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Plant growth promotion by streptomycetes: ecophysiology, mechanisms and applications

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Abstract

The genus *Streptomyces* comprises filamentous Gram-positive bacteria that are widely recognized for their ability to produce bioactive compounds such as antimicrobial, antiparasitic and immune-suppressing compounds via secondary metabolism. These bioactive compounds represent a third of all commercially available antibiotics. Streptomycetes have been found in beneficial associations with plants where they have improved plant growth and protected against pests, which have attracted the attention of researchers worldwide. This review focuses on the potential of streptomycetes as plant growth-promoting bacteria (PGPS) and considers features related to secondary metabolic pathways, interactions with host plants and recent advances in elucidating plant growth-promoting mechanisms. Such advances in basic knowledge have increased the prospects for streptomycetes to be used as bioinoculants for sustainable agriculture.

Keywords: *Streptomyces*, Actinobacteria, Biotechnological potential

Introduction

It has been estimated that the world's population will reach about nine billion by 2050 [1], which will require high levels of yield from agricultural systems. Centered on the Green Revolution model established in the last century, a range of research and technology transfer initiatives have been employed to meet the demand for food, fiber, and energy. However, it has become increasingly clear that the conventional systems of food production have many negative impacts on the environment [2].

To develop food production under environmentally and socially sustainable systems represents one of the twenty-first century's greatest challenges for agricultural researchers. One of the most promising initiatives for a new model of agriculture is based on converting the natural processes that occur in the soil–plant system into biological input technologies. In this context, microorganisms, their products and their processes are essential resources for a new generation of biotechnologies applicable to plant production and protection, and potentially a paradigm shift in agricultural practice.

Using plant growth-promoting bacteria (PGPB) for the benefit of agriculture has received increasing attention and acceptance [3–5]. Besides the well-studied Gram-negative plant-associated bacteria, Gram-positive bacteria can also have beneficial interactions with plants and promote plant growth [6–8]. *Streptomyces* is the most widely studied genus of Gram-positive PGPB and is the central subject of this review. This genus comprises a wide diversity of species that have a high G-C (guanine and cytosine) ratio in its DNA, up to 75 % of its genome [9]. This genus produces a wide variety of biologically active compounds; some with plant growth activity. It has been suggested by some authors that the increasingly intensive surveys of soil-borne microbes have resulted in a decreased frequency of newly discovered compounds [10]. However, the metabolic versatility and cosmopolitan behavior of *Streptomyces* species have enabled them to be isolated from different environments, some of

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which have not yet been explored, hence, presenting an opportunity to discover new bioactive compounds.

Morphogenetic and physiological aspects of the *Streptomyces* genus have been reviewed [11, 12]. Other reviews have focused on the biotechnological potential of plant-associated endophytic actinobacteria [10] and free-living plant growth-promoting actinobacteria [7]. This review presents an overview of the plant growth-promoting ability of various species from the genus *Streptomyces*; it considers historical aspects of their discovery, their physiological features, their plant growth mechanisms and their application as bioinoculants in agriculture.

Review

Historical and taxonomic aspects

Nearly 200 years after Antony van Leeuwenhoek reported the first observation of bacteria in 1684 using his own handcrafted microscope, other pioneers, such as Ferdinand Cohn and Robert Koch, founded modern concepts about bacteriology as a science domain [13]. It took another 200 years to identify and reach the current understanding of actinobacteria. Further, only 204 years after van Leeuwenhoek studies, the first description of a microorganism that eventually became known as an actinobacterium was described, when Armauer Hansen discovered a microorganism in the tissues of leprosy patients, which was later described as the etiologic agent of this disease in 1874 [14].

In 1875, Cohn described the first Actinobacteria species, which he named *Strepthrotrix foersteri*. He isolated this microbe from samples of human tear ducts provided by R. Foerster, a medical friend. Cohn supposed that *Strepthrotrix foersteri* was not associated with any disease, but that it reached the patient's eye through airborne soil particles. Later, he observed that *Strepthrotrix foersteri* had morphological features of fungi and bacteria [14]. However, the proposed nomenclature for the bacterial genus was deemed invalid because *Strepthrotrix* had already been classified as a true fungus by Corda in 1839 [15]. Then in 1877, Carl Otto Harz described the etiologic agent of "lampy jaw". Harz observed structures similar to reproductive bodies and hyphae of fungi; therefore, he considered the microorganism to be a fungus and named it *Actinomyces bovis* [14]. In 1882, Robert Koch discovered another microorganism during his observations using light microscopy that is now recognized as an actinobacterium: the tuberculosis pathogen *Mycobacterium tuberculosis* [16]. Koch observed that the microbes presented morphological characteristics that were similar to those of microorganisms previously described by Hansen associated with leprosy disease [17].

Although there was a clear relationship between these microorganisms, it was not until 1916 that R.E. Buchanan suggested a nomenclature and classification for this group. Buchanan proposed the order Actinomycetales, containing the family *Actinomycetaceae* and the following genera: *Actinobacillus*, *Leptotrichia*, *Actinomyces*, and *Nocardia* [18]. In 1943, Waksman and Henrici proposed a new classification for the actinomycetes, which was based on their ability to form branching cells. Waksman and Henrici observed that one actinomycete group formed a condensed mat of interlinked branching hyphae that produced reproductive spores. The *Streptothrix* described by Cohn fell into this group, but due to the invalid genus name, Waksman and Henrici named it *Streptomyces*, which means "twisted fungus" [19].

In the fourth decade of the twentieth century, *Streptomyces* was recognized. Many studies were performed during this time to find chemotherapeutic treatments to control tuberculosis [17]. In 1943, Waksman again received attention, this time due to his greatest discovery: the antibiotic streptomycin isolated from *Streptomyces griseus* is effective against the tuberculosis pathogen [19]. About 600 validated species of *Streptomyces* have now been described following their isolation from many environmental sources. They are now the subject of research to discover new bioactive compounds for the pharmaceutical and agricultural industries [20].

The first proposed nomenclature of actinobacteria was based on sporulation patterns. Although morphological characteristics are typically important for *Streptomyces* identification, some studies have demonstrated that classification based on cell morphology, colony pigmentation, and physiological features do not always reflect the natural phylogenetic relationship between actinobacteria and related organisms [21]. Introduction of the polyphasic taxonomic approach combined molecular and biochemical analyses which elucidated streptomycetes systematics. In addition, increased availability of 16S rRNA sequence data has enabled accurate studies of taxonomic affiliations and phylogenetic relationships [15, 21, 22].

The *Streptomyces* genus belongs to the Streptomycetaceae family and the single-order *Streptomycetales* [23]. This order belongs to both phylum and class Actinobacteria [23]. The actinobacteria from the *Streptomyces* genus are the most extensively studied mycelial actinobacteria. They are aerobic, Gram-positive bacteria that grow as branching filaments that consist of vegetative mycelia and aerial hyphae [15, 24]. Some morphological and physiological properties, along with the ability to produce a wide range of pigments, have been used not only to classify the *Streptomyces* genus [25, 26], but also to study its ecological distribution and biotechnological potential [27, 28].

Morphological differentiation and physiology

Streptomycetes have a markedly different cell envelope structure than Gram-negative bacteria, such that *Streptomyces* genus has been identified using cell wall composition [29, 30]. Similar to other actinobacteria, streptomycetes have no outer membrane and their cell walls have a thick peptidoglycan (or murein) layer [31]. The presence of LL-diaminopimelic (LL-DAP) in the cell wall confers a typical chemotaxonomic characteristic to all members of the *Streptomyces* genus [32, 33], and its presence together with glycine characterizes the cell wall as Type I [31, 34]. Teichoic acids (anionic glycopolymers) comprise another important cell wall component that confers a negative charge to the cell surface and contributes to physiological functioning and cell co-aggregation [35, 36].

The life cycle is initiated when favorable environmental conditions and nutrient availability promote spore germination [12] (Fig. 1). Next, germ tubes grow to form syncytial vegetative or substrate mycelia, which consist of interconnected feeding hyphae that are responsible for nutrient uptake [37]. When nutrients become scarce, or another stress condition occurs, programmed cell death of the substrate mycelia and cell differentiation at the center of the colony result in aerial hyphae [12, 38]. These aerial hyphae are subtly distinguishable from the feeding hyphae, as they are covered by a hydrophobic fibrous layer, perhaps to help the aerial hyphae break the surface tension on air pockets in the soil, whereas the feeding hyphae have a smooth hydrophilic surface [24].

The growth of *Streptomyces* involves hyphal tip extension and sub-apical branching [39]. Unlike the process in rod-shaped bacteria where cytokinesis is based on building a cross wall by depositing murein into lateral walls, *Streptomyces* growth occurs by hyphae production at the cell pole [37]. Although it is not clearly elucidated, this cell growth pattern is regulated by the apical protein complex DivIVA. In *Bacillus subtilis*, DivIVA interacts with the Min system to coordinate division at the middle of the cell. In contrast, in *Streptomyces*, the Min system is absent, thus DivIVA affects division at the cell tip. Another aspect of streptomycetes growth involves the conservation of two groups of proteins, the tubulin homolog FtsZ and several membrane proteins, which are both associated with cytokinetic Z-ring and septal peptidoglycan [11].

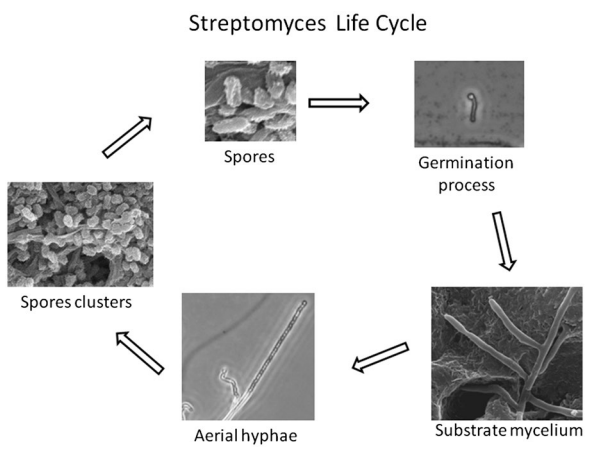

Fig. 1 Life cycle of *Streptomyces* [167] modified

The last phase of the *Streptomyces* life cycle consists of the apical cells of the aerial hyphae differentiating into a spore chain [12]. A differentiating apical compartment grows by tip extension and starts synchronous, multiple cell divisions into a developmentally controlled form [40]. Again, there is the participation of FtsZ, which leads to sporulation septa and then these pre-spores assemble thick spore walls by depositing actin [41]. The size of *Streptomyces* spores can range from 0.7 to 1.2 μm [42, 43]. These last two phases of the *Streptomyces* life cycle are closely related to antibiotic production [14]. During programmed cell death of the substrate mycelia, antibiotics are simultaneously produced, perhaps to protect the nutrient sources against competitor microorganisms [44, 45].

Among the 23,000 bioactive secondary metabolites produced by microorganisms, two-thirds are produced by actinobacteria, and *Streptomyces* spp. accounts for more than 70 % of these [46]. This production of secondary metabolites is attributed to the development of aerial hyphae as a result of nutrient limitation [47]. The biological activity of these compounds involves inhibitory or microbiocide activity against microorganisms (i.e., antibiotics), toxicity against metazoans, microbial hormone-like activity, and metal transport [48–50]. It has been well demonstrated that the secondary metabolites produced by streptomycetes increases adaptation to biological, physical, and chemical stresses; thus, they are recognized as 'stress metabolites' [36].

Structural genome studies tell us that most genes involved in regulating secondary metabolite pathways are arranged in clusters. These clusters might encode the highly phosphorylated guanosine nucleotide (p) ppGpp and some regulatory proteins involved in producing secondary metabolites [51]. In *Streptomyces* species under nutritional stress, alarmone ppGpp plays a role as a regulator of antibiotic production [52, 53]. Members of both the SARP and LAL families of regulatory proteins appear to be confined to actinobacteria, mainly genus *Streptomyces*, and have shown species-specific controls for secondary metabolism pathways [54–56]. Cell-to-cell communication is a determining factor for modulating antibiotic production, and γ-butyrolactones (GBLs) are the main intercellular signaling compounds [48].

Table 1 Biotechnological potential and cosmopolitan features of the *Streptomyces* species

Species	Strain	Isolated from	Major characteristics	References
S. coelicolor	A3(2)	Soil	The best genetically known representative of the genus	[145]
S. xiamenensis	DSM 41903^T	Mangrove sediment	Not described	[62]
S. axinellae	DSM 41948^T	Mediterranean sponge *Axinella polypoides* (Porifera)	Not described	[42]
S. griseus	DSM 40236^T	Soil	Producer of streptomycin antibiotic	[19]
S. chumphonensis	KK1-2^T	Marine sediments	Not described	[146]
S. rochei	SM3	Decomposed cow dung	Alleviates the stresses caused by *Sc. sclerotiorum* and salt in chickpea	[147]
S. fildesensis	GW25-5^T	Antarctic soil	Not described	[148]
S. scabies	ATCC 49173	Potato scab	Pathogen of potato scab	[149]
S. pseudovenezuelae	ACTA 1383	Rhizosphere of *Ebenus sibthorpii*	Antagonist activity against *Rhizoctonia solani*	[122]
S. oryzae	S16-07^T	Surface-sterilized stems of rice	Not described	[150]
S. wadayamensis	A23	Plant tissue of *Citrus reticulata*	Antagonist activity against *Xylella fastidiosa*	[151]
S. kebangsaanensis	SUK12^T	Inner tissue of *Portulaca oleracea* L. stems	Phenazine-1-carboxylic acid producer	[152]
S. phytohabitans	KLBMP4601^T	Surface-sterilized roots of *Curcuma phaeocaulis*	Not described	[153]
S. diastaticus	UENF AC01	Vermicompost of sunflower cake	Plant growth-promoting streptomycete. AIA and catalase producer	[154, 155]
S. variabillis	UENF AC31	Vermicompost of sunflower cake	Phosphate solubilizer	[154, 155]

^{T} Type strain

The overall ecophysiological traits of the *Streptomyces* genus support the concept of cosmopolitan biogeographical behavior. The traits include the ability to form spores under unfavorable abiotic conditions, a competitive ability related to antibiotic production, a broad pH range that is favorable for growth, and a wide pH range that is optimal for growth between different *Streptomyces* species (such as pH 4.3 for the acidophilic *S. yeochonensis* [57], pH 7.0 for the neutrophilic *S. roseus* [58], and pH 10 for the alkaliphilic *S. alkalithermotolerans* [59]). Streptomycetes are typically chemoorganotrophic with a great versatility for metabolizing a wide range of carbon sources including mono- and disaccharides, polyol, organic acids (glucose, dextrose, fructose, lactose, maltose, mannitol, rhamnose, sucrose, glycerol, and glycolic acid), polysaccharides (including cellulose and starch), and more complex and recalcitrant C-sources (such as humic and fulvic acids) [60–62].

Representatives of the genus *Streptomyces* are well recognized as soil-dwelling bacteria. Nevertheless, many reports have shown that they are widely distributed in both aquatic and terrestrial environments [60]. This cosmopolitan distribution of streptomycetes might be attributed to their production of spores, which are readily spread and thus could explain its presence in different environments (see Table 1). Several members of the genus *Streptomyces* have been isolated from various vegetative and reproductive plant parts, such as roots, tubers, stems, leaves, and seeds. There are many questions concerning the ecological and physiological significance of this interaction that would potentially converge for successful practical applications related to plant growth-promoting and plant-protection properties [63, 64].

Ecology of Streptomyces–plant host interaction

To acquire a better understanding and to manipulate the interactions between plant growth-promoting streptomyces (PGPS) and their hosts, it is necessary to elucidate those biochemical mechanisms that lead to compatible relationships. As shown above (Table 1), most of these streptomycetes are soil-dwelling bacteria with a free-living life cycle in the soil (i.e., saprophytic competence) and they are able to efficiently colonize the rhizosphere and rhizoplane compartments. Eventually, some PGPS might become endophytic and colonize the inner tissues of the host plant and partly or fully conduct their life cycle within them [65]. Therefore, before discussing plant responses to PGPS, it is necessary to describe the rhizosphere and rhizoplane colonization process.

The rhizosphere is the soil volume under the influence of plant root exudates, secretions, and loose cell deposition [66]. The rhizoplane plays a crucial modulatory role on the microbial community structure and microbial diversity that will ultimately influence plant growth and performance in the soil–plant system [67]. Additionally, microbial activity in the rhizosphere soil is markedly influenced by carbon-containing metabolites released from roots via the rhizodeposition process [68]. Rhizodeposition consists of numerous compounds such as ionic secretions, free oxygen and water, enzymes,

proteins, mucilage, amino acids, organic acids, sugars, and phenolics [69]. These compounds act as nutritional resources, chemoattractants, chemorepulsants, and signaling compounds that shape the microbial community structure and activity of different groups of microorganisms and have a significant influence on plant root–microorganism interactions [70].

The PGPS are widely recognized to be good rhizosphere colonizers and their rhizosphere competence may be partially explained by several chemotaxic features, such as bacterial rate multiplication, quorum sensing-controlled gene expression, amino acids, antibiotics, and siderophore synthesis [71]. Initially, soilborne or introduced streptomycete cells that respond to released compounds are actively attracted to the rhizosphere by chemotaxis [69, 72]. At this point, the versatile nutritional requirements and increased population rates coupled with bioactive compound production and detoxification mechanisms are determinants for successful rhizosphere establishment. The former properties play a pivotal role in overcoming complex competition and can be partially explained by the ability to produce antibiotics and other bioactive compounds that confer an ecological advantage and allow PGPS to colonize niches. Several biomolecules that are secondary metabolites of *Streptomyces* contribute to biocontrol and successful colonization; e.g., siderophores from *S. coelicolor* [73], the antifungal nigericin and antibiotic geldanamycin from *S. violaceusniger* YCED-9 [74], and chitinase from *S. violaceusniger* YH27A [75].

Some secreted proteins are important for successful root colonization by *Streptomyces* [76]. Differential protein expression was exhibited by *S. coelicolor* when it was cultivated in minimal medium with and without *Lemna minor* fronds. Bacterial enzymes involved in degrading cellulose, alkenes, and amino acids were induced in the presence of plant extracts, suggesting that the carbon and energy were acquired through degrading compounds present in *L. minor* exudates [77].

Isolates of PGPS can be screened for the attribute that only a minority of species are recognized as phytopathogenic agents; namely *Streptomyces scabies*, *S. acidiscabies*, *S. turgidiscabies*, and *S. ipomoeae,* which are all etiologic agents of common scab diseases [78]. *Streptomyces scabies* is a model organism for investigating plant host–pathogen interactions in Gram-positive bacteria in which a protein secretion system is essential for its pathogenesis [76]. The effector proteins can be secreted by the secretory (Sec) and twin-arginine translocation (Tat) pathway or, additionally, by the specialized Type VII secretion system (T7SS) [79]. Thaxtomin, a family of nitrated dipeptide phytotoxins, is an important pathogenicity factor secreted by *S. scabies* and plays a role in cellulose biosynthesis inhibition [80]. Nec1 is a protein that is required for root colonization by *S. scabies* [81]. Another important intercellular signal attributed to pathogenic streptomycetes and its host is nitric oxide (NO) [82]. Synthase-derived NO is produced by plant-pathogenic *Streptomyces* in response to cellobiose production, which expands plant tissues and appears to be involved in the nitration of thaxtomin [83].

In contrast, a wide variety of *Streptomyces* species establish beneficial plant–microbe interactions [84–86]. The ability of some *Streptomyces* species to gain access into root tissues and to establish an endophytic lifestyle without causing visible harm or symptoms in the host plant has been reported (Table 1). These species can be found mainly in the apoplastic compartments that comprise the intercellular spaces and lumen of differentiated dead cells (sclerenchyma and xylem cells) of the host plant organs (roots, stems, leaves, flowers, fruits, and seeds); intracellular occurrences seem to be less frequent [10]. Using a *Streptomyces* sp. strain EN27 tagged with green fluorescent protein, the endophytic colonization of embryos, endosperm, and emerging radicles of wheat seeds has been reported [87].

Unlike Gram-negative bacteria, *Streptomyces* and other filamentous actinobacteria possess active penetration structures that grow on the plant surface and infect intact cells [88]. The ability to attach and develop an infection point through the cell wall of sweet potato (*Ipomoea batatas* [L.] Lam.) has been reported for *S. ipomoea*. Subsequently, the tip-growth hyphae colonize the interior of parenchyma cells and establish an endophytic interaction [89]. Similarly, using short branches that emerged from the main hyphae, *S. scabies* was observed to penetrate the cell walls of potato plants [90]. Based on the described cell wall penetration process by these short hyphae within a short and uniform distance from the branching point, the authors suggested a specialized penetration function for this structure. Furthermore, *Streptomyces* might enter plant tissues by natural openings such as stomatal apertures, lenticels, hydathodes, wounds, broken trichomes, and root hair cracks formed by lateral root emergence zones [88]. A transmission electron microscope analysis demonstrated that *S. galbus* MBR-5 entered the leaves of *Rhododendron* sp. seedlings through stomatal openings [91].

Plants exhibit defense responses during infection by PGPS, but they are less aggressive than those expressed during pathogenic interactions [92]. Although the biochemical mechanisms involved in these plant responses are not clearly elucidated, the pivotal role of phytohormones such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) has been widely reported in the literature [93–96]. *Arabidopsis thaliana* inoculated with the

endophytic *Streptomyces* sp. strain EN27 induced low levels of gene expression related to the JA and ET pathways [93]. Furthermore, plant response to PGPS infection involves generating reactive oxygen species, which are cytotoxic [83]. This plant process can be subverted by enzymatic machinery related to antioxidant activity; e.g., catalase and superoxide dismutase by *S. coelicolor*, and aconitase by *S. viridochromogenes* strain Tü494. This process plays an important role in alleviating the cytotoxic effects induced by reactive oxygen species and in allowing successful plant tissue colonization [97–99].

Endophytic colonization usually represents an important ecological advantage to the microorganism, because the protected environment is less susceptible to abiotic stress (pH, redox, osmotic, and hydraulic variations) and microbial competition compared with the rhizosphere–soil system. Moreover, the intimate contact between plant host cells and microbial cells might be more effective for the bidirectional exchange of signals, functional metabolites, and nutritional sources for a successful beneficial interaction, which may promote growth of the host plant [88, 100]. The mechanisms involved in plant growth-promoting activity by both endophytic and rhizosphere streptomycetes will be discussed below.

Plant growth promotion by streptomycetes

Most of the fundamental and applied studies of beneficial plant–microbe interactions relate to Gram-negative bacteria [101–103]. Although less often studied, many representative groups of Gram-positive bacteria, particularly those belonging to genus *Streptomyces*, exhibit a range of traits that may improve plant growth by using different mechanisms [7]. As quoted for other beneficial interactions, the plant growth-promoting effects related to *Streptomyces*–plant interactions can be divided into biofertilization, biostimulation, and bioprotection [104].

Biofertilization effects

Due to the mineralogical and electrochemical properties of many soils, some essential mineral nutrients are unavailable to plants because they are present in insoluble forms [105]. Biofertilization consists of a direct mechanism that improves the macro or micronutrient acquisition (uptake and assimilation) by plants. Nutrients sequestered in the crystalline lattice of the mineral fraction of soil can be solubilized and released into solution by organic acids (such as gluconic acid, citric acid, succinic acid, and oxalic acid) that are secreted by different microorganisms [106]. Jog and colleagues [64] reported the release of free phosphate by acidification resulting from the release of malic acid and gluconic acids by *Streptomyces* mhcr0816 and *Streptomyces* mhce0811, respectively. These authors also observed an increase in the number of branches and lateral roots, shoot length, and mineral content of Fe, Mn, and P in wheat plants inoculated with these streptomycetes. Soil treated with a phosphate-solubilizing strain of *Streptomyces* that was isolated from a wheat field increased N, Fe, P, and Mn content in shoots of wheat [107]. In addition, solubilization of rock phosphate by *S. youssoufiensis* has been reported [108, 109]. Streptomycetes can further promote mineral supply by synthesizing siderophores and siderophore uptake systems [107]. *Streptomyces* sp. GMKU 3100, a siderophore-producing endophytic streptomycete, was capable of promoting the growth of rice and mungbean, whereas its siderophore-deficient mutant did not differ from the uninoculated control [86]. Until now, there is no convincing evidence for free-living or endophytic *Streptomyces* species able to fix nitrogen, since the controversial report related to *S. thermoautotrophicus* by Ribbe and colleges [110] was recently refuted [111].

Biostimulation effects

Plant growth can be directly improved by the microbial production of metabolic compounds with phytohormonal activity at micromolar to nanomolar concentrations [64]. Auxin and auxin-like compounds regulate many aspects of plant growth and development including cell plasticity, tissue elongation, embryogenesis, tip dominance, and emergence of lateral roots [112]. The production of indole-3-acetic acid (IAA) by *Streptomyces* spp. has been quoted in several reports [107, 113, 114]. For example, *S. atrovirens* ASU14 utilized tryptophan and produced 22 μg/mL of the IAA [115]. An auxin-like activity due to pteridic acid A was produced by *S. hygroscopicus* TP-A0451 isolated from *Pteridium aquilinum* (bracken) stems [116]. This compound stimulated root elongation and induced the formation of adventitious roots in *Phaseolus vulgaris* (kidney bean) hypocotyls. Another class of phytohormones that have an important function in plant growth is gibberellin. This phytohormone is involved in physiological process that includes seed germination, growth of stems and leaves, floral induction, and growth of flowers and fruits [117, 118]. *Streptomyces* species isolated from a marine environment exhibited the ability to produce a range of phytohormones, including gibberellic acid, and enhanced the agronomic performance of eggplant (*Solanum melongena*) by influencing its growth parameters, including root length and fresh or dry root weight [119].

Bioprotection

Plant-associated microbes might have the ability to minimize the challenges imposed by phytopathogens. This biocontrol activity can manifest as antibiosis, nutrient and space competition, parasitism, predation,

hypovirulence, and induced systemic resistance [69, 120], which are indirect mechanisms of plant growth promotion. The versatile production of secondary metabolites involved in biocontrol is primarily a competitive strategy to successfully colonize the root zone [71]. The genus *Streptomyces* is widely recognized as being able to synthesize several bioactive metabolites that act to control phytopathogen and to confer an advantage to rhizosphere or endophytic colonization [121]. It has been reported that antifungal metabolites produced by 213 *Streptomyces* strains isolated from different habitats exhibited in vitro antagonistic activity against *Rhizoctonia solani* [122]. An investigation into the nematicidal property of *Streptomyces roseoverticillatus* CMU-MH021 revealed the production of secondary metabolites that acted against the root-knot nematode *Meloidogyne incognita* [123]. *Streptomyces roseoverticillatus* CMU-MH021 produced fervenulin, which decreased the percentage of hatched eggs and increased the percentage mortality of second-stage juveniles; it produced isocoumarin, which also increased the percentage mortality of second-stage juveniles. A recently released draft genome sequence of the mushroom mycoparasite antagonist *Streptomyces* sp. strain 150FB, with close correspondence to the *S. avermitilis* MA-4680 genome, revealed possible factors related to disease suppression, namely, a set of genes encoding extracellular enzymes involved in degrading fungal cell wall polysaccharides, disrupting membranes and proteins, and also peroxidases and ribonucleases [124]. In addition, two terpenes and two siderophore biosynthetic gene clusters were detected. Streptomycetes can also stimulate plant defense by the *priming* phenomenon, resulting in induced systemic resistance [125]. *Streptomyces* sp. strain AcH505 suppressed oak powdery mildew infection [126]. This streptomycete strain elicited a systemic defense response in oak (*Quercus robur*), inducing the jasmonic acid/ethylene-dependent pathway and the salicylic acid-dependent pathway.

Secondary metabolites from streptomyces species include not only plant bioprotection effects (scope of the present review), but also other bioactivity properties related to application in medical science. Table 2 summarizes the examples of some of these compounds and their genes and operon structures. Advances in the genetic basis of secondary metabolite pathways enhance the perspectives for discovering new compounds in ecological surveys under distinct environmental conditions.

Plant-associated streptomycetes can also benefit the host plant by mitigating abiotic stress such as heat, cold, drought, and nutrient depletion, thus reducing their negative impacts and consequently increasing plant growth [127]. The application of *Streptomyces filipinensis* no. 15, a 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase and IAA producer, reduced the endogenous levels of ACC, the immediate precursor of ethylene, in both roots and shoots and subsequently enhanced plant fitness to the environment [128]. Plant growth-promoting and stress-alleviating activities have been demonstrated for a halo-tolerant and ACC deaminase-producing *Streptomycete* sp. strain PGPA39 applied to tomato (*Solanum lycopersicum*) plants under salinity stress [129].

Furthermore, a different approach that is based on the indirect mechanisms of plant growth by PGPS has received particular attention. In a study involving a tripartite culture system [130], streptomycete application seemed to act as a modulator in both mycorrhizal and nitrogen-fixing symbiosis and raised their ability to induce plant growth [131, 132]. An increased number, size, and vigor of root nodules were observed on young pea (*Pisum sativum*) seedlings cultivated in soil with naturally abundant *Rhizobium* and that was inoculated with *S. lydicus* WYEC108 [133]. *Streptomyces* sp. AcH505 isolated from the hyphosphere of a spruce (*Picea abies*) promoted mycelial growth and the mycorrhization rate by *Amanita muscaria* and *Suillus bovinus*, while it suppressed the mycelial extension of the plant pathogens *Armillaria obscura* and *Heterobasidion annosum* [134, 135].

Our group has recently proposed some different methods to enhance the plant growth-promoting ability of the endophytic diazotrophic bacteria *Herbaspirillum seropedicae* strain HRC54 (unpublished results). One method involved axenic studies combining *H. seropedicae* with the *Streptomyces bellus* strain UENF AC06 that was isolated from mature vermicompost. This mixed cultivation increased the population growth and nitrogen fixation rates of *Herbaspirillum* when measured by acetylene reduction activity. Therefore, *S. bellus* strain AC06 may be used to improve the plant growth-promotion response by *H. seropedicae* strain HRC54, and we suggest that this mixed cultivation is a potential bioinoculant for agricultural systems.

Biotechnological application of PGPS in agriculture

Using plant growth-promoting bacteria to improve nutrient availability to plants is an important practice for sustainable agriculture and is an alternative to chemical pesticides and fertilizers [136]. PGPS can enhance nutrient availability to plants by biosynthesizing metal chelators and phosphorus solubilizers, producing phytohormones, controlling phytopathogen, and alleviating abiotic stress. Although few *Streptomyces* strains are used as biofertilizers, commercial bioinoculants (microbe-based products) have been developed to improve plant growth promotion (Table 3) [63].

The first challenge to produce a bioinoculant using PGPS is to find the best strain of streptomycete (single

Table 2 Secondary metabolites produced by *Streptomyces* species, main bioactivity property, and their genes and structural organization

Streptomyces species	Secondary metabolite	Bioactivity	Genetic basis	References
S. clavuligerus	Clavulanic acid	Antibiotic	*herABCDEFG* genes	[156]
S. coelicolor	Actinorhodin	Antibiotic	*abeABCD;* α-*abeA* genes	[157]
S. griseus	Streptomycin	Antibiotic	*strFGHIK* genes	[158]
S. hygroscopicus	Geldanamycin	Antitumor	*ahba-B* locus	[159]
S. hygroscopicus var. ascomyceticus	Ascomycin	Immunosuppressant; neurotrophic; antifungal	FK520 gene cluster	[160]
S. thioluteus	Aureothin	Antitumor; antifungal; insecticidal	*aur* operon (*aurA* through *aurI*)	[161]
S. venezuelae	Chloramphenicol	Antibiotic	*sven*0916-*sven*0928 gene cluster	[162]
S. violaceusniger	Meridamycin	Neuroprotectant	*merA-D; mere; merP* genes	[163]
S. viridochromogenes Tu¨494	Phosphinothricin tripeptide	Herbicide	*phsB; orfM; phsC; pmi; ppm; ppd; phsA; pat; dea; prpA*	[164]
S. griseus	Griseobactin	Siderophore	*dhbACEBG* operon	[165]
S. scabiei	Indole-3-acetic acid	Auxin	*iaaM; iaaH*	[166]

formulation) or its combination with other microbes (mixed formulation). Screening studies involve different experimental assays in the laboratory and greenhouse. Elite strains must be tested under different environmental conditions and for different plant species and different genotypes of a target crop [4]. Following these steps, it is necessary to develop specific bioinoculant formulations, which involve determining the required physical and chemical characteristics of the carrier, and ascertaining which additives and metabolites would increase the viability, activity, and performance of the microorganism when introduced under field conditions [4]. Lastly, research to develop methods of bioinoculant delivery and timing must be carried out in the greenhouse and field to maximize the plant response to the applied bioinoculant. It has been found that applying streptomycetes is different to applying Gram-negative bacteria because better plant responses have generally been obtained when the streptomycete application to the soil or substrate occurred before sowing the seeds, thus allowing the selected strain to colonize and establish [6, 137, 138].

The viability and activity of the population inoculum is often affected by abiotic stress. Since the endophytic compartment represent a more protective niche for plant–bacteria interaction, formulations based on endophytic streptomycete strains had advantages over non-endophytic streptomycetes that would guarantee successful positive plant host response [139]. Representative streptomycetes possess the ability to colonize the rhizosphere or endophytic tissues of plants [6, 87], to produce spores resistant to irradiation, heat, and drought [12], and to have an impressive range of metabolites with a variety of biological activities [140]. *Streptomyces* may also convert plant exudates or macromolecules/supramolecules present in the rhizosphere into a form that can be used by other plant growth-promoting microbes. This proposition originated from our research group and represents a technological conversion of the fundamental concept of ecological succession of community members and metabolic cooperation. In this line of research, we combined the non-starch-degrading diazotrophic bacterium *H. seropedicae* strain HRC54 with *S. bellus* strain UENF AC 06, and verified that an increased population of the bacteria was probably sustained by C-sources from a starch degradation by-product. It is noteworthy that *Herbaspirillum* did not grow when *S. bellus* was absent in the medium and when starch was the sole C-source (unpublished results). It is another example of a simple idea that can be converted into a biotechnological product with a range of applications for sustainable crop production.

Concluding remarks and perspectives

The greatest challenge for agriculture in the current century is to produce food for the increasing world population and to reduce the dependence on non-renewable resources and environmental impact. The use of plant growth-promoting microbes to enhance crop production has emerged as a sustainable and alternative tool to meet this challenge [141]. The most studied and technologically developed plant growth-promoting microbes mainly include rhizobia and other Gram-negative bacteria. However, besides their widely known ability to produce antibiotics, representatives of the Gram-positive genus *Streptomyces* have been found in beneficial associations with plants, including those of agronomic importance [64, 142–144]. The diversity of bioactive compounds produced by *Streptomyces* spp.

Table 3 Commercially developed plant growth-promotion products from streptomycetes

Streptomycete active ingredients or their metabolites	Comercialized product	Target crop	Plant growth-promotion effects
Streptomyces lydicus WYEC 108	Actinovate® SP/Actinovate® AG (seed application)	Grass, ornamentals, vegetables, and forest species in greenhouses, nurseries, and more	Biocontrol by soil-borne plant pathogens and foliar diseases
	Micro108® soluble/Micro108® Seed Inoculant	Food and fiber crops, ornamentals, turf grass, landscape plants, including tree seedlings for transplanting into the forest	Enhances plant vitality and encourages more vigorous root systems
	Actino-iron®	For indoor/outdoor greenhouse, nursery, turf grass, ornamental plant, and field uses	Biocontrol of soil-borne plant pathogen
Streptomyces griseoviridis	Mycostop®	Seedling production, vegetables, herbs, and ornamentals	Biocontrol by soil and seed-borne pathogens
Streptomyces avermitilis	AVID® 0.15EC	Shadehouse, greenhouse, field-grown ornamentals, foliage plants, Christmas trees, and other woody ornamentals	Biocontrol of leaf miners, mites, and suppression of aphids, whiteflies, and thrips
	VERMITEC® (additional brands AGRI-MEK®)	Cotton, citrus, pome fruit, nuts and vegetables	Biocontrol of mites and insects
	PROCLAIM® (additional brands AFFIRM®, DENIM ™)	Vegetables (*Brassica*, leafy and fruiting vegetables) and cotton	Lepidoptera. Side effects on mites, leaf miners, and thrips
	AVICTA®	Cotton, corn, and soybean	Biocontrol of nematodes

Adapted from Hamedi and Mohammadipanah [63]

includes substances capable of improving plant growth; hence, they are recognized as PGPS. Increased knowledge of secondary metabolic pathways involving the production of bioactive compounds and mechanisms of plant growth promotion by *Streptomyces* will be assisted by the rapid development of functional genomics and bioinformatics over the coming years. PGPS can promote plant growth by colonizing the rhizosphere or the endophytic plant environment. However, the interactions between rhizosphere PGPS and indigenous microbiota as well as the infection process performed by endophytic PGPS are still not clearly elucidated. Metagenomic approaches and the use of molecular markers such as fluorescent proteins will certainly contribute to the study of dynamic microbial populations in the plant rhizosphere, PGPS inoculation, and streptomycetes endophytic plant colonization. In addition, the use of PGPS as commercial biofertilizers is developing, but research into the design of bioinoculant formulations (such as additives, carriers, and delivery methods) will increase the plant growth and yields and acceptance by farmers around the world.

Authors' contribution

JAJS and FLO contributed equally to this review. Both authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

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