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Review Article

Potentialities and Limit of Legume-Plant Growth Promoting Bacteria Symbioses Use in Phytoremediation of Heavy Metal Contaminated Soils

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Abstract

Heavy metals (HMs) pollution of soils is an environmental problem which had negative impact on agriculture and human health. In this review, we focused on the use of legumes co-inoculated by HMs tolerant plant growth promoting bacteria (PGPB) in phytoremediation of HMs contaminated soils.

Legume-HMs resistant PGPB symbiosis is an eco-friendly approach for phytoremediation of HMs contaminated soils, since it provides additional N-compounds to the soil by symbiotic nitrogen fixation(SNF) through nodule of rhizobia, in addition, PGPB were very effective and possessed plant growth promoting (PGP) traits such as solubilization of phosphate, production of phytohormones and siderophores which induced plant growth, as well as changing bioavailability of HMs in soil through various mechanisms such as bioaccumulation, chelation, acidification, protonation, precipitation and complexation.

HMs stress induced a wide range of physiological and biochemical tolerance mechanisms such as the expression of metal binding proteins involved in chelation and HMs transporting proteins employed in active transport of ligand-metal complex into vacuole such as Glutathion GSH, Phytochelatins PCs, Metallothionin MTs, organic acid and amino acid

HMs contamination caused generation of reactive oxygen species (ROS) in plant organs that causes oxidative stress. Plants respond by activation of enzymatic and non enzymatic antioxidant defense system suggesting that certain of them could be markers of HMs tolerance.

HMs tolerant PGPB improve the performance of phytoremediation in legumes either by reducing HMs accumulation in the aerial part of plants and it's enhancing to roots and nodules in phytostabilization process, or by increasing the uptake of HMs in plant organ and their translocation to the aerial parts in phytoextraction approach. So, selection of suitable resistant PGPB and legumes species for an efficient symbiosis in phytoremediation can be developed.

However, each contaminated ecosystem should be considered for their specificity, which presents the main difficulty for large spectre PGPB biofertilizer development.

ABBREVIATIONS

HMs: Heavy Metals; PGPS: Plant Growth Promoting Substance; PGPB: Plant Growth Promoting Bacteria; PSB: Phosphorus Solubilizing Bacteria; SNF: Symbiotic Nitrogen Fixation; GSH: Glutathion; Pcs: Phytochelatins; Mts: Metallothionins; ROS: Reactive Oxygen Species; SOD: Superoxide Dismutase; POX: Peroxidase; APX: Ascorbate Peroxidase; CAT: Catalase; GR: Glutathion Reductase

INTRODUCTION

Pollution of biosphere by toxic metals have been accelerated by industrialization and technological advancement, it has become one of the most severe environmental problems today [1]. HMs ions were non-biodegradable and persist in the soil, their presence at toxic level reduce or inhibit plant growth by hampering essential plant functioning and metabolic processes [2-5], like photosynthesis, respiration, and enzymatic activities

[6]. HMs toxicities in plants were due to their similarities with the nutrient cations, thus, a competition for nutrient absorption at root surface such as Cd competes with P and Zn [7].

In plants, excessive amount of HMs can impair important physiological and biological process by generation of ROS, such as superoxide free radicals (O_2^-), hydroxyl free radicals (OH^-) and hydrogen peroxide (H_2O_2) which cause multiple deteriorative disorders in protein, lipids and DNA [8,9]. Generally, plants have evolved a range of protective and repair systems to minimize the occurrence of oxidative damage by non-enzymatic antioxidants, essentially glutathione, proline, ascorbic acid, carotenoids and enzymatic anti-oxidative systems including superoxide dismutase (SOD), peroxidase (POX), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) [10].

Remediation of HMs by physico-chemical treatments still remains the most effective strategies, but, they are expensive, impracticable, no specific for metal-binding properties, energy-intensive and intrusive for the environment [11,12]. The development of phytoremediation, which are low cost and eco-friendly strategy for HMs contaminated soils, is necessary. The use of plants and soil microorganisms in phytoremediation enhances activity and diversity of soil microorganisms to maintain healthy ecosystems [1].

Phytoremediation is composed of different forms such as, phytoextraction which increases the concentration of metals into plants, rhizofiltration which is the use of plant roots to absorb HMs and phytostabilization that reduce the mobility and bioavailability of heavy metals through absorption in the roots and precipitation by plants [13].

Recently, another efficient alternative in phytoremediation technology is to provide legumes in symbiosis with HMs resistant PGPB belonged to rhizobia and endophytes genera [13-16]. Therefore, the rhizosphere contains a large microbial population with high metabolic activity that affect HMs motilities' and availabilities to legumes, through different mechanisms; including intracellular complexation or chelation of metal ions by molecular chelators and transporters [17,18]. PGPB are able to produce plant growth promoting substances (PGPs) such as phytohormones and siderophores that had beneficial effects on plant growth and nutrition [19]. Additionally, rhizobia were able to fix atmospheric nitrogen through symbiotic N_2 fixation, nitrogen- fixing and plant growth promoting traits of PGPB affect plant biomass, bioavailability of HMs, their uptake and translocation from soil to plants [20].

Recent research demonstrated that symbiotic relationship with legumes and PGPB can be applied in metal contaminated soils to improve soil fertility and ameliorate the quality of contaminated soils by extracting or stabilizing metals simultaneously [14,15,21]. In fact, many symbioses have been successfully used in phytoremediation of HMs contaminated soils [15,22-28]. This review focused on underlying the effectiveness of legume co-inoculated by HMs tolerant PGPB symbioses in phytoremediation of HMs contaminated soils. A second main point is to investigate the enzymatic antioxidant responses under HMs stress in order to evaluate biochemical tolerance mechanisms and create suitable metal tolerant symbioses useful in phytoremediation strategies.

EFFECT OF PGPB TRAITS ON HMS TOLERANCE MECHANISMS

Heavy metals contamination altered structures of microbial community; the decline of microbial biomass is an indicator of soil pollution with HMs [3]. Analysis of bacterial diversity showed that mine tailing soils contained abundant bacteria that tolerate multiple HMs and have plant growth-promoting abilities, generally composed by genera belong to *Bacillus, Pseudomonas, Arthrobacter* and *Rhizobia* [29].

A large diversity of tolerant bacteria nodulating *Vicia faba, Lens culinaris* and *Sulla coronaria* cultivated in HMs contaminated soil belonged to different genera such as *Rhizobium leguminosarum, Rhizobium phaseolus, Agrobacterium* and others [30]. HMs resistant PGPB that were able to survive in HMs contaminated soils showed the presence of HMs resistance genes located on plasmids or chromosomes that could regulate HMs resistance [31]. Several works demonstrated the existence of HMs resistances genes, thus, PGPB nodulating *Lens culinaris* revealed Pb resistant genes [24], similarly those nodulating *Sulla coronaria* showed the presence of Cd resistant genes [32] and *Sinorhizobium meliloti*, isolated from *Medicago lupulina* revealed copper tolerance genes [33].

In addition, plant growth promoting bacteria (PGPB) possessed single or multiple traits such as symbiotic nitrogen fixation capacity, solubilization of phosphate, production of phytohormones and siderophores, these PGP traits assist in plant growth and roots development by enhanced nutrient availability as well as by changing bioavailability of HMs [34]. Some non-symbiotic PGPB had the ability to fix lesser amount of nitrogen than rhizobia [35]. However, in spite of their low fixing capacity, some PGPB are very effective and augmented nutrient and nitrogen availability to plants [36].

Symbiotic nitrogen fixation is a characteristic of rhizobia, consisted in providing nitrogen to the plants through nodules [37]. Nodulation process is induced by root exuded (flavonoids) which are the key components of legume-rhizobia symbiosis [38], they promote the growth of host-specific rhizobia by serving as chemo attractants and inducers of nodulation (**nod**) genes involved in the synthesis of nod factors [39].

Recently, it has been demonstrated that other components control the expression of nodulation genes such as the transcriptional regulators nodulation signaling pathway (NSP1)/NSP2, nuclear factor YA1 (NF-YA1)/YA2, ethylene-responsive factor required for nodulation and nodule (NIN), Micro- RNA172 (miR172) [40].

PGPB help plant hosts in the absorption of mineral nutrients (such as N, Ca, Fe, Mg, and P) in metal contaminated soils, and improved plant growth and nodulation. Phosphorus is an essential macronutrient for plant. However, in the soil, P is present in the insoluble form and PGPB identified as Phosphate Solubilizing Bacteria (PSB) like *Pseudomonas, Bacillus, Enterobacter*and *Rhizobium* [41] can solubilize P by enzymes, organic acids and/or chelating agents excreted by both plants and microbes [42].

Siderophores play a crucial role in the enhancement of plant Fe uptake, most PGPB produce this iron chelators which are an important metabolite used as iron chelating agents and regulate the availability of iron in the plant rhizosphere [37], siderophores production was widely demonstrated in rhizobial species, such as *S. meliloti, R. tropici, R. leguminosarum* bv. *viciae, R. Leguminosarum* bv. *trifolii, R. leguminosarum* bv. *Phaseoli* and *Bradyrhizobium* sp. [43].

PGPB produce phytohormones, essentially indole-3-acetic acid (IAA)under stress conditions which promotes root growth directly by stimulating plant cell elongation or cell division [44], in fact, its production was demonstrated in many PGPB nodulating *Vicia faba* [23], *Lens culinaris* [45,24,25] and *Sulla coronaria* [32]. Besides IAA, the synthesis of ethylene production inhibitors 1-aminocyclopropane-1-carboxylate (ACC) that hydrolyses the plant ethylene precursor ACC into ammonia and α-ketobutyrate, is one key PGPB produced element related to plant growth [46].

All these PGPs were not only effective plant growth promoting traits, but also essential to the legume-PGPB symbiosis for effective nodulation and nitrogen fixation as well as on phytoremediation performance (Figure 1).

MECHANISMS OF HMS PHYTOREMEDIATION IN LEGUME-HMS RESISTANT PGPB SYMBIOSES

Heavy metals resistant PGPB have been widely proposed as effective inoculants for legumes and the appropriate symbioses involved in applied processes enhanced phytoremediation efficiency, increase plant biomass and facilitate metal mobilization or immobilization in soil [47].

In legume-PGPB symbioses, root exudates and PGPs secreted by PGPB play important roles in changing the bioavailability of metals and nutrients. The interactions between root exudates and PGPB have been recognized as a critical component of plant growth [48-50]. Root exudates enhances mobility of metals and nutrients by different manners, protonation or acidification of the rhizosphere that change metal availability through alteration of soil pH [51], chelation to intracellular binding compounds such as phytochelatins, organic acids, and amino acids. The formed complexes will be transported into cell vacuoles [52] by transporter families like ABC, CDF, HMA, and NRAMP transporters [7].

In return root exudates stimulates PGPB activity manifested by PGP traits marked by PGPs production and secretion of organic acids such as gluconic, oxalic, acetic, and malic acids which are natural chelating agents of HMs [2], indicating that microorganisms can develop important defense mechanisms for re-establishing polluted sites.

PGPB reduce HMs uptake by immobilization and decreasing metal bioavailability in soil via enzymatic precipitation, or interaction with inorganic acids alkalinization activity. PGPB help to remove or recover metals from the rhizosphere through bioaccumulation, by complexation with exopolysaccharides EPSs secreted by PGPB [53] such as polysaccharides, glycoprotein, lipopolysaccharide, and soluble peptide [54], which possess substantial quantity of anion functional groups (Figure 1).

HMs resistant PGPB can survive in HMs contaminated soils, bioaccumulate metals and reduced plant metal toxicity [55]. The biosorption and bioaccumulation processes involved different helper proteins which contribute to incorporate nutrients and reduced metal penetration [5] by different processes including complexation, coordination, chelation, ion exchange and microprecipitation [56], these phenomena has been widely described in the literature. Thus, PGPB had the capacity to reduce plant metal toxicity and uptake [57,58]. In *Vicia faba* co-

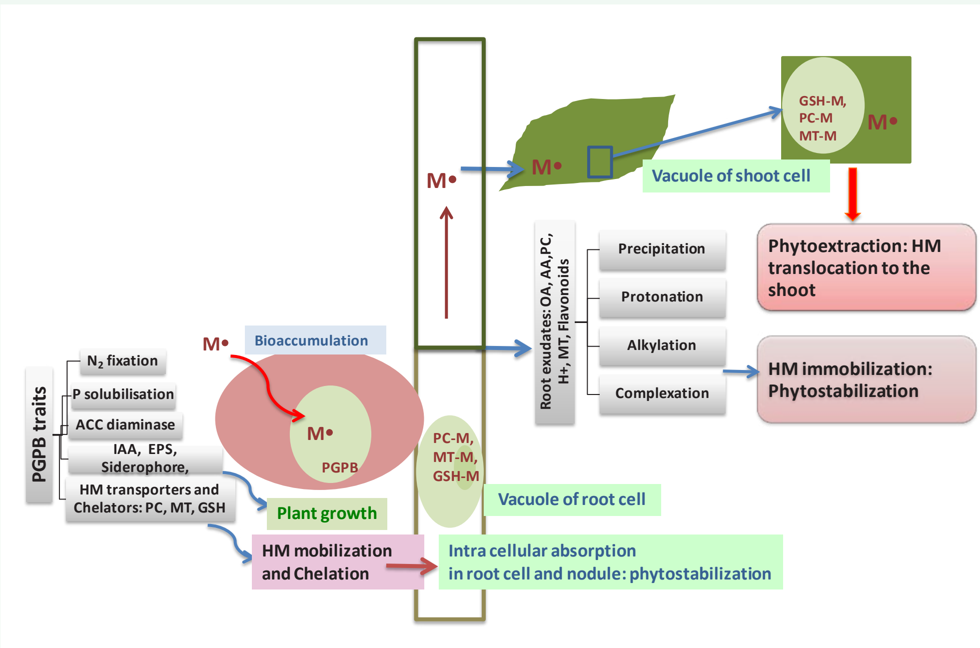

Figure 1 Mechanisms of phytoremediation of heavy metals contaminated soils by using heavy metals resistant Plant Growth Promoting Bacteria-legume symbiosis. OA: organic acids, PC: phytochelatins, MT: metallothionins, GSH, Glutathion, M: heavy metal.

inoculated by Cu resistant PGPB in hydroponic medium added with 0.5 mM Cu, phytostabilization was due to the capacities of PGPB to bioaccumulate Cu [23]. In lentil associated with the most Pb-resistant bacteria, Pb bioaccumulation enhanced in the cell wall with the time of incubation, indicating that Pb bioaccumulation was related to cell growth and the enhancement of cell biomass [33].

All these HMs tolerance process in plants and microorganisms induced the over expression or inhibition of certain genes involved in chelation and active transport of ions into cell vacuoles [52], including thiol compounds (Glutathion GSH, Phytochelatins PCs, and Metallothionin MTs containing sulfhydryl–SH groups) for binding a variety of metals [59]. GSH is a precursor for the synthesis of phytochelatins in metal-exposed plants [60]. PCs are synthesized from GSH by phytochelatin synthase (PCS) activity [61]. In higher plants, PCs are mainly responsible for detoxification of toxic heavy metals rather than metallothioneins (MTs) and have higher metal-binding capacity than MTs [62]. MTs are non specific chelators and exhibit their high affinity for both essential and non-essential metals such as Cu, Cd, Pb, and Zn [63]. Thus MTs protect cells against the toxicity of heavy metals and maintain cell homeostasis by bounding to essential metal such as Zn and Cu ions [61].

Furthermore a number of non-thiol compounds (organic acid and amino acids such as proline, histidine, cysteine, arginine, glutamate and nicotianamine) have been credibly evidenced to contribute the metal-chelation in plants [64-66].

Recent findings have established that under heavy metals stress condition, plants have developed other molecular responsive mechanisms involving regulatory mechanisms such as micro RNA target genes (miRNAs) which regulate plant gene expression at the post transcriptional level [67] and play a crucial role adaptation of plants to metal toxicity [68], such as Al-stress responsive miRNAs in common bean plants inoculated with **Rhizobium tropici** CIAT899 [67] and **Medicago truncatula** [69]. Similarly, Cd stress induced differential expression of miRNAs in *B. napus* [70]. These findings demonstrated that miRNAs is a critical post-transcriptional regulators of gene expression under heavy metal [71].

POTENTIAL OF USING LEGUMES-HMS RESISTANT PGPB SYMBIOSES IN PHYTOREMEDIATION OF HMS CONTAMINATED SOILS

PGPB including rhizobia and endophytes may play an important role in phytoremediation, essentially in symbiosis with legumes, it is one of plant-microbe interactions that provide nitrogen to plant and enhance plant growth [72]. Many studies demonstrated the beneficial effects of using this symbiotic relationship in phytostabilization or phytoextraction of HMs contaminated soils [14,15,73,74].

Previous studies demonstrated that co-inoculation of legumes by heavy metal resistant PGPB could be useful in phytoremediation process. The cultivation of *Vicia faba* co-inoculated by specific Cu-resistant PGPB (*Rhizobium* sp. *CCNWSX0481, R. leguminosarum* bv*. viciae, E. clocae* and *Pseudomonas* sp.) in a moderately Cu contamination, enhanced plant biomass and reduced the Cu accumulation in plant [22], whereas, *S. meliloti* increase the copper concentration in *Medicago lupine* tissues growing in medium supplied with 100 µM Cu2+ by 39% [33].

Lens culinaris cultivated in moderately Pb contaminated soil and its co-inoculation by Pb-resistant PGPB (*Agrobacterium tumefaciens*, *Rahnella aquatilis* and two *Pseudomonas* sp.) induced a reduction in Pb accumulation in roots and shoots. However, in highly Pb contaminated soil; we registered a diminution in concentration of Pb in shoots and an enhancement of Pb uptake in roots [25]. Co-inoculation of lupines with a mixture of metal-resistant bacteria, including *Bradyrhizobium* sp, *Pseudomonas* sp. and *Ochrobacterium cytisi* induced a reduction in Pb accumulation both in shoots and roots, indicating the usefulness of inoculation in phytostabilization of moderated HMs contaminated soils [15].

Sulla coronaria co-inoculated by Cd-resistant inoculums (*Pseudomonas* sp, *Pseudomonas fluorescens* and *Rhizobium sullae)* cultivated in Cd contaminated soils showed that the inoculation enhanced Cd accumulation especially in roots [28]. In fact, plant responses to HMs contamination depended on PGPB that enhance plant uptake of HMs in certain case, and reduce or have no significant effect in other case [75]. Thus, the inoculation with PGPB, could improve the metal extraction potential of hyperaccumulator plants, whereas, there were other opposites results and certain metal resistant soil bacteria decreased the uptake of metals by the plants [76]; since these PGPB alleviate metal toxicity by alteration of metal availability through bioaccumulation capacity of PGPB and the production of biochelators such as organic acids, amino acids and exopolysaccharides [50]. For example, the inoculation of pea plant by the *Rhizobium* RP5 decreased the concentration of nickel and zinc grown in contaminated soils [37], while, the co-inoculation of Alfalfa by *Pseudomonas fluorescens* and *Rhizobium leguminosarum* bv *phaseoli* under copper stress improved Cu and Fe from the roots to the shoots [77]. Generally, the uptake and translocation of metals from soils to plants due to their bioavailability depending on their concentrations, electron acceptors, moisture content, nutrients, osmotic pressure, oxygen, pH, redox potential, soil structure, temperature, and water activity [78].

Analysis of recent studies revealed that each contaminated ecosystem and environment present a single case and should be considered for their specificity which present the main difficulty for large spectre PGPB biofertiliser development for industrialization and large use.

ROLE OF INOCULATION IN THE MOBILIZATION OF ANTIOXIDANT ENZYMES

Heavy metals contamination cause oxidative damage to plants, through reactive oxygen species (ROS) formation that adversely affect biochemical and physiological process by impairing photosynthetic and respiratory [79,19]. Plants possess sophisticated defense strategies to avoid or tolerate HMs intoxication, enzymatic and non-enzymatic antioxidant defence systems that scavenge ROS and protect plants from oxidative damage [80]. One of these mechanisms is the employment of an enzymatic antioxidant system such as SOD, POX, CAT, GR and APX [10]. It is known that SOD is the first antioxidant enzyme functioning as a superoxide radical scavenger; POX, CAT and APX are involved in the removal of H_2O_2 [81]. Plants might create balance between ROS and the antioxidant system to tolerate HMs contamination [82]. In addition, the modulation of antioxidant levels constitutes an important adaptive response to heavy metal contamination in plant tissues. Different responses of enzymatic antioxidant were registered in legumes treated by HMs and inoculated with PGPB. *Vicia faba* treated by 0.5 mM Cu and inoculated with *Rhizobium* sp. *CCNWSX0481*, *Rhizobium leguminosarum* bv *viciae, Enterobacter cloacae* and *Pseudomonas* sp. increased activities of SOD, APX and POX but reduced CAT activity [23]. *Lens culinaris* grown hydroponically with 2 mM Pb and inoculated by a consortium formed by *Agrobacterium tumefaciens, Rahnella aquatilis,* and *Pseudomonas* sp*.* demonstrated an activation of SOD and POX whereas CAT was inhibited [24,25]. In *Sulla coronaria* cultivated hydroponically and co-inoculated by *Pseudomonas fluorescens, Pseudomonas* sp and *Rhizobium sullae*, the application of 50 μM $CdCl_2$ stimulated all enzymes in shoots and decreased SOD and CAT activities in roots, whereas, 100 μM of $CdCl_2$ increased SOD, APX, CAT and GPOX activities in shoots and increased significantly CAT activity in roots [28]. This differential response of antioxidant enzymes to Cd was due to the metal concentration, period of treatment and inoculation, generally antioxidant enzyme responses diverge among plant species and different tissues [80,83].

Furthermore, legumes required protection from HMs by PGPB inoculation, the symbiotic interaction involves formation of nodules, which have a high potential for ROS production due to the elevated rate of respiration that is required for nitrogenase in the nitrogen fixation process. In fact, nodules are rich in antioxidants that protect plant structures against high rates of nodules respiration [80], and the enhancement in the antioxidant enzymes activities supported a role of PGPB co-inoculation to alleviate the heavy metals induced stress [26].

DISCUSSION AND CONCLUSION

The contamination of soils by heavy metals caused threat to the environment and population; it is transferred through the food chain and are a serious hazard to human health [81,84]. Phytoremediation is an effective method used to remediate heavy metal-polluted sites. Therefore plant-microbe partnerships are an effective way utilized to improve biomass production and remediation [50]. For this purpose we used HMs resistant PGPB, consisted by rhizobia and endophytes to inoculate legumes species in phytoremediation of HMs contaminated soils. Rhizobia was characterized by its nitrogen fixing capacity, which could improve soil fertility, in addition PGPB had PGP traits such as solubilizing phosphate, production of plant growth-promoting substances, which assist in plant growth and root development by enhancing nutrient availability as well as by changing bioavailability of HMs [19]. The overall published data presented in this review demonstrated that symbiotic relationship of legumes and HMs resistant PGPB could be successful in phytoremediation of HMs contaminated soils. Thus, it had an excellent potential to ameliorate plant growth and reduce metal availability, this has been reviewed periodically and verified in field experiments [15,26]. Generally, either legumes or PGPB possess a basic defense system upon HMs contamination either by mobilization, or immobilization of HMs in the rhizosphere. In addition, a wide range of physiological and biochemical mechanism of tolerance was demonstrated to cope with the negative consequences of HMs toxicity such as the expression of bounding molecules essentially GSH, PCs and MTs [60]. These chelators act as cellular homeostatic or detoxifying agents that interact directly or indirectly with plant antioxidant defense system to mobilize or immobilize ion metals in plant cells. In this case, realizing transgenic plants overexpressing these chelators could ameliorate plants HMs tolerance [13]. HMs toxicities in plants resulted from the strong similarities with the nutrient cations that caused a competition for absorption at root surface [5], which is the first contact with heavy metals. Roots respond to HMs contamination by the excretion of root exudates containing organic chemical compounds and flavonoids chemoattractants, which improved PGPB activities. All these process induce root growth, nodulation, and detoxification of HMs by adsorption, chelation, precipitation and complexation influencing metals and nutrients mobilities [53], therefore enhancing phytoremediation efficacy [85].

This review showed that HMs, inducing ROS and some antioxidant components such as SOD, POX, APX, and CAT were activated by co-inoculation and raise plant tolerance to HMs stress [24,25]. Enzymatic and non-enzymatic antioxidant defence mechanisms are involved in detoxification mechanisms and comprehension of these antioxidant mechanisms must be further investigated to understand HMs tolerance mechanism in legume-HMs resistant PGPB symbioses.

The response of legume-PGPB symbiosis to HMs contamination depend on plant species, HM type, and concentration as well as oxidation state of HMs. In fact, PGPB can reduce HMs availability in phytostabilization, or enhance their plant uptake in phytoextraction. In this case, HMs absorbed by roots was translocated into shoots via xylem and several classes of proteins called heavy metal-transporting ATPases [7]. After translocation the complexes formed MHs-Metal bounding agents were transported to the vacuole [86].

In conclusion, the nitrogen- fixing and plant growth promoting traits of PGPB induce phytoremediation performance of legumes. However, legumes-PGPB differs in their response to HMs contamination and further research should be focused on the tolerance mechanisms of legume-PGPB. Nevertheless, the specificity of each ecosystem presents a handicap for the generalization of the results for a large-scale fertilizer production.

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