

Review Article

The Role of Rhizosphere Microorganisms Containing the Abiotic Stress Tolerance in Plants

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Abstract

Rhizosphere can be defined as the region extending a few millimetres from the root surface in which the microbial population of soil is influenced by the chemical activities of plant roots. A major characteristic of the rhizosphere is the release of organic compounds into the soil by plant roots. These compounds called root exudates which make the environment different in rhizosphere and bulk soil. The exudates increase the availability of nutrients in the rhizosphere & also provide a carbon source for heterotrophic microorganisms. Most commonly, bacteria such as *Azospirillum*, *Herbaspirillum*, *Acetobacter*, *Azotobacter* and *Azoarocus* are used as biofertilizers, mainly because of their ability to fix atmospheric nitrogen. Various inoculant mixtures from these bacteria are currently commercially available for agricultural applications. Other species of bacteria such as *Bacillus*, *Streptomyces* and *Pseudomonas* which have shown a positive effect on plant biofertilization could be developed for commercialization.

However, future commercially available biocontrol agents should simultaneously provide cross-protection against various stress factors, making agricultural systems environmentally and economically more sustainable by reducing the need for pesticides, irrigation and other ecologically problematic and costly crop management strategies.

Keywords: Rhizosphere, Microorganisms, Biofertilizers, Biocontrol agents, Cross-protection

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Introduction

Organisms in the rhizosphere can affect the plant roots by altering the movement of carbon compounds from roots to shoots. Many microorganisms are beneficial and are called Plant growth promoting rhizobacteria [PGPR]. Various root microbes association can increase nutrient uptake by plants in nutrient poor environment such as symbiosis [eg. Mycorrhizal or Rhizobia] & specific association [Associative N₂ fixing bacteria with grasses etc. – *Azospirillum*]. Some microorganisms produce hormones that stimulate plant growth and some microorganisms are antagonistic to plant pathogens. But some soil microorganisms are pathogenic & attack living plant roots.

The majority of known higher plant species is associated with Mycorrhizal fungi, which can increase the tolerance of plants against abiotic stress, e.g. by an improved nutrient supply or by detoxification of pollutants. Rhizosphere bacteria can strongly promote the growth of plants solely and in interaction with mycorrhizal fungi. They can contribute to the mobilization of nutrients and degradation of organic pollutants. The main reason the rhizosphere is a far more attractive habitat than bulk soil is the organic carbon provided by plant roots. More than 85% of the total organic carbon in the rhizosphere can originate from sloughed-off root cells and tissue [1]

Root-colonizing non-pathogenic bacteria can increase plant resistance to biotic and abiotic stress factors. Bacterial inoculates have been applied as bio fertilizers and can increase the effectiveness of phytoremediation. Inoculating plants with non-pathogenic bacteria can provide 'bioprotection' against biotic stresses, and some root-colonizing bacteria increase tolerance against abiotic stresses such as drought, salinity and metal toxicity. Rhizobacteria respond to root exudates by means of chemotaxis towards the exudate source and in such scenario, competent bacteria tend to modulate their metabolism towards optimizing nutrient acquisition [2, 3]

Microorganisms contribute essentially to the protection of plants against unfavourable soil conditions. A narrow zone of soil affected by the presence of plant roots is defined as rhizosphere. Soil conditions, and the amount and composition of root exudates play important role in the specificity of those interactions. Dense populations of microorganisms colonize the root zone of plants. The main reason the rhizosphere is a far more attractive habitat than bulk soil is the organic carbon provided by plant roots. More than 85% of the total organic carbon in the rhizosphere can originate from sloughed-off root cells and tissues. Moreover; plants supply organic carbon to their surroundings in the form of root exudates. Rhizobacteria respond to root exudates by means of chemotaxis towards the exudate source

and in such scenario, competent bacteria tend to modulate their metabolism towards optimizing nutrient acquisition. In this regard, the role of bacterial motility in their interaction with plants has been demonstrated [4]. However, it has also been indicated that flagella synthesis is an energy-consuming event which, consequently, induces a rapid metabolic switch from a motile to non-motile form, upon bacteria reaching the root epidermis. Moreover, aside from locomotion, adhesive properties have also been attributed to bacterial flagella. In contrast to the notion of flagella motility, non-flagella-producing rhizobacteria such as *Streptomyces* spp. establish beneficial interactions with plants via development of hyphae in plant tissues [5].

Plant-bacteria interactions in the rhizosphere

Microorganisms present in the rhizosphere play important roles in ecological fitness of their plant host. Important microbial processes that are expected to occur in the rhizosphere include pathogenesis and its counterpart, plant protection/growth promotion, as well as the production of antibiotics, geochemical cycling of minerals and plant colonization [6]. Plant-microbe interactions may thus be considered beneficial, neutral, or harmful to the plant, depending on the specific microorganisms and plants involved and on the prevailing environmental conditions [7]. Exploring these microorganisms by unravelling their possible relationships with plants has launched a new and fascinating area of investigations in the rhizosphere research.

Pathogenic interactions

Roots exudates can attract beneficial organisms, but they can also be equally attractive to pathogenic populations [8], that many express virulence on only a limited number of host species. Many pathogenic organisms, bacteria as well as fungi, have coevolved with plants and show a high degree of host specificity [9]. In nature however, plant disease is the exception rather than the rule because the conditions that are optimized for the plant growth may not be favourable for pathogens [10]. Plants are not defenceless. In fact, it is estimated that only about 2% of the known fungal species are able to colonize plants and cause disease.

Even though plants are in permanent contact with potential pathogens such as fungi, bacteria or viruses, successful infection is rarely established. Such a general resistance against most pathogens has been named “horizontal resistance” or “non-host-resistance”. This reflects the fact that the plant is not a suitable target for infection by a specific pathogen due to preformed, passive resistance mechanisms resulting in “basic incompatibility”. These resistance mechanisms comprise structural barriers and toxic compounds that are present in the unaffected, healthy plant and limit successful infection to specialized pathogens that have the ability to overcome these factors and therefore exhibit “basic compatibility”. If contact is nevertheless established with the plant tissue, pathogens are often confronted with preformed chemical components named phytoanticipins [3]. This term comprises a variety of compounds produced by different biosynthetic pathways which possess antimicrobial properties. These low molecular weight secondary metabolites are mainly stored in inactive form in the vacuoles or organelles and are released upon destruction of the cells. Since destroying the integrity of the plant tissue is part of the colonization strategy by fungi, phytoanticipins represent an important resistance mechanism against these pathogens.

However, in some instances, pathogens can overcome the pre-formed barriers and develop virulent infection processes leading to plant disease. Plant diseases play a direct role in the destruction of natural resources in agriculture. In particular, soil-borne pathogens cause important losses, fungi being the most aggressive. The extent of their harmful effects ranges from mild symptoms to catastrophes where large fields planted with agricultural crops are destroyed. Thus, they are major and chronic threats to food production and ecosystem stability worldwide. Common and well investigated bacterial agents include Gram- bacteria *Erwinia carotovora*, *Pseudomonas*, *Ralstonia* spp and the Gram+ bacterium *Streptomyces scabies*. The fungal and oomycete phytopathogens includemembers of *Fusarium*, *Phytophthora*, *Pythium*, *Rhizopus*, *Rhizoctonia* and *Verticillium*. From the forest pathogens, among the most important are the filamentous fungi *Heterobasidion* and *Armillariella* [11], and *Phytophthora* spp. [12].

Beneficial microorganisms and modes of action

Plant-beneficial microbial interactions can be roughly divided into three categories. First, those microorganisms that, in association with plants, are responsible for its nutrition [*i.e.*, microorganisms that can increase the supply of mineral nutrients to the plant]. In this case, while most may not directly interact with the plant, their effects on soil biotic and abiotic parameters certainly have an impact on plant growth. Second, there is a group of microorganisms that stimulate plant growth indirectly by preventing the growth or activity of pathogens. Such microorganisms are referred to as bio control agents, and they have been well documented. A third group involves those microorganisms responsible for direct growth promotion, for example, by production of phytohormones. There has been a large body

of literature describing potential uses of plant associated bacteria as agents stimulating plant growth and managing soil and plant fitness [13].

On another hand, apparently neutral interactions are found extensively in the rhizosphere of all crop plants. Saprophytic microorganisms are responsible for many vital soil processes, such as decomposition of organic residues in soil and associated soil nutrient mineralization or turnover processes. Whereas these organisms do not appear to benefit or harm the plant directly [hence the term neutral], their presence is obviously vital for soil dynamic, and their absence would clearly influence plant health and productivity [14].

Rhizosphere-living bacteria that exert a global beneficial effect on plant growth are referred as plant growth promoting rhizobacteria [PGPR] [15]. The number of bacterial species identified as PGPR increased recently as a result of the numerous studies covering a wider range of plant species and because of the advances made in bacterial taxonomy and the progress in our understanding of the different mechanisms of action of PGPR. Presently, PGPR include representatives from very diverse bacterial taxa and in the following sections we are not giving a thorough description of all the genera and species of PGPR, but rather a few examples to illustrate the diversity and modes of action of these beneficial bacteria. Diverse PGPR strains have been used successfully for crop inoculations. These comprise members of the bacterial genera *Azospirillum* [16], *Bacillus* [17], *Rhizobium* [18], *Serratia* [19], *Stenotrophomonas* [20], and *Streptomyces* [21].

Pseudomonas and *Bacillus* genera are the most commonly investigated PGPR, and often the dominating bacterial groups in the rhizosphere [22]. One has to mention that, in many cases of individual beneficial plant-microbe interactions, several mechanisms are involved. *Ad planta*, direct mechanisms of plant growth promotion are difficult to differentiate from disease suppression and the relative importance on a specific mechanism can vary within different pathosystems [23].

There are some common principles at work, particularly with regard to root/soil interactions and the physiological changes in the root system induced by microorganisms, namely:

- Stimulation of root growth through bacterially produced IAA [and/or nitric oxide] under drought, nutrient deficiency, salinity and metal toxicity stress
- Decrease in host plant stress ethylene level by bacterial ACC deaminase activity under drought, salinity, heavy metal toxicity and flooding conditions and
- Induced changes in cell wall/cell membrane under drought and suboptimal temperature conditions.

Some plant species, however, contain bacteria under the seed coat or within the embryo. Such bacteria will still have to compete with beneficial bacteria, even when the latter are applied as early as seed stage. Thus, providing a continuous supply of carbon and energy sources will contribute to a successful establishment of the beneficial bacteria [24]. Moreover, breeding efforts should consider the abilities of plants to interact with beneficial bacteria in order to promote specific beneficial plant-bacteria combinations. Studies on the practicability of the application of beneficial microorganisms in real-life agricultural systems are, thus, urgently needed.

Mechanisms of Bacteria-Mediated Stress

The availability of specific substrates as precursors for phytohormones, such as l-tryptophan for IAA, therefore, is a major factor determining the degree of bacterial stimulation of plant growth. Another widespread characteristic among endophytic and rhizosphere bacteria is ACC deaminase activity, and regulation of ACC is a principal mechanism by which bacteria exert beneficial effects on abiotically stressed plants. Bacteria possessing this enzyme can use the immediate ethylene precursor ACC as a source of nitrogen.

Bacterial hydrolysis of ACC leads to a decrease in plant ethylene level, which, in turn, results in increased root growth. Nevertheless, changes in root morphology are not the only consequence of bacterial ACC deaminase activity, as bacterial nitric oxide has also been implicated, for instance, in *Azospirillum*-mediated changes in root morphology however; decreasing the level of ethylene alters the general stress status of the plant, as ethylene plays a key role in stress-related signal transduction pathways. Its synthesis increases when the plant is exposed to different types of stress. For a detailed review on the so-called stress ethylene and the alteration of plant ethylene levels by bacterial ACC deaminase. Like ethylene, proline is often synthesized by plants in response to various abiotic, as well as biotic, stresses, mediating osmotic adjustment, free radical scavenging and sub cellular structure stabilization. Proline synthesis has been shown to be increased in abiotically stressed plants in the presence of beneficial bacteria such as *Burkholderia*, as well as *Arthrobacter* and *Bacillus*] however, in pepper, proline was also accumulated in the absence of abiotic stress in *Arthrobacter*- and *Bacillus*-treated plants, suggesting that these bacteria could cause some biotic stress on the pepper.

Cross-protection against abiotic and biotic stress

The non-specificity of plant perception of abiotic stress can lead to a general response, the basis of cross-protection. For example, an increase in the synthesis of quaternary amines, such as glycine betaine, increases plant resistance to water deficiency, but also provides protection against frost and salinity. Likewise, the up-regulation of anti-oxidative enzymes, for example, superoxide dismutases [SODs], is a general response to different abiotic stress conditions. Obviously, plant enzymatic anti-oxidative response to abiotic stress is by no means limited to SODs. There were numerous studies undertaken to elucidate the plant beneficial effects of non-pathogenic rhizobacteria under different abiotic stress conditions. Interestingly, the beneficial effects of inoculation with plant growth-promoting root zone bacteria have been reported to be most significant under unfavourable conditions such as flooding drought [metal toxicity or nutrient deficiency]. This is consistent with results from a computer simulation showing that the survival rate of introduced rhizobacteria in any given microbial community is an important factor determining the degree of plant stimulation. Because competition for limited resources is crucial, and bacteria are also susceptible to environmental stressors, the most prominent beneficial effects of inoculation with a potential PGPR is to be expected in poor soils [25], when the development of the indigenous microbial community is inhibited.

Some of the bacteria that have been used to study beneficial effects under abiotic stress conditions, such as *Bacillus* sp., have been shown to induce ISR and the primed physiological state of an inoculated plant could, therefore, be one explanation for increased tolerance against abiotic stresses. Indeed, the phenomenon of priming, although not yet fully understood at the molecular level, is thought to be associated with an accumulation of inactive signalling proteins which become activated and transduced, upon subsequent exposure of the plant to similar stresses. In addition, observed changes in gene expression in *Arabidopsis thaliana*, first inoculated with *Paenibacillus polymyxa* and then exposed to drought or infected with the pathogenic bacterium *Erwinia carotovora*, support the conclusion that genes involved in plant response to biotic and abiotic stresses may be coregulated. Consistent with this, constitutive expression of the rice *Osm5b4* gene encoding a transcription factor involved in cold acclimation, resulted in elevated tolerance of transgenic *A. thaliana* to both abiotic [salt, UV, ozone, drought] and biotic [viruses, bacteria, fungi] stresses. Studies using the promoter: *GUS* [beta-glucuronidase] reporter system have shown that the promoter of osmotins, a family of small [25–50 kDa] protective proteins that accumulate under salt stress, is responsive to the phytohormones ABA and ethylene; to viral and fungal infections; to wounding; as well as to the abiotic stresses salinity, drought and UV radiation.

However, the accumulation of osmitine proteins, which leads to salt tolerance, only occurs upon salt stress and fungal infection, indicating that the regulatory mechanisms of cross-protection are very complex and occur not only on the level of gene expression, but also on the translational and post-translational levels. Consistent with this showed that disease resistance and abiotic stress tolerance in rice are inversely modulated by an ABA-inducible mitogen-activated protein kinase [MAPK]. This MAPK is induced by biotic [pathogen infection], as well as abiotic [wounding, drought, salt and cold], stresses, and increases tolerance to drought, salinity and cold stress when over-expressed.

Suppression of the MAPK gene, however, significantly enhances resistance to fungal [*Magnaporthe grisea*] and bacterial [*Burkholderia glumae*] pathogens, whereas tolerance to drought, salinity and low temperature was significantly reduced.

Drought tolerance

Bacteria occurring on root surfaces containing ACC deaminase have been shown to modify the sensitivity of root and leaf growth to soil drying, apparently by influencing ethylene signalling. The ACC deaminase activity of *Achromobacter piechaudi* was shown to confer tolerance to water deficit in tomato and pepper, resulting in significant increases in fresh and dry weights. Ethylene production was reduced in inoculated plants compared to non-inoculated controls, with improved recovery from water deficiency, although inoculation did not influence relative water contents [26]. Under water deficiency, maize seedlings inoculated with *Azospirillum brasilense*, however, displayed improved relative and absolute water contents, in comparison to non-inoculated treatments. Bacterial inoculation has also been shown to prevent a significant drop in water potential, in parallel with a concomitant increase in root growth, total aerial biomass and foliar area, as well as proline accumulation in leaves and roots.

Tolerance to high soil salinity

Azospirillum-inoculated seeds of lettuce [*Lactuca sativa* L., cv. Mantecosa], for instance, showed better germination rates and vegetative growth than non-inoculated control plants when exposed to NaCl. The relevance of decreased endogenous ethylene levels in bacterially mediated tolerance to salt stress has been highlighted by some studies. In

groundnut grown under saline field conditions, the plant growth-promoting effects of ACC deaminase possessing *Pseudomonas fluorescens* TDK1 were more pronounced, compared to strains lacking the enzyme [27]. Consistent with this, transgenic canola expressing a bacterial ACC deaminase gene was shown to be more tolerant to high concentrations of salt than non-transformed control plants.

Tolerance to extreme temperatures

Temperature extremes present a stress condition for plants. For example, root elongation only occurs above a certain, species-dependent minimum temperature, and increases almost linearly with increasing temperature up to specific maximum temperature when elongation rates rapidly decrease. The beneficial effects of various bacterial strains on soya bean growth and physiology under suboptimal root zone temperatures, and found that bacterial stimulation is interactively dependent on temperature. It has often been claimed that growth-promoting effects are caused by the bacterial nitrogen-fixing activities, but in this case, positive effects on the plant's physiology were detected before start of nitrogen fixation, indicating that mechanisms independent of nitrogen status are involved.

Tolerance to nutrient deficiency and heavy metal toxicity

Nutrient elements, such as phosphorus, potassium, iron, zinc and copper, possess limited mobility in the soil. In the case of phosphorus, its insoluble form can be mobilized by plant exudates such as phosphatases and organic acids. Exuded carbohydrates also indirectly contribute to phosphorus mobilization by serving as a carbon source for P-solubilizing microorganisms. Release of carbohydrates by P-deficient plants increased by 52% upon treatment with IAA, whereas no significant change was observed in plants sufficiently supplied with P. This led to the speculation that bacterially produced IAA could also provoke higher amounts of plant carbohydrate exudates, and, therefore, result in a better nutrient status of the bacteria. In turn, the bacteria are able to mobilize more P; thus, plant growth-promoting effects of P-solubilizing bacteria would be more pronounced under P-deficient conditions.

Inoculation with *Pseudomonas alcaligenes* PsA15, *Bacillus polymyxa* BcP26 and *Mycobacterium phlei* MbP18, respectively, promoted growth and nutrient uptake in maize. In nutrient-deficient calcisols, however, promotion of nitrogen, phosphorus and potassium uptake was found to be much greater than on rich loamy sand soil, where stimulation was only detected in root growth, as well as in N and K uptake [28].

Many root zone bacteria release into the rhizosphere metal-chelating substances, such as iron-chelating siderophores. Siderophore-producing bacteria have been shown to influence plant uptake of various metals, including iron, zinc and copper. This way, rhizobacteria can also impact on the bioavailability of heavy metals that can be toxic to plants in low concentrations. Because soil conditions influence metal valencies, microorganisms also affect metal bioavailability by acidification of the micro-environment, and by influencing changes in redox potential; Autotrophic and heterotrophic leaching, volatilization through methylation and release of chelators can mobilize metals, whereas sorption to cell components followed by intracellular sequestration or precipitation as insoluble organic or inorganic compounds reduces heavy metal mobility.

Barley plants grown on cadmium-contaminated soil obtained 120% higher grain yield and twofold decreased Cd contents in grains when inoculated with the commercially available PGPR *Klebsiellamobilis* CIAM 880. Simulation of these effects with a mathematical model showed that it is a complex process, with one of the underlying mechanisms being bacterial migration from rhizoplane to rhizosphere. Here, free Cd ions can be bound by bacteria into complex forms that cannot be taken up by the plant. Moreover, all bacterial strains tested in the study possessed nitrogen-fixing ability, and produced IAA or ethylene, characteristics, which, most likely, played key roles in mediating stress tolerance. Indeed, the possession by some bacteria of cell wall components with metal-binding properties] may help in bacterial accumulation of metals such as Cd.

In turn, this feature can contribute in the reduction of Cd uptake by plants with which such bacteria are associated. In contrast, in *Brassica juncea* inoculated with IAA- and siderophore-producing bacteria, chromium uptake was not altered, whereas chromium tolerance was enhanced. Indeed, the ability of some bacteria to protect plants against either nickel, lead or zinc toxicity has previously been shown to be related to the production of siderophores. Because microbial iron-siderophore complexes serve as an iron source for both monocot and dicot plants, iron deficiency symptoms, genuine or metal induced, common in plants grown under high heavy metal concentrations can be prevented. However, iron, although essential, can cause oxidative stress in plants when absorbed in high concentrations. Indeed, iron intoxication, similar to other metals, was shown to cause the modification of enzymes related to oxidative stress.

However, for the first time, microbial siderophores were shown to be able to alleviate metal-induced oxidative stress in plants. Apparently, by chelating and reducing toxic metal concentrations in the root zone, siderophores exerted a bioprotective effect by lowering the formation of cell-damaging free radicals, thereby enabling a microbial

IAA-mediated plant biomass increase, which contributed in the dilution of toxic metal effects on the plants [29]. Iron toxicity is a serious constraint in wetland rice production. Preliminary findings, however, indicate that several *Bacillus* strains possess the ability to mitigate the symptoms of iron toxicity in rice. The underlying mechanisms still remain elusive, although they seem to depend on the *Bacillus* strain and on the rice genotype. *Bacillus* sp., as with most other bacteria, possess SODs which, as mentioned previously are key enzymes involved in the alleviation of oxidative stress in living systems. Similar to plants, bacterial SODs play an important role in their survival in the rhizosphere, which as noted is an environment characterized by free radical-generating activities. As such, bacterial survival ensures their contribution to the amelioration of abiotic stress, and hence, to plant growth promotion.

Bacterially Mediated Plant Tolerance to Abiotic Stress

Selected representation of studies published on beneficial effects of bacterial inoculation on plant physiology and growth under abiotic stress conditions

Stress type	Bacterial inoculate	Plant species
Salt	<i>Azospirillum brasilense</i>	Pea [<i>Phaseolus vulgaris</i>]
Salt	<i>Pseudomonas syringae</i> , <i>Pseudomonas fluorescens</i> , <i>Enterobacteraerogenes</i>	Maize [<i>Zea mays</i>]
Salt	<i>Azospirillum</i>	Lettuce [<i>Lactuca sativa</i>]
Salt	<i>Achromobacter piechaudii</i>	Tomato [<i>Lycopersicon esculentum</i>]
Drought	<i>Achromobacter piechaudii</i>	Tomato [<i>L. esculentum</i>], pepper [<i>Capsicum annuum</i>]
Drought	<i>A. brasilense</i>	Common bean [<i>P. vulgaris</i>]
Drying soil	<i>Variovoraxparadoxus</i>	Pea [<i>Pisum sativum</i>]
Drying soil	<i>Bacillus</i>	Lettuce [<i>L. sativa</i>]
Osmotic stress [45% PEG]	<i>Arthrobacter</i> sp., <i>Bacillus</i> sp.	Pepper [<i>C. annuum</i>]
Flooding	<i>Enterobacter cloacae</i> , <i>Pseudomonas putida</i>	Tomato [<i>L. esculentum</i>]
Temperature	<i>B. phytofirmans</i>	Potato [<i>Solanum tuberosum</i>]

Phytoremediation is a method to clean up contaminated soils based on the ability of certain plants to stabilize, extract, degrade or volatilize pollutants. Despite this ability, plants often suffer from the toxic effect of metals which affects their phytoremediation potential. However, supplementation of such plants with soil bacteria can enhance phytoremediation, hence the term microbe-assisted phytoremediation. In comparison to conventional clean-up methods where the soil is removed and cleaned in complicated technical processes, phytoremediation is very cost-effective and non-destructive to the soil structure. Ideally, plants used for phytoremediation should produce high amounts of biomass and/or hyper-accumulate the contaminant. However, although some plants may tolerate high amounts of a pollutant, their growth might still be constrained by such pollutants. Thus, rhizobacteria enhancing the tolerance of plants to high concentrations of a pollutant and/or promoting plant growth could provide a useful tool for making the process of phytoremediation more efficient.

Commonly with metal-induced oxidative stress, ACC-induced ethylene production is a major factor affecting plant growth in metal-polluted environments, leading to reduced plant biomass and, therefore, lowered phytoremediation efficiency [30]. As plants do not possess ACC deaminase activity, transgenic plants have been developed with this capability, based on bacterial ACC deaminase genes. Such applications have contributed in enhancing plant growth, tolerance to metal stress and ultimately, to augmenting metal accumulation for phytoremediation.

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