jones, 2009; Nakashima and Yamaguchi-Shinozaki, 2013). These phytohormones work in harmony with one another, responding to developmental and environmental signals, through synergistic and antagonistic activities known as signaling cross talk. Knowledge of the key communication signals that define favorable or negative plant–microorganism interactions is critical for improving defensive responses while maintaining advantageous relationships such as symbiosis (Boivin et al., 2016).

Auxin (indole-3-acetic acid; IAA) was the first phytohormone to be discovered and can stimulate plant growth at low concentrations. Since auxin plays a vital role in plant growth, the search to unravel the processes behind its action is both exciting and daunting (Perrot-Rechenmann, 2010). It has been noted that Auxin might be more of a signal transduction molecule, which triggers a pre-set system, than a hormone with a specific function (Bennett and Leyser, 2014). Auxin can cause extremely quick non-transcriptional reactions, like stimulation of the cellular membranes' proton gradient and signal transduction, as well as microtubule reorientation (Weijers and Wagner, 2016). It can, in combination with cytokinin at physiological concentrations, induce cell division which increases plant cell growth, and plays key roles in nutrient source-sink interactions, root shape, and rhizosphere activity (Paque and Weijers, 2016). Cytokinins and auxins have been noted to induce cell division and undifferentiated growth in tissue cultures by interacting synergistically. Similarly, cytokinin and gibberellin stimulate seed germination in certain plants. Auxin also interacts antagonistically with cytokinins in the regulation of growth of stem and hypocotyl segments and opposes lateral bud development in plants (Splivallo *et al.,* 2009).

Since most of these plant hormones do not work alone on a specific developmental process, maintaining balance amongst them is usually paramount, in order to avoid reversibly inactivating any phytohormone. There is more research on the effect of exogenous applications of plant produced phytohormones and how they influence plant development than studies on endogenous concentrations and how they affect plant growth. There should be more studies focused on understanding how endogenously produced phytohormones influence the molecular and physiological responses of plants. This would go a long way in enhancing phytoremediation of toxic metals and organic pollutants from the environment.

Microbial Synthesized Phytohormone

Microbial phytohormones influence the metabolism of plant hormones produced endogenously by the plant's tissues and are involved in root morphological changes caused by drought, salinity, heavy metal toxicity and severe temperatures (Sorty *et al.,* 2016). However, the degree of substantiation for their participation might vary considerably depending on the individual plant hormone and the examined microbial strain (Spaepen, 2015). The use of microbial mutant strain defective in phytohormonal production, further establishes the microbial phytohormone's participation, as detecting if a particular phytohormone in a microbial culture's supernatant is inadequate.

Historically, there are five different classes of phytohormones produced by rhizobia microbes (symbiotic, free-living or endophytic) namely; auxins, gibberellins, cytokinins, abscisic acid and ethylene. Jasmonic and salicylic acid are two more modulators discovered as microbial phytohormones that contribute to long-term plant growth and production. The fungus *Lasiodiplodia theobromae* produces jasmonic acid, while *Penicillium patulum* produces salicylic acid. The microbial synthesis of phytohormones such as auxin (one of the most important phytohormones) occurs through numerous pathways with tryptophan being the most important precursor. With tryptophan as the precursor, only six biosynthetic routes for the synthesis of IAA in microorganisms have been identified, with majority of the pathways predicated on the presence of metabolic intermediates in the culture medium and most of the pathways resembling those found in plants, while some intermediates may differ (Spaepen *et al*., 2007). IAA synthesis by rhizobia is regulated by certain genes, and overexpression of this auxin has been observed in a number of bacterial mutants, notably *Ensifer (Sinorhizobium) meliloti* RD64 as compared to the wild type (Defez *et al.,* 2019). Free amino acids such as valine, alanine, aspartic acid, and glutamic acid, as well as photosynthetic products, have been significantly enhanced by IAA-producing rhizobia (Tsikou *et al.,* 2013; Erice *et al.,* 2014; Defez *et al.,* 2019).

Plant beneficial bacteria such as *Azospirillum, Bacillus, Bradyrhizobium, Enterobacter cloacae, Paenibacillus, Pseudomonas,* and *Rhizobium* make use of a pathway where an aromatic aminotransferase transaminase, the precursor tryptophan to *IPyA* in the *IPyA* pathway as the first step. The second step which is the rate limiting stage involves the decarboxylation of indole-3-pyruvate IPyA to indole-3-acetaldehyde (IAAld) by an important enzyme indole-3-pyruvate decarboxylase (encoded by the *ipdC* gene). IAAld is finally transformed to IAA. The regulation and biochemical characterization of the second stage in this pathway has been researched extensively in a variety of bacterial species (Patten *et al*., 2013).

APPLICATIONS OF MICROBIAL SYNTHESIZED PHYTOHORMONES IN PHYTOREMEDIATION

In the light of global climate change and unsustainable food security, exogenous phytohormone supplementation plays a pivotal role in remediation of heavy metal contaminated soils and in modulating plant stress response (Saini *et al.,* 2021). Heavy metal concentrations in uncontaminated soils are quite low (Ma *et al.,* 2016a). Rapid urbanization, uncontrolled use of agricultural chemicals, and anthropogenic activities due to industrialization ultimately lead to increased accumulation of heavy metals in soils (Kumar and Verma, 2018). These have detrimental impact on plants and humans. Thus, for conservation and protection of the ecosystem from the deleterious impacts of these pollutants, it is of utmost importance that sustainable and effective remediation techniques be employed for the removal of the pollutants. Multifaceted traits have proved the effectiveness of microbially synthesized phytohormones in combating these challenges (Chirakkara *et al.,* 2016; Ma *et al.,* 2016b).

Microbial synthesized phytohormones and mechanism of heavy metal removal

Plants have been known to exist in beneficial synergistic relationship with rhizobacteria, and exudates from such interactions have been implicated in variety of biogeochemical processes that have a significant impact on plant development and survival (Glick, 2010; Dharni *et al.,* 2014). It has been proposed that using phytohormone-producing heavy metal-tolerant PGPR may be a feasible method for tackling the serious problem of heavy metals contamination in agro – ecosystems (Sytar *et al.,* 2019; Nazli *et al*., 2020). Apart from growth promotion, phytohormone heavy metal-tolerant rhizobacteria have the potential to remediate heavy metal polluted soils and improve agricultural system productivity. Phytohormones produced by these rhizobacteria can be utilized exogenously in removing contaminating heavy metals through biosorption and bioaccumulation (Luo *et al*., 2011). The possibility of using such exogenous synthesized phytohormones in heavy metal removal and stress endurance in plants holds great promise due to its sustainability and cost effectiveness (Nguyen *et al.,* 2021).

Varieties of microalgae produce phytohormones which enable them to withstand and survive biotic and abiotic stress. It has been observed that in multi-metal-challenged environments, phytohormones increase heavy metal uptake by raising the concentrations of primary metabolites in the microalgae *Chlorella vulgaris L*. (Tassi *et al.,* 2008; Cassina *et al.,* 2011). Similar studies also showed a reduction in mercury toxicity by the exogenous application of salicyclic acid (Zhou *et al.,* 2009). Exogenously administered cytokinins assist in heavy metal uptake by raising plant transpiration rate (Pospisilova, 2003). The majority of heavy metals taken up from the soil are retained in root cells, where they are detoxified via chelation in the cytoplasm or sequestration into vacuoles, whereas hyperaccumulator plants translocate these elements to the shoot via the xylem quickly and efficiently (Monferrán and Wunderlin, 2013). As a result, the flow of water-soluble soil components or pollutants to the plant's upper portions (through xylem sap) rises (Dodd, 2003).

Metal chelation process is quite crucial in heavy metal entrapment and deposition in plant cell vacuoles. An Auxin derivative, 1-Naphthaleneacetic acid (NAA), has been reported to increases the concentration of hemicellulose 1 in plant root cell wall. This enhances cadmium (Cd) fixation in roots, decreasing its upward migration towards the shoot and providing resistance to heavy metals (Saini *et al.,* 2021). These phytohormones stimulate the release of root exudates, which are metal chelators (Mahmood *et al.*, 2015). Alterations in phytohormones concentrations, in most cases, signal the activation of heavy metal chelators. Abscisic acid has been suggested to be a stress signaling molecule which induces plant responses under stress conditions (Hayward *et al.* 2013). Heavy metals are absorbed into the roots where they form complexes with various chelators, such as organic acids. These complexes are immobilized in the apoplastic cellular walls or vacuoles, where they can be degraded by intracellular enzymes (Rascio and Navari-Izzo, 2011; Seth, 2012; Ali *et al.,* 2013; van der Ent *et al.,* 2013).

The phytoremediation of lead (Pb) using maize crop (*Zea mays*) was studied by Fuentes *et al*. (2000) and they reported an increased uptake by bioaccumulation when treated with either indolebutyric acid (IBA) or naphthylacetic acid (NAA). Treatment with microbially synthesized IBA showed a 41.2% Pb removal, and 87.4% Pb removal using NAA. Some other study showed that application of 28-homobrassinolide, a phytohormone, reduced soil nickel and cadmium heavy metal concentration (Janeczko *et al.,* 2005).

Mechanisms of action of Auxin during phytoremediation

Apart from its pivotal role in plant growth regulation, exogenously applied auxin induces plant response to stressors by regulating biosynthetic, transduction, and disintegration activities (Potters *et al.,* 2007; Saini *et al*., 2017; Bücker-Neto *et al.,* 2017). In mutant plants, Krishnamurthy and Rathinasabapathi (2013) discovered that aux1 seedlings were more resistant to arsenic. Similar study by Elobeid *et al.* (2012) found enhanced bioaccumulation and absorption of Cadmium (Cd) by cottonwood (Poplar) following exogenous auxin treatment Cd was shown to increase Gretchen Hagen 3 (GH3) activity, facilitating auxin conjugation and degradation. The specific role of endogenous levels of auxin in plants is unknown due to heavy metal stress; however, amendments with exogenous auxins have been demonstrated to decrease the detrimental effect of these heavy metals in plants (Saini *et al.,* 2013). Exogenous application of indole-3-acetic acid (IAA) also reduced heavy metal toxicity, stimulating the increased upregulation of the *AUX1* and *PIN2* genes (Wang *et al.,* 2015).

Aside from direct phytoremediative action, phytohormones can also stimulate rhizobacteria to produce gluconic, oxalic and citric acids. These have been implicated in the mobilization and enhancement of the availability of heavy metals to plants (Janoušková *et al.,* 2006; Ullah *et al.,* 2015). Phytohormones can also induce rhizobacteria to bio-methylate heavy metals like lead (Pb), mercury (Hg), selenium (Sn) and arsenic (As). This invariably increases the bioavailability of the methylated heavy metals for phytoremediation.

Mechanisms of action of exogenously applied cytokinins (CK) during phytoremediation

Even though the precise role of cytokinin application in relieving heavy metal stress is still not well defined, investigations have demonstrated that its treatment significantly improves phytoremediation of Zn, As, and Pb (Vitti *et al.,* 2013; Mohan *et al.,* 2016; Piotrowska-Niczyporuk *et al.,* 2020). Zhou *et al*. (2019) reported the modulation of heavy metal stress adaptation and biosorption action of exogenously applied cytokinins. Similarly, when supplemented with abscisic acid, cytokinin stimulates tomato plants to bioaccumulate Co through regulating the mechanism of its absorption and translocation. The mechanism of action of exogenously applied cytokinin during Cd toxicity has been suggested to be by increasing the expression concentration of *IPT gene* and the up-regulation of *CKX* gene in roots and down-regulation in shoots. This enhanced the CK content, leading to effective translocation of Cd in Arabidopsis plant (Vitti *et al.,* 2013).

Roles of other phytohormones during phytoremediation

Phytohormones have been known to stimulate the activation of metal chelating agents which contribute significantly in heavy metal sequestration and subsequent absorption in plant intracellular vesicles (Nguyen *et al.,* 2021). Exogenously applied Gibberellin has been shown to stimulate the phytoextraction of copper (Cu) from polluted soil using pea plants (Javed *et al.,* 2021). According to Bücker-Neto *et al.* (2017), thiol/phytochelatin production was promoted by exogenous application of abscisic acid, thus enhancing heavy metal resistance and bioaccumulation. Likewise, increasing abscisic acid concentration during Cd contamination stimulated the synthesis of phytochelatin in *Deschampsia cespitosa* (Hayward *et al.,* 2013).

Table 1: Summary of the mode of action of exogenously applied microbial synthesized phytohormones

Phytohormones	Plant/Microbial species	Heavy metal	Mode of heavy metal removal	References
Auxin	Cottonwood (Poplar)	Cd	Enhanced bioaccumulation and absorption in plant specie	Elobeid *et al.,* 2012
	Arabidopsis	Cd, As	Increased up regulation of the *AUX1* and *PIN2* genes in plants, leading to enhanced bioaccumulation of the pollutant.	Wang *et al*., 2015.
	Rhizobacteria	Pb, mercury (Hg), selenium (Sn) and arsenic (As).	Induces rhizobacteria to produce gluconic, oxalic and citric acids induce rhizobacteria to bio-methylate	Ullah *et al.,* 2015; Janouškova *et al.,* 2006;
Cytokinins	Tomato plants	Zn, As, Co and Pb	Enhanced biosorption and bioaccumulation	Vitti *et al.,* 2013; Mohan *et al.,* 2016; Zhou *et al*., 2019; Piotrowska-Niczyporuk *et al.,* 2020
	Arabidopsis	Cd	Increases the expression of IPT gene and the up-regulation of CKX gene in roots and down-regulation in shoots. This enhances the bioaccumulation of heavy metal by plant.	Vitti *et al.,* 2013.
Gibberellin	Pea plants	Zn,	Induces thiol/phytochelatin production which enhances the bioaccumulation and phytoextraction of heavy metals by the plant.	Javed *et al.,* 2021
Abscisic acid	*Deschampsia cespitosa*	Cd	Enhanced bioaccumulation and absorption.	Hayward *et al.,* 2013
	Sedum alfredii	Cd and Zinc	Improve the metal uptake by up regulating the ABA biosynthetic.	Song *et al*., 2019; Lu *et al.,* 2020; Saini *et al.,* 2021
IAA and siderophores	*Brassica oxyrrhina*.	Cu and Zn	Increased metal mobilization and enhanced absorption by plants	Braud *et al*., 2009; Rajkumar *et al*., 2010; Ma *et al*., 2016b
IAA	*Helianthus annuus* (Sunflower)	Cd	Enhanced biosorption and bioaccumulation	Prapagdee *et al*., 2013
Brassinosteroids		Pb, Cu, Cr, Cd, and Zn	Enhanced biosorption and bioaccumulation	Hayat *et al*., 2010; Hasan *et al.,* 2011; Ramakrishna and Rao, 2015.

Ma *et al*. (2016b) recently demonstrated that the application of IAA and siderophores enhanced the absorption of Cu and Zn by *Brassica oxyrrhina*. Similarly, Prapagdee *et al.* (2013) investigated and found that inoculating *Helianthus annuus* (Sunflower) with IAA yielding microbes increased cadmium absorption and its effective removal from the soil. Braud *et al.* (2009) and Rajkumar *et al.* (2010), in separate studies, reported an increased metal mobilization and absorption by plants in siderophores treated soil. A summary of the heavy metal removal mechanism of exogenously applied phytohormones are highlighted in Table 1 below.

Multiple plant defense mechanisms were elicited after soil treatment with ethylene during Zn contamination, through the uptake regulation of peroxidase, ascorbate peroxidase (APX), glutathione peroxidase (GPX), superoxide dismutase (SOD) and glutathione S-transferase (GST) (Khan *et al.,* 2019; Saini *et al.,* 2021).

Sedum alfredii was able to uptake and bioaccumulate Cd and Zinc by treating soil with abscisic acid (ABA) by boosting the activities of ABA biosynthetic enzymes (zeaxanthin epoxidase (ZEP), 9-cis-epoxycarotenoid dioxygenase (NCED), and abscisic aldehyde oxidase (AAO)) (Lu *et al.,* 2020). Furthermore, the administration of ABA increased the expression of the zinc/iron-regulated transporter (ZRT/IRT)-related protein (ZIP) family (which participates in metal transport across the cell membrane and inhibits heavy metal buildup) (Song *et al*., 2019; Saini *et al.,* 2021). Zn detoxification related genes and enhanced Zn bioaccumulation by plants were boosted by application of ABA during phytoremediation (Saini *et al.,* 2021).

Brassinosteroids were shown to regulate the accumulation of heavy metals such as Pb, Cu, Cr, Cd, and Zn in plants during heavy metal contamination (Hasan *et al.,* 2011; Hayat *et al*., 2010; Ramakrishna and Rao, 2015). To maintain BR homeostasis, brassinosteroids biosynthesis genes are expressed at high BR levels (Kim *et al.,* 2006). Exogenous applications of certain phytohormones during phytoremediation have been linked to enhanced absorption and bioaccumulation of heavy metals in dose dependent manner, but the major challenge lies in understanding the intricate signaling mechanisms of action.

Current Status of Exogenous Applications of Phytohormone-Producing Microbes in Growth Modulation or Stress Tolerance

To meet up with the various demands of an exponentially growing global population, together with the challenges of climate change, a “new” bio-revolution would be needed which will be characterized by less inputs with minimal environmental impacts. One of such beneficial approaches is the inoculation of PGPRs in heavy metal stressed environments, both as a form of bioremediation and enhancer of plant growth (Kumar and Trivedi, 2016). Rhizobacteria-produced phytohormones have been demonstrated to enhance stress tolerance and plant development under a variety of abiotic and biotic stress conditions (Liu *et al.,* 2013; Sgroy *et al.,* 2019)

Auxins are presently the most researched microbially synthesized phytohormones, with most microorganisms being able to produce them and having significant impact on root structure and growth (Gupta *et al.*, 2015). The effects of phytohormones concentrations have been investigated and reported in many studies, with high levels sometimes encouraging favorable root growth benefits. It has been found that auxins regulate plant growth and development through alterations of the plant gene expression patterns (Ljung, 2013). Despite the fact that its production may be decreased under stress situations, it stimulates growth modulation by the induction of abscisic acid (ABA) (Kazan, 2013). Application of auxin has been used to mitigate the harmful effect of Pb on sunflower. This increased the shoot biomass, indicating the metal phytoextractive nature of the phytohormone (Fässler *et al*., 2010). Singh and Jha, (2016) and Sorty *et al*. (2016) showed the ability of auxin generated by the root-colonizing halotolerant bacteria *B. licheniformis HSW-16, B. subtilis*, and *Arthrobacter* spp, salt-tolerant strain *Enterobacter sp*. NIASMVII to improve the salinity stress of wheat plants.

IAA-producing bacteria like *Pseudomonas* species, *Serratia sp*. and *B. megaterium* also induced drought and nutrient limited tolerance in clovers plants (Marulanda *et al.,* 2009; Zaheer *et al.,* 2016). Salicylic acid, ethylene, and brassinosteroids have been shown to increase photosynthesis in heavy metal-stressed plants by lowering ROS levels and lipid peroxidation by improving its antioxidative enzyme systems (Bashar *et al.,* 2019). Brassinosteroids were shown to decrease copper buildup in plants under copper stress in a study conducted by Sharma and Bhardwaj, (2018).

Similar study was undertaken by Choudhary *et al.* (2007) and it showed reduced copper in *Raphanus raphanistrum* subsp. Nickel heavy metal concentration has been reported to be reduced by the exogenous application of 28-homobrassinolide, a phytohormone. An increase in the antioxidative enzyme system, with a proportionate rise in glutathione reductase, superoxide dismutase, peroxidase, catalase, carbonic anhydrase, and nitrate reductase enzymes, resulted in enhanced plant growth, chlorophyll content, and photosynthesis (Yadav *et al.,* 2018). Salicylic acid and Jasmonates, multifunctional hormones generated in plants under abiotic stressors, have long been known to reduce heavy metal toxicity (Dar *et al.,* 2015).

Most bacteria are capable of producing a variety of phytohormones in response to various physiological and biochemical changes in plants, particularly electrolyte and chemical balance (Egamberdieva *et al.,* 2017). All of these investigations revealed the role of phytohormone regulation in plant tissue by plant-associated microorganisms in inducing plant stress tolerance.

CONCLUSION AND FUTURE PROSPECTS

The knowledge of activities around the rhizosphere of plants has helped to explain how soil microbes interact with plants, thereby enhancing plant growth and productivity. This has facilitated in-depth understanding of hormone signaling and how plants react to unfavorable conditions in the soil. Microbial synthesis of phytohormones is a powerful tool used in influencing plant physiology and resistance to pathogens. To cope with the different soil environmental stressors that plants are exposed to, plants utilize microbially synthesized phytohormones. As a result, plant-associated microorganisms can alter hormone balance and physiology in plant cells, notably in metabolic activities that might shield plants against the negative effects of environmental stimuli.

Exogenous treatments of microbially produced phytohormones have been demonstrated to promote abiotic and biotic stress tolerance in plants, providing significant practical advantages amid fluctuating or severe abiotic factors. As stated above, the production and participation of phytohormones in plant interactions have been thoroughly researched and confirmed by genetic evidence. The use of phytohormone-producing microorganisms under heavy metal stress is one of the sustainable crop production strategies in changing conditions. Phytohormone-mediated remediations have been demonstrated to be potentially viable methods for inducing stress tolerance in agricultural plants under severe environmental conditions.

Notwithstanding, for a better knowledge of phytohormone metabolism, it is essential that a mutant defective in each pathway is isolated and that the stability and bioavailability of phytohormones in the soil environment are studied. Further research on different plant species is needed to see if microbial phytohormones are plant-specific features and to learn more about the interactions at work between them. There is a large gap in our understanding of these features that have to be filled through agronomical research at the grass root level. Furthermore, there is need to select and evaluate possible strains with the ability to produce specific phytohormones so that an appropriate strain for a specific purpose can be employed efficiently. More research is needed to discover the beneficial soil microbial populations capable of producing phytohormones that can create significant metal stress tolerance in certain plant species.

Furthermore, more study is required to identify the beneficial soil microorganisms with the ability to generate phytohormones that can promote heavy metal stress tolerance in certain agricultural crop specie. It is important to conduct specific research to examine the processes involved in the synthesis of different metabolites, as well as their harmful and beneficial associations with selected plant species. Plant–microbe interactions should be enhanced by the use of molecular genetics, bioinformatics, and modeling techniques to increase agricultural production, soil and environmental conservation.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

Authors are thankful to the Centre for Environmental Management and Control, University of Nigeria, Nsukka for the mentorship opportunity and significant contributions to the success of this work. No specific funding was received for this research.

AUTHOR CONTRIBUTIONS

All the authors contributed to the study conception and design. The review was conceived and designed by MAN and ECC. The first draft was written by OCJ and ECC. MAN revised the manuscript. The final draft was read and approved by all the authors before submission.

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