

Biotechnological application and taxonomical distribution of plant growth promoting actinobacteria

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Abstract Plant growth promoting (PGP) bacteria are involved in various interactions known to affect plant fitness and soil quality, thereby increasing the productivity of agriculture and stability of soil. Although the potential of actinobacteria in antibiotic production is well-investigated, their capacity to enhance plant growth is not fully surveyed. Due to the following justifications, PGP actinobacteria (PGPA) can be considered as a more promising taxonomical group of PGP bacteria: (1) high numbers of actinobacteria per gram of soil and their filamentous nature, (2) genome dedicated to the secondary metabolite production (~5 to 10 %) is distinctively more than that of other bacteria and (3) number of plant growth promoter genera reported from actinobacteria is 1.3 times higher than that of other bacteria. Mechanisms by which PGPA contribute to the plant growth by association are: (a) enhancing nutrients availability, (b) regulation of plant metabolism, (c) decreasing environmental stress, (d) control of phytopathogens and (e) improvement of soil texture. Taxonomical and chemical diversity of PGPA and their biotechnological application along with their associated challenges are summarized in this paper.

Keywords *Actinobacteria* · Bacterial hormones · Bioactive metabolites · Biodiversity · Endophyte · Symbiosis

Introduction

The population of earth will increase to 9 billion by 2050, 35 % more than today. To produce the food needed by this larger population, cereal production should increase to 60 % relative to today. This was estimated to consist of a 77 % increase in developing countries and a 24 % increase in developed countries [2]. Changes in agricultural strategies and techniques will be needed, but the challenge is great and all options for improving yield, including chemical pesticides and fertilizers as well as alternative options need to be utilized to the fullest to meet this global demand for food. However, critics have warned since 1958 that widespread use of pesticides in agriculture causes adverse effects on wildlife, useful insects and human health [17]. Some of these potential local and global adverse effects of agricultural chemicals are evident today and may include loss of species diversity [143]. Chemical pesticides and fertilizers, when used responsibly, can be part of sustainable development, however, the paradigm of sustainable development can prompt researchers to consider alternatives to the established chemical strategies for facilitating plant growth in agriculture, horticulture and silviculture toward assured agricultural purposes [40].

There has been a sustainable relationship between plant growth-promoting bacteria (PGPB) and plants during the billion years of evolution and PGPB are associated with nearly all plant species studied so far. Regarding to the vast distribution of actinobacterial genera among PGPB and high abundance of these bacteria in soil (10^7 – 10^8 per g^{-1})

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compared to other bacteria (10^8 – 10^9 per g^{-1}) [92] and the importance of ecophysiological concept of PGPB, here we review plant growth-promoting actinobacteria (PGPA) as members of *Actinobacteria* which have beneficial association with plants.

This review summarizes mechanisms of action of free-living or endophytic PGPA, their taxonomical distribution and potential of their recruitment in biological enhancement of agricultural crops.

Biology of actinobacteria

The class “Actinobacteria” is well-supported by analyses of the 16S and 23S rRNA genes, presence of conserved insertions and deletions in certain proteins, and characteristic gene rearrangements [83]. At the time of writing this review, this class is one of the largest taxonomic units within the domain *Bacteria* including 15 orders, 57 families and more than 300 genera. Among these 15 orders, *Actinomycetales* (commonly called actinomycetes) often have filamentous life cycle [83]. Among the widely diverse microbial taxa, actinobacteria are the most prolific source for production of bioactive metabolites including herbicides, fungicides and biofertilizers.

Actinobacteria are Gram positive or Gram stain variable, aerobes, facultative anaerobes or anaerobes. Most are chemoorganotrophs and have rigid cell wall containing muramic acids or teichoic acids. Growth at neutral pH and ambient temperature is common, but some are acidophiles, alkaloophiles or halophiles or thermophiles. Most are saprophytic, but a few are pathogenic to plants and animals. Phenotypically, they are diverse organisms from cocci to highly differentiated mycelia. Actinobacteria are widely distributed in aquatic and terrestrial habitats. The genome of actinobacteria vary in size from 0.93 Mb (*Tropheryma whipplei*) [144] to 12.7 Mb (*Streptomyces rapamycinicus*) [8]. The natural product-rich actinobacteria generally have large genomes of >5 Mb which contain large contiguous secondary metabolite gene clusters (at a typical length of 20–150 kbp) each genome contains more than 20 sets of putative biosynthetic genes for secondary metabolites [19]. This genetic potential makes actinobacteria potent producers of secondary metabolites with a vast spectrum of different biological activities which are applicable to agriculture and industry.

A prominent characteristic of using actinobacteria as PGPB is that phytopathogenic actinomycetes constitute only a minority of plant-associated actinobacteria which include *Streptomyces scabies*, *Streptomyces acidiscabies*, *Streptomyces turgidiscabies*, *Streptomyces ipomoeae* causing common scab diseases [80] and *Rhodococcus fascians* that cause leafy gall [91].

Members of actinobacterial taxa which are regarded as PGPA have been isolated from various sections of plants, such as root, tubers, seeds and leaves which their study as growth influencing agents is of vital importance. Also, they are useful to investigate the PGPA compounds because of their potential as a source of agroactive compounds that may aid in growth enhancement or prevention of plant diseases. In addition to the inoculation of PGPA cells or spores to plant, its seed or surrounding soil, agroactive metabolites of PGPA also can be formulated as natural pesticides or alternatives of chemical fertilizers.

Actinobacteria as plant colonizers

Bacteria which colonize plant surfaces in competitive conditions of natural habitats in soil are considered true colonists. Actinorhizal plants comprise around 200 plant species belonging to 25 genera in eight families [18]. Actinobacteria may establish compact or tight associations as it is exemplified by rhizospheric or endophytic actinobacteria. Despite their different ecological niches, free-living and endophytic bacteria use similar mechanisms to promote plant growth [122].

Ectophytic colonizers

There is a symbiotic relationship between microbial residents in rhizosphere and their host plants. The plant roots excrete various chemical attractants in rhizosphere, including organic acids, amino acids and specific carbohydrates. Some exudates can be effective as antimicrobial agents and thus give ecological niche advantage. The quantity and composition of chemoattractants and antimicrobials exuded by plant roots are under genetic and environmental control [7]. PGPA detected from the rhizospheric habitats include *Streptomyces*, *Thermobifida*, *Microbispora*, *Saccharopolyspora*, *Nocardia* and *Kitasatospora* [37].

Phytohormones or related substances of actinobacterial origin may take part in the infection and nodulation process of nodule-forming species. Actinomycetes-inoculated *Ochetophila trinervis* have effected higher development of dense zones of root hairs than control plants without inoculation or with *Frankia* alone. This may be induced by changes in the primary plant cell wall structure by helper rhizoactinomycetes [117].

Strains from *Streptomyces rochei* and *Streptomyces thermolilacinus* which were isolated from wheat rhizosphere showed high PGP activities and soil enzyme production capability which led to an increase of 12.2–24.5 % in shoot length and 1.8–2.3-fold in biomass of wheat [57].

Endophytic colonizers

It is estimated that each of the nearly 300,000 plant species on earth host endophytic bacteria [121]. Many of rhizobacteria including actinobacteria can cross from the root cortex to the vascular system, and subsequently thrive as endophytes in stem, leaves, tubers, and other organs [44]. Colonization may also originate from other part of plant such as phyllosphere, anthosphere or spermosphere [47]. Majority of endophytic actinomycetes have been isolated from roots rather than other organs. Most of the reported actinomycetes belong to *Streptomyces* genus. Members of *Microbispora* spp. were isolated more frequently from plant leaves than soil. It is plausible that endophytic actinomycetes adhere firmly to the host plant surfaces and acquire the nutrition from host surfaces using extracellular polymers containing adhesive compounds and hydrolytic enzymes [113].

Pteridic acids A and B have been found from endophytic *Streptomyces hygrosopicus* TP-A0451 isolated from a stem of bracken, *Pteridium aquilinum* [51]. Pteridic acid A promoted the root elongation of rice and induced the adventitious root formation of the kidney bean hypocotyls as effectively as indole acetic acid (IAA).

Two endophytic *Streptomyces* isolates recovered from a stress-tolerant dicotyledenous plant *Artemisia annua* L. showed protection against agronomic diseases mediated by *S. scabies*. It was revealed that these strains do not produce thaxtomin A and activate the salicylic acid (SA)-mediated plant defense responses upon pathogen challenge. Moreover, defense deficiency in *eds5* gene (enhanced disease susceptibility) which is at the upstream of SA accumulation in the signaling pathway of systemic acquired resistance (SAR) can be compensated by the salicylic acid produced by these *Streptomyces* strains [80].

Endophytic actinobacteria from the genus *Pseudonocardia* effectively stimulate certain plant defense responses and increased production of artemisinin (anti-malarial compound) by up-regulation of cytochrome P450 oxidoreductase [76]. Due to the typical trace amount production of artemisin, inoculation of *Artemisia annua* with endophytic PGPA is of significant potential economic value [76].

Endophytic strains of *Actinoplanes campanulatus*, *Micromonospora chalcea* and *Streptomyces spiralis* individually or in combination promote cucumber growth. Internal tissues of roots, stems and leaves can be colonized by these species which persist up to 8 weeks after seedling inoculation. These strains also reduce seedling damping-off and crown rots of cucumber (*Cucumis sativus*) by *Pythium aphanidermatum* [31].

Micromorphology of *Frankia* strains have the same appearance in soil as in culture, *i.e.* hyphae, sporangia with spores and vesicles (under low environmental nitrogen). Hyphae are always present in root nodules and vesicles are

found in nodules of all studied genera as well except *Casuarina* and *Allocasuarina*. Vesicle shape and size, presence or absence of septa in vesicles, and the spatial distribution of vesicles within an infected plant cell differ among symbionts and are varied by the host [18].

Symbiont-Actinobacteria specificity

Bacteria commonly enter plant tissues via stomata, wounds, lenticels, projecting areas of lateral roots, and broken trichomes by forming cell aggregates. Most of actinobacteria, however, form branching hyphae that grow on plant surfaces and enter their host plants through natural (stomatal) openings and mechanical and insect wounds [113].

Symbiont-actinobacteria specificity is observed in some bacterial-plant relationships. An individual strain may exert growth enhancing effects on some plants while inhibiting growth of some others. To begin with, the interaction between PGPA species and their plant symbionts appears to be specific, even within a crop or cultivar [40].

Phylogenetic diversity of PGPA

Proteobacteria and actinobacteria form the most common of the dominant populations found in the rhizosphere of many different plant species [115]. Actinobacteria belonging to taxonomically diverse genera (Table 1) are isolated from different plant hosts. Strains within the following 33 genera of bacteria are described for their plant growth promoting traits: *Acetobacter*, *Acinetobacter*, *Agrobacterium*, *Alcaligenes*, *Allorhizobium*, *Azoarcus*, *Azorhizobium*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Beijerinckia*, *Bradyrhizobium*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Delftia*, *Derrxia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Gluconoacetobacter*, *Herbaspirillum*, *Klebsiella*, *Mesorhizobium*, *Ochrobactrum*, *Pantoea*, *Paenibacillus*, *Pseudomonas*, *Seropedicea*, *Serratia*, *Stenotrophomonas*, *Xanthomonas* and *Zoogloea*. At the time of writing this review, around 52 genera of agroactive PGPA have been reported (Table 1). As seen, PGPA are detected among member of all *Actinobacteria* (12 orders) other than *Bifidobacteriales*, *Catenulisporales* and *Propionibacteriales*. Among reported plant-associated species, *Streptomyces* spp. has been the most predominant species followed by the *Microbispora*, *Micromonospora*, *Nocardioidea*, *Nocardia* and *Streptosporangium* [100].

Regulation of plant metabolism

Rhizospheric and soil actinobacteria have been shown to produce various phytohormones. They also can regulate

Table 1 Taxonomic distribution of reported PGPA

Family	Genera	Host plants	Reference
<i>Streptomycetaceae</i>	<i>Streptomyces</i>	<i>Maytenus Austroyunnanensis</i>	[20]
		<i>Sedum</i> sp.	[75]
		<i>Artemisia annua</i>	[146]
		<i>Alnus nepalensis</i>	[81]
		<i>Triticum aestivum</i>	[23]
<i>Streptovercillium</i>	<i>Streptovercillium</i>	<i>Oryza sativa</i>	[126]
		<i>Triticum aestivum</i>	[23]
<i>Kitasatospora</i>	<i>Kitasatospora</i>	<i>Triticum aestivum</i>	[23]
		<i>Triticum aestivum</i>	[23]
<i>Tsukamurellaceae</i>	<i>Tsukamurella</i>	<i>Triticum aestivum</i>	[23]
		<i>Maytenus austroyunnanensis</i>	[97]
<i>Intrasporangiaceae</i>	<i>Janibacter</i>	<i>Cucumis melo</i>	[141]
<i>Streptosporangiaceae</i>	<i>Herbidospora</i>	<i>Osyris wightiana</i>	[73]
		<i>Nonomuraea</i>	<i>Artemisia annua</i> <i>Maytenus austroyunnanensis</i>
<i>Actinophytocola</i>	<i>Actinophytocola</i>	<i>Oryza sativa</i>	[54]
		<i>Oryza sativa</i>	[54]
<i>Pseudonocardiaceae</i>	<i>Amycolatopsis</i>	<i>Dendranthema indicum</i>	[138]
		<i>Saccharopolyspora</i>	<i>Tripterygium hypoglaucum</i> <i>Gloriosa superba</i> <i>Maytenus austroyunnanensis</i>
<i>Kibdelosporangium</i>	<i>Kibdelosporangium</i>	<i>Heterospatha</i> sp.	[56]
		<i>Pandanus</i> sp.	[56]
<i>Pseudonocardia</i>	<i>Pseudonocardia</i>	<i>Jatropha curcas</i>	[104]
		<i>Artemisia annua</i> <i>Eucalyptus microcarpa</i> <i>Maytenus austroyunnanensis</i> <i>Lobelia clavata</i> <i>Acacia auriculiformis</i> <i>Oroxylum indicum</i>	[144] [60] [63] [103] [21] [30] [45]
<i>Streptoalloteichus</i>	<i>Streptoalloteichus</i>	<i>Dendranthema indicum</i>	[138]
		<i>Dendranthema indicum</i>	[138]
<i>Glycomycetaceae</i>	<i>Glycomyces</i>	<i>Sambucus adnata</i>	[46]
		<i>Scoparia dulcis</i> <i>Maytenus austroyunnanensis</i>	[94]
<i>Micromonosporaceae</i>	<i>Actinoplanes</i>	<i>Triticum aestivum</i>	[23]
		<i>Catellatospora</i>	<i>Castanea sativa</i> <i>Corylus avellana</i> <i>Equisetum arvense</i>
<i>Dactylosporangium</i>	<i>Dactylosporangium</i>	<i>Tripterygium wilfordii</i>	[38]
		<i>Plantactinospora</i>	<i>Maytenus austroyunnanensis</i>
<i>Polymorphospora</i>	<i>Polymorphospora</i>	<i>Bruguiera gymnorhiza</i>	[38]
		<i>Sonneratia alba</i>	[38]
<i>Jishengella</i>	<i>Jishengella</i>	<i>Acanthus illicifolius</i>	[38]
		<i>Phytomonospora</i>	<i>Artemisia annua</i>
<i>Phytohabitans</i>	<i>Phytohabitans</i>	<i>Orchid</i>	[38]
		<i>Micromonospora</i>	<i>Pisum sativum</i> <i>Lupinus angustifolius</i> <i>Pisum sativum</i> <i>Tulbaghia violacea</i>
<i>Cellulomonadaceae</i>	<i>Oerskovia</i>	<i>Ginkgo</i> sp.	[64]
<i>Nocardiaceae</i>	<i>Rhodococcus</i>	<i>Cercidiphyllum Japonicum</i>	[70]
		<i>Artemisia annua</i>	[147]
<i>Gordonia</i>	<i>Gordonia</i>	<i>Maytenus austroyunnanensis</i>	[97]
		<i>Nocardia</i>	<i>Jatropha curcas</i> <i>Callitris preissii</i>
<i>Geodermatophilaceae</i>	<i>Blastococcus</i>	<i>Cercidiphyllum japonicum</i>	[70]
<i>Microbacteriaceae</i>	<i>Leifsonia</i>	<i>Ginseng</i> sp.	[105]

Table 1 continued

Family	Genera	Host plants	Reference
<i>Thermomonosporaceae</i>	<i>Actinoallomurus</i>	<i>Oryza sativa</i> <i>Acacia auriculiformis</i>	[55] [125]
	<i>Actinocorallia</i>	<i>Duranta repens</i> <i>Millettia reticulata</i>	[97]
<i>Nocardiopsaceae</i>	<i>Actinomadura</i>	<i>Maytenus austroyunnanensis</i>	[102]
	<i>Nocardiopsis</i>	<i>Maytenus austroyunnanensis</i>	[97]
<i>Nocardiodaceae</i>	<i>Nocardioides</i>	<i>Carex scabrifolia</i> Steud	[119]
	<i>Kribbella</i>	<i>Pittosporum angustifolium</i>	[64]
	<i>Flindersiella</i>	<i>Eucalyptus microcarpa</i>	[61]
<i>Mycobacteriaceae</i>	<i>Mycobacterium</i>	<i>Triticum aestivum</i>	[23]
		<i>Paris yunnanensis</i>	[97]
<i>Microbacteriaceae</i>	<i>Microbacterium</i>	<i>Triticum aestivum</i> <i>Maytenus austroyunnanensis</i>	[23] [97]
<i>Promicromonosporaceae</i>	<i>Promicromonospora</i>	<i>Maytenus austroyunnanensis</i>	[96]
<i>Dietziaceae</i>	<i>Dietzia</i>	<i>Cercidiphyllum japonicum</i> <i>Schima</i> sp.	[77]
<i>Micrococcaceae</i>	<i>Arthrobacter</i>	<i>Triticum aestivum</i>	[23]
	<i>Micrococcus</i>	<i>Polyspora axillaris</i> <i>Aquilaria sinensis</i>	[145] [22]
<i>Actinosynnemataceae</i>	<i>Lechevalieria</i>	<i>Triticum aestivum</i>	[23]
	<i>Lentzea</i>	<i>Triticum aestivum</i>	[23]
<i>Kineosporiaceae</i>	<i>Kineosporia</i>	<i>Tripterygium wilfordii</i>	[71]
	<i>Kineococcus</i>	<i>Limonium sinense</i>	[12]
<i>Streptosporangiaceae</i>	<i>Herbidospora</i>	<i>Osyris wightiana</i>	[78]
		<i>Alpinia galangal</i> <i>Triticum aestivum</i>	[123] [19]
	<i>Planotetraspora</i>	Not specified	[56]
	<i>Streptosporangium</i>	<i>Maytenus austroyunnanensis</i> <i>Orchid</i>	[97] [53]
		<i>Sphaerisporangium</i>	<i>Oryza sativa</i>
	<i>Nonomuraea</i>	<i>Maytenus austroyunnanensis</i> <i>Artemisia annua</i>	[96] [72]

level of phytohormones production in plants or degrade phytohormones. Current information of actinobacterial phytohormones and their effects on plants are summarized in Table 2. There are a number of examples on regulation of phytohormones by PGPA. In vitro treatment of winter rye seeds with auxin producing endophytic actinobacteria increased the germination capacity and enhanced an intensive seedling growth [85]. An increased availability of growth regulators produced by applying *Streptomyces* spp. as a seed-coating has been shown to improve tomato growth. *Streptomyces olivaceoviridis* and *Streptomyces rochei* produce substantial amounts of growth-regulating substances, including auxins, gibberellins and cytokinins which increase the shoot length and shoot fresh mass, respectively [1]. The supernatant of *Micromonospora* sp. MM18 was shown to have a definite positive effect on plant growth and evidence suggested that the supernatant contains IAA and gibberellic acid (GA) at the level of autoregulation of nodulation [116]. The culture filtrates of

S. olivaceoviridis enhance spikelet number, spike length and mass of the developing grain of wheat plants. This activity attributed to increase in bioavailable auxins (IAA), as well as gibberellins and cytokinins which are produced by the bacterium [85].

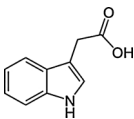
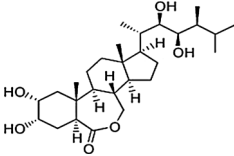
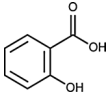
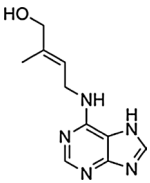
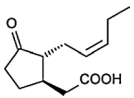
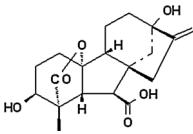
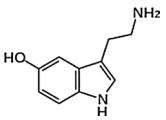
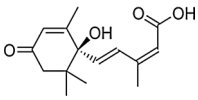

Enhancement of nutrient availability

Actinorhiza have great impact on mineralization and mobilization of nutrients required for plant growth as well as production of vitamins and other growth factors and promoting mycorrhizal function.

Nitrogen fixation

Endophytic PGPA such as *Frankia* species can improve the growth of their plant host by fixation of nitrogen. Enzymatic conversion of molecular nitrogen to ammonia

Table 2 Phytohormones metabolites produced or modulated by plant symbiotic actinobacteria

Hormone	Structure	Functions in plant [81]	Actinobacterial producer or modulator	References
Indole-3-acetic acid (Auxin)		Stimulates seed and tuber germination, initiates lateral and adventitious root formation; affects biosynthesis of metabolites	<i>Micromonospora</i> , <i>Streptomyces</i> <i>Frankia</i>	[117] [49]
Brassinolide		Increase content of chlorophyll, stimulate protein synthesis, activate certain enzymes and regulate cellular differentiation	<i>Streptomyces</i>	[85]
Salicylic acid		Induce SAR, prolong life of flowers, inhibit ethylene biosynthesis, and facilitate pollination of certain plants	<i>Streptomyces</i>	[80]
Cytokinins		Key role in plant morphology, leaf senescence and source-sink relationships, key regulators of the plant growth-defence	<i>Micromonospora</i> , <i>Streptomyces</i> , <i>Actinoplanes</i>	[111]
Jasmonic acid		Induce ISR against necrotrophs, activates Phylloptosis, tuber formation, fruit ripening, and pigment formation	<i>Streptomyces</i>	[85]
Gibberellins		Stimulate stem elongation by stimulating cell division and elongation. Stimulates bolting/flowering	<i>Micromonospora</i> , <i>Frankia</i> , <i>Actinoplanes</i>	[117] [87]
Serotonin (5-hydroxytryptamine)		Structural analog of auxins. Plant metabolize serotonin to IAA	<i>Streptomyces</i>	[130]
Absciscic acid (ABA)		Phylloptosis, closure of stomata and aging	<i>Streptomyces</i>	[6]
Ethylene		Disrupts geotropism, promotes phylloptosis, and accelerates Fruit maturation and aging	*	[39] [1]

* Actinobacteria can stimulate its degradation

is catalyzed by nitrogenase, an oxygenlabile enzyme complex highly conserved in free-living and symbiotic diazotrophs.

Frankia is characterized by a slow growth rate and formation of vesicles and spores which are developmental structures for survival in environment. Vesicles are the site for actinorhizal nitrogen fixation, while spores contained in multilocular sporangia are the reproductive structures of *Frankia*.

Nitrogenase (*nifH*) genes are also detected in non-*Frankia* symbiont actinobacteria, including *Thermomonosporaceae* and *Micromonosporaceae* families, which are isolated from *Casuarina equisetifolia* root [132]. In another study, it was observed that *Micromonospora* sp. promotes both the *Discaria trinervis*-*Frankia* [116] and the *Medicago sativa*-*Sinorhizobium meliloti* nitrogen-fixing symbioses by producing IAA and GA [118]. Other actinobacteria in addition to *Micromonospora* also stimulate alfalfa

nodule formation, even in the presence of abundant inorganic nitrogen in soil [49].

Biosynthesis of metal chelators

Actinobacteria produce siderophores to facilitate iron uptake by binding to Fe^{3+} from the environment. Siderophores have various chemical structures and form a family of at least 500 different compounds. The most prevalent structural groups include catechols (such as in streptobactin from *Streptomyces* spp.) and hydroxamate (such as desferrioxamine from *S.coelicolor* and amyachelin from *Amycolatopsis*) [135].

Some PGPA can produce siderophoric compounds that can deprive pathogenic fungi by their higher affinity for iron while some may draw iron from heterologous siderophores produced by cohabiting microorganisms [82].

Phosphorus solubilization

Being a critical macronutrient for plant growth and development, most part of the total soil phosphorus is unavailable for uptake due to rapid immobilization by soil organic and inorganic components [59]. Among the several potential mechanisms for phosphate solubilization those involving the production of chelating compounds, like organic acids or by means of a modification of pH are the more often described [107]. In addition to solubilizing the bound phosphorus to soil particles, microorganisms are able to mineralize organic phosphorus and release soluble inorganic phosphate into soil by decomposition of phosphate-rich organic compounds [3].

The secretion of organic acids from plant roots enhances phosphorus availability by chelating cations such as Fe^{+2} , Al^{+3} or Ca^{+2} , which form insoluble phytates and also helps in the solubilization of insoluble phytates. Actinobacteria can hydrolyze phytate (which constitutes up to 60 % of soil organic phosphorus) by secreting phosphatases such as phytases and acidic/alkaline phosphatases [114]. Phosphate solubilization by *Micromonospora endolithica* is reported in growth promotion of beans (*Phaseolus vulgaris* L.) [33].

Antagonism of PGPA against phytopathogens

Phytopathogens can be categorized to major and minor pathogens, which kill or suppress the growth of their hosts, respectively. Actinobacteria, not only support their host plant indirectly, they can also directly antagonize phytopathogens as biocontrol agents. Actinobacteria have high capacity to produce antimicrobial agents, siderophores, hydrolytic or detoxifying enzymes and therefore can directly antagonize phytopathogens. Also, they can cope

indirectly with phytopathogens by supporting the growth of host plants by their competition with phytopathogens for iron acquisition, nutrients, minerals and colonization site. These strategies are especially useful for minor pathogens, which reduced plant growth without distinct symptoms. Symbiotic actinobacteria inhibit growth of minor phytopathogens. For example, applications of *Streptomyces lydicus* WYEC 108 as a soil mix are expected to control *Fusarium*, *Rhizoctonia*, *Pythium*, *Phytophthora*, *Phytomatotricum*, *Aphanomyces*, *Monosporascus*, *Armillaria*, *Sclerotinia*, *Postia*, *Verticillium*, *Geotrichum*, and other root decay fungi [127, 131, 142] and it is marketed as an antifungal agent for greenhouses, nurseries, turf grasses, and agricultural use sites [35, 48, 79]. It was also shown that endophytic actinobacteria, including *Actinoplanes campanulatus*, *Micromonospora chalcea* and *Streptomyces spiralis* reduce seedling damping-off, and root and crown rots of mature cucumber (*Cucumis sativus*) caused by *Pythium aphanidermatum*, *S. spiralis* produces IAA, GA, indole-3-pyruvic acid (IPYA), and isopentenyl adenine (iPa), *A. campanulatus* produces IAA, IPYA, and GA, whilst *M. chalcea* produced only IAA and IPYA [32].

PGP activity of some strains of *Streptomyces* having biological control activity against chickpea wilt caused by *Fusarium oxysporum* f. sp. *ciceri* was shown effective in the greenhouse on sorghum [42]. In the rice field, *Streptomyces* strains significantly enhanced tiller numbers, panicle numbers, filled grain numbers, weight stover yield, grain yield, total dry matter and root length, volume and dry weight, over the control. In the rhizosphere soil, the PGPA significantly enhanced microbial biomass carbon, total nitrogen, dehydrogenase activity, available phosphorous and amount of organic carbon over the control [42, 43].

Stimulation of immune responses in plants by PGPA

Immunity response of plant cells can be stimulated by entrance of phytopathogenic actinobacteria. Signal transduction system of the host plant can recognize the phytopathogens in contaminated cell(s) and triggers other cells of the plant to express defense genes and induce systematic resistance (ISR). Cell components of phytopathogens have important roles in ISR. Also, when a pathogen induces a hypersensitive reaction, systemic acquired resistance (SAR) activates in plants to limit the infection to a local necrotic lesion.

ISR is associated with an increase in sensitivity to jasmonate and ethylene hormones (JA/ET) in plants [40]. The endophytic actinobacteria appeared to be able to “prime” both the SAR and JA/ET pathways (Fig. 1). Upon diverse pathogen challenge, either, the SAR or JA/ET pathway was triggered in the *Micromonospora*-inoculated roots leading to greater host resistance [49]. *Streptomyces*

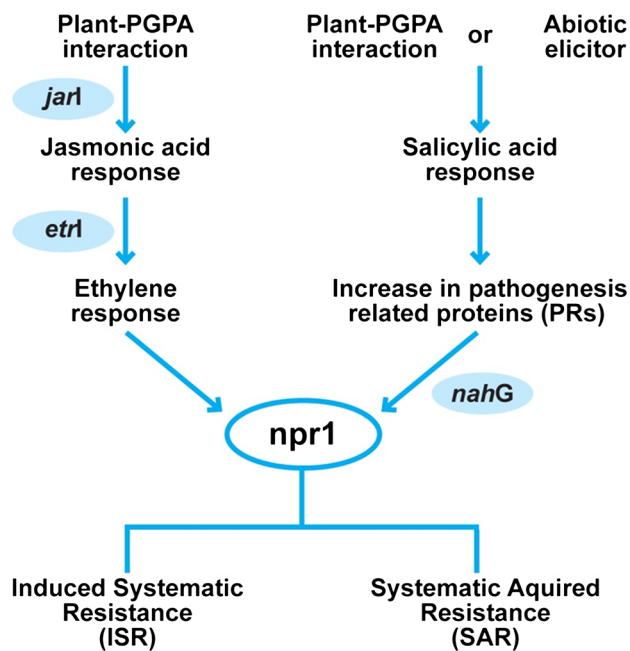


Fig. 1 Induced systemic resistance (ISR) and systematic acquired resistance (SAR) mechanisms in relation to interaction with PGPA. Adapted from Van Loon et al. [133]

padanus-colonized plants induced expression of proteins or enzymes that functioned directly in defense or stress response classes of glutathione *S*-transferase, although endochitinases were exclusively suppressed [84].

Antibiotic production as principle function of PGPA

Kasugamycin, from *Streptomyces kasugaensis*, is widely used in Japan for the control of rice blast, which is caused by *Pyricularia oryzae* Cavara and has also been shown effective in control of bacterial fire blight [93]. Polyoxin B and D produced by *Streptomyces cacaoi* var. *asoensis* can inhibit chitin synthase. Polyoxin B is applied against a number of fungal pathogens in fruits, vegetables and ornamentals and Polyoxin D is marketed as Endorse™ for controlling rice sheath blight caused by *Rhizoctonia solani* [26]. Validamycin A isolated from *Streptomyces* sp. affects on invertebrates is an inhibitor of trehalase [88]. Mildiomycin, from *Streptoverticillium rimofaciens*, is active against several powdery mildews on various crops and acts as an inhibitor of the fungal protein biosynthesis [36]. Mycostop™ is a biofungicide that contains *Streptomyces griseoviridis* as the active ingredient. *S. griseoviridis* strain K61 which colonize specific plant rhizosphere is used in root dipping or growth nutrient treatment of flowers, potted plants, greenhouse cucumbers and various other vegetables [35, 66]. Production of geldanamycin by *Streptomyces violaceusniger* YCED9 [10] and *S. hygroscopicus* was effective

in protection of lettuce and potato against *P. ultimum* and scab, respectively [128].

A number of secondary metabolites of actinobacteria which are involved in interaction with plants or phytopathogens cannot be produced in axenic conditions in the lab. The value of co-cultivating different organisms to find novel compounds is undisputed [111]. Recent studies show that activation of dormant gene clusters in actinobacteria and other microorganisms can be assessed by co-culturing. It is shown that metabolites of *Streptomyces* sp. were able to induce biosynthesis of Opolyketides including orsellinic acid, lecanoric acid, cathepsin K inhibitors, S-9775A and S-9775B in *Aspergillus nidulans* [112].

Enzyme producing PGPA as biocontrol agents

Actinobacteria have high potential in enzyme production in which some are used as biocontrol agents. These enzymes can degrade or detoxify virulence factors of phytopathogens. Examples of the best characterized defense enzymes are peroxidases, polyphenol oxidases and phenylalanine ammonia-lyases [68]. Some actinobacteria produce extracellular enzymes such as chitinase, glucanases and peroxidases which can affect the cell walls of fungal hyphae, e.g. *Streptomyces lydicus* WYEC108 is capable of destroying germinating oospores of *Pythium ultimum* [24]. This strain is commercialized as Actinovate® which causes plant growth promotion even in the absence of pathogen. Antagonistic *Streptomyces* isolates against *Fusarium oxysporum* produced hydrocyanic acid and showed activity against *Rhizoctonia bataticola* (dry root rot and sorghum disease) [41].

Micromonospora carbonaceae isolate can lyse, via cellulase production, the cell walls of *Phytophthora cinnamomi*, a pathogen that causes root rot. Moreover, a synergism was observed when the cellulase-producing *M. carbonaceae* was co-inoculated with the antibiotic producing *Streptomyces violascens* in that more of the fungal hyphae were degraded [34].

Thaxtomin A is a dipeptide phytotoxin produced by the plant pathogen *S. scabies*. It is a potent inhibitor of cellulose biosynthesis and triggers the release of cello-oligosaccharides from expanding plant tissue.

Thaxtomin A can be degraded by some members of the actinomycetes and they protected growing potato plants against common scab [29]. Alkaline protease inhibitors, as a novel class of antifungal proteins are reported among metabolites of *Streptomyces* species. They can inhibit the fungal serine alkaline protease as it was used against phytopathogenic fungi such as *Alternaria*, *Fusarium* and *Rhizoctonia* by this mechanism [134].

Biotransformation of fomannoxin, a fungal phytotoxin, by soil actinobacteria is also reported.

Streptomyces-mediated modulation of spruce infection with *Heterobasidion abietinum* 331 does not depend on the availability of fomannoxin and some soil *Streptomyces* isolates were able to change fomannoxin to its three new derivatives without phytotoxic activity [50].

Most bacterial plant pathogens rely upon autoinducer-mediated quorum-sensing to turn on gene cascades for their key virulence factors (e.g. cell-degrading enzymes and phytotoxins). Certain PGPB quench pathogen quorum-sensing capacity by degrading autoinducer signals, thereby blocking expression of numerous virulence genes [89]. Degradation of signaling molecules led to lack of biofilm formation by pathogenic or growth-retarding bacteria.

Alleviation of environmental stresses

Drought, high temperature, radiation, heavy metals and other toxic pollutants, damage and wound by insects, other invertebrates and phytopathogens are important environmental stresses for plants. Actinobacteria can reduce biotic and abiotic stresses by regulation of phytohormones and increasing plant growth. For example, IAA biosynthesis is related to environmental stress, including acidic pH, osmotic and matrix stresses and carbon limitation [120].

Ethylene is also a stress hormone which can exacerbate some of the symptoms of the stresses or it can lead to responses that enhance plant survival under adverse conditions by transcription of genes encoding defensive proteins [40]. Ethylene is also required to break seed dormancy but, following germination, a sustained high level of ethylene may inhibit root elongation. PGPA bounded to the seed coat of a developing seedling may reduce the ethylene level by producing 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase to the point where root growth has occurred [39]. Deaminase production is also reported for *Kibdelosporangium phytohabitans* isolated from the oil-seed medicinal plant *Jatropha curcas* L. which adjusts levels of ethylene during climacteric fruit development and damage during stress responses [58, 137].

Drought-tolerant endophytic actinomycetes of *S. coelicolor*, *S. olivaceus* and *S. geysiriensis* which are isolated from plants in arid and drought regions can enhance the intrinsic water stress tolerance of plants from -0.05 to -0.73 MPa by production of IAA phytohormones [140].

Beside altering bioavailability of metals, secondary metabolites of PGPA can sequester the heavy metals in rhizosphere. The hydroxamate siderophores contained in culture filtrates of *S. acidiscabies* E13 promotes Cowpea growth under nickel contamination by binding iron and nickel, thus playing a dual role of sourcing iron for plant use and protecting against nickel toxicity [27].

Competition between pathogens and PGPB can limit disease incidence and severity. PGPA and abundant PGPB rapidly colonize plant surfaces and use most of the available nutrients, making it difficult for pathogens or growth-retardant strains to colonize. PGPB can contribute to ecological fitness by ameliorating crop abiotic stresses (particularly decreased water and nutrient availability) which sustain crop yields despite decreased nutrient and water inputs [40]. Bacterial modulation of phytohormone status promotes root growth, increasing access to soil moisture [28].

Improving the soil texture

Implementation of agricultural chemicals including fertilizers and pesticides caused a rapid increase in the productivity of agricultural products in a short course, but lead to negative impact on soil texture and quality in long term of their application during decades. Many of chemical fertilizers are produced from fossil fuels; therefore their using can deplete non-renewable energy. Other adverse effects of chemical fertilizers are erosion of soil, damaging natural flora and biodiversity, making the crop more susceptible to the attack of diseases and reducing the soil fertility [3]. It was shown that higher organic matter caused more water retention. A bare land with poor soil structure and poor soil fertility cannot effectively support plant growth. Prohibition of chemical use and implementation of biopesticides results in more organic matter that increase yields for farms in drought years, when organic farms have had yields 20–40 % higher than their conventional counterparts [143]. Microbial cooperation in the rhizosphere reflects the formation and stabilization of soil aggregates where in soil particles are held together by bacterial products followed by hyphae of filamentous actinobacteria which form stable microaggregates of size 2–20 μm diameters [9].

Field implementation of PGPA

Treatments of plants with PGPA include drench application [4] and seed bacterization [67], seedling treatment [5], bioformulation, biopreparation, spray on the folia and a combination of these treatments [69]. Field-tested formulations, mostly based on dry powder (charcoal, lignite, farmyard manure, etc.) have inherent problems of appropriate shelf-life and cell viability. Peat [108] or biodegradable gel matrices [110] at seed sowing may enhance bacterial survival in the rhizosphere [28].

Despite a number of bacteria which are used commercially as adjuncts to agricultural practice, only a few strains of actinobacteria such as *Streptomyces griseoviridis* and *Streptomyces lydicus* are developed as commercial biofertilizers. A number of issues for commercializing the PGPB

Table 3 Commercially developed PGP products from actinobacteria. Adapted from Palaniyandi et al., 2013 [90] and Rezzonico et al. [106]

Commercialized product	Bioactive actinobacterium or their metabolites	Application
Actinovate® AG/Actinovate® SP	<i>Streptomyces lydicus</i> WYEC108	Plant growth promotion and fungicide
Micro108® soluble/Micro108® Seed Inoculant	<i>Streptomyces lydicus</i> WYEC108	Plant growth promotion
Actino-Iron®	<i>Streptomyces lydicus</i> WYEC108	Plant growth promotion and fungicide
Thatch Control	<i>Streptomyces violaceusniger</i> strain YCED 9	Fungicide and nematocide
Mycostop®	<i>Streptomyces griseoviridis</i> strain K61	Fungicide
YAN TEN <i>Streptomyces saraceticus</i>	<i>Streptomyces saraceticus</i> KH400	Fungicide
AFFIRM ^{WDG}	Polyoxin D (<i>Streptomyces cacaoi</i> var. <i>asoensis</i>)	Fungicide
PH-D® Fungicide	Polyoxin D (<i>Streptomyces cacaoi</i> var. <i>asoensis</i>)	Fungicide
Keystrepto™	Streptomycin (<i>Streptomyces griseus</i>)	Bactericide
Agri-Mycin 17 WP	Streptomycin (<i>Streptomyces</i> sp.)	Bactericide
Strepto	Streptomycin (<i>Streptomyces griseus</i>)	Bactericide
Plantomycin WG	Streptomycin (<i>Streptomyces griseus</i>)	Bactericide
Ag-Streptomycin	Streptomycin (<i>Streptomyces griseus</i>)	Bactericide
Kasumin™	Kasugamycin (<i>Streptomyces kasugaensis</i>)	Bactericide
Biomycin	Kasugamycin (<i>Streptomyces kasugaensis</i>)	Fungicide and bactericide
Omycin	Kasugamycin (<i>Streptomyces kasugaensis</i>)	Fungicide and bactericide

strains need to be addressed, including (1) determination of most important traits for efficacious functioning and subsequent selection of PGPB strains with appropriate biological activities; (2) consistency among regulatory agencies in different countries regarding which strains can be released to the environment; (3) concluding the advantages and disadvantages of using rhizospheric versus endophytic strains; (4) selection of PGPB strains that have optimal function under extreme or specific environmental conditions; (5) development of more effective means of applying PGPB to plants in various settings (e.g., in the field versus in the greenhouse) and (6) understanding the potential interactions between PGPB and mycorrhizae and other soil fungi [40]. Commercially developed PGP products from actinobacteria are shown in Table 3.

PGPA versus other PGPB

Strong colonization [66], production of resistant spores to irradiation, heat and drought [140] are among other advantageous traits of PGPA towards other PGPB. Actinobacteria may convert plant exudates into a form that can be used by another PGPB in rhizosphere. Some PGPA species have appeared to promote plant growth by acting both as biofertilizers and biopesticides. Unlike the adverse effect of the continuous use of chemical fertilizers, PGPA when applied to the soil improve the soil structure because of their filamentous biomass.

One of the advantages of PGPA over other PGPB is that a number of PGPB have emerged as opportunistic human pathogens. Some members of the plant-associated genera

including, *Burkholderia*, *Enterobacter*, *Herbaspirillum*, *Ochrobactrum*, *Pseudomonas*, *Serratia*, *Staphylococcus*, and *Stenotrophomonas* can enter into interaction with humans [11].

Future perspective of PGPA and concluding remarks

Integrated pest management (IPM) are based on two important principles in modern agriculture: (1) increasing the productivity of agriculture to provide food needed for increasing world population and (2) confining environmental destruction to the lowest possible level. The aim of IPM is not eradication of pest; it is reducing their number at level with less economic effects [143]. Chemical pesticides and fertilizers can meet IPM aims when properly used; however, misuse can have various adverse effects [3]. Considering PGPA as natural antagonists of pests and phytopathogens, high potential to promote the growth of agricultural plants, a member of ecosystems and biological resources are driving forces for replacing chemical pesticides with PGPA.

Although phytoprotection using symbiont actinomycetes is widely discussed, extensive field experiments are required to investigate the involved mechanisms and consequences of cocultivation or inoculation of PGPA. Population dynamics, metabolic activity and spatial distribution of PGPA in field can be investigated by bioluminescent gene transformation approach. Evidence for the horizontal transfer of a pathogenicity island carrying the virulence gene is considered as a related risk of implementation of actinobacteria for biocontrol [16]. Effect of introduced actinobacteria

on non-target plants, animals and microorganisms has also to be evaluated.

More progress in identification and diversity of PGPA along with their colonization ability and mechanism of action will facilitate their application as a component in the management of sustainable agricultural system. Therefore, diversity of commercial PGPA formulations for plant growth and protection will increase in future.

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