

ACTINOMYCETES AND BIOPREPARATIONS IN AGRICULTURE

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<https://doi.org/10.55251/jmbfs.13032>

ARTICLE INFO

Received 7. 7. 2025
Revised 20. 1. 2026
Accepted 20. 1. 2026
Published 1. 2. 2026

Review



ABSTRACT

In recent decades, it has been confirmed that the application of biopreparations containing microorganisms in vegetative or resting (spore) form is a promising ecological alternative to the application of industrial fertilisers and pesticides. In addition to traditionally applied vegetative and spore forms of bacteria, with different physiological abilities, mycorrhizal fungi and algae, it is confirmed that actinomycetes can be used in biopreparations as a prospective. The advantage of actinomycetes is their presence in any, even dry, stressed environment, their easy isolation, especially in the case of species of the genus *Streptomyces*, and also the production of a wide variety of metabolites that promote plant growth by direct or indirect mechanisms. Their most effective direct mechanisms for plant growth include phosphate solubilization, production of phytohormones and siderophores, nitrogen fixation, ethylene regulation, and indirectly induced systemic resistance, production of chitinases, antibiotics, and antifungal agents. Actinomycetes grow more slowly than other bacteria, so the addition of biostimulants is advisable to improve their growth and metabolic activity in field conditions. Streptomyces are key biocontrol agents in agriculture due to their ability to produce diverse secondary metabolites with strong antimicrobial effects. Species such as *Streptomyces avermitilis*, *S. lydicus*, *S. griseus*, *S. kasugaensis* and *S. hygroscopicus* suppress a wide range of plant pathogens by inhibiting protein or cell wall synthesis or by disrupting membrane integrity. These preparations are commonly applied as foliar sprays, seed treatments or soil drenches and represent a sustainable alternative to synthetic pesticides.

This review aimed to summarise the latest knowledge about the occurrence, mechanisms and effects of actinomycetes isolated from different environments on the growth of agriculturally important plants and their possible application, in the form of biopreparations, in crop production with an ecological approach.

Keywords: soil, plant growth, *Streptomyces*, bioactive metabolites, ecology

INTRODUCTION

The interaction between the plant and microorganisms, which has arisen from the natural evolution of plants, forms the basis for plant growth. Selected groups of algae, microscopic fungi, bacteria (especially lactic acid bacteria), actinomycetes, and yeasts are potentially effective microorganisms in agriculture (Naik *et al.*, 2019). Their potential is currently being explored in environmentally sustainable land management practices, particularly those that promote the use of biopreparations (such as biostimulants and biofertilizers), soil conditioners, and other soil-improving agents, either applied directly to the soil or used in combination with conventional fertilizers. Typically, these preparations contain either live microorganisms, their dormant forms, or metabolites produced during their growth. When applied to soil, seeds, seedling roots, or the surface of plants, they colonise the rhizosphere or interior of the plant and promote its growth by increasing the supply or availability of primary nutrients to the host plant (Vessey, 2003). In addition, they also influence soil porosity, particularly when applied to post-harvest plant residues, where they accelerate residue decomposition and thereby improve soil workability and physical structure. (Lekavičienė *et al.*, 2021). Biopreparations containing beneficial microorganisms, especially bacteria, actinomycetes and non-pathogenic fungi, also induce plant protective mechanisms and reduce the reproduction of pathogens. Metabolites produced by soil-associated and endophytic actinomycetes are commonly described not only as antibacterial agents, but also as antifungal compounds capable of eliciting induced systemic resistance in host plants. (Bhat *et al.*, 2022). Endophytic actinomycetes colonise various tissues (obligate or facultative) in plants and play an important role in strengthening plant defences and plant survival strategies during biotic and abiotic stress (Gopalakrishnan *et al.*, 2019). It has been confirmed several times that actinomycetes produce a wide range of bioactive substances and have a great ability to promote plant growth (Bhatti *et al.*, 2017; Rehan *et al.*, 2021) and are therefore a suitable active ingredient in biopreparations or soil conditioners applied to agriculturally used soils. Bioactive metabolites are compounds that exert effects on other living organism, tissue, or cell, while they may not have a demonstrable effect on their producer, provide them with various ecological benefits (e.g. defence mechanisms). In recent years, the use of actinomycetes as a biocontrol agent, especially against phytopathogenic fungi, has become an alternative to the application of synthetic fungicides with pronounced antifungal activity (Boukaew

et al., 2022). These are mainly representatives of genera *Streptomyces*, *Micromonospora*, and *Nocardioopsis* that have been isolated from different environments such as terrestrial, marine, saline and wetland (Jing *et al.*, 2020). The main antagonistic mechanisms of actinomycetes for the control of phytopathogenic fungi are competition for space and nutrients (Fadhilah *et al.*, 2021), production of antibiotics (Xia *et al.*, 2022), siderophores (Meena *et al.*, 2022), lytic enzymes (Gebily *et al.*, 2021), volatile organic compounds (VOCs) (Gong *et al.*, 2022), and induction of host resistance (Kaari *et al.*, 2022). Currently, there is a constant increase in the number of biopreparations containing cocci and rod-shaped bacteria, as well as mycorrhizal fungi, whether in vegetative or spore form. However, so far, few also contain filamentous bacteria and actinomycetes.

Therefore, the presented study aimed to summarise the most up-to-date scientifically based information on the occurrence, mechanisms of action, importance and possibilities of application of soil actinomycetes in biopreparations used in agriculture.

CHARACTERISTICS AND OCCURRENCE OF ACTINOMYCETES IN SOIL

Bouzigarne (2022) states that actinomycetes are prokaryotic microorganisms, mostly obligate aerobes. They mainly populate soils with a neutral soil reaction (Tarafdar, 2022), but are also well adaptable to higher soil reaction values (Yaradoddi *et al.*, 2022). While many soil-dwelling *Streptomyces* thrive at near-neutral pH, several actinobacterial taxa, including representatives of the families *Streptacidiphilus* and *Acidotherrmus*, are well adapted to acidic environments, whereas others tolerate alkaline soils. This wide pH tolerance contributes to the ubiquity of actinomycetes in terrestrial ecosystems (Barka *et al.*, 2016). It is believed that 10^4 to 10^8 actinomycetes are present in soils in 1 g of soil, with a higher abundance in soils with an alkaline soil reaction and a high concentration of organic matter (Bhatti *et al.*, 2017). Actinomycetes occur in soil primarily in the upper layers, which are best aerated and have a high content of available sources of organic matter (Ngamcharungchit *et al.*, 2023). According to several authors (Das *et al.*, 2021; Javed *et al.*, 2021; and Ravi *et al.*, 2022), actinomycetes are often present in the rhizosphere of plants, and their presence in this area has a significant positive effect on plant health (Kontro &

Yaradoddi, 2022). The occurrence of actinomycetes in the rhizome area is controlled by the plants themselves, as they are mostly beneficial for the plant, help plants overcome various forms of biotic and abiotic stress, improving nutrient uptake by using molecular nitrogen fixation, solubilization, and chelation (**Dow et al., 2023**). **Kontro et al. (2022)** state that actinomycetes are capable of completely suppressing pathogenic microscopic filamentous fungi and bacteria in the rhizosphere, or at least reducing the negative effects of some pathogenic representatives of this group. **Javed et al. (2021)** emphasise that such antagonistic activity toward phytopathogens in the root zone helps maintain the so-called biotic balance. **Dow et al. (2023)** indicate that actinomycetes are

generally most abundant in the root endosphere compared to the rhizosphere, bulk soil or the aerial parts of plants. Endophytic actinomycetes are more metabolically active than those living in open soil, producing a wide range of specific metabolites that facilitate signalling between the host and the surrounding microbiome. Frequently occurring endophytic actinomycetes include members of the genera *Streptomyces*, *Frankia*, *Micromonospora*, *Microbispora*, *Streptosporangium*, *Nocardioides* and *Nocardia* (**Katti et al., 2022**).

Table 1 Estimated and real numbers of species of the order *Actinomycetes* (**Sharma et al., 2014/** List of Prokaryotic names with Standing in Nomenclature (**LPSN, 2025**))

Family/ Genus	Number of species	Family/ Genus	Number of species
Streptomycetaceae:		Thermomonosporaceae:	
<i>Streptomyces</i>	8000/1384	<i>Actinomadura</i>	345/126
<i>Streptoverticillium</i>	258/54	<i>Saccharothrix</i>	68/33
<i>Kitasatosporia</i>	37/47	<i>Microbispora</i>	54/32
<i>Chainia</i>	30/moved to <i>Streptomyces</i>	<i>Actinosynnema</i>	51/2
<i>Microellobosporia</i>	11/4	<i>Nocardioipsis</i>	41/74
<i>Nocardioides</i>	9/198	<i>Microtetraspora/Nonomuraea</i>	26/21/inconsistent records /68
Micromonosporaceae: (Actinoplanetes)		<i>Thermomonospora</i>	19/ small number of child records
<i>Micromonospora</i>	740/168	<i>Micropolyspora/Faenia</i>	13/3/small numbers 1-3
<i>Actinoplanes</i>	248/77	<i>Thermoactinomyces</i>	14/ small number of child records
<i>Dactylosporangium</i>	58/17	<i>Thermopolyspora</i>	1/small number of child records
<i>Ampullariella</i>	9/is not in the LPSN database	<i>Thermoactinopolyspora</i>	1/small number of child records
<i>Glycomyces</i>	2/32	Mycobacteriaceae: (Actinobacteria)	
<i>Catenuloplanes</i>	3/7	<i>Nocardia</i>	357/192
<i>Catellatospora</i>	1/17	<i>Mycobacterium</i>	57/294
Pseudonocardiaceae:		<i>Arthrobacter</i>	25/155
<i>Saccharopolyspora</i>	131/51	<i>Brevibacterium</i>	17/90 of which 40 were verified by LPSN
<i>Amycolatopsis</i>	120/108	<i>Proactinomyces</i>	14/not correct published
<i>Kibdellosporangium</i>	34/11	<i>Rhodococcus</i>	13/89
<i>Pseudonocardia</i>	27/79	Other (unclassified) genera:	
<i>Amycolata</i>	12 genus synonym <i>Amylolactopsis</i>	<i>Actinosporangium</i>	30/4
<i>Saccharomonospora</i>	2/19	<i>Microellobosporia</i>	11/4
<i>Actinopolyspora</i>	1/14	<i>Frankia</i>	7/24
Streptosporangiaceae: (Maduromycetes)		<i>Westerdykella</i>	6/not a bacterium, but an LPSN fungus
<i>Streptosporangium</i>	79/47	<i>Kitasatoa</i>	5/only nomenclature variants LPSN
<i>Streptoalloteichus</i>	48/2	<i>Synnenomyces</i>	4/not validly published correct name LPSN
<i>Spirillospora</i>	11/3	<i>Sebekia</i>	3/not validly published correct name Nonomuraea
<i>Planobispora</i>	10/4	<i>Elaktomyces</i>	3/not validly published correct name
<i>Kutzneria</i>	4/5	<i>Excelsospora</i>	3/not validly published correct name LPSN
<i>Planomonospora</i>	2/6	<i>Waksmania</i>	3/preferred name LPSN
		<i>Alkalomyces</i>	1/not validly published correct name LPSN
		<i>Catellatospora</i>	1/not validly published correct name LPSN
		<i>Erythrosporangium</i>	1/not validly published correct name LPSN
		<i>Streptoplanospora</i>	1/not validly published correct name LPSN
		<i>Microechinospora</i>	1/not validly published correct name LPSN
		<i>Salinospora</i>	1/9

Das et al. (2021) note that because actinomycetes grow more slowly than many other soil microorganisms, they must rely on mechanisms that compensate for this disadvantage in the continual competition for accessible energy sources and nutrients. Key mechanisms include the production of secondary metabolites such as antimicrobial compounds, hydrolytic enzymes, volatile organic compounds (VOCs), and siderophores (**Yan et al., 2021**). According to **Javoreková et al. (2019)**, these biomolecules are usually synthesized via polyketide synthases (PKS) and non-ribosomal peptide synthetases (NRPS).

Yaradoddi et al. (2022) highlight the extensive production of secondary metabolites, most commonly within the genus *Streptomyces*, including antibiotics, antivirals, antihypertensives, cytostatics, fungicides and immunosuppressive

compounds. As shown in Table 1, the most frequent and significant producers are species belonging to the genus *Streptomyces* (**Sharma et al., 2014**).

The predicted numbers of most of the actinomycetes reported by these authors were significantly higher than they are currently reported according to the LPSN (List of Prokaryotic names with Standing in Nomenclature listed on the site). This is a consequence of new knowledge, classification and the use of new methods of identification of individual species (**Parte et al., 2020**).

Hungund et al. (2022) list streptomycetes (*Streptomyces griseus*, *S. kanamyceticus*, *S. fradiae*, *S. hygrosopicus*, *S. pristinaespiralis*, *S. mediterranei*) as major producers of substances such as streptomycin, kanamycin, neomycin, hygromycin, pristinamycin, and rifamycin. In addition to medicine, these substances are also used in agriculture and especially in biotechnology (**Aallam et**

al., 2022). Edison and Pradeep (2020) describe the significant use of cellulolytic enzymes, e.g. β -glucanase, in the production of wine, alcohol and animal feed, as well as in coffee processing, waste management, the textile industry and agriculture. The use of species of the genus *Streptomyces* in the production of biofuels is also interesting (Lakshmikandan *et al.*, 2021). They reported that the co-cultivation of *Streptomyces* spp. with microalgal cells enhances overall biomass yield, increases lipid accumulation, and promotes efficient bioflocculation. These effects are attributed to extracellular polymeric substances and biosurfactants secreted by *Streptomyces*, which facilitate cell aggregation and significantly simplify biomass harvesting – a major economic bottleneck in algal biodiesel production. In addition, microalgae provide oxygen and organic metabolites that support bacterial growth, establishing a mutually beneficial interaction. This co-culture strategy therefore represents a promising, cost-effective and environmentally sustainable approach to improving biodiesel production efficiency. *Streptomyces rosealbus* MTTC11016 was used for co-cultivation with *Chlorella vulgaris*, which increased the production of biomass and polyunsaturated fatty acids. *Streptomyces coelicolor* COB KF977550 has been used in the production of bioethanol from sugarcane waste (Buraimoh *et al.*, 2021). In practice, representatives of the genus *Streptomyces* are used in the bioremediation of contaminated soils or as producers of nanoparticles. Silver nanoparticles are produced by the species *S. albidoflavus*, *S. hygrosopicus* and *S. rochei*, and in the case of gold, they are the species *S. aureofaciens*, *S. glaucus* and *S. viridogens* (Hungund *et al.*, 2022). In their work, Bhatti *et al.* (2017) also report the effectiveness of antimicrobials produced by representatives of the genus *Streptomyces* against biocorrosion caused by some species of bacteria, such as *Bacillus pumilus* and *Desulfovibrio alaskensis*.

Although the genus *Streptomyces* is associated with positive effects on plant growth, several representatives are also capable of producing phytotoxins and exhibiting pathogenicity to plants (Dow *et al.*, 2023). According to Bouizgarne (2022), these are the species *Streptomyces scabiei*, *S. acidiscabies*, *S. brasilscaibiei*, *S. caviscaibiei*, *S. europaeiscaibiei*, *S. ipomea*, *S. stelliscaibiei* and *S. turgidiscabies*. According to the latest studies, species of the genus *Streptomyces* have the potential to produce at least 150,000 additional, as yet unexplored specific metabolites. This metabolic potential can be attributed to their diversity of biosynthetic gene clusters (BGCs), which is the highest of all known bacteria so far (Dow *et al.*, 2023).

METABOLIC PATHWAYS OF FORMATION OF BIOACTIVE METABOLITES OF ACTINOMYCETES

Streptomycetes are filamentous soil-dwelling actinomycetes characterised by complex morphological differentiation and a remarkable capacity to produce extracellular enzymes, siderophores and signalling molecules. Their genomes harbour numerous biosynthetic gene clusters encoding polyketide synthases (PKS), nonribosomal peptide synthetases (NRPS) and hybrid systems, underpinning both their ecological competitiveness and their importance as producers of bioactive secondary metabolites (Fischbach & Walsh, 2006; Medema & Fischbach, 2015). These molecules (especially polyketides, non-ribosomal peptides, carbohydrates, alkaloids, and terpenoids), encompass an astonishing variety of chemical structures and are produced by metabolic pathways encoded by chromosomally adjacent genes: biosynthetic gene clusters (BGCs). These BGCs encode enzymes, regulatory proteins, and transporters that are required for the production, processing, and export of the specialised metabolite (Medema & Fischbach, 2015).

Secondary metabolites of actinomycetes can be divided into the nuclear (conserved) metabolome and the specific metabolome. The nuclear metabolome includes metabolites that are present in most actinomycetes and play an essential role in ecological adaptation, morphogenesis and regulation of cell growth. These include, in particular, siderophores, pigments, antioxidants, and regulatory signalling molecules (Barka *et al.*, 2016). These biosynthetic pathways are located predominantly in stable sections of the chromosome and show low variability across species. In contrast, a specific metabolome includes the products of biosynthetic gene clusters that are present only in certain species or strains, often localised at the edges of a chromosome or on plasmids, and undergo horizontal gene transfer (Medema & Fischbach, 2015). These pathways include the synthesis of polyketides (PKS), non-ribosomal peptides (NRPS), hybrid PKS-NRPS products, metabolites arising from the shikimate pathway, β -lactam structures, and glycosidic derivatives. The products of these pathways form a large group of clinically relevant bioactive agents, including antibiotics (e.g., penicillins, vancomycin, erythromycin), antifungal agents (nystatin), antitumor agents (ansamitocin, bleomycin), antiparasitic preparations (avermectin), and immunomodulatory drugs (rapamycin) (Ayuso-Sacido & Genilloud, 2005).

Intermediates and terminal compounds derived from primary metabolism in actinomycetes provide essential precursors for the biosynthetic pathways leading to the formation of secondary bioactive metabolites. In the metabolism of microorganisms, and therefore actinomycetes, there are 6 pathways responsible for the production of secondary metabolites: peptide pathway, pathway in which polyketide synthase (PKS) or non-ribosomal peptide synthase (NRPS) is involved,

hybrid (non-ribosomal polyketide) synthetic pathway, shikimic acid formation pathway, β -lactam synthetic and carbohydrate pathway. The genes encoding enzymes of synthetic pathways are mostly present in chromosomal DNA and are often arranged in clusters. The resulting products of these pathways are active polyketides and peptide substances that are usable in medicine, agriculture and biochemical research. These structurally distinct metabolites include antibiotics (penicillins, vancomycin, and erythromycin), antifungals (nystatin), antitumor agents (ansamitocin, bleomycins), anthelmintic agents (avermectin), and immunosuppressants (rapamycin) (Ayuso-Sacido & Genilloud, 2005).

Important producers of polyketides are, for example, *Streptomyces hygrosopicus*, producing rapamycin (Dutta *et al.*, 2005), *Streptomyces antibioticus* producing oleandomycin (Rodríguez *et al.*, 2001), *Streptomyces coelicolor* producing actinorodine (Elilob, 2004), *Streptomyces peucetius* producing daunorubicin (Pokhrel *et al.*, 2016) and caprazamycins-producing *Streptomyces* sp. MK730-62F2 (Igarashi *et al.*, 2005).

Nonribosomal peptide synthetases (NRPSs) are multifunctional enzymes that catalyse the synthesis of a wide variety of biologically active compounds with important applications in the pharmaceutical industry and agriculture (Manulis *et al.*, 1994). Well-known examples include penicillin, an antibiotic; cyclosporine, an immunosuppressant, gliotoxin, a compound with antiviral, antibacterial, and immunosuppressive effects; and siderophores, essential for iron uptake in plants (Finking, Marahiel, 2004). NRPSs are organised in a modular fashion, with each module responsible for the incorporation of a specific monomer. Modules are further divided into domains, each catalysing a specific reaction during chain elongation. The number, arrangement, and type of modules and domains determine the structural variability of nonribosomal peptides by controlling the number, order, and selection of amino acids incorporated into the final product. Polyketides are a large and structurally diverse group of natural products, most often classified as secondary metabolites. Their biosynthesis is carried out by enzymes known as polyketide synthases (PKSs), which utilise precursors such as acetyl-CoA (Shen, 2000). Polyketides display a wide range of biological activities, including antibacterial, antifungal, anticancer, antiviral, immunosuppressive, anticholesterol, and anti-inflammatory properties. They are produced by bacteria, fungi, plants, insects, and especially by actinomycetes, in particular the genus *Streptomyces*. Streptomycetes produce important polyketides such as rapamycin, oleandomycin, actinorodin, daunorubicin, and caprazamycin (Risidian *et al.*, 2019). The biosynthesis of polyketides depends on three main PKS types: I, II, and III. Types I and II are primarily found in microorganisms, while type III occurs mostly in plants but has also been identified in actinomycetes (Yu *et al.*, 2012). The genus *Streptomyces* is one of the most prolific producers of both NRPS- and PKS-derived secondary metabolites and plays a central role in pharmaceutical and agricultural research. A list of representative type I, II, and III polyketides produced by streptomycetes is provided in Table 2.

Type I PKSs are large multidomain proteins that can be organised into modules. Each module contains several catalytic domains required for the synthesis of carbon chains. These systems are responsible for the biosynthesis of complex macrolides such as erythromycin, rapamycin, and rifamycin B. Macrolides are polyketides characterised by a macrocyclic lactone ring, which confers antibacterial, antifungal, immunosuppressive, and anticancer activities (Risidian *et al.*, 2019). According to Table 2, the producers are mainly *Streptomyces venezuelae* (methymycin, neomethymycin, narbomycin, pikromycin), *S. avermitilis* (avermectin), *S. bikiniensis* (chalkomycin), *S. griseus* (candicidin) and others.

Type II PKSs are typically found in microorganisms and are responsible for the biosynthesis of aromatic polyketides. These compounds often exhibit strong antibacterial or anticancer activities. Based on the polyphenolic ring system and their biosynthetic pathways, aromatic polyketides produced by PKS type II are generally divided into seven groups, i.e., anthracyclines, angucyclines, halolic acids, tetracyclines, tetracenomycins, pramimicin-type polyphenols, and benzoisochromanquinones (Hertweck *et al.*, 2007). Aromatic polyketides produced by *Streptomyces* include actinorodine (benzoisochromanquinones), doxorubicin (anthracyclines), jadomycin B (angucyclines), oxytetracycline (tetracyclines), mitamycin (halolic acids), tetracenomycin C (tetracenomycins) and benastatin A (pramimicin-type polyphenols). Producers are, for example, representatives of *Streptomyces peucetius*, *S. rimosus*, *S. griseoflavus*, *S. antibioticus*, *S. chartreusis* and others (Table 2).

Type III PKSs are the simplest of all PKS systems. Unlike types I and II, they catalyse chain elongation and cyclisation without requiring an acyl carrier protein. Initially thought to occur only in plants, type III PKSs were later confirmed in bacteria as well (Nakano *et al.*, 2009; Yu *et al.*, 2012). In actinomycetes of the genus *Streptomyces*, type III PKSs have been studied in detail; for example, the *RppA* gene in *Streptomyces griseus* encodes an enzyme responsible for the synthesis of 1,3,6,8-tetrahydroxynaphthalene. In *Streptomyces coelicolor* A3, the *Gcs* gene plays a crucial role in the biosynthesis of germicidin, an antibacterial compound active against Gram-positive bacteria (Funa *et al.*, 2005; Song *et al.*, 2006; Aoki *et al.*, 2011).

Table 2 Representative type I, II and III polyketides produced by streptomycetes

Polyketides	Structure	Producer	PKS gene cluster	References
Type I PKS (modular polyketide synthases)				
Avermectin	16-membered macrocyclic lactone	<i>Streptomyces avermitilis</i> K139	AveA1-AveA4	Ikeda <i>et al.</i> , 1999
Chalcomycin	16-membered macrocyclic lactone	<i>Streptomyces bikiniensis</i> NRRL2737	ChmGI-ChmCIV	Ward <i>et al.</i> , 2004
Candididin	38-membered polyene macrolide	<i>Streptomyces griseus</i> IMRU 3570	CanA, CanE	Gil <i>et al.</i> , 2003; Campelo <i>et al.</i> , 2002
FK506 (Takrolimus)*	23-membered macrocyclic lactone	<i>Streptomyces tsukubaensis</i> 9933, <i>Streptomyces</i> sp. MA6858	FkbA-FkbP	Motamedi <i>et al.</i> , 1998; Kino <i>et al.</i> 1987
FK520 (Ascomycin)*	23-membered macrocyclic lactone	<i>Streptomyces hygroscopicus</i> var. <i>ascomyceticus</i> ATCC 14891	FkbA-FkbP	Wu <i>et al.</i> , 2000
Methymycin, Neomethymycin, Narbomycin, Picromycin	12 or 14 -membered macrolides	<i>Streptomyces venezuelae</i> ATCC15439	PikAI-PikAIV	Xue <i>et al.</i> , 1998
Pimaricin (Natamycin)	26-membered polyene macrolide	<i>Streptomyces natalensis</i> ATCC27448	PimS0- PimS4	Aparicio <i>et al.</i> , 1999
Rapamycin	31-membered macrocyclic lactone ring	<i>Streptomyces hygroscopicus</i> NRRL5491	RapA=RapC	Schwecke <i>et al.</i> , 1995
Spiramycin	16-membered macrolide	<i>Streptomyces ambofaciens</i> ATCC23877	SrmGI-SrmGV	Karray <i>et al.</i> , 2007
Tautomycetin*	linear	<i>Streptomyces</i> sp. CK4412	TmcA, TmcG	Choi <i>et al.</i> , 2007
Tylosin	16-membered macrolide	<i>Streptomyces fradiae</i>	TYLGI-TYLGV	Fiers <i>et al.</i> , 2015
Type II PKS (aromatic polyketide synthases)				
Medermycin	Octaketid	<i>Streptomyces coelicolor</i> CH999	Med-1, Med-2, Med-23	Ichinose <i>et al.</i> , 2003; Takano <i>et al.</i> , 1976
Doxorubicin	Decaketid	<i>Streptomyces peucetius</i> ATCC29050	DpsA-DpsD, Dps-G	Grimm <i>et al.</i> , 1994
Oxytretracyklin	Decaketid	<i>Streptomyces rimosus</i> ATCC 10970	OxyABCD	Pickens, Tang, 2010
Gilvocarcin	Decaketid	<i>Streptomyces griseoflavus</i> Gö 3592	GilA-GilC	Fisher <i>et al.</i> , 2003
Oviedomycin	Decaketid	<i>Streptomyces antibioticus</i> ATCC 11891	OvmPKS	Lombó <i>et al.</i> , 2009
Chartreusin	Decaketid	<i>Streptomyces chartreusis</i> HKI - 249	ChaABC	Xu <i>et al.</i> , 2005
Cervimycin	Decaketid	<i>Streptomyces tendae</i> HKI-179	CerABC	Bretschneider <i>et al.</i> , 2011; Herold <i>et al.</i> , 2004
Resistomycin	Decaketid	<i>Streptomyces resistomycificus</i>	RemABC	Jakobi <i>et al.</i> , 2004
Chromomycin	Decaketid	<i>Streptomyces griseus</i> subsp. <i>griseus</i> ATCC13273	CmmPKS	Menendez <i>et al.</i> , 2004
Hedamycin	Dodecaketid	<i>Streptomyces griseoruber</i> ATCC15422	HedCDE	Bililign <i>et al.</i> , 2004
Frederikamycin	Pentadecaketid	<i>Streptomyces griseus</i> ATCC 49344	FdmF-FdmH	Das <i>et al.</i> , 2010; Chen <i>et al.</i> , 2008
Type III PKS				
THN (1,3,6,8-tetrahydroxynaphthalene)	aromatic precursor	<i>Streptomyces griseus</i> IF 013350	RppA	Funa <i>et al.</i> , 1999
Germicidin A / B	Small cyclic polycetide	<i>Streptomyces coelicolor</i> A3	Gcs (PKS III)	Aoki <i>et al.</i> , 2011
Alkylresorcinol (ARs)	Resorcinolic lipids	<i>Streptomyces collinus</i> DSMZ 40733	ArsA	Rückert <i>et al.</i> , 2013
Flaviolin	Naphtoquinone pigment (oxidised THN)	<i>Streptomyces coelicolor</i> A3	RppA → derived	Thanapipatsiri <i>et al.</i> , 2015

*Several compounds listed under type I PKS (e.g. FK506, FK520, tautomycetin) are synthesised by hybrid PKS–NRPS systems, reflecting the modular and combinatorial nature of secondary metabolite biosynthesis in streptomycetes

ACTINOMYCETES AND PLANT GROWTH SUPPORT

According to **Javed et al. (2021)**, actinomycetes belong to a group referred to as PGPB - plant growth-promoting bacteria or, as stated in their paper, **Bhatti et al. (2017)** and **Dasila et al. (2020)**, they belong to the category labelled PGPR - plant growth-promoting rhizobacteria. The potential of actinomycetes, especially streptomycetes, to promote plant growth has been noted on a variety of plants (beans, tomato, wheat, sorghum, rice, and chickpeas). Plant growth is affected by direct or indirect mechanisms, such as the ability to produce substances that directly affect plant growth or to suppress the growth and

occurrence of pathogens, either in the form of colonisation or by antibiosis. **Bouizgarne (2022)** also mentions the stimulation of induced plant defences from indirect mechanisms. **Bhatti et al. (2017)** report that interactions of actinomycetes with non-pathogenic microorganisms can also positively affect plant growth. This ability is often stimulated, especially by the positive relationship between actinomycetes and mycorrhizal fungi (**Chen et al., 2020; El-Sharkawy et al., 2022; Wang et al., 2024**). The most common mechanisms carried out by actinomycetes include the production of metabolites supporting plant growth, solubilization of phosphates, fixation of atmospheric nitrogen, and production of siderophores or phytohormones (Fig. 1).

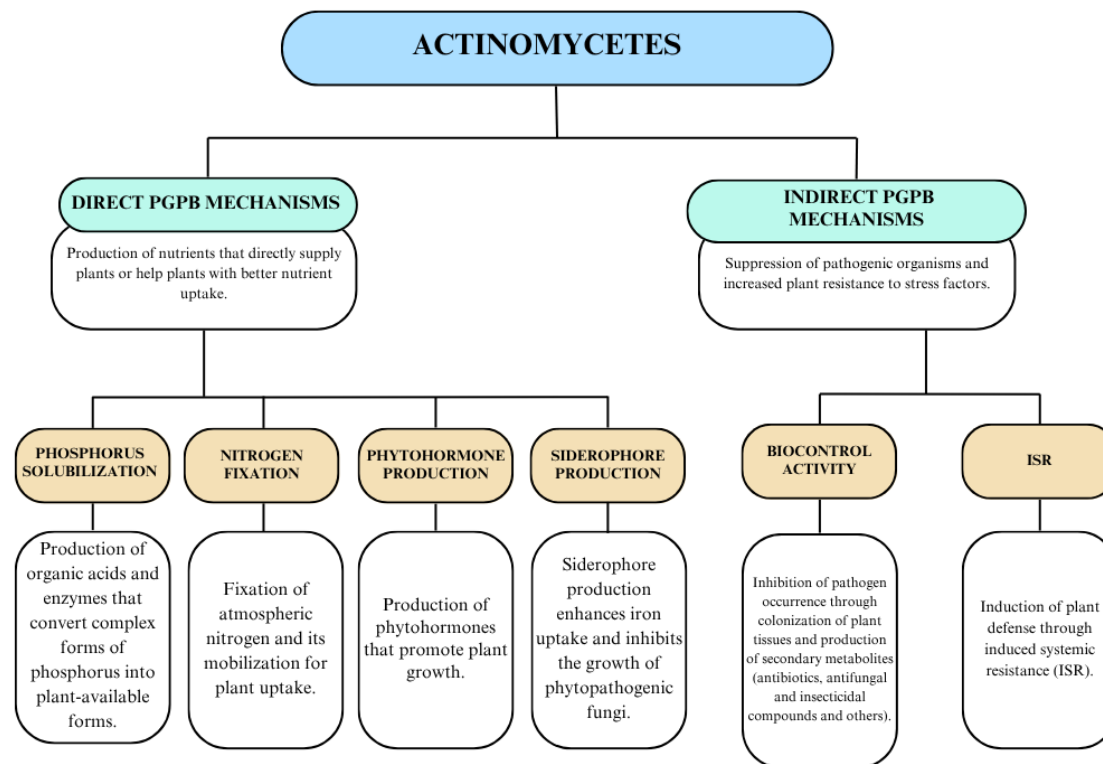


Figure 1 Mechanisms of actinomycetes supporting plant growth

Solubilization of phosphates in soil

Phosphorus is the second most important macroelement required for plant growth after nitrogen (**Bouizgarne, 2022**). However, it is known that the usability of natural or applied industrial phosphate fertilisers is low (only 25%), as the applied phosphate fertilisers create insoluble chemical complexes in the soil, in an insoluble form for the plant (**Tian et al., 2021**). **Mohammed (2020)** states that microorganisms, and especially actinomycetes, species of the genus *Streptomyces*, are the natural key in the processes of converting these complex forms of phosphates (superphosphate, tricalcium phosphate) into forms acceptable to plants. According to **Chouyia et al. (2020)**, isolates of *Streptomyces roseocinereus* and *S. natalensis* demonstrated the greatest phosphate-solubilization efficiency after barley plants were inoculated. **Aallam et al. (2021)** examined ten *Streptomyces* isolates originating from the rhizosphere of sugar beet under conditions containing natural phosphorite and tricalcium phosphate. The study showed that these isolates exhibited significant phosphate-solubilising activity, primarily mediated by the secretion of organic acids and siderophores. The best results of solubilization were shown in the case of representatives of *S. enissocaesilis* and *S. bellus*, which were able to release phosphorus from both applied forms of phosphorus. **Bousselham et al. (2022)** confirmed the ability of actinomycetes to solubilise phosphorus from phosphorite in 143 isolates out of 235 isolated, using the excretion of chelating agents rather than the production of organic acids. The phosphate-dissolving ability of actinomycetes has also been confirmed by **Moscol et al. (2020)**, **Cinkocki et al. (2021)**, **Boubekri et al. (2021)**, and **Djebaili et al. (2021)**. These were mainly representatives of the genera *Streptomyces* and *Nocardioopsis*. **Vargas Hoyos et al. (2021)** demonstrated that *Streptomyces rishiriensis* 3AS4 produced a rare combination of gluconic and 2-ketogluconic acid in phosphorus solubilization, which can have extensive uses in the development of new biofertilizers. In his work, **Bouizgarne (2022)** recommends the use of a combination of less soluble forms of phosphorus with actinomycetes and with mycorrhizal fungi or other bacteria. The advantages of this application are justified by the slower release of phosphorus into the soil, which he describes as an "intelligent" method of fertilisation, that even though it does not reach the qualitative and quantitative level compared to the application of bacterial representatives of the genera *Bacillus* or *Pseudomonas*. **Moscol et al. (2020)** also indicate that actinomycetes are still very little used in practice as bioinoculants.

Nitrogen fixation

The molecular nitrogen (N_2) present in the atmosphere is metabolically unavailable to higher plants. Only microorganisms can convert it into an available form; Atmospheric nitrogen is mostly reduced to the form of ammonia available to plants during the biological nitrogen fixation process. Microorganisms that fix nitrogen are referred to as diazotrophs. They are able to fix nitrogen either in free life or in symbiotic association with higher plants (**Swarnalakshmi et al., 2016**). Another direct mechanism by which actinomycetes affect plant growth is the ability of some representatives to fix molecular nitrogen and subsequently make it available to plants (**Lawal et al., 2021**). The diazotrophic genus *Frankia* plays a key role in soil nitrogen cycling due to its capacity to establish actinorhizal symbioses with a wide range of non-leguminous dicotyledonous plants. These interactions involve the formation of specialised root nodules in which nitrogen fixation occurs, mediated by *nif* gene expression under low-nitrogen and microaerophilic conditions (**Hungund et al., 2022; Silva et al., 2022**). **Javed et al. (2021)** reported in their work that representatives of the genus *Frankia* sp. is responsible for about 15% of the total biological fixation of molecular nitrogen by soil microorganisms. According to **Bhatti et al. (2017)**, species of the genus *Frankia* are also able to provide the entire nitrogen requirement for the plant. **Bhattacharyya et al. (2024)** report that species of the genus *Frankia* in actinorhizal symbiosis with alder can enrich the soil with 240-350 kg of nitrogen per hectare of land per year by fixing atmospheric nitrogen. **Qi et al. (2022)** published a study that looked at the effects of *Frankia*F1 microbial inoculants on ginseng growth and found that total soil nitrogen content increased by 50.78% after inoculation. However, the ability of representatives of the genus *Frankia* to form root nodules and thus fix atmospheric nitrogen depends on several factors. The most important is the soil reaction, which should be in the pH range of 4.5-6. Furthermore, successful nodulation requires optimal moisture, temperature, soil salinity, availability of organic matter, and sufficient nutrient concentration in the soil (mainly P, Fe, Mo), as well as a favourable composition of the surrounding microbiocenosis (**Bhattacharyya et al., 2024**). The negative effect of soil salinity on the efficiency of air nitrogen fixation by representatives of the genus *Frankia* was demonstrated, for example, by **Chen et al. (2022)**, who found that although green alder (*Alnus alnobetula*) benefited from this relationship, the efficiency of soil nodule formation was reduced by 56% due to soil salinity. However, according to **Mishra et al. (2022)**,

actinomycetes are capable of fixing nitrogen even in extreme conditions, such as those found in saline soils, and are a crucial component for plants in overcoming this abiotic stress.

For nearly four decades, *Frankia* was considered the sole actinomycete genus capable of establishing nitrogen-fixing symbioses with plants. Recent evidence summarised by **Silva et al. (2022)**, however, indicates that species belonging to other genera, particularly *Streptomyces* and *Micromonospora*, may also possess nitrogen-fixing ability. **Wei et al. (2024)** also demonstrated N₂ fixation by the *Streptomyces rochei* S32 isolate in their experiment.

The process of N₂ fixation is mediated by the enzyme complex oxygen-sensitive nitrogenase (encoded by the *NIF* genes), which is present in bacteria. Molecular studies have demonstrated the presence of *nif* H genes in other non-frankial actinobacteria, such as *Slackia exigua*, *Rhithia mucilaginoso* and *Gordonibacter pamelaee*; however, their nitrogen-fixing potential has not been estimated (**Gtari et al., 2012**). It has been confirmed that the presence of *Streptomyces* species can increase frankial nodulation, and *Micromonospora* in nodules can affect rhizobial symbiosis in alfalfa (**Tokala et al., 2002**; **Martinez-Hidalgo et al., 2014**). Endophytic inoculations of actinomycetes of commercially important crops such as rice, sugarcane, and wheat have been found to reduce the input of nitrogen fertilisers (**Govindarajan et al., 2008**). The application of nitrogen-fixing bacteria in combination with nitrogen fertilisers to the soil can reduce the amount of fertiliser that needs to be applied, but the presence of inorganic nitrogen can inhibit both nodulation and nitrogen fixation (**Murray et al., 2017**).

Production of siderophores

Iron is an essential element required for numerous physiological and biochemical processes in living organisms. **Mondal and Baksi (2022)** report that iron constitutes approximately 2–4% of soil content; however, under aerobic and neutral to alkaline soil conditions, iron predominantly occurs as poorly soluble Fe³⁺ oxides, which strongly limit its bioavailability. Iron deficiency in the soil environment therefore stimulates the secretion of chelating agents, such as phyto siderophores produced by plants and microbial siderophores synthesised by soil microorganisms.

Siderophores are low-molecular-weight biomolecules with a high affinity for ferric iron (Fe³⁺), forming stable Fe³⁺-siderophore complexes that can be transported into microbial or plant cells, where iron is subsequently reduced to Fe²⁺ (**Hungund et al., 2022**; **Nazari et al., 2023**). In soils, iron mainly exists in two oxidation states, Fe³⁺ and Fe²⁺, with Fe³⁺ being largely inaccessible to plants, making siderophore-mediated acquisition a key strategy for iron uptake (**Mishra et al., 2022**).

Based on their chemical functional groups, siderophores are commonly classified into hydroxamates, catecholates (phenolates), carboxylates, and mixed-type siderophores containing two or more coordinating moieties. In streptomycetes, hydroxamate siderophores (e.g. deferroxamine, albisporachelin), catecholates (e.g. heterobactin), phenolates, and carboxylate-type siderophores have been reported (**Torres-Rodriguez et al., 2022**).

From a biosynthetic perspective, siderophores are synthesized via two principal biosynthetic systems,

non-ribosomal peptide synthetase (NRPS)-dependent pathways, which are typical for many hydroxamate and catecholate siderophores, and NRPS-independent siderophore (NIS) pathways, which rely on acyl transfer and condensation reactions and are characteristic of siderophores such as desferrioxamine. Genomic analyses of *Streptomyces* spp. have revealed numerous gene clusters encoding both NRPS and NIS systems responsible for siderophore biosynthesis (**Gao et al., 2022**).

Actinomycetes enhance iron availability through multiple mechanisms: by secreting organic acids that solubilise insoluble iron minerals and by producing siderophores that chelate Fe³⁺ and facilitate its uptake by plants (**Hungund et al., 2022**). Numerous studies have confirmed siderophore production by actinomycetes, particularly *Streptomyces* species (**Chouiya et al., 2020**; **Moscol et al., 2020**). **Cinkocki et al. (2021)** reported siderophore production in up to 88% of tested *Streptomyces* isolates, while **Wei et al. (2024)** demonstrated siderophore synthesis by *Streptomyces rochei* S32. Additionally, siderophore-producing *Streptomyces* strains have been identified in saline and stressed soils (**Nozari et al., 2022**; **Zhu et al., 2024**).

Beyond iron acquisition, siderophores and siderophore-producing actinomycetes play an important role in the mobilisation and uptake of other essential nutrients, including nitrogen, phosphorus, magnesium, potassium, zinc, and manganese. **Hungund et al. (2022)** demonstrated that siderophore-producing actinomycetes can enhance plant uptake of Fe, N, P, and Mg, thereby contributing to the phytoremediation of heavy metals, such as cadmium, through metal chelation. **Boubekri et al. (2021)** further demonstrated that siderophore-producing actinomycetes improve potassium availability, reporting soluble potassium concentrations ranging from 2.6 to 41.45 mg·L⁻¹, particularly under conditions of sufficient phosphorus availability. Moreover, siderophores indirectly suppress phytopathogens by competitively limiting iron availability in the rhizosphere, thereby contributing to plant health and growth promotion (**Hungund et al., 2022**). In addition to iron, siderophores produced by actinomycetes are also capable of chelating and mobilising other transition metals, particularly zinc (Zn²⁺) and nickel (Ni²⁺), which are essential micronutrients for plant metabolism and microbial

enzymatic activity. Zinc plays a crucial role as a structural and catalytic cofactor of numerous enzymes, while nickel is required for the activity of enzymes such as urease and hydrogenase. Several studies have demonstrated that siderophores, especially catecholate- and hydroxamate-type siderophores, exhibit affinity not only for Fe³⁺ but also for divalent metal ions, including Zn²⁺ and Ni²⁺, thereby enhancing their solubility and bioavailability in soil environments. **Hungund et al. (2022)** reported improved uptake of Zn in plants inoculated with siderophore-producing actinomycetes, while other studies indicate that microbial siderophores can complex Ni²⁺ and facilitate its controlled uptake at low concentrations, or conversely reduce its toxicity under elevated metal levels through chelation. This multifunctional metal-binding capacity highlights the broader ecological significance of siderophore-producing actinomycetes in nutrient cycling and plant growth promotion.

Production of phytohormones

Phytohormones are a heterogeneous group of low-molecular-weight organic compounds that regulate plant growth, development and responses to biotic and abiotic stresses even at very low concentrations. The major classes of phytohormones include auxins, cytokinins, gibberellins, ethylene, abscisic acid, jasmonates, salicylic acid and strigolactones (**Binder, 2020**). In addition to plants, several plant growth-promoting bacteria (PGPB), including actinomycetes, are capable of synthesising phytohormones or modulating their endogenous levels in plants (**Vurukonda et al., 2016**; **Hungund et al., 2022**). Actinomycetes, particularly members of the genus *Streptomyces*, are known producers of auxins, cytokinins and gibberellins, while some species can also produce jasmonates, salicylic acid, abscisic acid and strigolactones or stimulate the expression of plant genes responsible for their biosynthesis (**Thenappan et al., 2024**; **Wei et al., 2024**). Through these mechanisms, actinomycetes significantly contribute to plant growth promotion, root architecture modulation and increased tolerance to environmental stresses (**Myo et al., 2019**; **Hungund et al., 2022**).

Streptomyces as PGPB are ranked among the most important producers of phytohormones (**Myo et al., 2019**). Among the most famous producers of the IAA genus *Streptomyces* are *S. nobilis*, *S. kunningensis*, *S. olivaceoviridis*, *S. rimosus*, *S. rochei*, *S. griseoviridis*, *S. lydicus*, *S. djakartensis*, *S. griseorubens*, *S. globosporus*, *S. caviscaabies*, and *S. enissocaesilis* (**Anwar et al., 2016**).

Hungund et al. (2022) report that some actinomycetes produce only auxins, members of the genera *Streptomyces*, *Actinomyces* and *Nocardia*, in turn, produce gibberellins. However, the species *Streptomyces rhimosus*, *S. olivaceoviridis* and *S. rochei* can produce various hormonal substances as part of their secondary metabolism. The species *S. rochei* has been confirmed to produce up to 39 different forms of phytohormones belonging to the groups of auxins, cytokinins, jasmonates, gibberellins, salicylic acid, strigolactones and abscisic acid (**Wei et al., 2024**). Actinomycetes of the genus *Streptomyces* are also able to stimulate the expression of plant genes themselves, which are responsible for the production of auxins, cytokinins and gibberellins (**Thenappan et al., 2024**).

Among phytohormones, 3-indoleyl acetic acid (IAA) is the most physiologically active growth hormone, belonging to the auxins (**Vurukonda et al., 2016**). The level of this phytohormone fluctuates during plant development, resulting in effects that differ both between growth stages and among plant species. IAA microorganisms produce two different pathways referred to as the "L-tryptophan-dependent pathway" and the "L-tryptophan-independent pathway". However, the production of IAA by microorganisms is most often carried out through the L-tryptophan-dependent pathway, with microorganisms using L-tryptophan as a precursor to IAA (**Goswami et al., 2020**). **Rai et al. (2021)** report that almost 80% of microorganisms in the rhizosphere are capable of producing IAA. **Hungund et al. (2022)** confirmed that actinomycetes, which are near the roots, secrete IAA, thereby promoting lateral root growth. However, **Nazari et al. (2023)** warn that too much IAA inhibits plant growth and can be a trigger mechanism for ethylene formation.

The production of IAA by streptomycetes has been confirmed by several authors, e.g. **Chouiya et al. (2020)** with *S. roseocinereus* MS1B15 isolate, **Cinkocki et al. (2021)** for 9 isolates with the highest activity for *Streptomyces* sp. isolate. **KimRC20A118, Djebaili et al. (2021)** confirmed 12 isolates of the genera *Streptomyces* and *Nocardiopsis* producing IAA in their work. **Boubekri et al. (2021)**, in turn, demonstrated high IAA production by the strain *Streptomyces griseorubens* BC10 and the strain *Nocardiopsis alba* BC11. **Wei et al. (2024)** confirmed the production of IAA by the strain *Streptomyces rochei* S32 by an L-tryptophan-dependent pathway. They confirmed that actinomycetes produce IAA even under saline conditions by *Streptomyces* sp. isolates HU2014, *Streptomyces paradoxus* D2-8 and *Nocardioides* sp. NIMMe6 (**Meena et al., 2020**; **Gao et al., 2022**; **Zhu et al., 2024**).

Ethylene is a gaseous phytohormone produced by plants to regulate growth, development and responses to biotic and abiotic stresses. Its immediate biosynthetic precursor in plants is 1-aminocyclopropane-1-carboxylic acid (ACC), which is synthesised from S-adenosyl-L-methionine (**Yang and Hoffman, 1984**; **Binder, 2020**). Under stress conditions, elevated ACC levels lead to increased ethylene production, which can negatively affect plant growth and root elongation (**Vurukonda et al., 2016**; **Hungund et al., 2022**). According to **Binder (2020)**, ethylene is a gaseous hormone produced by plants to regulate plant development,

growth, and stress responses. However, a high concentration of this hormone is undesirable for the plant. Actinomycetes can regulate the production of this stress hormone in plants through the production of the enzyme ACC deaminase. This enzyme can break down ACC into ketoglutarate and ammonia, reducing the amounts of subsequent ethylene in plants (Hungund *et al.*, 2022). Stressful conditions that can induce ethylene production in plants also include a saline soil environment; even in these conditions, the ability of actinomycetes to produce ACC deaminase by *Streptomyces paradoxus* D2-8 isolate has been confirmed in the case of soybeans (Gao *et al.*, 2022). Djebaili *et al.* (2021) demonstrated this enzyme in 12 isolates of actinomycetes belonging to the genus *Nocardioopsis* or to the genus *Streptomyces* when monitoring the growth of wheat.

BIOPREPARATIONS WITH ACTINOMYCETES

Biopreparations may contain live microorganisms, their resting forms, or their secondary metabolites (Bouizgarne, 2022). In agriculture, biopesticides and biofertilizers are mainly used, which are defined as preparations containing microorganisms that are applied to the soil, seeds, plant roots or their surface (Chaudhary *et al.*, 2024). According to Bouizgarne (2022), one of the advantages of using actinomycetes in biopreparations, compared to gram-negative bacteria, is their ability to sporulate. Thanks to this, such preparations can be in a dry state, in the form of powder or granulate. Another advantage of such biopreparations is their strong competitive ability in the rhizosphere, supported by the extensive production of secondary metabolites (especially in *Streptomyces* species), their biocontrol potential, and their capacity to survive in soil for several months or even years due to spore formation (Seipke *et al.*, 2012; Schlatter *et al.*, 2017). The biotechnological potential of actinomycetes has led to the emergence of new biocontrol agents and biopreparations that can replace conventional fungicides in particular, while supporting bioremediation efforts, including the degradation of pesticides and toxic residues (Kovaleski *et al.*, 2025). Gao *et al.* (2022) report that antifungal biopreparations containing streptomycetes include Actinovate (*Streptomyces lydicus*), Mycostop (*Streptomyces griseoviridis*) and Rhizovit (*Streptomyces* DSMZ 12424). Djemouai *et al.* (2023) report that Mycostop and Actinovate are the longest-used actinomycete-based biopreparations on the market.

Aggarwal *et al.* (2016) and Torres-Rodriguez *et al.* (2022) list in Table 3 other preparations containing streptomycetes and their biologically active metabolites, which are used in agricultural practice. These preparations are mainly effective against fungal and bacterial pathogens of plants, but in the case of Agri-Mek, the preparation has insecticidal/acaricidal effects. Pacios-Michelena *et al.* (2021) report that preparations such as Agrimycin, Paushak, Cuprimicin 17 and Astrepto 17 contain the species *Streptomyces griseus* and are effective against the phytopathogens *Xanthomonas oryzae*, *X. citri* and *Pseudomonas tabaci*. Bouizgarne (2022) also lists commercial products such as Actofit, Actin, Action Iron, Micro 108, Bialaphos and Bactophil. Secondary metabolites of actinomycetes are also part of the bioinsecticides Entrust SC and Tracer, whose active insecticidal substances are spinosad and spinosyn D, or Vertimec and Agri-Mek SC, which contain abamectin, which is active against nematodes and produced by *Streptomyces avermitilis*. This representative is also a producer of avermectin with similar insecticidal effects and is found in the biopreparations Avicta and Tervigi (Silva *et al.*, 2022). Gupta *et al.* (2022) state that representatives of the genus *Frankia* are part of a biopreparation called N-fixer, which is produced in India with the declared effect of symbiotic fixation of atmospheric nitrogen.

Bouizgarne (2022) reports that Mycostop is the only commercial biopreparation containing only actinomycetes. According to Silva *et al.* (2022), the preparation Actinovate, which is effective against the phytopathogens *Pythium ultimum*, *Rhizoctonia solani*, *Fusarium* sp., *Phytophthora* sp. and *Verticillium* sp., is readily available in the countries of the European Union. Betz and Punja (2021) and McGrath (2023) note that many biofungicides act primarily through contact. Because powdery mildew develops mainly on the underside of leaves, where the product may not reach as effectively, the performance of such biopreparations can be reduced. In contrast, Silva *et al.* (2022) demonstrated biocontrol activity against several phytopathogens by application already in seeds, including *Ceratocystis radicola*, *Alternaria* sp., *Rhizoctonia solani*, *Fusarium* sp., *Phytophthora* sp. and *Pythium* sp., and the fungus *Verticillium dahliae* (Pacios-Michelena *et al.*, 2021). In Slovakia, we have also approved several foreign products containing actinomycetes. It is a biopreparation, Bi Safe (Ukraine), which contains non-pathogenic bacterial representatives of the genera *Bacillus* sp. and *Streptomyces* sp., in combination with a mycorrhizal fungus of the genus *Trichoderma* spp., as well as biopreparations Biofil (Hungary) and Mycofriend (Ukraine), which, in addition to other species of bacteria and mycorrhizal fungi, also contain representatives of the genus *Streptomyces*. Other registered biopreparations with actinomycetes are Streptomyces Linea Greenspore and MicoSeed plus (Italy), which contain representatives of the genera *Pseudomonas*, *Bacillus* and *Streptomyces*. Mycostop is a powdered biopreparation containing *Streptomyces griseoviridis* K61, containing aromatic heptaene polyene, which acts against soil pathogenic microscopic filamentous fungi (Al-Quwaie, 2024). According to Lebedev *et al.* (2022), Mizorin (Russia), which contains actinobacteria of the species *Arthrobacter mycoides*, had a positive effect on the cultivation of spring mustard (*Brassica campestris*). Seed inoculation resulted in a 16% increase in

germination capacity, a 36% increase in plant height, a larger leaf area and a 47% increase in dry biomass production compared to the control group. The authors also found that monoinoculation with Mizorin was more effective as a result of competition, compared to bionoculation of Mizorin with Flavobacterin.

Survival and activity of actinomycetes in soil biopreparations

Actinomycetes are widely incorporated into agricultural biopreparations due to their capacity to produce antimicrobial metabolites, induce systemic resistance in plants, and improve nutrient transformation in soils. However, the ecological success of introduced strains depends on their ability to establish, survive, and remain active in competitive soil environments. The persistence of viable actinomycete cells and their bioactive metabolites is influenced by environmental conditions, microbial competition, soil physicochemical properties, and application formulations (Schrey & Tarkka, 2008).

Commercial inoculants provide well-documented examples of survival performance under field conditions. *Streptomyces griseoviridis* strain K61 (Mycostop), applied as a biological control agent, has been shown to persist for 6–12 weeks in rhizosphere soils, with the highest recovery rates at moderate soil moisture and near-neutral pH (Tahvonen & Avikainen, 1987). Similarly, *Streptomyces lydicus* WYEC108, used in formulations such as Actinovate, exhibits effective root colonisation when applied to germinating seeds or seedlings, though its persistence significantly declines in soils with high microbial competition or elevated organic carbon turnover (Mawarda *et al.*, 2020). These findings highlight the importance of application timing and microhabitat selection (rhizosphere vs. bulk soil) for maintaining introduced populations.

The environmental longevity of actinomycete secondary metabolites also varies widely. Antibiotics such as streptomycin and tetracyclines, frequently produced by *Streptomyces* species, can persist in soils for days to several weeks, depending on mineral composition, sunlight exposure, and microbial degradation capacity (Mousavi *et al.*, 2024). For instance, streptomycin exhibits a reported half-life ranging from 1 to 14 days in agricultural soils, with rapid degradation under warm, aerobic, and microbially active conditions (Kumar *et al.*, 2020). In contrast, more structurally complex metabolites such as polyene macrolides (e.g., nystatin or amphotericin-like compounds) may bind strongly to soil organic matter, reducing their bioavailability while prolonging environmental residence times (Bérdy, 2005).

Key environmental variables influencing the longevity and bioactivity of introduced actinomycetes include soil pH, moisture content, temperature, and nutrient availability, as well as the presence of plant hosts that support rhizosphere colonisation. Competitive exclusion by native soil microbiota is often the dominant factor limiting persistence, suggesting that successful establishment frequently requires either repeated application, co-inoculation with plant growth-promoting rhizobacteria, or delivery in protective formulations such as encapsulated granules or biochar carriers (Vassilev *et al.*, 2020).

Overall, the ecological performance of actinomycete biopreparations is determined not only by the metabolic capabilities of the introduced strains but also by the dynamic interactions within soil microbiomes and physicochemical processes affecting metabolite stability. However, in contrast to controlled laboratory conditions, comparable positive results are often not achieved in field conditions (Alkemade *et al.*, 2022). The authors attribute the variability of the results to environmental factors such as temperature, humidity and soil conditions. Bouizgarne (2022) lists the factors that slow down the development and sale of biopreparations. These are the issues of the complexity of isolation procedures, the identification of the microbial inoculant, the development of cost-effective conditions for its growth and prevention of possible contamination, the selection of a suitable carrier for bioformulation that would ensure a long shelf life and its appropriate form and method of application of preparations in field conditions. In addition to these factors that influence the effectiveness of biopreparation application, Folli-Pereira *et al.* (2022) also identify temperature, humidity, possible resistance of the harmful organism, and the intensity of infectious pressure as important variables. Both Bouizgarne (2022) and Folli-Pereira *et al.* (2022) point out that despite the proven positive effects of biopreparations on plant growth, there are still doubts about the possibility of their general use in agriculture, in such a complex environment as soil.

Risks of applying biopreparations to the soil

The application of biopreparations containing bacteria, including actinomycetes, is widely regarded as an environmentally friendly alternative to chemical inputs. However, their use may involve certain ecological and biosafety risks. One of the main concerns is the potential dissemination of antimicrobial resistance genes (ARGs) and mobile genetic elements (MGEs) in the soil. Actinomycetes, as a major component of soil microbial communities and a historical source of clinically relevant antibiotics, often possess self-resistance mechanisms encoded on MGEs such as plasmids, transposons, or integrons, enabling horizontal gene transfer (HGT) among soil microorganisms, including plant-associated bacteria and opportunistic pathogens (Wright, 2007; Nesme & Simonet, 2015; Wellington *et al.*, 2013; van Hoek *et al.*, 2011).

Genomic analyses of plant growth-promoting bacteria, including *Streptomyces* spp., have confirmed that some strains carry ARGs on plasmids or other MGEs, raising concerns about their potential mobility in soil (Berg et al., 2017). Metagenomic surveys indicate that the introduction of well-characterised inoculants does not necessarily increase the overall ARG abundance in soil; however, strain-specific effects cannot be excluded, particularly when transferable resistance determinants are present (Berglund et al., 2017). Compared with inputs from manure or wastewater, the risks from biopreparations appear lower, yet rigorous genomic screening and risk assessment remain essential (Cycoń et al., 2019).

Beyond ARG-related risks, actinomycetes can influence soil microbial communities due to their competitive abilities and production of bioactive secondary metabolites. Repeated or high-dose applications of specific strains may disrupt indigenous microbial diversity, alter nutrient cycling, or exert phytotoxic effects on plants and non-target soil organisms (Mendes et al., 2011; Shade et al., 2012). Their ecological plasticity may occasionally lead to dominance in microbial

networks, indirectly affecting the functional stability of the soil ecosystem (Weller et al., 2002).

Intensive agricultural practices, such as repeated application of manure, organic biosolids, or wastewater residues, further drive the dissemination of ARGs in soils by introducing both antibiotic residues and resistant microorganisms, applying selective pressure on microbial populations (Chee-Sanford et al., 2001; Heuer et al., 2011; Martínez, 2008). Soil thus acts as both a reservoir and active hotspot for ARG exchange among indigenous bacteria, opportunistic pathogens, and plant-associated microbiota (Berendonk et al., 2015; Cycoń et al., 2019).

To mitigate potential risks, current recommendations advocate the use of well-characterised strains lacking clinically relevant ARGs and mobile resistance determinants, supported by whole-genome sequencing, ecological monitoring, and management practices that maintain soil microbial diversity (Berg et al., 2017; Berendonk et al., 2015; Glick, 2020). Such preventive measures are essential for ensuring the biosafety of microbial biopreparations while preserving their benefits in sustainable agriculture.

Table 3 Characteristics of biopreparations containing streptomycetes or their biocontrol metabolite (adapted to Aggarwal et al., 2016 and Torres-Redriguez et al., 2022)

Biopreparation/ Biocontrol metabolite	Actinomycetes	Crop	Target pathogen/pest	Main impact	Application method (form)
Agri-Meck®SC, Avid®, Vertimec®/Abamectin (avermectin B1 mixture)	<i>Streptomyces avermitilis</i>	Ornamental plants, cotton, citrus, potatoes, core crops	Dust mites, beetles, ants <i>Pythium, Fusarium, Phytophthora, Rhizoctonia, Verticillium, Botrytis, Alternaria, Geotrichum, Sclerotinia</i>	Binds to glutamate-and GABA-gated chloride channels, causing paralysis and death of arthropods Induction of systemic resistance and production of extracellular chitinases	foliar spray, soil drench; also seed treatment in some formulations soil drench, root dip, seed coating, foliar spray
Actinovate®	<i>S. lydicus</i>	Various crops (roots and foliage)	<i>Xanthomonas spp. Pseudomonas spp.</i>	Inhibition of bacterial protein biosynthesis and cell wall formation	foliar spray (orchard & field application), post-harvest dip in storage management
Agrimycin®, streptomycin formulations/ Streptomycin	<i>S. griseus</i>	Pome and stone fruits, citrus, olives, vegetables, potato, tobacco, cotton, and ornamentals	<i>Pyricularia oryzae</i>	Inhibition of protein biosynthesis by binding to the 50S ribosomal subunit	seedling root dip, foliar spray, field water irrigation incorporation
Blasticidin-S	<i>S. griseochromogenes</i>	Rice	<i>Fusarium oxysporum, Candida, Aspergillus, Cephalosporium, Fusarium, Penicillium</i>	Binding to fungal membrane sterols increases the permeability of the membrane and leakage of cellular contents	bulb dip before planting, soil surface drench, post-harvest antifungal coating
Delvolan®/ Natamycin	<i>S. natalensis, S. chattanoogensis</i>	Ornamental bulbs and plants	<i>Alternaria, Rhizoctonia solani, Fusarium, Botrytis, Phytophthora, Pythium</i>	Competition for space and nutrients; production of polyene antibiotics	Seed treatment, root dip, soil drench, substrate incorporation
Mycostop®	<i>S. griseoviridis</i>	Various crops (root zone)	<i>Erwinia amylovora, Pseudomonas spp., Xanthomonas spp.</i>	Inhibition of bacterial protein synthesis (30S and 50S subunits of ribosomes) and inhibits the binding of aminoacyl-tRNA and termination factors RF1 and RF2.	trunk injection (systemic) for trees, foliar spray for row crops
Mycoshield®, oxytetracycline formulations/ Oxytetracycline	<i>S. rimosus</i>	Various crops	<i>Erysiphe spp., Uncinula necator, Podospaera spp. Sphaerotheca spp. Cercospora spp., Venturia spp., Phytophthora sojae, Botrytis cinerea, Sclerotium spp., Alternaria alternata, Helminthosporium spp.</i>	Inhibition of fungal protein biosynthesis by blocking peptidyltransferase	Foliar spray, flower cluster spray
Mildiomyacin (no widely standardised commercial formulation)	<i>S. rimofaciens</i>	Ornamental grapevine	<i>Phytophthora sojae, Botrytis cinerea, Sclerotium spp., Alternaria alternata, Helminthosporium spp.</i>	Inhibition of protein biosynthesis	Foliar spray, soil drench
Kasumin® /Kasugamycin	<i>S. kasugaensis</i>	Sugar beet, celery, pear, apple, soybean	<i>Alternaria alternata, Helminthosporium spp.</i>	Inhibition of cell wall biosynthesis, the formation of spores and hyphae.	Foliar spray, soil drench
Polyoxin-Z®/Polyoxins	<i>S. cacao</i>	Vegetables, fruit, trees, and ornamentals	<i>Rhizoctonia solani,</i>	Inhibition of trehalase disrupts fungal energy metabolism and pathogenicity	Soil drench, seedling dip, paddy-water application
Validacin®, Valimun®, /Validamycin	<i>S. hygroscopicus</i>	Rice, potato, vegetable, strawberry, tobacco, ginger, cotton, sugar beet			

CONCLUSION

In this review, we bring the latest knowledge about the possibilities of use and benefits of applying biopreparations with actinomycetes to the soil. Of the bacteria, biopreparations include mainly representatives of the genera *Bacillus* and *Pseudomonas*, as well as actinomycetes, especially species of the genus *Streptomyces*. Bacteria of the genera *Streptomyces* spp., *Nocardopsis* spp., or *Frankia* spp. can support plant growth in various ways, convert macroelements from their unavailable form to a form acceptable to plants, and also protect plants from phytopathogens. Actinomycetes are a natural component of the soil microbiocenosis, and their use is not expected to negatively affect the ecosystem, soil quality and health, plant growth, or the health of humans and animals. The positive effect of the application of biopreparations containing actinomycetes or their secondary metabolites should be reflected in increased mineralisation and thus better availability of nutrients (nitrogen, phosphorus, iron), in the soil for plants, and reduction of the occurrence of phytopathogens. We expect that the application of biopreparations will reach the level of impact of the application of industrial fertilisers and pesticides. The effectiveness of individual representatives of actinomycetes against specific phytopathogens is often different and species-specific, and their application against phytopathogens inhabiting the underside of the leaf surface is also often ineffective. The challenge for the future will be to minimise the difference in the effectiveness of biopreparations in "in vitro" and "in vivo" conditions, as in field conditions, this efficiency is often lower due to changing environmental conditions and self-regulatory relationships between microorganisms. Biopreparations have proven themselves especially in small and controlled conditions (gardens, greenhouses). They are also usable for large areas, but it is necessary to take into account a higher price, variable efficiency and the need for integrated protection.

Acknowledgements: This publication was supported by the Slovak Research Grant No. VEGA 1/0573/23 (Compost microbiome and its role in quality improvement of soil and crop production).

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