

Plant growth-promoting actinobacteria: a new strategy for enhancing sustainable production and protection of grain legumes

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Abstract Grain legumes are a cost-effective alternative for the animal protein in improving the diets of the poor in South-East Asia and Africa. Legumes, through symbiotic nitrogen fixation, meet a major part of their own N demand and partially benefit the following crops of the system by enriching soil. In realization of this sustainability advantage and to promote pulse production, United Nations had declared 2016 as the “International Year of pulses”. Grain legumes are frequently subjected to both abiotic and biotic stresses resulting in severe yield losses. Global yields of legumes have been stagnant for the past five decades in spite of adopting various conventional and molecular breeding approaches. Furthermore, the increasing costs and negative effects of pesticides and fertilizers for crop production necessitate the use of biological options of crop production and protection. The use of plant growth-promoting (PGP) bacteria for improving soil and plant health has become one of the attractive strategies for developing sustainable agricultural systems due to their eco-friendliness, low production cost and minimizing consumption of non-renewable resources. This review emphasizes on how the PGP actinobacteria and their metabolites can be used effectively in enhancing the yield and controlling the pests and pathogens of grain legumes.

Keywords Plant growth-promoting actinobacteria · Legumes · Metabolites · Biocontrol · Stress control

Introduction

Grain legumes also called ‘Poor man’s meat’ are an essential entity in food and feed due to its protein, minerals, and other bioactive molecules. Increasing nutritional awareness increased the per-capita consumption of grain legumes across the world (Amarowicz and Pegg 2008). The symbiotic association of leguminous crops with rhizobia contributes 65% of nitrogen (N) needs. Their better adaptation as an inter-crop with cereals or tuber crops helps in increased income generation and livelihood resilience of small holder farmers. However, production level of such leguminous crops has constraints in various forms such as pest and pathogen attacks, infertile soils, and climate changes. Development of improved cultivars through breeding and molecular techniques had been practiced; still, the productivity remains stagnant for the last two decades. All these together attracted the attention at global level, and thus, the general assembly of United Nations has announced this year as ‘International Year of Pulses (2016 IYOP)’ to emphasize the need for focusing on pulses for food and nutritional security and to create awareness and understanding of the challenges faced in pulse farming and trading (FAO 2014).

A cleaner and greener approach towards the improvement of leguminous crop production is the use of a category of microbes called Plant Growth-Promoting Rhizobacteria (PGPR), a group of heterogeneous bacteria found in rhizosphere or plant tissues (Kloepper and Schroth 1978). They induce plant growth by enhancing the availability of soil nutrients, supplying phytohormones, and inducing systemic resistance against phytopathogens. There are voluminous data available on PGPR, but most of it belongs to the phylum Bacteroidetes, Firmicutes, and Proteobacteria, of which the most commonly studied are

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Azospirillum, *Azotobacter*, *Bacillus*, *Pseudomonas*, *Gluconacetobacter*, *Enterobacter*, *Serratia*, *Paenibacillus*, and *Rhizobium* (Bhattacharyya and Jha 2012). However, the reports on the plant growth-promoting (PGP) traits of bacteria belonging to the phylum Actinobacteria are limited, despite its ubiquitous existence in bulk soil, rhizospheric soil, and plant tissues and their usefulness in agriculture (Bhattacharyya and Jha 2012; Jog et al. 2012). Hence, this review emphasizes to document mainly on PGP traits of actinobacteria and how far it was studied in the context of growth-promotion, biocontrol against pests, and pathogens, as mitigators of abiotic stress, as a tool for enhanced phytoremediation and bio-fortification.

Actinobacteria diversity

The bacteria belong to the phylum Actinobacteria are Gram-positive filamentous bacteria, with 6 classes, 25 orders, 52 families, and 232 genera and represent one of the largest taxonomic units among the 18 major lineages currently recognized within the domain Bacteria (Stackebrandt and Schumann 2000). They can thrive in either bulk soil or rhizospheric soil, and due to spore forming characteristics, they can remain dormant in agricultural soil for a longer period. The actinobacteria population increases with the soil depth up to horizon 'C'. It is estimated that actinobacteria are distributed with average 10^4 – 10^6 spores g^{-1} soil in various crops fields (Shaharokhi et al. 2005; Ul-Hassan and Wellington 2009). Though they are mesophilic organisms, species of the family such as Thermoactinomycetaceae are commonly found in compost and manures at thermophilic growing temperature (Ul-Hassan and Wellington 2009). They also stay as either epiphyte or endophyte in plant tissues of wide host range including barley, wheat, rice, soybean, cowpea, chickpea, banana, tomato, and medicinal plants. Among them, *Streptomyces* is the predominant genus followed by *Actinonmadura*, *Microbispora*, *Micromonospora*, *Nocardia*, *Nonomurea*, *Mycobacterium*, *Frankia*, *Actinoplanes*, *Saccharopolyspora*, and *Verrucosipora* (Martinez-Hidalgo et al. 2014; Vijayabharathi et al. 2016).

PGP traits of actinobacteria

As like other PGPR, actinobacteria also employ both direct and in-direct mechanisms to influence the plant growth and protection. The direct mechanisms involve the production of vital factors for crop growth such as growth hormones and the assistive actions on nitrogen fixation, phosphate solubilization, and iron acquisition. PGP actinobacteria indirectly influence the plant growth by controlling and

minimizing the deleterious effects of external stresses of either biotic or abiotic sources through the following modes: competition for nutrients, production of low molecular inhibitory substances such as ammonia, cyanogens, alcohols, aldehydes, sulfides, and ketones, cell-wall degrading enzymes, and secondary metabolites with bio-cidal properties, in which the latter, two are the key phenomenon deployed by the actinobacterial community (El-Tarabily and Sivasithamparam 2006; Glick 2012; Bouizgarne 2013; Dey et al. 2014).

Nitrogen fixation

Nitrogen is the major essential crop nutrient available through the process called symbiotic N fixation. This was aided by the relationship between the members of the family Rhizobiaceae, Bradirhizobiaceae, and Phyllobacteriaceae with the leguminous plants through the formation of N-fixing specialized structure called nodules (Schultze and Kondorosi 1998). *Frankia*, a versatile N fixing actinobacteria, fixes N in non-legumes under both symbiotic and free-living conditions. It infects the root cells of actinorhizal plants through either intracellular root-hair infection or intercellular root invasion (Benson and Silvester 1993). Besides this, several other endophytic actinobacteria exhibited N-fixing ability which includes *Arthrobacter*, *Agromyces*, *Corynebacterium*, *Mycobacterium*, *Micromonospora*, *Propionibacteria*, and *Streptomyces* (Sellstedt and Richau 2013). This was demonstrated long back by Fedorov and Kalininskaya (1961) by their ability to grow on N-free medium and acetylene reduction activity. Recent studies using ^{15}N isotope dilution analysis and identification of *nif* genes further support this phenomenon (Valdes et al. 2005; Ghodhbane-Gtari et al. 2010). Molecular studies have established the fact that many actinobacteria can occur as endophytes in various leguminous and non-leguminous plants without forming nodule. This is supported by the existence of *nif* sequence homology in both *Rhizobium* and *Frankia*, the absence of *nod* genes in the latter (Ceremonie et al. 1999). Even under field conditions, enhanced nodulation of chickpea and soil N content observed upon the application of *Streptomyces* inoculants indicates their promotional effect and influence of rhizobia-legume symbiosis in a non-specific manner (Gopalakrishnan et al. 2015a, b). However, a detailed understanding of the mechanisms on this symbiotic mode needs to be established.

Phosphate solubilization

Influence of PGPR in enabling the availability of phosphate to plants through various mechanisms is highlighted by various researchers across a range of soil conditions. In

the context of actinobacteria, *Arthrobacter*, *Rhodococcus*, *Gordonia*, *Streptomyces*, and *Micromonospora* have been reported for P solubilization in vitro and glass house conditions (Chen et al. 2006; Hamdali et al. 2008; Jog et al. 2014). Initial report on P solubilizing capacity of a non-streptomycete *Micromonospora endolithica* and its subsequent effect on the growth of bean plants have been reported by El-Tarabily et al. (2008). Similar effect has also been demonstrated on wheat by *Micromonospora aurantiaca*, *Streptomyces griseus*, and *Streptomyces* sp., under P-deficient soil (Hamdali et al. 2008; Jog et al. 2014). In these actinobacterial strains, production of various organic acid including citric acid, gluconic acid, lactic acid, malic acid, oxalic acid, propionic acid, and succinic acid which aids for P solubilization has been demonstrated (Chen et al. 2006; Hamdali et al. 2010; Jog et al. 2014).

Iron acquisition

Iron in soil is known for its un-availability to both plants and microbes due to its normal presence as insoluble hydroxides and oxyhydroxides. This is made available by the synthesis of siderophores, the low molecular weight compounds which have high affinity towards iron. Iron chelation by microbial siderophores from soil depends on its pH, concentration, redox potential, stability constant, and receptor availability to exchange with phytosiderophores (Crowley 2006). Microbes produce variety of siderophores and a major class includes catechols and hydroxamate. Numerous strains of actinobacteria have been reported as siderophore producers (Wang et al. 2014). The genus *Streptomyces* is well known for its siderophores, including its own characteristic types such as hydroxamate siderophores: desferrioxamines and coelichelin (Imbert et al. 1995; Challis and Ravel 2000); siderophore of other actinobacteria members: heterobactin, a siderophore of *Rhodococcus* and *Nocardia* (Lee et al. 2012); and also siderophores of other bacterial members: enterobactin, siderophore of the family Enterobacteriaceae (Fiedler et al. 2001). Besides the context of plant nutrition, siderophore also offers for plant protection through the control of phytopathogens. They acquire iron thereby create a competitive environment for other pathogenic microbes in the root vicinity (Glick 2012). This is an effective phenomenon in controlling fungal pathogens as they produce low-affinity siderophores, which can be eliminated by high affinity siderophores of actinobacteria (Wang et al. 2014). Such siderophore producing *Streptomyces* was also found to show control against *Fusarium oxysporum* f. sp. *ciceri* under wilt sick field conditions on chickpea (Gopalakrishnan et al. 2011).

Phytohormones

Phytohormone producing capacity of several rhizospheric and endophytic actinobacteria was demonstrated by various researchers for indole acetic acid (IAA), cytokinins, and gibberellins (El-Tarabily and Sivasithamparam 2006; Vijayabharathi et al. 2016). In recent years, endophytic actinobacteria are getting greater interest. *Nocardiosis*, an endophytic actinobacterium associated with mandarin recorded highest IAA production (222.75 ppm) (Shutsrirung et al. 2013). IAA producing endophytic *Streptomyces atrovirens*, *Streptomyces olivaceoviridis*, *Streptomyces rimosus*, *Streptomyces rochei*, and *Streptomyces viridis* showed improved seed germination and root elongation and growth (El-Tarabily 2008; Khamna et al. 2010; Abd-Alla et al. 2013). IAA also triggers cell differentiation, hyphal elongation, and sporulation in *Streptomyces atroolivaceus* (Matsukawa et al. 2007). Metabolites such as pteridic acids A and B produced by endophytic *Streptomyces hygrosopicus* TP_A045 were found to show auxin-like activity and induce root elongation in common bean (Igarashi et al. 2002). Hence, the phytohormone producing potential and metabolites with phytohormone mimicking activity of actinobacteria can be exploited for enhancing crop productivity of not only legumes and also other crops.

Cell wall degrading enzymes

Majority of soil actinobacteria are saprophytic in nature and core of decomposition, which was aided by the synthesis of various classes of extracellular enzymes including nucleases, lipases, glucanases, xylanases, amylases, proteinases, peptidases, peroxidases, chitinases, cellulases, ligninases, pectinase, hemicellulase, and keratinase. All these enzymes together contribute to its biocontrol potential against a wide range of phytopathogens, because the cell wall of most fungal and bacterial pathogens consist of polymers such as chitin, glucan, cellulose, proteins, and lipids (Gupta et al. 1995; Fodil et al. 2011). Among them, chitinases are of great importance and many *Streptomyces* spp. are observed to inhibit both fungal pathogens and insect pests (Tahmasebpour et al. 2014; Karthik et al. 2015; Yandigeri et al. 2015).

Other secondary metabolites

According to the literature survey, there are around 300,000 to 600,000 natural compounds derived from living sources. Among them, the major contributors are found to be microbes (60–80,000), of which actinobacteria accounts for ~60% of new antibiotics. This is supported by the genetic makeup of biosynthetic pathways and their enzyme activities for branching, alkylations, condensations,

isomerizations, and oxidations. The single genus, *Streptomyces*, is the major producer (39%) of secondary metabolites (Olano et al. 2008; Berdy 2012). In addition, they have the capacity to produce a wide variety of compounds including polyene macrolides, actinomycins, aminoglycosides, streptothricins, anthracyclines, cyclopolylactones, and quinoxaline peptides. Non-*Streptomyces* actinobacteria also found to produce compounds such as glycopeptides and orthosomycins (Nicolaou et al. 2009).

It is also noted that half of the microbial metabolites express one or multiple bioactivities including antibiotic or enzyme inhibitory activities or other activity. In the context of agriculture, more than 3000 pesticide and herbicide activities, including phytotoxic, plant growth regulatory, insecticide, larvicide, acaricide, algicide, and nematocidal activities were reported. The major advantage of using secondary metabolites from actinobacteria over the fungal metabolites is lower phytotoxic activity. More than 50% of fungal metabolites were observed to be phytotoxic which contrasts with the 2% of phytotoxic actinoproducts (Berdy 2012). These kinds of actinobacteria have a competitive edge over other microbial communities as it increases their chances of survival. This characteristic has been exploited more than five decades ago and studied by several researchers for the biological control of plant pathogens and disease suppression (Weindling et al. 1950; Chamberlain and Crawford 1999; Meschke et al. 2012). Several commercial formulations with the antibiotic or microbes as an active ingredient are marketed as biocontrol products. Representatives include, Actinovate[®] and Actino-Iron[®] by *Streptomyces lydicus* WYEC 108 (Crawford et al. 2005), Arzent[™] by four different strains of *Streptomyces hygroscopicus* (Hamby and Crawford 2000) and Mycostop[®] by *Streptomyces griseoviridis* K61 (Figueiredo et al. 2010). Besides this, Blastocidin-S from *Streptomyces griseochromogenes* and kasugamycin from *Streptomyces kasugaensis* against rice blast disease, mildiomycin from *Streptomyces rimofaciens* against powdery mildew disease, oxytetracycline form *S. rimosus* for the control of bacterial diseases, and polyoxins from *Streptomyces cacaoi* for the control of fungal incidences at field levels demonstrates the importance of secondary metabolites from actinobacteria for sustainable agriculture. Several reviews depicting the importance of actinobacteria and its compounds as biocontrol agents are available (Copping and Menn 2000; Copping and Duke 2007).

Host plant resistance

Host plant resistance is one of the key tools for management of phytopathogens and pests in which the protection is conferred systemically even in the non-exposed parts of the plant. Plants were reported with two types of non-

specific defense systems: (1) induced systemic resistance (ISR) primed by the influence of beneficial microbes and (2) systemic acquired resistance (SAR) primed by the influence of pathogens (Schuhegger et al. 2006). The ISR mediated by rhizobacteria predisposes the plants to resist further attacks. On the contrary, the SAR is induced by pathogens, resulting in the activation of resistance mechanisms in other uninfected parts of plants. In general, the defense systems are mediated by signaling molecules such as jasmonic acid (JA), salicylic acid (SA), and ethylene (ET) (Pieterse et al. 1996). JA activates defense-related genes: defensins, thionins, and pectinase inhibitors (Hause et al. 2002). The SA induces genes that encode the pathogenesis-related proteins (PRs) such as chitinase, β -1,3 glucanases, and thaumatin such as proteins and peroxidases (Uknes et al. 1992). Actinobacteria are demonstrated as inducers of plant immunization against different pathogens such as *Rhizoctonia*, *Fusarium*, *Pythium*, *Phytophthora*, and *Colletotrichum* (Raaijmakers et al. 2009). Endophytic actinobacterium *Streptomyces* sp. was able to control take-all disease of wheat and potato scab under the field conditions (Liu et al. 1996; Coombs et al. 2004). Conn et al. (2008) observed that endophytic *Streptomyces* sp. EN27 and *Micromonospora* sp. EN 43 are able to induce resistance in *Arabidopsis thaliana* by up-regulating genes involved in SAR. Culture filtrates of EN 43 also induced SAR and the JA/ET pathway. The bacterial determinants involved in triggering ISR include secondary metabolites, siderophores, and colonization efficiency. Recently, many studies on *Streptomyces*-induced host plant resistance were evaluated on range of crops including forage crops, vegetable crops, and economically important woody species such as *Arabidopsis* (Bernardo et al. 2013), potato (Arse-neault et al. 2014), oak (Kurth et al. 2014), and *Eucalyptus* (Salla et al. 2016), and such an opportunity for encasing actinobacteria for grain legumes needs to be exploited.

PGP actinobacteria as helper bacteria

Actinobacteria are able to promote N-fixing symbiosis (Solans 2007; Solans and Vobis 2013) and also in other symbiotic relationships of legumes and non-legumes plants by their role as helper bacteria; however, it is documented in very few reports. Actinobacteria are found to promote mycorrhizal symbioses via the promotion of hyphal elongation of symbiotic fungi (Schrey and Tarkka 2008). Such an enhanced mycorrhizal symbiosis was observed on the roots of sorghum and clover by *Streptomyces coelicolor* and *Streptomyces* spp. MCR9 and MCR24, respectively (Abdel-Fattah and Mohamedin 2000; Franco-Correa et al. 2010).

Solans and their research group have studied the helper effect of actinobacteria with various host plants. This was

demonstrated in the system of *Ochetophila trinervis* and *Frankia*, with the co-inoculation of *Streptomyces* MM40, *Actinoplanes* ME3, and *Micromonospora* MM18 (Solans 2007). The same actinobacteria were studied in other symbiotic systems of *Medicago sativa*–*Sinorhizobium meliloti* (Solans et al. 2009) and *Lotus tenuis*–*Mesorhizobium loti* (Solans et al. 2015). It was noticed that the plants co-inoculated with actinobacteria and rhizobium showed increased nodulation and plant growth compared to the plants with single inoculations. Similar results were noted by other researchers as well. The combination of *Streptomyces kanamyceticus* and *Bradyrhizobium japonicum* increased nodulation and shoot N composition of soybean by up to 55 and 41%, respectively (Gregor et al. 2003). Soe and Yamakawa (2013) examined the effect of co-inoculation of *Bradyrhizobium yuanmingense* MAS34 and *Streptomyces griseoflavus* P4 in enhancing nodulation, N₂ fixation, and seed yield in different soybean varieties. The results of these researchers clearly demonstrated the importance of actinobacterial inoculants in growth promotion of leguminous and non-leguminous plants.

PGP actinobacteria as stress relievers

Abiotic stress factors such as extreme temperatures, drought, flooding, salinity, metal stress, and nutrient stress are likely to cause serious impacts on crop yields and impose severe pressure on soil and water resources. According to the estimates from Food and Agricultural Organization (FAO), abiotic stress factors will result in 30% land degradation in the next 25 years and up to 50% by the year 2050 if precautionary measures are not taken (Munns 2002).

Actinobacteria are known to possess better tolerance towards temperature, salinity, and metals; inoculation of such tolerant strains is observed to promote plant growth. Aly et al. (2003, 2012) observed the PGP effect of *Streptomyces* sp. on maize and wheat under saline conditions. Palaniyandi et al. (2014) observed enhanced biomass and lateral roots of *Arabidopsis* seedlings under in vitro conditions of 1 mol l⁻¹ NaCl upon the inoculation with *Streptomyces* sp. PGPA39 exhibiting salt tolerance and other PGP traits. Srivastava et al. (2015) attempted to study the mechanism underlying actinobacteria-mediated stress tolerance in chickpea. They used *Streptomyces rochei* SM3 against the challenges of *Sclerotinia sclerotiorum* and NaCl on chickpea. Treatment with SM3 suppressed chickpea mortality due to *S. sclerotiorum* infection (48%) and increased biomass accumulation (20%) in the salt-stressed conditions. Physiological responses showed increased phenylalanine ammonia lyase and catalase activities, along with the accumulation of phenolics and

proline in SM3-treated plants. Investigation at genetic level further showed that the strain SM3 triggered the ET responsive ERF transcription factor (CaTF2) under the challenged conditions. Drought tolerant endophytic actinobacteria, *Streptomyces coelicolor* DE07, *Streptomyces olivaceus* DE10, and *Streptomyces geysiriensis* DE27, with intrinsic water stress tolerance from -0.05 to -0.73 MPa and IAA production were isolated from arid and drought affected regions. Co-inoculation of endophytes DE10 and DE27 recorded the highest yield in wheat (Yandigeri et al. 2012). In addition, induction of higher osmotic pressure of plant cells, callose accumulation, and cell wall lignification as a strategy for drought tolerance has been documented for *Streptomyces padanus* (Hasegawa et al. 2004, 2005). Recent studies on *Streptomyces pactum* Act12, a multi-functional strain with drought resistance, metal resistance (Cao et al. 2016), and antagonistic traits against phytopathogenic fungus (Zhao et al. 2011) explores the role of these in-kind actinomycetes for arid and semi-arid regions.

Responding to stress, plant synthesizes higher level of ET called 'stress ethylene' which leads to plants' premature death. In fact, some of the effects of stress cannot solely be attributed to the stress itself but are also due to autocatalytic ethylene synthesis (Van Loon 1984). These effects can be controlled by the action of an enzyme of microbial origin, 1-aminocyclopropane-1-carboxylate (ACC) deaminase which converts the ethylene precursor ACC to ammonia and α -ketobutyrate. Characterization of this enzyme effects on stress management is observed for the past two decades, and now considered as a key phenomenon of PGP traits (Glick 1995). Many of the actinobacteria are shown to produce ACC deaminase such as *Streptomyces*, *Amycolatopsis*, *Nocardia*, *Mycobacterium*, *Rhodococcus*, and others (Nascimento et al. 2014). Siddikee et al. (2010) isolated several halotolerant actinobacteria strains with ACC deaminase, from the soil of barren fields and the rhizosphere of naturally growing halophytic plants and found that they can increase canola plant growth. Similarly, Selvakumar et al. (2015) identified ACC deaminase producing *Citricoccus zhacaiensis* B-4, an osmotolerant actinobacterium from the banana rhizosphere and observed improved percent germination, seedling vigor and germination rate on onion seeds (cv. Arka Kalyan) at osmotic potentials up to -0.8 MPa. El-Tarabily (2008) showed that ACC deaminase producing *Streptomyces filipinensis* 15 and *S. atrovirens* 26 could reduce tomato endogenous ACC levels in both roots and shoots, resulting in increased plant growth. Similarly, Palaniyandi et al. (2013) also showed that some *Streptomyces* spp. of yam rhizospheres could produce ACC deaminase. Dastager et al. (2010) indicated that the cowpea PGP bacterium *Micrococcus* sp. NII-0909 produced ACC deaminase under free-living conditions. Idris et al. (2004) isolated

endophytic *Curtobacterium*, *Okibacterium*, and *Rhodococcus* strains with ACC deaminase activity from *Thlaspi goesingense*. All these suggest that, irrespective of habitat, i.e., rhizospheric/endophytic or stressed/non-stressed soil, actinobacteria with ACC deaminase can be used for the dual purposes of enhancing productivity and stress control.

PGP actinobacteria in bioremediation of metals

Metal pollution of agricultural lands has risen mainly by anthropogenic activities, led to the shrinkage of healthy agricultural cropland, and hence demands the farmers to use contaminated sites for crop cultivation. According to the Environmental Protection Agency (EPA) report, the United States had more than 40,000 contaminated sites. In addition, 100,000 ha of cropland, 55,000 ha of pasture, and 50,000 ha of forest have been lost by heavy metal contamination and demands for reclamation process (Ragnarsdottir and Hawkins 2005). PGPR reside in metalliferous soil with higher metal solubilizing and extracting capacity can play decisive role in the context of bioremediation besides enhancing phytoremediation

process. Metal mobilizing property of these microbes is aided by its own substances such as siderophores, organic acids, polymeric substances, biosurfactants, and glycoprotein and also by the reactions such as metal reduction and oxidization and biosorption. Mechanism behind the metal mobilization was reviewed in detail by Ma et al. (2011), Rajkumar et al. (2012), and Sessitsch et al. (2013), and a review on current research status of bioremediation involving actinobacteria has been given by Alvarez et al. (2017). From the published data, it is understood that actinobacteria with metal mobilizing and PGP traits were evaluated mostly on non-edible/hyper accumulating plants and on toxic metals in the area of phytoremediation. Such works on edible crops were a few. Some of the representative reports stating the potential of PGP actinobacteria with metal mobilization traits were given in Table 1.

PGP actinobacteria as nutrient enhancer

Actinobacteria influence the soil fertility through the involvement of many components and serve as nutrient enhancer. Besides producing siderophores and solubilizes

Table 1 Metal mobilization potential of PGP actinobacteria

Actinobacteria	Source	Identified PGP/metal mobilization traits	Plant studied	Exhibited effects	References
<i>Azotobacter chroococcum</i> HKN-5	Agronomic soils in Hong Kong	N fixation, P and K solubilization, metal mobilization	<i>Brassica juncea</i>	Increased plant aboveground biomass	Wu et al. (2006)
<i>Rhodococcus</i> sp. Fp2 <i>Rhodococcus erythropolis</i> MTCC 7905	Cr-contaminated site situated in the Indian Himalayan Region	Metal detoxification mechanism	<i>Pisum sativum</i>	Increased plant growth	Trivedi et al. (2007)
<i>Streptomyces acidiscabies</i> E13	Former uranium mine, Wismut, in eastern Thuringia, Germany	IAA and Siderophore: desferrioxamine E desferrioxamine B, and coelichelin	<i>Vigna unguiculata</i>	Increased height and biomass	Dimkpa et al. (2008)
<i>Streptomyces tendae</i> F4	Former Uranium mine, Wismut in Eastern Thuringia, Germany	Siderophore: Desferrioxamine B, desferrioxamine E and coelichelin	<i>Helianthus annuus</i>	Enhanced Cd and Fe uptake by plants through facilitating their mobilization	Dimkpa et al. (2009)
<i>Azotobacter</i> spp.	Manganese mine spoil dump near Gumgaon, India	Extracellular polymeric substances or cell wall lipopolysaccharides	<i>Triticum aestivum</i>	Immobilized Cd and Cr and decreased their uptake	Joshi and Juwarkar (2009)
<i>Arthrobacter</i> sp. MT16, <i>Azotobacter vinelandii</i> GZC24, <i>Microbacterium</i> sp. JYC17, <i>Microbacteriumlactium</i> YJ7	Cu-tolerant plant species growing on a Cu mine wasteland, Nanjing, China	ACC deaminase, siderophore, IAA, P solubilization	<i>Brassica napus</i>	Increased root length promotion	He et al. (2010)
<i>Streptomyces mirabilis</i> P16B-1	Heavy metal-contaminated soil derived from a former uranium mining site in Ronneburg, Germany	Siderophore: Ferrioxamines E, B, D, and G	<i>Sorghum bicolor</i>	Increased plant biomass	Schütze et al. (2014)

phosphate, they are known to produce cocktail of enzymes which include amylase, chitinase, cellulase, invertase, lipase, keratinase, peroxidase, pectinase, protease, phytase, and xylanase which make the complex nutrients into simple mineral forms. This nutrient cycling capacity makes them as an ideal candidate for natural fertilizers (Jog et al. 2016). In addition, the metal mobilizing ability can be applied for biofortification approaches for enhancing seed mineral nutrients such as Fe, Zn, and Se. However, limited studies are available on legumes. A recent study had revealed that arbuscular mycorrhizal fungal colonization on chickpea roots enhanced the crop growth, and grain Fe and Zn contents (Pellegrino and Bedini 2014). Verma et al. (2013) documented the effect of two PGPR isolates, *Mesorhizobium* sp. and *Pseudomonas* sp., on chickpea in enhancing yield and Fe acquisition under greenhouse and field conditions. Similar results were reported by Rudresh et al. (2005) using a consortium of *Rhizobium* sp., phosphate solubilizing *Bacillus megaterium* sub sp. *phosphaticum* and *Trichoderma* sp. on chickpea under greenhouse and field conditions. Recent study of Khalid et al. (2015) on chickpea further supports the ability of PGP bacterial strains with siderophore producing capacity in increasing Fe concentration. Some of the PGP *Streptomyces* from our microbial collection were found to increase the grain Fe and Zn contents by 38 and 30%, respectively, in chickpea (Sathya et al. 2016). Though the effects of actinobacteria were not reported in the context of biofortification, previously demonstrated effects on their metal mobilization property along with PGP reveals that, actinobacteria are capable of mobilizing minerals and metals in a wide range of food crops including cereals, oil seeds, and leguminous crops.

Conclusion

The present review documents the potential of PGP actinobacteria and highlights its unique properties in plant growth induction, defense pathways, and stress management. The available information suggests that actinobacteria represent a hidden repertoire and sustainable source for bioactive and chemically novel natural products, which can be explored to a great extent in various fields of agricultural sector. However, such an extent of success especially on legumes under field conditions is limited. This indicates the existence of large gaps between research and development of potential actinobacterial inoculums for field application. Therefore, generation of comprehensive knowledge on screening, characterization, and formulation strategies and understanding of molecular mechanisms behind their action and evaluation at field levels are necessary.

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Compliance with ethical standards

Conflict of interest The authors declared that they have no competing interest.

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