



The role of *Streptomyces* species in controlling plant diseases: a comprehensive review

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Abstract

Numerous factors contribute to the decline in crop yields, including plant diseases caused by bacteria, fungi, and viruses. The management of these diseases with chemical fertilizers is not a sustainable approach. This review briefly summarizes the role, mechanisms, advantages, and disadvantages of using *Streptomyces* species in plant disease management as an alternative method is needed to address the problems of using chemicals. One promising alternative is to use microbes to manage plant diseases. *Streptomyces*, a gram-positive saprophytic bacterium, is particularly effective at combating plant diseases. They produce bioactive-rich antimicrobial metabolites and enzymes that can kill or inhibit the growth of plant pathogens. *Streptomyces* species are widely distributed in nature but are especially abundant in the rhizosphere, the soil region surrounding plant roots. *Streptomyces* can be used as bioinoculants to protect plants from diseases. In addition to their disease-fighting abilities, they can promote plant growth in many ways. They produce plant growth-promoting substances, such as indole-3-acetic acid (IAA), cytokinin, and siderophores. They also suppress diseases through antibiosis, mycoparasitism, and nutrient competition. *Streptomyces* can also supply plants with essential minerals, i.e., iron, copper, phosphorus, and sulfur. Therefore, it is concluded that *Streptomyces* species can be used as an alternative to chemicals to control plant diseases.

Keywords Antimicrobial compounds · Biological control · Plant Diseases · Plant growth promotion · *Streptomyces*

Introduction

The pressure to meet rising food demands propelled the adoption of chemical fertilizers and pesticides to maximize agricultural production (Bhardwaj and Agrawal 2014), and the decline in agricultural productivity can be attributed to many factors, with pests and pathogens being the most prominent. The prevalence of pathogen infections among crops can range from 20 to 40%, significantly impacting overall yields (Savary et al. 2012). The widespread application of chemical substances in agriculture can lead to a cascade of detrimental effects, including the accumulation of harmful residues in the environment, the evolution of fungicide resistance in plants, and the unintended proliferation of non-target and beneficial microbes (Bharathi et al. 2004).

Developing genetically resistant crops is a lengthy process that requires innovative methods to overcome agricultural productivity limitations (Rey and Dumas 2017). Consequently, focusing on microorganisms is a viable strategy for enhancing agricultural productivity. Microbes are essential in plant disease management due to their environmental friendliness.

Plant beneficial microbes are abundant in the rhizosphere region, which is used as bio inoculants and can maintain the soil environment by fixing the nitrogen, solubilizing nutrients like phosphate and potassium, liberating plant growth stimulating constituents, synthesis of antibiotic compounds, and improvement of soil organic matter content through biodegradation processes (Bhardwaj and Agrawal 2014). Among all microbes, actinomycetes receive wide attention because of their potential antibiotic production, which is used for controlling various plant pathogens. Their mechanism includes mycoparasitism, nutrient competition, production of hydrolytic enzymes and antimicrobial metabolites, and regulation of plant defense. As per Bergey's Manual of Systematic Bacteriology (Whitman et al. 2012),

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actinomycetes are renamed actinobacteria, of which *Streptomyces* is widely studied since it can be grown in the laboratory on artificial media. *Streptomyces* sp. contributes about 10% of soil microflora with antifungal, antibacterial, antiviral, and antioxidant activities. 60% of antibiotic production is by *Streptomyces*, besides producing hormones like IAA and siderophore, which are responsible for improving plant growth. In a nutshell, using actinomycetes possessing antimicrobial activity might be an alternative for chemical fertilizers in plant disease management owing to their low cost of production, environmental safety, and reduction in natural non-replenishable resources. Considering its importance and potentiality, the application of *Streptomyces* spp. as a bioinoculant and alternative to chemical additives, besides its mechanisms in managing plant diseases and causes of diseases, is reviewed here.

Actinobacteria

Combining the characteristics of bacteria and fungus, actinobacteria are widespread in compost, atmosphere, and freshwater basins at varying depths worldwide. This gram-positive bacterium is classified under the Actinomycetes class and Actinomycetales order of the kingdom of bacteria's Actinobacteria phylum, Actinomycetes order, and Actinomycetaceae family. It possesses a high genomic G+C content of 74% by molecular weight (Elamvazhuthi and Subramanian 2013). Nonthakaew et al. (2022) and Peng et al. (2020) isolated many isolates from plant rhizosphere, including *Streptomyces* spp., and explored their potential antimicrobial activity.

Waksman and Henrici (1943) familiarized *Streptomyces* for the first time as the type genus of the family *Streptomycetaceae*, distinguished by physiological and morphological characteristics, type of fatty acids chains, phospholipids, peptidoglycan, GC content (%), chemical constituents of cell walls, 16 S rRNA analysis and DNA hybridization (Bhardwaj and Agrawal 2014).

Actinobacteria produces an array of secondary metabolites with high commercial interest, among which genus *Streptomyces* tops in the production with the discovery of actinomycin. Functions employed include degrading organic substrates like proteins, fats, and cellulose; therefore, its ability to produce microbial bioactive compounds makes actinobacteria one of the most explored microbes among prokaryotes. The secondary metabolites of actinobacteria are known for their role in various physiological, cellular, and biological processes (Selim et al. 2021).

Streptomyces is a significant genus representing over 500 species of chemoorganotrophic, filamentous Gram +ve, and non-acid-fast organisms. The majority of the species

are mesophile (10–37 °C) while some are thermophile (45–55 °C) with pH of 6.5–8.0 (e.g.) *Streptomyces thermoflavus*, *S. thermonitrificans* and *S. thermovulgaris* (Gowdar et al. 2018). They are sensitive to water-logged conditions, form arthrospores, and are more drought-resistant. Few reports illustrated that sandy loam and calcareous soil possess more *Streptomyces* than heavy clay soil. Substrate and aerial mycelium production occur in which substrate hyphae are 0.5–0.1 µm diameter. As it ages, the production of aerial mycelium begins, forming a chain of spores (conidia) (Wildermuth 1970; Wildermuth and Hopwood 1970). The spores are formed by fragmentation and are arranged in helical, wavy, or straight chains. The colonies grow slowly with initial smooth edges and progress into crosswise mycelial threads that appear velvety, powdery, floccose, or granular with the typical earthy odor.

Actinomycetes distribution

Actinomycetes are widely distributed in natural ecosystem habitats such as soil, rhizosphere soil, actinmycorrhizal plants, hypersaline soil, limestone, freshwater, marine, sponges, volcanic cave—hot spot, desert, air, insects' gut, earthworm castings, goat feces, and endophytic actinomycetes. The most important features of microbial bioactive compounds are that they have specific microbial producers: their diverse bioactivities and their unique chemical structures. Actinomycetes represent a source of biologically active secondary metabolites like antibiotics, biopesticide agents, plant growth hormones, antitumor compounds, antiviral agents, pharmacological compounds, pigments, enzymes, enzyme inhibitors, anti-inflammatory compounds, single-cell protein feed, and biosurfactant (Farda et al. 2022; Selim et al. 2021). The rhizospheric streptomycetes can prevent the fungal infection of plant roots by producing antifungal drugs. Actinomycetes are also excellent sources of lytic enzymes, antibiotics, and other bioactive compounds due to their metabolic diversities (Vurukonda et al. 2018).

According to the recent study conducted by Ambikapathy et al. (2022b), the insect gut microbiota significantly contributes to the nutrition of termites, cockroaches, and aphids. *Apis mellifera*, the honeybee, has a complex digestive tract, which makes it an attractive model for studying gut bacteria. Occasionally, *Streptomyces* spp. can dominate the bee stomach. The bee guts have also been recorded to contain *Nocardiopsis* sp., which expresses an antibiotic biosynthesis gene. The *Bacillus* strains native to the bees and the actinomycetes have selectively killed two other drug-resistant Gram-positive pathogens.

The *Nocardiopsis alba* has been detected in the guts of honeybees. In earthworm casting, the actinomycetes and

industrial enzymes have rarely been studied. The casting action of *Actinomyces* sp. nourishes and enriches the soil. By burrowing and eating, the earthworms redistribute the organic materials in the soil, increase the soil's permeability, improve the exchange of gases with the atmosphere, and increase microbial activity. Several medicinal applications can be recognized for casting actinomycetes in animal and human medicines (Salcedo-Porras et al. 2020). Most actinobacteria are environmental residents, as opposed to the obligate pathogens. Actinobacteria play vital roles in the life and reproduction of many insects. The streptomycetes protect the European beewolf pups against microbial pathogens infection. *Oerskovia* and *Nocardiosis* spp. are the major bacterial species detected in goat feces, generating more antifungal agents than antibacterial ones. Antibiotics from *Streptomyces* spp., such as monensin and flavomycin, have been utilized to promote the growth rate of cattle (Selim et al. 2021). An endophyte is a microorganism that lives entirely or partially inside the plant's tissues. The longstanding relationship between the endophytic bacteria and their host plants has increased their numbers (Huang et al. 2021).

Actinomycete-derived bioactive compounds effectively control silver scurf disease in potatoes, which is caused by the fungus *Helminthosporium solani* (Gao et al. 2021). *Streptomyces* species are particularly good at producing antifungal compounds. One example is Amycolatopsis CP2808, which makes ansa carbamitocins antibiotics. Ansamitocin also has anticancer properties. Another example is *Nocardia* sp., an endophytic actinomycete with ansamitocin (Selim et al. 2021).

Chen et al. (2021) found that marine actinomycetes interact with various marine organisms, such as sponges, corals, echinoderms, and puffer fish. These interactions may promote the evolution of secondary metabolic pathways in marine actinomycetes, producing diverse chemical compounds. These interactions may have significant ecological and biotechnological implications. These compounds may have novel biological activities, including antimicrobial, antitumor, and antiviral ones. In addition to the interaction with the other species of marine organisms, the marine actinomycetes may thrive in both the planktonic and the biofilm habitats, and most of these actinomycetes strains have been identified in the sediments (Schmidt et al. 2019).

What factors encourage and result in actinomycetes adopting one of these life choices is unknown. In general, the planktonic and biofilm-forming bacteria have diverse species compositions. Many physicochemical characteristics, such as temperature, pH, pressure, total organic carbon, and salinity, affect the abundance of actinomycetes in ocean sediment. The optimal conditions for actinomycetes vary depending on the location. *Streptomyces*, *Micromonospora*, and *Actinomyces* strains have been discovered at depths up to

500 m (Jagannathan et al. 2021). For instance, *Micromonospora* sp. may be more abundant at 450 m than lower levels. Furthermore, several investigations have demonstrated that the actinomycetes samples taken from the coastal sediments are more heat resistant than those collected from the salt water, suggesting that the heat-resistant spore forms of the actinomycetes dominate the deposits over their vegetative states (Jagannathan et al. 2021).

Actinomycetes isolation

Isolation of the soil actinomycetes

Actinomycetes can be isolated from soil samples using several general bacterial isolation procedures, such as serial dilution, pouring plates, streaking, and centrifugation (Majhi 2021). Centrifugation followed by repeated dilutions can improve the growth of actinomycetes in soil samples. However, none of these techniques can specifically isolate actinomycetes, making it difficult to purify them (Shivabai and Gutte 2019).

A pure culture of non-actinomycete bacterium can inhibit the growth of actinomycetes. Therefore, six methods have been developed for selective isolation of the soil actinomycetes mainly (i) nutritional selection, in which the media contain nutritional components that the actinomycetes preferentially consume; (ii) selective inhibition, in which the growth inhibitors such as antifungal drugs and antibiotics are included to prevent growth of the non-actinomycete bacteria, (iii) physical or chemical sample pretreatments; to limit the non-actinomycete bacteria, (iv) enrichment approaches; where the nutritional medium can be supplemented with extra nutrients, which favor growth of the actinomycetes, and/or inhibit the growth of the other microorganisms, (v) the membrane filter method, which does not require pretreatment, specific medium, and/or antibiotics; and (vi) the integrated method that can use combinations of various procedures (Kumar and Jadeja 2016). Pretreatment of the soil can either increase the growth of actinomycetes or remove most of the unwanted Gram-negative bacteria. Several pretreatment methods have been developed for the different actinomycetes taxonomy. Under natural settings, the streptomycetes play a significant role in the actinomycetes population. As a result, physical pretreatment can facilitate the isolation of the streptomycetes. In contrast, chemical pretreatment and/or a combination of physical and chemical pretreatments may reduce the isolation of the other bacteria (Ezeobiora et al. 2022).

Isolation of the marine actinomycetes

The phylum Actinobacteria adapts to and colonizes many hostile habitats, including the deep sea; its metabolic capability, morphology, and metabolism are incredibly varied. Generally, the growth conditions of unusual marine actinomycetes differ from terrestrial actinomycetes (Subramani and Sipkema 2019). A considerable proportion of the bacteria in underexplored habitats are viable but not culturable since only around 1% of these bacteria can form colonies on the isolation media using the standard techniques. For this reason, high-throughput molecular methods, such as metagenomics, are becoming increasingly popular for studying microbial communities in environments where culture-based approaches are largely ineffective (El-Tarabily et al. 2009; Gutleben et al. 2018). Furthermore, culture-independent studies on the functional features of actinomycetes have improved methods for growing and cultivating the previously uncultivable actinobacteria (Kumar and Jadeja 2016).

The actinomycetes' taxonomy, physiology, and environmental parameters, including pH, culture temperature, oxygen, and nutritional requirements, must be understood and controlled to isolate the undiscovered or uncommon actinomycetes (El-Tarabily 2003; Subramani and Sipkema 2019). The growth media should usually have osmotic values similar to seawater since sodium (Na^+) is a critical medium for developing marine microorganisms such as *Salinispora* spp. Furthermore, different carbon sources (i.e., soluble starch, glucose, dextrose, maltose, trehalose, mannitol, raffinose, fucose, chitin, glycerol, and oatmeal), and combined carbon-nitrogen sources (i.e., peptone; yeast extract, casein, malt extract, meat extract, beef extract, and tryptone) should be added to the isolation media. Furthermore, sediment extracts, sponge extracts, and genuine saltwater should be introduced alone or as supplements to simulate the natural growth conditions of marine life (El-Tarabily et al. 1996; Subramani and Sipkema 2019).

Before isolating the uncommon actinomycetes, marine materials, mainly sediments, may be added to eliminate the common terrestrial actinomycetes and undesirable microorganisms. Isolation of the rare Actinomycetes from the marine samples is commonly done by diluting and mixing the samples with sterile natural and/or artificial seawater, deionized dist (El-Tarabily 2006; Siro et al. 2022). Water with NaCl, multi-salts, vitamin B mixtures, Ringer's solution, and/or saline solution. The marine actinomycetes have been preferentially isolated using a variety of pretreatment procedures; most commonly, the environmental sample is to be dried within a laminar airflow cabinet and then diluted with seawater or saline before it is heated (Siro et al. 2022). Due to their resistance to desiccation and heat, the

actinomycetes spores can be used to select against the other Gram-positive bacteria.

The actinomycetes spores resist various substances, including benzethonium chloride, chlorhexidine gluconate, phenol, sodium dodecyl sulfate, and several antibiotics. Selective separation of the actinomycete taxa has been achieved using these substances (Hayakawa 2008). These substances kill or inhibit the aerobic Gram-negative bacteria, endospore-forming bacteria, and pseudomonads within 30 min., thus increasing the possibility of selective isolation of the actinomycetes while reducing the other forms of bacteria. Moreover, the ultrasonic waves can disperse the actinobacterial propagules from the soil particles, thereby increasing the actinobacterial strains and lowering those of undesirable bacteria (Rasuk et al. 2017).

Streptomyces as a bio inoculant

Streptomyces spp. may decompose biopolymers such as lignocellulose, starch, and chitin in soil, water, and organic debris (Fig. 1). *Streptomyces* as a bioactive chemical became apparent following the discovery of streptomycin, which paved the door for detecting antimicrobial substances. Malviya et al. (2009) and Gopalakrishnan et al. (2011) isolated many actinomycetes from rhizosphere soil from diverse sites. They screened them for their new microbial chemicals. *Streptomyces* sp. alone accounted for 75% of the antibiotics used in agrochemicals and medicines among actinobacteria (Berdy 2005). Through the synthesis of extracellular hydrolytic enzymes, they have also gained significance in plant disease control (Joo 2005; Prapagdee et al. 2008). The formation of thread-like filaments in the soil is helpful for the effective colonization of the rhizosphere (Al Raish et al. 2021; Elnahal et al. 2022). In addition, they encourage plant development, make nutrients accessible, and combat infections. They are administered as spore suspension, culture filtrate, wettable granules, wettable powder, and emulsifiable concentrates for synthesizing antibiotics, bactericides, insecticides, fungicides, acaricides, and herbicides (Chouyia et al. 2022).

The mechanism employed by *Streptomyces* against plant pathogens

Streptomyces species can inhibit infections by providing bioactive chemicals, extracellular enzymes, and antibiotics (Fig. 2). Table (1): summarizes the effectiveness of *Streptomyces* isolates and its secondary metabolites in managing plant pathogens.

Fig. 1 Applying *Streptomyces* to plants (via spray or soil inoculation) can improve their uptake of metals, production of hydrolytic enzymes, phytohormones, osmolytes, and antioxidants

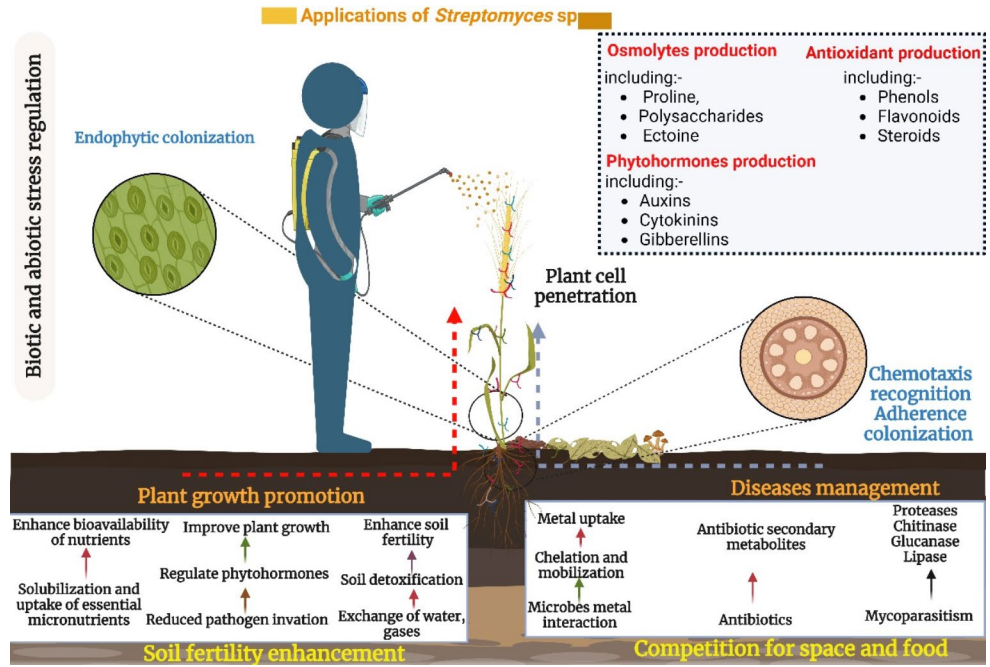
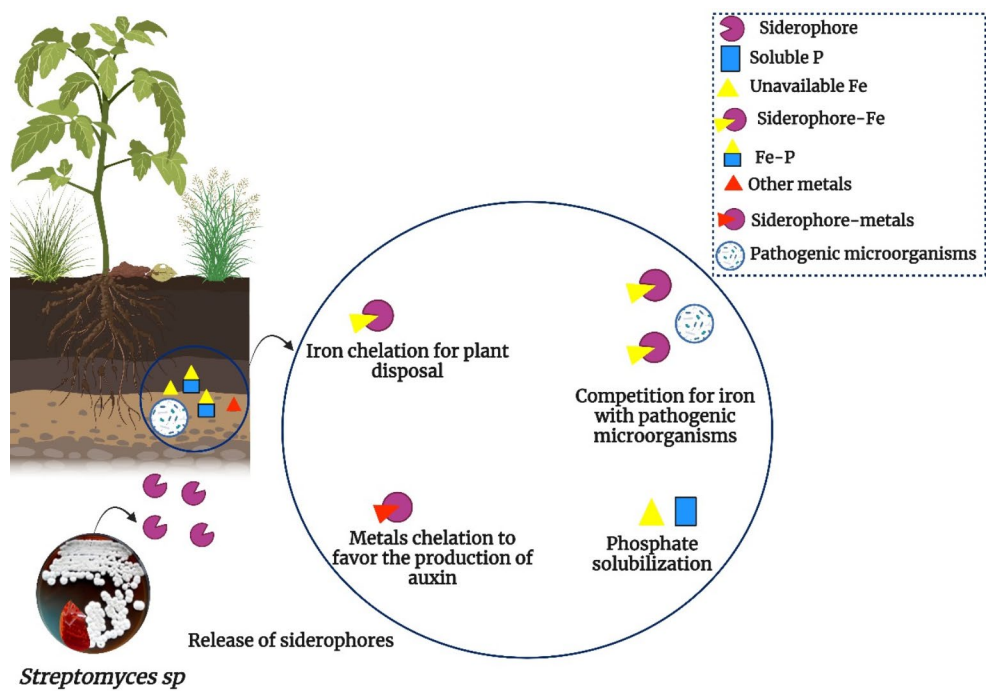


Fig. 2 Mechanism of *Streptomyces* in control plant pathogens



Mycoparasitism / hydrolytic enzymes

Like parasitism and antibiosis, enzymes play a crucial role in the biocontrol of plant diseases. Antifungal activity needs cell wall disintegrating enzymes such as 1,3-glucanase, chitinase, cellulase, and protease (Haggag and Mohamed 2007). Actinobacteria are potential makers of -1, 3-glucanase, chitinase, amylase, pectinase, cellulase, xylanase, lipase, and protease and are isolated from agricultural soil actinomycetes (Sonia et al. 2011). The complete dissolution

of *Sclerotium rolfsii*, *Sclerotinia minor*, *Aspergillus*, and *Fusarium oxysporum* was caused by glucanase and chitinase (Hassan et al. 2011; El-Saadony et al. 2022).

Two hundred and eighty-three chitinolytic actinomycetes were isolated from rhizosphere soils of Sisaket Province and Ubon Ratchathani, Thailand was separated by Pattanapitpaisal and Kamlandharn (2012), among which 13 isolates showed potentiality for inhibiting the fungal growth emphasizing its usage as a biocontrol agent. Srividya et al. (2012) reported β -1, 3 and β -1, 4 glucanases, chitinase, protease

Table 1 The effectiveness of *Streptomyces* isolates and its secondary metabolites in managing plant pathogens

Plant	Disease	Pathogen	<i>Streptomyces</i>	Active compounds	Reference
Lemon	Sour rot	<i>Geotrichum candidum</i>	<i>Streptomyces</i> sp. RO3	Oligomycins A	(Goudjal et al. 2014)
Turfgrass	Crown disease	<i>Rhizoctonia solani</i>	<i>S. violaceusniger</i> YCED9	Natamycin; 4-Phenyl-3-butenoic acid	(Gao et al. 2021)
Porphyra	Red rot	<i>Pythium porphyrae</i>	<i>Streptomyces</i> sp. AP77	Rapamycin	(Zhang et al. 2016)
Chilli	Root rot, blight	<i>Alternaria brassicae</i> , <i>C. gloeosporioides</i>	<i>Streptomyces</i> spp.	4-Phenyl-3-butenoic acid	(Srividya et al. 2012)
Sweet pea	Powdery mildew	<i>Oidium</i> sp.	<i>Streptomyces</i> sp.	Natamycin	(Sangmanee et al. 2009)
Ginger	Rhizome rot	<i>F. oxysporum</i> f. sp. <i>zingiberi</i>	<i>Streptomyces</i> spp.	Antimycin A17	(Manasa et al. 2013)
Tomato	Damping-off	<i>R. solani</i> <i>Rhizoctonia solani</i>	<i>Streptomyces</i> spp. <i>Streptomyces</i> sp. S30	Oligomycins A and C Rapamycin	(Goudjal et al. 2014) (Gao et al. 2021)
	Fusarium wilt	<i>Fusarium oxysporum</i> f.sp. <i>lycopersici</i>	<i>S. rochei</i> ACTA 1551	Pyrroles (Pyrroles [1,2- a] pyrazine-1,4-dione	(Kanini et al. 2013)
	Root rot	<i>R. solani</i>	<i>Streptomyces vinaceusdrappus</i> S5MW2	1 H-Pyrrole-2- carboxylic acid (PCA)	(Yandigeri et al. 2015)
		<i>R. solani</i>	<i>S. toxytricini</i> vh6	Propanoic acid	(Patil et al. 2011)
Pepper	Blight	<i>Phytophthora capsici</i>	<i>Streptomyces</i> spp. 47W08, 47W10	Avermectins	(Yandigeri 2021)
		<i>Colletotrichum gloeosporioides</i>	<i>S. cavurensis</i> NRRL 2740	Lucensomycin	(Intra et al. 2011)
Chickpea	Fusarium wilt	<i>Fusarium</i> spp.	<i>Streptomyces</i> (CAI-24, CAI-121, CAI-127, KAI-32 and KAI90)	Natamycin	(Gopalakrishnan and Ganeshkumar 2013)
	Basal rot	<i>Macrophomina phaseolina</i>	<i>Streptomyces</i> sp. RO3	Oligomycins A and C	(Goudjal et al. 2014)
Cucumber	Damping-off	<i>Pythium</i> spp.	<i>S. griseoviridis</i>	4-Phenyl-3-butenoic acid	(Junaid et al. 2013)
Onion	Bacterial rot	<i>Erwinia carotovora</i>	<i>S. lavendulae</i> HHFA1	Natamycin	(Gopalakrishnan and Ganeshkumar 2013)
Wheat	Root rot	<i>Fusarium cloumorum</i>	<i>S. aurantiogriseus</i> VSMGT1014	Oligomycins A and C	(Harikrishnan et al. 2014)
Rice	Blast	<i>Bipolaris oryzae</i> , <i>Curvularia oryzae</i> , <i>Fusarium oxysporum</i> , <i>Pyricularia oryzae</i> , <i>Rhizoctonia solani</i> and <i>Rhizoctonia oryzae-sativae</i>	<i>S. hundertgensis</i> strain MBRL 251; <i>Streptomyces</i> sp. KH-614	Antimycin A17	(Nimaichand et al. 2013)
	sheath blight	<i>R. solani</i>	<i>S. aurantiogriseus</i> VSMGT1014	Oligomycins A and C	(Harikrishnan et al. 2014)
	brown spot	<i>Helminthosporium oryzae</i> , <i>R. solani</i>	<i>S. misionensis</i> NBRC	Rapamycin	(Poomthongdee et al. 2015)
	brown spot	<i>Pyricularia</i> sp.	<i>Streptomyces</i> strain PC 12, <i>Streptomyces</i> strain D 4.1, <i>Streptomyces</i> strain D 4.3 and <i>Streptomyces</i> strain W1	Pyrroles (Pyrroles [1,2- a] pyrazine-1,4-dione	(Chaiharn et al. 2020)
Groundnut	Stem rot	<i>Sclerotium rolfsii</i>	<i>Streptomyces</i> sp. CBE	1 H-Pyrrole-2- carboxylic acid (PCA)	(Adhilakshmi et al. 2014)
Pepper and cherry tomato	Anthracnose	<i>Colletotrichum gloeosporioides</i>	<i>Streptomyces</i> sp. A1022	Lucensomycin	(Gao et al. 2021)
Lettuce	Basal drop	<i>Sclerotinia minor</i>	<i>S. viridodiasticus</i>	Natamycin; 4-Phenyl-3-butenoic acid	(Gao et al. 2021)
	Damping off	<i>Pythium ultimum</i> ; <i>Rhizoctonia solani</i>	<i>Streptomyces</i> sp. YCED9	Natamycin	(Chen et al. 2018)
Apple		<i>Botryosphaeria dothedia</i>	<i>Streptomyces rochei</i> A1	Propanoic acid	(Zhang et al. 2016)
Strawberries		<i>B. cinerea</i>	<i>Streptomyces</i> sp. 3–10	Avermectins	(Lyu et al. 2017)

Table 1 (continued)

Plant	Disease	Pathogen	<i>Streptomyces</i>	Active compounds	Reference
Banana		<i>C. musae</i> , <i>C. gloeosporioides</i>	<i>Streptomyces spectabilis</i> NBRC 13,424	Lucensomycin	(Chen et al. 2018)
	wilt	<i>Fusarium oxysporum</i>	<i>S. violaceusniger</i> G10	Propanoic acid	(Chaiharn et al. 2020)
Red chili	Anthracnose	<i>Colletotrichum gloeosporioides</i>	<i>S. ambofaciens</i> S2	Avermectins	(Lyu et al. 2017)
Soybean	Blight	<i>Xanthomonas campestris</i> pv. <i>glycines</i>	<i>Streptomyces</i> sp.	Antimycin A17	(Chaiharn et al. 2020)
Many	Root rot, botrytis blight	<i>Alternaria alternata</i> , <i>Botrytis cinerea</i>	<i>S. spororaveus</i> RDS28	PCA	(Yandigeri et al. 2015)
	Leaf blight	<i>Coriolus versicolor</i> ; <i>Phanerochaete chrysosporium</i>	<i>S. violaceusniger</i> XL-2		(Chaiharn et al. 2020)
	Wood rot	<i>Sclerotium rolfsii</i>	<i>S. hygroscopicus</i>	Antimycin A17	

and lipase-producing isolates from Solanaceae rhizosphere having possible role against fungal pathogens like *Alternaria alternata*, *A. brassicola*, *A. brassicaceae*, *Rhizoctonia solani*, *Colletotrichum gloeosporioides*, and *Phytophthora capsici*. The second most abundant organic compound in the cell wall next to cellulose is chitin, and the chitinase enzyme produced by *Streptomyces* spp. can depolymerize it. Hence, it could be exploited as a promising tool in biocontrol either directly or indirectly by using purified proteins (Sonia et al. 2011). Chitinase-producing chili rhizosphere isolates exhibited antimicrobial potential against *Colletotrichum capsici* and *Fusarium oxysporum* (Ashokvardhan et al. 2014). *S. griseoloalbus* from cucumber rhizosphere suppressed the damping-off pathogen *Pythium aphanidermatum* when compared with metalaxyl by producing cell wall degrading enzymes (El-Tarabily and Sivasithamparam 2006). The conidial germination of cucumber wilt pathogen *F. oxysporum* f. sp. *cucumerinum* was inhibited by the actinobacteria *S. bikiniensis* strain HD-087, which triggered defense-related enzyme β -1,3, glucanase, phenylalanine ammonialyase and peroxidase against the pathogen (Zhao et al. 2012).

Antibiosis

Actinobacteria are capable of producing several volatile compounds, poisons, and antibiotics. *Streptomyces* are potential makers of numerous secondary metabolites that can function as fungicides against plant diseases and ensure environmental safety among actinomycetes (Siupka et al. 2021). *S. padanus* Strain JAU4234, which generated fungichromin, actinomycin X2, and antifungalmycin 702, exhibited antifungal activity in *Rhizoctonia solani* via altering the structure of cell membranes and the cytoskeleton in addition to interacting with cellular organelles (Xiong et al. 2013). Similarly, *S. olivaceiscleroticus* AZ-SH514 and *S. antibioticus* AZ-Z710 were known to produce mycangimycin and 4-phenyl-1-naphthyl-phenyl acetamide with antibacterial and

antifungal activity against *Staphylococcus aureus*, *Micrococcus lutea*, *Bacillus subtilis*, *B. pumilus*, *Klebsiella pneumonia*, *Escherichia* (Atta 2015). Similarly, the antibiotic compounds geldanamycin, guanidylfungin A, and nigericin produced by *S. violaceusniger* YCED9 showed antifungal activity against *Phytophthora*, *Pythium* and *Fusarium* spp, besides making the chitinases and β -1,3-glucanase enzymes (El-Tarabily et al. 1997; Trejo-Estrada et al. 1998).

Polyoxins B and D were obtained from *S. cacaoivar* function by inhibiting the chitin syntheses (Isono et al. 1967). Mildiomycin from *Streptoverticillium rimofaciens* inhibits protein biosynthesis in powdery mildew (Harada and Kishi 1978). Polyene from *Streptomyces plumbeus* effective against *Botrytis cinerea* (El-Tarabily et al. 2010; Han et al. 2020), macrolide antibiotic oligomycin A from *S. libani* was active against pathogenic fungi *Botrytis cinerea*, *Cladosporium cucumerinum*, *Colletotrichum lagenarium*, *Magnaporthe grisea* and *Phytophthora capsici* ((Kim and Xiao 2011), and isochainin from an *S. marokkonensis* AP1 strain inhibitory towards *F. oxysporum* f. sp. *albedinis* and *V. dahliae* (Bouizgarne et al. 2009; Saxena 2014). Kasugamycin, a bactericidal and fungicidal metabolite from *Streptomyces kasugaensis*, is effective against rice blast *Pyricularia oryzae* by inhibiting the protein biosynthesis in microorganisms (Law et al. 2017) and *Pseudomonas* diseases of several crops (Sharma et al. 2014). Cyclic lipopeptide daptomycin from *S. roseosporus* (Liu et al. 2013), geldanamycin, nigericin, and Oligomycin A of *S. diastatochromogenes* exhibited inhibitory activity against many pathogenic fungi (Yang et al. 2010). The antibiotics 2,5-Piperazinedione and Pyrrolo [1,2-a] pyrazine-1,4-dione, hexahydro functions by reducing or scavenging the volume of free radicals (Morales-Gonzalez et al. 2018) exhibiting antioxidant activity.

It has been reported that actinomycetes spores can be present in the air. Moreover, it has been suggested that airborne actinomycetes, such as *Nocardia* spp., have antibacterial activity (Seratnahaei et al. 2022). Several unique bioactive

microbial compounds have been produced by symbiotic and transitory bacteria in the insect digestive tracts, which include streptanoate; alpiniamide A, the alteramides A and B, coproporphyrin III, deferoxamine, demethylenocardamine, dihydropicromycin, nocardamine, picromycin, surugamides A, B, C, D, and E, tirandamycins A and B, and valinomycin (Ambikapathy et al. 2022a; Li et al. 2022).

Volatile organic compounds (VOCs)

Propyl ester of octadecanoic acid produced by *S. albolongus* S9 was highly inhibitory to *Corynespora cassiicola*, causing spot disease in tomatoes (Devi and Rao 2017). Volatile organic compounds are diffusible and low molecular weight compounds produced by many *Streptomyces* spp. and exhibit potent antifungal activity. Aldehydes, alkanes, aromatic hydrocarbons, alcohols, alkenes, ketones, furans, esters, and ethers were created. *S. platensis* strain F-1 volatiles conferred resistance to *Rhizoctonia solani* on rice, *Sclerotinia sclerotiorum* on oilseed rape, and *Botrytis cinerea* on strawberries (Wan et al. 2008). Phenol, 2-methyl-5-(1-methylethyl) (Carvacrol) from *Streptomyces griseus* has a cytotoxic effect on peroxidant activity, antifungal activity against *Penicillium glabrum*, *P. capisci*, *R. solani*, *F. moniliforme*, *S. sclerotiorum*, and *Cladosporium herbarum* (Danaei et al. 2014). Cyclohexanol, benzaldehyde, and naphthalene possessed antimicrobial effects (Danaei et al. 2014). VOCs secreted by *S. alboflavus* TD-1 include activity against *Aspergillus ochraceus* (Yang et al. 2018). Inhibition of *Sclerotinia sclerotiorum* mycelial growth and spore germination was achieved by the VOCs Cyclohexanol, decanol, 2-ethyl-1-hexanol, nonanol, benzothiazole, and dimethyl trisulfide (Fernando et al. 2005; Al Hamad et al. 2021; Alwahshi et al. 2022).

Bacterial pathogens

S. termitum ATC-2 developed the antibacterial chemical aloesaponarin II, which is effective against the rice bacterial blight disease (Donghua et al. 2013). Similarly, Mingma et al. (2014) reported that *Streptomyces* sp. strain RM 365 inhibited *Xanthomonas campestris* pv. glycines, which causes bacterial pustule on soybean, and *Streptomyces* sp. strain OE7 inhibited *Pectobacterium carotovorum* and *P. atrosepticum*, which causes soft rot of potatoes, by up to 90% (Baz et al. 2012).

Root colonizer and defense activator

The rhizosphere is a reservoir for all chemical and biological interactions in the soil matrix, and it contains a variety of helpful and hazardous bacterial species. (Glick 2012;

Raaijmakers et al. 2009). One of the fundamental characteristics of biocontrol agents is their ability to colonize the roots efficiently, with more colonization resulting in greater efficiency against plant infections. Unlike pathogenic microorganisms, helpful microorganisms mobilize plant nutrients and guard against plant illnesses (Solanki et al. 2013).

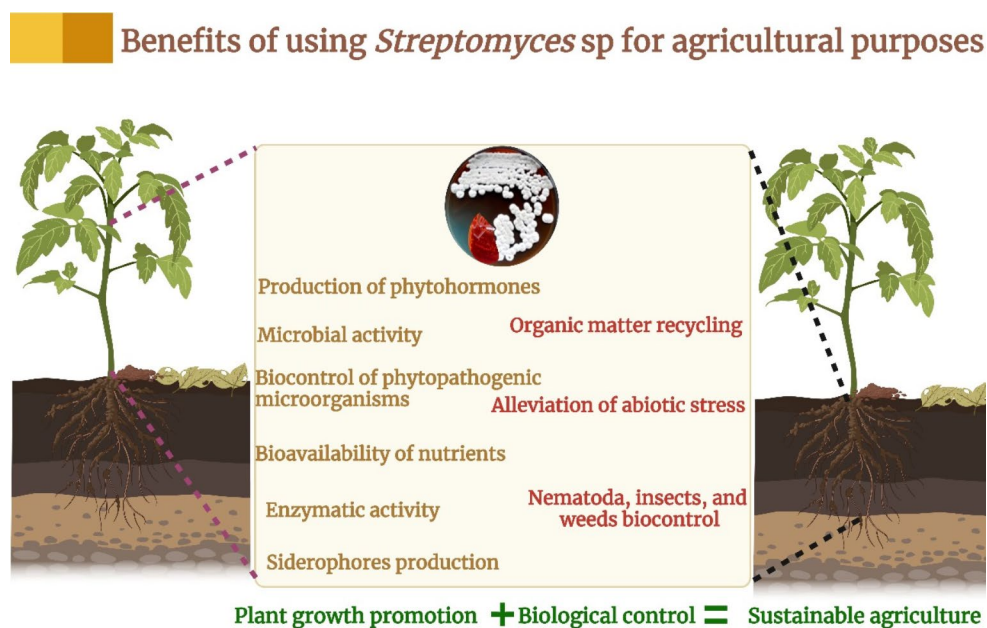
A superior model of actinomycetes for rhizosphere colonization is *S. griseoviridis* isolated from sphagnum peat (Tahvonen 1982) used against cucumber root rot, damping-off in crucifers and carnation fusarial wilt. Cheng et al. (2019) reported the colonization of *Sclerotinia sclerotiorum* in oilseed rape by *S. felleus* YJ1 and enhanced activities of Peroxidase (PO), polyphenol oxidase (PPO), superoxide dismutase (SOD) associated with plant disease resistance (Kim and Hwang 2007). POD aids in lignin formation by enhancing the thickness of the cell wall, PPO oxidizes phenols to quinone, and phenylalanine ammonia-lyase (PAL) strengthens the production of phenolic compounds lignans and phytoalexin which promotes systemic resistance in the plant (Wang et al. 2013).

Plant growth promotion

Like other PGPRs, *Streptomyces* can stimulate plant growth and enhance crop output by obtaining nutrients or secreting growth regulators (Fig. 2). The inoculation of *Streptomyces* strains into plants such as tomato, wheat, Sorghum, and rice increased plant biomass (Palaniyandi et al. 2011). Several pathways enhanced plant growth, including phosphate solubilization, N₂ fixing, ACC deaminase synthesis, sulfur oxidation, and iron acquisition (Nassar et al. 2003; Jaemsaeng et al. 2018). Tomato plants infected with the endophytic *Streptomyces* sp. GMKU 336 strain that produces 1-amino-cyclopropane-1-carboxylate deaminase (ACCD) was water-logged resistant (Jaemsaeng et al. 2018). Five *Streptomyces* isolates, i.e., *S. tsusimaensis*, *S. caviscabies*, *S. setonii*, and *S. africanus*, were significantly efficient against chickpea wilt induced by *F. oxysporum* and *F. ciceri* besides improving plant development ability on Sorghum and rice crops (Gopalakrishnan and Ganeshkumar 2013).

Phosphate solubilization

Phosphorus is necessary for plant growth, but its availability in soil is limited and must be supplemented with artificial fertilizers (Fig. 2). Due to its quick immobilization, most are leached out, and little is accessible for the plants (Shigaki et al. 2006). Being a potential root colonizer and an agent for transforming insoluble phosphorus into available (Hamdali et al. 2008) through the production of solubilizing acids such as propionic acid, lactic acid, citric acid, gluconic acid, malic acid, succinic acid, and oxalic acid, the filamentous

Fig. 3 Advantages of using *Streptomyces* in agriculture

Streptomyces sp. are given due consideration; consequently, *S. griseus* and other *Streptomyces* (Jog et al. 2014).

Siderophore production

The siderophore-producing rhizobacteria prevent the proliferation of pathogenic microorganisms mainly belonging to *Streptomyces*, *Serratia*, *Pseudomonas*, *Rhizobium* and *Bradyrhizobium* genera (Fig. 2) (Kuffner et al. 2008). *Streptomyces* spp., produces hydroxamate-type siderophore that protects the plants against pathogens (Khamna et al. 2009). *Streptomyces rochei* IDWR 19 produces a hydroxamate siderophore at 34.17 mg/l (Jog et al. 2014).

IAA production

The synthesis of growth regulators also stimulates plant development. Principal auxin is IAA, which performs several tasks, including cell differentiation, elongation, division, embryonic and fruit development, vascular tissue differentiation, organogenesis, root patterning, apical hook creation, and apical dominance (Khamna et al. 2009). *Streptomyces* species from the tomato rhizosphere, such as *S. rochei*, *S. rimosus*, and *S. olivaceoviridis*, can create IAA and promote plant development through higher seed germination (Fig. 2), root elongation, and root dry weight (El-Tarabily 2008). It has been discovered that *Streptomyces* produces natural auxin (IAA) (El-Tarabily 2008; Khamna et al. 2009). Gibberellins and cytokinin-like substances produced by *S. rimosus*, *S. olivaceoviridis*, and *S. rochei* have also been reported to stimulate plant development (Palaniyandi et al. 2011). Auxins also aid in promoting root hairs,

lateral root development, and sugar production, all of which play a crucial part in microorganisms' early colonization of roots. *Streptomyces* sp., which generates IAA and siderophore, enhances the availability of trace elements such as zinc and iron and promotes root development and elongation (Çakmakçi et al. 2006).

Commercially available strains

Ten *Streptomyces* species have been registered as commercial products (Vurukonda et al. 2018), and a few others are in the early phases of formulation development for commercial use. Mycostop and Actinovate, two actinobacterial compositions, have been commercially exploited for decades. Due to the presence of the antifungal antibiotic aromatic heptacene polyene, Mycostop (*S. griseoviridis* K61 strain isolated from sphagnum peat) is authorized for treatment against seed and soil-borne fungal infections in Canada, the European Union, and the United States. Additionally, to stimulate plant development, the Actinovate produced from the *S. lydicus* WYEC 108 strain inhibits the growth of *Pythium ultimum* and *Rhizoctonia solani*. Additionally, Actinovate has been utilized to prevent *Fusarium*, *Phytophthora*, *Verticillium*, and foliar diseases, including powdery and downy mildew (Vurukonda et al. 2018). Blasticidin-S against rice blast and Kasugamycin against *Phytophthora*-led root rot and leaf spot in diverse crops have been registered in the United States and Ukraine, respectively (Aggarwal et al. 2016). The wettable *Streptomyces* sp. Di-944 formulation reduces *Rhizoctonia solani*-caused damping off disease in tomatoes (Sabaratnam and Traquair 2002).

Advantages and disadvantages of *Streptomyces* bio-inoculant

Actinomycete metabolites are naturally occurring and are growing in relevance in plant disease control. Due to its prevalence, dominance, and promise as an agrochemical, it might be economically marketed (Solanki et al. 2013). Less hazardous and environmentally benign; Targets the specific organism and decomposes rapidly; Provides micronutrients and balances the soil nutrient cycle; Regulates the plant's metabolism to protect it from illness. Effective colonizer of roots and promoter of mycorrhizal colonization. Storage is a significant issue; the Failure rate is low. The growth rate is sluggish compared to other bacterial inoculants (Fig. 3).

Conclusion and future perspectives

Due to its potential and diverse mechanisms, *Streptomyces* sp. might be utilized as a bio-inoculant for disease control. The limitation is that all strains that perform well under in vitro conditions cannot function similarly under in vivo conditions. Therefore, a practical approach must be created to identify the strain that thrives under both environments. In general, microorganisms play a vital role in plant disease control. Researchers have concentrated on *Streptomyces*, whose metabolites are employed in commercial goods, signifying its usage as a bio-inoculant for disease management. Only active *Streptomyces* species have been identified from rhizosphere soil yet. The research should focus on discovering unique, uncommon *Streptomyces* sp. from undiscovered habitats with enormous antibiotic production potential. Research should be conducted on elution techniques to commercialize the discovered antibacterial chemicals. In addition, the optimization of a suitable carrier, the avoidance of harmful metabolites, and the genetic engineering of a successful strain will aid in producing agricultural products for commercial use.

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Declarations

Conflict of interest The authors have no conflict of interest to declare that are relevant to this article.

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