

Review Article

***Streptomyces* at the Heart of Several Sectors to Support Practical and Sustainable Applications: a Review**

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Abstract: This article emphasizes the various contributions of actinobacteria to the well-being of human life on our planet. Agrarian virtues begin with the substitution of chemical fertilizers with bio-fertilizing microorganisms which have a versatile potential for the benefit of soil and plants by playing complementary and interconnected roles. Thus, these microorganisms improve soil health through bioremediation phenomena and the elimination of several non-beneficial microorganisms. In agriculture, these microorganisms can be added to compost as inoculants to speed up the composting process and provide an additional source of beneficial microorganisms for the compost-treated soil. *Streptomyces* and other actinobacteria can also be used as biotechnological sources of herbicides and insecticides. In the medical and therapeutic sectors, this paper emphasizes the potential of actinobacteria, in particular *Streptomyces* species, in the production of antibiotics, antioxidant, and anticancer agents, opening up avenues for the creation of molecules with high benefits. In biotechnology, these totipotent microorganisms produce enzymes widely used in several industries, generating considerable revenue. Sporadic data accumulated on these types of microorganisms opens up many new avenues for exploiting these natural biocatalytic resources. Papers published in the last decade have exploded the amount of information that can be put to practical use. To maximize the value of these microorganisms, it would be advisable to create common threads between the themes that bring together the areas of expertise where these microorganisms could potentially be exploited. This bibliographical synthesis is a contribution to the development of a targeted database.

Keywords: *Streptomyces*, bio-fertilizers, antibiotics, antioxidant, anticancer, enzymes, compost, soil

1. Introduction

The widespread adoption of chemical fertilizers in modern agriculture has become common. Nonetheless, the excessive application of these fertilizers has resulted in environmental contamination, soil degradation, and soil fertility loss ^[1–3]. Chemical fertilizers can also be harmful and toxic to humans and animals by food, feed, and water as shutter transmitters ^[4]. To address these issues, biofertilizers, such as compost, have become increasingly popular in agriculture. Composting is a widely used method for recycling organic waste and producing a nutrient-rich soil amendment ^[5]. Actinobacteria, a significant bacterial group commonly present in compost, have a vital role in the decomposition of organic matter and the transformation of nutrients ^[6]. In particular, the *Streptomyces* genus is known to be implicated in compost processing and has been recognized for its potential as a biofertilizer. The *Streptomyces* genus, part of the Streptomycetaceae family, consists of over 700 species of filamentous bacteria that are gram-positive, neutrophilic, and facultative aerobic with a G+C DNA content higher than 70% ^[7]. *Streptomyces* bacteria life cycle is intricate and encompasses various stages, including vegetative growth, aerial hyphae formation, and sporulation phenomena ^[8,9]. The *bld* genes control aerial hyphae formation, while the *whi* genes control cell division and spore maturation ^[8,10]. *Streptomyces* is renowned for its ability to produce a huge number of secondary metabolites ^[11,12], such as antibiotics, antifungals, phytotoxins, plant growth regulators, herbicides, antivirals and antitumor ^[13–15] (Figure 1). These bacteria can colonize different ecological niches and use a wide range of carbon and nitrogen sources ^[16]. Optimal pH growth is between 6.5 and 8, but some strains can tolerate 9 or higher levels ^[9]. *Streptomyces* are widespread in soils and can resist drastic conditions such as long drought and nutrient scarcity, thanks to their mycelial growth and spore-forming abilities, so they are known for their ability to conquer different environmental biotopes ^[17], making them valuable biocontrol tools in agriculture.

Streptomyces and other actinobacteria can be added to compost as inoculants to enhance composting process and improve final product quality ^[18–21]. These microorganisms can improve organic matter degradation, increase nutrient availability, and inhibit harmful microorganisms proliferation, leading to a more stable and high-value compost. Additionally, they can produce a wide range of secondary metabolites and plant hormones, which can improve their growth and health.

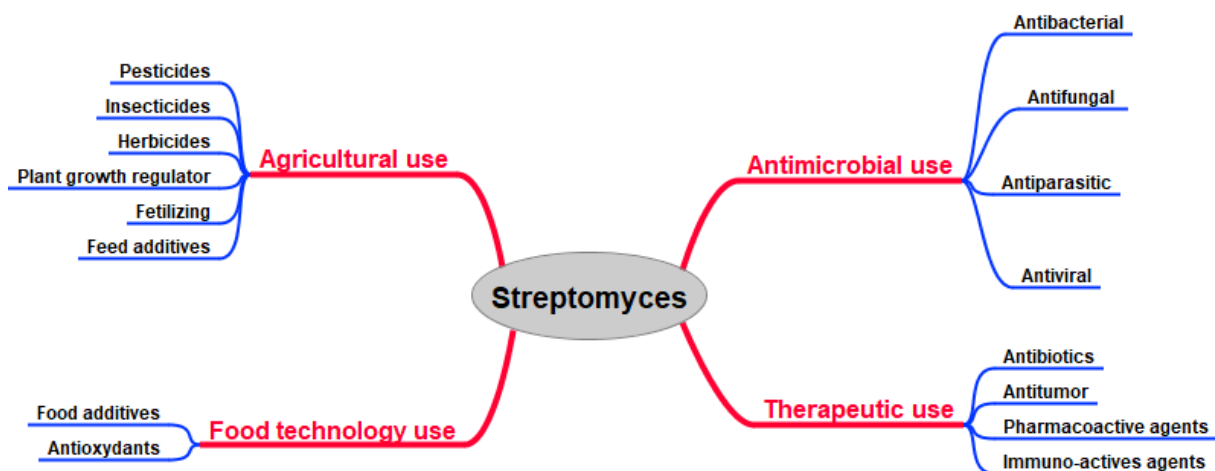


Figure 1. Mental map of *Streptomyces* virtues in various fields.

The adverse impacts of chemical fertilizers are not limited to environmental and health concerns but also contribute to antibiotic-resistant bacteria development. The continuous application of these antimicrobial substrates in agriculture can lead to resistant strains emergence, which can give rise to serious threats to human health. Therefore, biofertilizers use, such as compost inoculated with *Streptomyces*, can help to reduce chemical fertilizers and antibiotics dependency in agriculture. The use of actinobacteria, especially *Streptomyces*, has been shown to be effective on herbicides and insecticides in soil [14,22,23]. However, despite their potential, very few actinobacteria-based products are currently available on the market. For this reason, lots of research is being conducted to develop efficient formulations containing actinobacteria as active ingredients and improve their shelf life and stability.

One of the most notable applications of actinobacteria and their valued enzymes is the composting process. These microorganisms play a critical role in breaking down refractory plant materials, such as lignocellulose polymers, into easily metabolizable monomeric compounds [18,20]. This process not only helps to improve compost quality but also enhances soil fertility, making it an important basement for sustainable agriculture. In addition to composting, actinobacteria and their enzymes were found to have important applications in biotechnology and used in different industrial processes [24]. Therefore, further research and development of biofertilizers should be supported to reduce chemical fertilizers' negative impact and essentially promote sustainable agricultural practices.

The Moroccan government took proactive measures by implementing the Green Morocco Plan (GMP 2008-2020). This strategy was designed to revitalize agricultural sector and foster sustainable practices. With a specific focus on promoting organic agriculture and

compost utilization as a natural soil amendment, the GMP underscores the importance of environmentally sustainable approaches. To ensure the success of this endeavor, the government enacted regulations to support the adoption of compost in agricultural practices.

In this review, we will discuss the potential of actinobacteria, especially *Streptomyces*, as antibiotics and their potential applications in sustainable agriculture, with a focus on their role in compost. We will examine the mechanisms by which they enhance compost quality and composting process.

2. Overview of *Streptomyces* life cycle

Actinobacteria is a large phylum within the Bacteria domain widely distributed in both terrestrial and aquatic ecosystems [25]. These Gram-positive bacteria are characterized by their high guanine and cytosine (G + C) content in DNA and are known for their filamentous nature, capable of forming both substrate and aerial mycelium [26]. The phylum encompasses 374 genera, with *Streptomyces* being the most dominant group. Non-*Streptomyces* actinobacteria such as *Actinomyces*, *Kitasatospora*, *Micromonospora*, *Nocardia*, *Micrococcus*, *Arthrobacter*, and *Rhodococcus* are also present but are less frequently located under normal conditions and demand specialized methods for their isolation, preservation, and cultivation methods [26,27].

Streptomyces species' life cycle begins with spore germination, initiated by the emergence of one or two germ tubes. Emerging shoots emerge at locations behind the tip and grow into a mesh-like structure of hyphae, known as vegetative mycelium (MV) (stage 1). Following nutrient depletion, the vegetative mycelium undergoes differentiation, transforming into aerial hyphae (stage 2). Ultimately, the aerial hyphae differentiate into elongated chains of spores (stage 3). The regulation of the polarisome, the *bld* gene family, and the *whi* gene family allow for manipulation and control of all three stages of this process (Figure 2) [8].

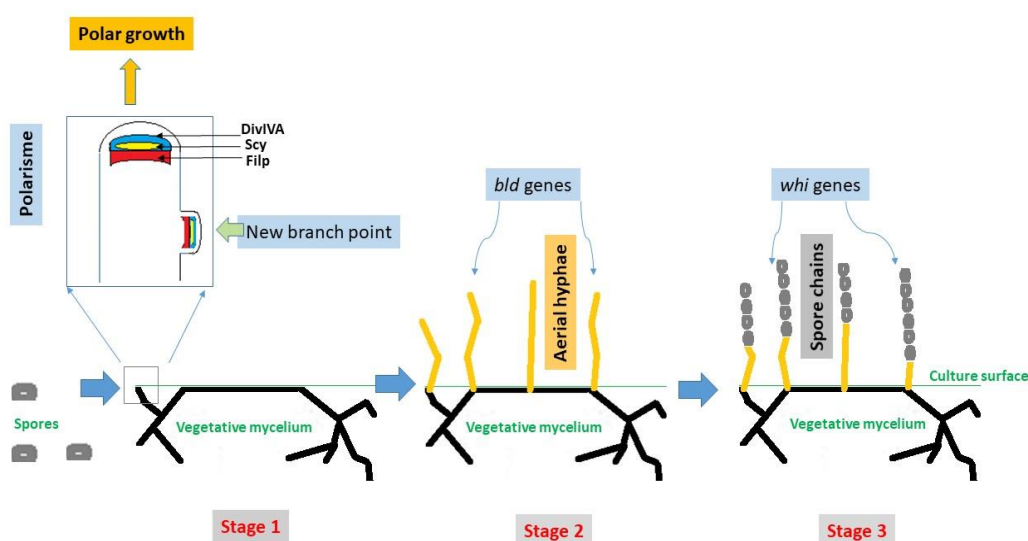


Figure 2. *Streptomyces* life cycle (Reproduced from [8]).

Streptomyces life cycle can be divided into vegetative and reproductive phases [28], with some differences in solid and liquid cultures medium [28] and it is characterized by compartmentalized hyphae formation, which is a process that begins with spore germination in solid cultures or mycelial fragmentation in liquid cultures. In solid cultures, cycle life begins with spore germination and vegetative mycelium development, which grows deep into solid medium culture [29]. After a period of time, programmed cell death (PCD) occurs, leading to antibiotic production and aerial mycelium growth. In contrast to solid culture where spore germination is the initial step, liquid cultures of *Streptomyces* begin with compartmentalized hyphae formation (MI), which is followed by programmed cell death and secondary metabolite-producing mycelia development. In some *Streptomyces* strains, spores formation and aerial mycelium may be hindered. *Streptomyces coelicolor* proteomics analysis has demonstrated that expressed proteins during mycelial growth (MII) second stage are responsible for secondary metabolites production (Figure 3). Despite these findings, the mechanisms behind *Streptomyces* differentiation in liquid medium are not yet fully understood, and researchers are still trying to explore the relationship between pellet formation and secondary metabolite production [28].

The sporadic data accumulating on actinobacteria, and streptomycetes in particular are due to the mass discovery of a very high number of new species [30–33] which can solve thorny problems where there are blockages in medical, cosmetic and agri-food procedures [34]. These new species give hope of finding anti-cancer molecules, drugs to treat emerging diseases [35] or improve the living environment of mankind [36].

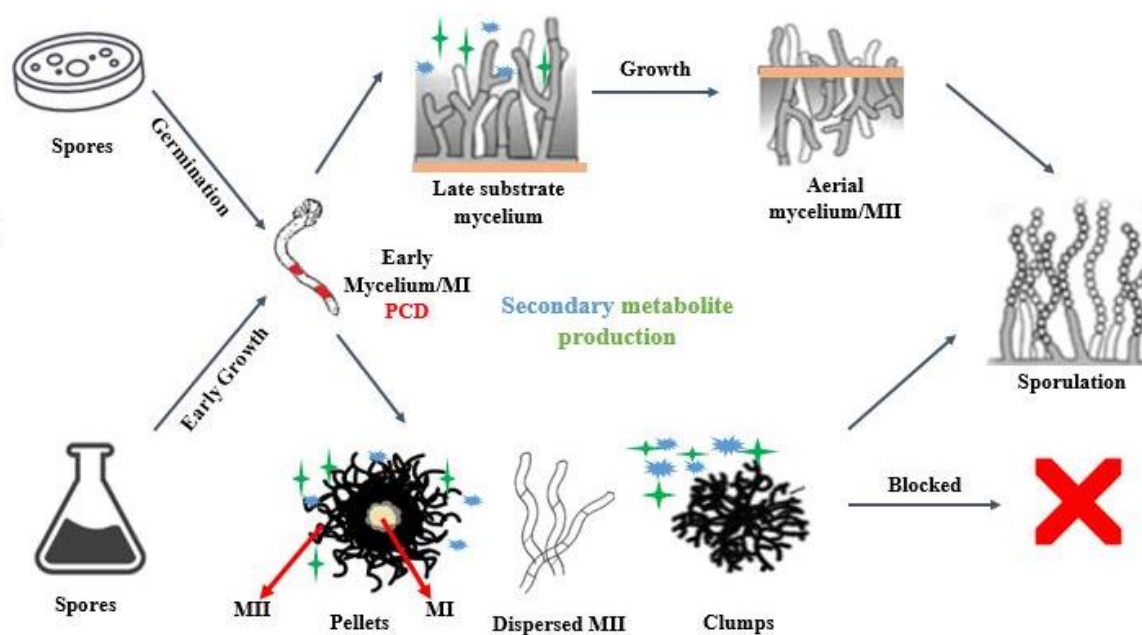


Figure 3. General life cycle of *Streptomyces* in solid cultures (upper panels) and liquid cultures (lower panels) (Reproduced from [28]).

3. Industrial application: extracellular enzymes from *Streptomyces spp.*

Microbial-derived enzymes are widely sought after in the industrial sector because of their exceptional stability, productivity, and availability, as well as their economical nature and environmentally sustainable production methods. From an industrial standpoint, their practicality and ecological soundness further justify their use [37]. *Streptomyces sp.* constitutes a group of bacteria that are well-known for their unique characteristics and capabilities to produce a wide range of extracellular enzymes [38]. The latter finds many applications in various industrial fields (figure 4) [39]. Among the most commonly used enzymes produced by *Streptomyces* are amylase, protease, chitinase, xylanase, lipase, cellulase and laccase.

3.1. Amylase

Amylase (EC 3.2.1.1) is an enzyme responsible for the hydrolysis of starch into more accessible sugars like glucose and maltose. These simpler sugars serve as essential raw materials for diverse fermentative bioconversions, including ethanol, lactic acid, and citric acid fermentation. Amylases are highly regarded as one of the most significant enzymes for industrial use, due to their extensive applications [40], including brewing, detergent manufacturing, tanning, papermaking, textile production, biofuel production, bakery, and food processing [41]. This enzymatic activity (amylase) is still a subject of research and development to select new species with significant physico-chemical potential [42]. Many

species of *Streptomyces* have been used for amylase production [43–48]. *Streptomyces* amylase has been used in the field of medicine [43], and starch processing industry [49], especially raw starch processing [50]. Table 1 presents some of Amylase-Producing *Streptomyces* and their applications.



Figure 4. Diversity and functionality of extracellular enzymes produced by *Streptomyces spp.*

Table 1. Amylase-producing *Streptomyces* strains and their applications.

Strains	Industry	Application	References
<i>Streptomyces spp</i> NAA-28	Biotechnology	Food, paper, detergent, fermentation, textile, and pharmaceutical sectors	[51]
<i>Streptomyces griseus</i> (SGAmy)	medicine	Antibiofilm agent	[52]
<i>Streptomyces lonarensis</i> NCL 716	Food	Maltooligosaccharides production	[53]
<i>Streptomyces erumpens</i> MTCC 7317	Food	Soluble starch and cassava starch hydrolysis	[54]
<i>Streptomyces enissocaesilis</i> NRRL B-16365	Food	High fructose corn syrup production	[55]
<i>Streptomyces spp</i>	Food	Bakery	[56]
<i>Streptomyces spp</i> SNAJSM6	Biotechnology	α-amylase production	[57]

3.2. Protease

Numerous research studies have documented the production of proteases from *Streptomyces*, making them extensively utilized in various industrial applications, notably in fields of food processing, cosmetic manufacturing, detergency, pharmaceuticals, chemical application, and waste management due to their adaptable nature [58]. They are also used in leather processing industries in the dehairing phase, thus leading to the total elimination of chemical application [59]. Proteases (EC 3.4) have been shown to exhibit a high degree of tolerance to diverse environmental challenges, including extreme pH levels, temperature, and salinity conditions, with most of them displaying this characteristic [60]. Additionally, proteases derived from *Streptomyces spp.* have been found to be effective in agro-industrial waste processes recycling, such as feathers, nails, hair, and plant waste [61]. Table 2 highlights a range of protease-producing *Streptomyces* strains and the various practical applications of these proteases.

Table 2. Protease-producing *Streptomyces* strains and their applications.

Strains	Industry	Application	References
<i>Streptomyces gulbargensis</i>	Healthcare industry	Surgical instruments washing	[62]
<i>Streptomyces koyangensis</i> TN650	Detergents	Detergent formulations and non-aqueous peptide biocatalysis	[63]
<i>Streptomyces mutabilis</i> TN-X30	Detergent	Serine alkaline protease formulation	[64]
<i>Streptomyces griseus</i> K-1	Medicine, cosmetics, textiles	Pronase P preparation	[65]
<i>Streptomyces coelicolor</i> A3(2)	Biotechnology	Actinorhodin production	[66]
<i>Streptomyces pactum</i>	Feather industry	Chicken feathers disintegration	[67]
<i>Streptomyces flavogriseus</i> HS1	Detergents	Laundry detergent (Detergent additive)	[68]
<i>Streptomyces nogalotor</i> Ac 80	Leather industry	Goatskin depilation	[69]

3.3 Chitinase

Chitinase (EC 3.2.1.14) is a type of enzyme that is highly valuable in industrial settings due to its ability to break down chitin. Chitinases produced by certain actinobacteria have demonstrated remarkable characteristics, such as thermostability and pH tolerance, which make them highly appropriate for various industrial applications [70]. *Streptomyces spp* produces chitinases, which are used in the production of chitin derivatives, such as chitosan, a natural biopolymer with applications in the medical, agricultural, and food industries [71–73]. Various *Streptomyces* strains, including *Streptomyces thermoviolaceus*, have been identified as producers of chitinases. These chitinases have been used to extract chitobiose, a compound that shows potential as an antioxidant with applications in both biomedical and food industries [74,75]. Table 3 displays certain *Streptomyces* strains that produce chitinase and their industrial applications.

Table 3. Chitinase-producing *Streptomyces* strains and their applications.

Strains	Industry	Application	References
<i>Streptomyces alfalfa</i> ACCC 40021	Agriculture	-Fungal Biocontrol -Chitine conversion to N-acetyl-D-glucosamine	[76]
<i>Streptomyces sampsonii</i> XY 2–7	Agriculture	N-acetyl chitobiose production	[77]
<i>Streptomyces spp</i> CT02	Agriculture	Biocontrol agents against phytopathogenic fungi	[78]
<i>Streptomyces thermocarboxydus</i> TKU045	Medicine	Chitin oligomers	[79]
<i>Streptomyces violaceoruber</i> pChi	Food industry	Chitinase food enzyme	[80]
<i>Streptomyces griseorubens</i> E44G	Agriculture	<i>Fusarium</i> biocontrol	[81]
<i>Streptomyces cavourensis</i> SY224	Agriculture	Anthracnose biocontrol	[82]
<i>Streptomyces hygrosopicus</i> SRA14	Agriculture	Phytopathogenic fungi biocontrol	[83]
<i>Streptomyces rochei</i> A-1	Food industry	<i>Botryosphaeria dothidea</i> post-harvest biocontrol	[84]

3.4. Xylanases

The principal constituent of hemicelluloses is xylan, a complex polysaccharide that is predominantly used in the pulp and biobleaching industry to improve pulp quality [85]. Xylanases (EC 3.2.1.8) are highly sought after in numerous industries due to their broad utility across various sectors, including pharmaceuticals, food processing, paper and cellulose manufacturing [86–88]. In addition, they are also utilized in beverage production, bakery, and probiotics [89]. *Streptomyces* sp. produce xylanases, which are utilized in the pulp and paper industry [90,91] and are also able to break down various agricultural residues such as straw waste and oil cake, resulting in enhanced biogas production [91,92]. The industrial application of certain *Streptomyces* strains that produce xylanase is presented in Table 4.

Table 4. Xylanase-producing *Streptomyces* trains and their applications.

Strains	Industry	Application	References
<i>Streptomyces galbus</i> NR	Pulp and paper industry	Softwood kraft pulp bleaching	[93]
<i>Streptomyces</i> sp. AOA40	Food industry	Fruit juice and bakery	[94]
<i>Streptomyces</i> sp. Strain MS-S2	Biofuels industry	Bioethanol	[95]
<i>Streptomyces</i> sp. FA1	Food industry	Chinese bakery	[96]
<i>Streptomyces</i> spp ER1	Beverage industry	Fruit juice clarification	[97]
<i>Streptomyces megasporos</i> DSM 41476	Beverage industry	Brewing	[98]
<i>Streptomyces thermovulgaris</i> TISTR1948	Food industry	Xylooligosaccharide	[99]
<i>Streptomyces</i> spp QG-11-3	Pulp and paper industry	Eucalyptus kraft pulp bleaching	[100]

3.5. Lipases

Lipases (EC 3.1.1.3) have numerous applications in various industries, they are used in biodiesel production [101] through lipase-catalyzed transesterification and in flavor compounds synthesis by esterification in food, cosmetics, perfumery, and medicine [102]. Lipases are also used in bioremediation by lipid hydrolysis, in detergent formulation for hydrolyzing greasy and oily stains, plastic degradation, agrochemicals production, waxes, and biopolymers, along with their application in tea processing. *Streptomyces*-derived lipases serve as biosensors in probe technologies as well [102–104]. Additionally, they serve as degreasing agents in leather industry, in paper industry (for pitch treatment), and in textiles

(as dewaxing, desizing, and scouring agents) ^[104]. Other important applications of lipases include treating oily wastewater ^[105]. *Streptomyces exfoliates* are known to produce lipases, enzymes that break down ester bonds in triglycerides into glycerol and fatty acids ^[106]. These lipases have a wide range of potential applications ^[107], including their use in fats catalyzing, cosmetics, diagnostics, and detergents ^[108]. Table 5 presents industrial application of some lipase-producing *Streptomyces* strains.

Table 5. Lipase-producing *Streptomyces* strains and their applications.

Strains	Industry	Application	References
<i>Streptomyces</i> sp. DPUA1566	Detergent	Biosurfactant	[109]
<i>Streptomyces chromofuscus</i>	Food industry	Phospholipase D	[110]
<i>Streptomyces violascens</i> OC125-8	Wastewater treatment	Oily wastewater	[111]
<i>Streptomyces</i> spp OC119-7	Biodiesel production	Enzymatic catalyst	[112]
<i>Streptomyces</i> spp CS133	Biodiesel production	Oils transesterification	[113]
<i>Streptomyces</i> sp. SC734	Pharmaceutical industry	Phosphatidylserine synthesis	[114]
<i>Streptomyces thermocarboxydus</i> ME168	Cosmetic and food industry	Sugar ester synthesis	[115]
<i>Streptomyces clavuligerus</i> CKD1119	Pharmaceutical industry	Tacrolimus	[116]

3.6. Cellulases

Cellulases, also known as glucan 1,4- β -glucosidase (EC 3.2.1.74), break down cellulose, yielding glucose, cellobiose, and cello-oligosaccharides as primary products ^[117]. These enzymes work synergistically to degrade cellulose ^[118] and are the focus of numerous studies due to their vital role in biomass hydrolysis ^[119]. Due to the potential of cellulases to break down cellulosic biomass into glucose, these enzymes are in great demand in the global commercial market due to their wide-ranging applications across diverse industries ^[120,121]. In order to apply cellulases in different industries, such as detergents and leather, it is crucial to identify enzymes that are highly stable and capable of functioning under extreme pH and temperature conditions ^[122]. Certain *Streptomyces* sp. such as *Streptomyces ruber*, and *Streptomyces rutgersensis*, produce highly thermostable cellulases ^[123]. The use of cellulases is prevalent across multiple industries such as food, brewery and wine, agriculture, textile, detergent, animal feed, pulp and paper, as well as in research and development ^[120]. Table 6 presents some of cellulase-producing *Streptomyces* sp. and their industrial applications.

Table 6. Cellulase-producing *Streptomyces* strains and their applications.

Strains	Industry	Application	References
<i>Streptomyces drozdowiczii</i>	Detergent and textile	Cellulase	[124]
<i>Streptomyces</i> sp. MS-S2	Biofuels industry	Sugar bioconversion to ethanol	[95]
<i>Streptomyces</i> sp. C48	Agriculture	Agricultural waste hydrolyzsis	[125]
<i>Streptomyces ruber</i>	Textile	Cellulase	[126]
<i>Streptomyces roseochromogenes</i> ATCC 13400	Waste treatment	Cellulase	[127]
<i>Streptomyces</i> sp. NAA2	Biofuels industry	Biomass saccharification	[128]
<i>Streptomyces</i> sp. T3-1	Biofuels industry	Sugar bioconversion to ethanol	[129]
<i>Streptomyces clavuligerus</i> MAC 9	Waste treatment	Biogas production	[130]
<i>Streptomyces griseoaurantiacus</i> ZQBC691	Biotechnology	Ethanol production	[130]

3.7. Laccases

Laccases are enzymes containing copper that have a widespread presence in nature ^[131] and have a diverse range of applications. Laccases have the potential to be used in various industrial applications due to their ability to act on a large range of substrates. These applications include treating industrial effluent, producing biofuels, bleaching, metabolizing drugs, remediating pollutants, decolorizing dyes, developing biosensor probes, and bioprinting ^[132]. These diverse applications make laccases a promising candidate for use in multiple industries. Laccase production by *Streptomyces* is influenced by various factors ^[133], including culture conditions, substrate composition, and enzyme inducers ^[134,135]. Despite having a relatively low redox potential, small laccases produced by *Streptomyces* possess a range of exceptional traits that make them appealing for use in commercial applications. Notably, their ability to exhibit unique substrate specificity and demonstrate remarkable effectiveness over a broad pH range, particularly. Additionally, their unusual resistance to inhibitors further broadens the scope of potential applications in various industries ^[136]. The presented table (Table 7) provides an overview of the different types of *Streptomyces* strains that produce laccase enzyme and their industrial applications.

Table 7. Laccase-producing *Streptomyces* strains and their applications.

Strains	Industry	Application	References
<i>Streptomyces psammoticus</i>	Wastewater treatment industry	Phenolic compounds removal	[137]
<i>Streptomyces ipomoeae</i> SilA	Lubricant industry	Eco-friendly oleogels production	[138]
<i>Streptomyces psammoticus</i> MTCC7334	Textile	Dye decolourization	[139]
<i>Streptomyces cyaneus</i> CECT 3335	Pulp and paper industry	Kraft pulp bleaching	[140]
<i>Streptomyces mutabilis</i> A17	Environmental remediation	Detoxification and bioremediation of sulfonamides and synthetic dyes	[141]
<i>Streptomyces ipomoeae</i> CECT 3341	Textile	Dye degradation	[142]

In addition to previously cited enzymes, *Streptomyces* is renowned for its ability to produce an extensive array of other enzymes that hold significant importance in various fields. For instance, *Streptomyces* strains are capable of producing azoreductase, which is used in azo dyes biodegradation in textile and paper industries [143]. Peroxidase is another enzyme produced by *Streptomyces* that has applications in environmental bioremediation, pulp and paper bleaching, and food processing [144]. Pectinase is an enzyme produced by *Streptomyces* strains that has applications in fruits and vegetables processing industries [145]. Phenazine-1-carboxylic acid dioxygenase is another enzyme derived from *Streptomyces*, which plays a role in organic pollutants [146]. Finally, *Streptomyces* is known to produce transglutaminase, an enzyme used in food processing to improve the texture and quality of meat products [147]. The wide range of enzymes produced by *Streptomyces* makes it a valuable organism for industrial and biotechnological applications.

4. *Streptomyces* as a source of antibiotics

Since the discovery of the first antibiotic in 1942, the genus *Streptomyces* has gained widespread acknowledgment as an invaluable reservoir of antibiotics, with 80% of today's antibiotics originating from this group. The first antibiotic, actinomycin, was isolated from *Streptomyces antibioticus*, followed by streptothricin and streptomycin, obtained from *S. lavendulae* and *S. griseus*, respectively [148–150]. Various antibiotics, including cephalosporins, chloramphenicol, tetracycline, nystatin, viomycin, lincomycin, vancomycin, rifamycin, kanamycin, and daptomycin, have been derived from different *Streptomyces* spp, as reviewed by [150–152]. *Streptomyces* is known to release antibiotics to hinder competitors in its telluric environment, which has led to the discovery of new compounds of commercial

interest with marketable yields ^[153]. For *Streptomyces* strains, interactions with biotic or abiotic factors are essential to increase chemical diversity and compound production, as is naturally found in soil. However, recent studies have shown that antibiotic production is commonly observed when closely related strains grow together or share biosynthetic pathways for secondary metabolites, but not in defense against toxins from competitors. Moreover, nutrient limitations and competitor's presence can decrease antibiotic production output by *Streptomyces* ^[154]. As has been reviewed by Tyurin et al. ^[155], elicitors are also used to enhance antibiotic production by *Streptomyces* bacteria, and several abiotic or biotic compounds such as metals, rare earth elements, dimethyl sulfoxide, ethanol, nanoparticles, and enzymes have been identified as elicitors ^[153]. In a recent study conducted by Quinn et al. ^[156] it was observed that *Streptomyces* strains isolated from soil possess the ability to combat multi-resistant *Staphylococcus aureus* and *Pseudomonas aeruginosa* infections. Genetic analysis of these strains revealed the synthesis of antibiotics resembling griseochelin, macrolactams, candicidin, and cypemycin ^[150]. Among the *Streptomyces* strains investigated, *Streptomyces sp.* 7NS3 was found to be associated with the freshwater snail *Physa acuta* ^[150], producing an angucycline-like aromatic polyketide with a broad-spectrum antibiotic activity against Gram-positive bacteria ^[157]. The genomic analysis of the 7NS3 strain unveiled a gene cluster that may be responsible for emycin A biosynthesis. Faddetta et al. ^[158] reported the importance of extracellular vesicles produced by Streptomyces. These vesicles were found to contain a diverse array of metabolites, including antibiotics that can be delivered ^[150]. Also, *Streptomyces thermoviolaceus* is capable of producing a pigmented and pH-sensitive antibiotic known as granaticin. This antibiotic is synthesized at high temperatures, specifically at 45 °C, with optimal synthesis occurring at temperatures as high as 55 °C ^[159]. More than 50% of clinically effective antibiotics are derived from *Streptomyces* ^[160,161]. The exploitation of actinobacteria can be recommended to combat multidrug-resistant (MDR) pathogenic strains ^[162] and eradicate biofilms, which are the focus of much effort in the medical field to solve emergency public health problems; in particular, MRSA infections associated with medical devices ^[163–166]. Table 8 lists some of *Streptomyces* strains that have been shown to produce antibiotics.

Table 8. Selection of known antibiotic-producing *Streptomyces* strains.

Streptomyces strains	Antibiotics	References
<i>Streptomyces</i> sp. SM01	Picolinamycin	[167]
<i>Streptomyces avermitilis</i> phiSASD1	Endolysin and Holin	[168]
<i>Streptomyces</i> sp. PAL114	Mzabimycin A and B	[169]
<i>Streptomyces</i> sp. HS-NF-780	Glutarimide	[170]
<i>Streptomyces lusitanus</i> OUCT16-27	Grincamycin L and angucycline	[171]
<i>Streptomyces althioticus</i> MSM3	Desertomycin G	[172]
<i>Streptomyces globosus</i> DK15	Factumycin and tetrangomycin	[173]
<i>Streptomyces edersensis</i> ST13	Factumycin and tetrangomycin	[173]
<i>Streptomyces thermoviolaceus</i> SRC3	Streptazolin	[174]
<i>Streptomyces puniceus</i> AS13	Dinactin	[175]
<i>Streptomyces lydicus</i> AZ-55	Natamycin	[176]
<i>Streptomyces avermitilis</i>	Avermectin	[177]
<i>Streptomyces griseus</i> IFO 13350	Streptomycin	[178]
<i>Streptomyces bingchenggensis</i> CP002047	Milbemicin	[179]
<i>Streptomyces fradiae</i> Tü 2717	Urdamycins	[180]
<i>Streptomyces lunaelactis</i> MM109T	Lunaemycins	[181]
<i>Streptomyces cinnamonensis</i>	Monensin	[182]
<i>Streptomyces justiciae</i> RA-WS2	Setomimycin	[183]
<i>Streptomyces cattleya</i> NRRL 8057	Thienamycin, cephamycin C, penicillin N	[184]
<i>Streptomyces diastaticus</i> TUA-NKU25	Surugamide	[185]
<i>Streptomyces</i> sp. P-56	Nonactin	[186]
<i>Streptomyces pluripotens</i> MUM 16J	Glycopeptide antibiotic	[187]

5. *Streptomyces* as sources of antioxidants and anticancer molecules

Microbial diversity offers a rich assortment of unique chemicals, serving as a valuable resource for cutting-edge biotechnology. Actinobacteria account for 42% of the more than 23,000 documented microbial secondary metabolites, while fungi produce a similar proportion (42%), and eubacteria contribute the remaining 16% [188]. The investigation of molecules derived from *Streptomyces* for their anticancer effects remains relatively understudied. Indeed, the majority of cytotoxic antibiotics in current use are sourced from *Streptomyces* species. Among the "classic" drugs originating from *Streptomyces* is the anthracyclines family, which includes well-known medications like doxorubicin and daunorubicin [189,190]. Although limited in number, studies on the potential anticancer activities of *Streptomyces*-derived EPS (Exopolysaccharides) have shown promising results. Ramirez-Rodriguez et al. [191] conducted research on three *Streptomyces* strains (*S. aburaviensis*, *S. gramineus*, and *S. psammoticus*) [150]. These strains exhibited notable

cytotoxic activity against specific cancer cell lines, including prostate cancer (PC3), breast cancer (MDA-MB-231), and lung cancer (A549) [150]. In another study, *Streptomyces carpaticus* strain, isolated from marine sediments, was exploited to produce a high-value exopolysaccharide with significant toxicity against human breast (51.7%) and colon (59.1%) tumor cells [192]. Similarly, a marine *Streptomyces hirsutus* NRC2018-produced exopolysaccharide named EPSNC2, displayed notable and selective anticancer activity specifically against the Caco-2 cell line, without affecting other cell lines [150,193]. Besides this cell line (Caco-2), cancer cells models (HCT-116, HT-29, and SW480) were the subject of *Streptomyces* antioxidant and anticancer activity confirmation [194].

Streptomyces are occasionally competent in the biosynthesis of compounds with anticancer activity, powered by new molecules such as streptocarbazoles A and B, streptomyceamide C and neoantimycins A and B [195]. In a study by Ser et al. [196], a *Streptomyces* strain, namely MUSC 136T, produces an extract containing cyclic peptides that have the potential to induce apoptotic cell death through the p53-associated pathway in colon cancer cells. Moreover, the researchers from the same group have discovered that in a mangrove environment, two *Streptomyces* strains, namely *Streptomyces pluripotens* MUSC 137^T and *Streptomyces sp.* MUM 256, produced intriguing cyclic dipeptides. The presence of these cyclic dipeptides, particularly in *Streptomyces pluripotens* MUSC 137^T, has demonstrated the regulation of genes associated with essential biological processes, including cell cycle regulation, differentiation, apoptosis, cell adhesion, and angiogenesis [196]. These compounds exhibit similarities to anthracyclines and can induce apoptosis by modifying histones and inhibiting topoisomerase I activity [29]. Moreover, they have the potential to enhance the efficacy of DNA-targeted anticancer drugs. Some specific cyclic dipeptides, like pyrrolo[1,2a]pyrazine-1,4-dione, hexahydro-3-(phenylmethyl) [29], have been extensively studied and demonstrated growth inhibitory effects on various cancer cell lines, including MCF-7, HT-29, and HeLa [196].

Streptomyces also exhibit efficient production of a diverse array of bioactive compounds, including antioxidants. Through a screening program focused on actinobacteria, researchers have isolated numerous compounds with antioxidant properties [188,197]. Among these compounds, *Streptomyces spp.* has been found to produce various antioxidant isoflavonoids, such as 4', 7, 8-trihydroxyisoflavone. Notably, these compounds have also shown promising antitumor activity [198]. Extract derived from *Streptomyces spp.* LK-3 (JF710608) has been found to possess antioxidant activity, containing key components like daidzein-8-C-glucoside (puerarin), (-) gallic acid gallate, sesamol, cyanidin-3-O-rutinoside, and delphinidin [199]. *Streptomyces*, isolated from various environments, have

been discovered to possess antioxidant activity. For instance, *Streptomyces lydicus* A2 [200], *Streptomyces spp.* SRDP-H03 [201], and BI244 have demonstrated antioxidant activity as evaluated by the DPPH assay [188,202]. In a study conducted by Tan et al. [203], a strain called MUM212, isolated from mangrove soil, was found to possess remarkable antioxidant properties. The extract derived from MUM212 exhibited strong scavenging activity against various free radicals, such as superoxide anion, DPPH, and ABTS radicals. Furthermore, the extract demonstrated the ability to chelate metal ions. Another example is *Streptomyces misionensis*, which was isolated from soil in a mountain forest. This particular strain exhibited significant antioxidant capacity against nitric oxide, DPPH, and hydrogen peroxide free radicals [204]. According to the study conducted by Tan et al. [205], *Streptomyces spp.* MUM256 extract was found to possess antioxidant activity. It demonstrated the ability to scavenge superoxide anion radicals, with its effectiveness being dependent on the dosage. Table 9 presents some of the recently discovered *Streptomyces* strains with antioxidant capacities.

Table 9. Recent discovered *Streptomyces* strains with antioxidants and anticancer capacities.

Activity	Strain	Source	Secondary metabolites/Gene/Compounds	References
Antioxidant	<i>Streptomyces carpaticus</i> K-11	Semi-desert soil	flavonoids, alkaloids, glycosides, organic acids, alcohols, aldehydes, hydrocarbons, ethers	[206]
	<i>Streptomyces tunisiensis</i> W4MT573222	Sediments	Pigment (divaric acid)	[207]
	<i>Streptomyces flavogriseus</i> ADEM7	Soil	<i>sprA</i> Gene	[208]
	<i>Streptomyces telluris sp.</i> AA8 ^T	Rhizosphere soil	3,4-dihydroxybenzaldehyde	[209]
	<i>Streptomyces sp.</i> QZS11	Soil	Ethyl-acetate crude extract	[210]
	<i>Streptomyces sp.</i> MA4	Soil	Selenium nanoparticles	[211]
	<i>Streptomyces sp.</i> Sae4034	Rhizosphere soil	Alkaloid, terpenoid, flavonoid, and polyphenol	[212]
	<i>Streptomyces levis</i> HFM-2	Human gut	2-Isopropyl-5-methyl-1-heptanol; 1-Octanol, 2-butyl-, 3-Octadecene and 3-Eicosene	[213]
	<i>Streptomyces sp.</i> MUSC 11, 125, 14, 273b, 292, 5	Mangrove soil	Phenolic compounds, <i>PKS I</i> , <i>PKS II</i> genes, 2,4-dihydroxy-6-propyl benzoic acid, 2,4-bis(1,1-dimethylethyl), pyrazine, pyrrole, cyclic dipeptides, hydrocarbons, alcohols, triterpene	[214–219]
	<i>Streptomyces sp.</i> MUM265, 14, 256	Mangrove soil	Hydrocarbons, alcohols, phenolics, cyclic dipeptides, thioholgamide A/thioholgamide B, pyrrole, pyrazine	[220–222]
Anticancer	<i>Streptomyces colonosanans</i> MUSC 93J ^T	Mangrove soil	Ectoine synthesis gene	[223]
	<i>Streptomyces monashensis</i> MUSC 1J ^T	Mangrove soil	phenolic compounds, pyrazines and pyrrolopyrazines, Benzoic acid, 9H-Pyrido[3,4-b]indole	[224]

6. Importance of *Streptomyces* in agriculture

6.1. *Streptomyces* in agricultural biocontrol

Actinobacteria produce a number of bioactive metabolites that are beneficial to both soil and plants. They also have the capacity to act as biocontrol agents [225], making plants more resistant to biotic and abiotic stresses [225,226]. A study done by Wang et al. [227] showed that certain actinobacteria (*Streptomyces pactum* Act12, *S. globisporus* Act7, and *S. globisporus* subsp. *globisporus* C28) can destroy the membrane of fungal pathogens attacking celery leaves. *Streptomyces griseoviridis*, a light-colored actinomycete isolated from *Sphagnum* peat, is an example of a biocontrol agent that reduces damage caused by various soil and seed pathogens [228,229]. Antibiotic production by actinobacteria in soil, as shown in a study done by Trejo-Estrada et al. [230], is also helpful against plant pathogens. For instance, *Streptomyces violaceusniger* YCED9 produces antibiotics such as headache, Geldanamycin, and Guanidylfingine to counteract plant pathogens. Previous studies have demonstrated actinobacteria ability to enhance plant growth and effectively manage plant diseases [226,228,231,232]. *Streptomyces* strains are primarily recognized for their capacity to act as a biocontrol agent by producing potent volatile compounds, metabolites, and antibiotics that exhibit antipathogenic properties [233]. The illustration below (Figure 5) conceptually summarizes the virtues of *Streptomyces spp* consortium on good *Vicia Faba L* plant growth.

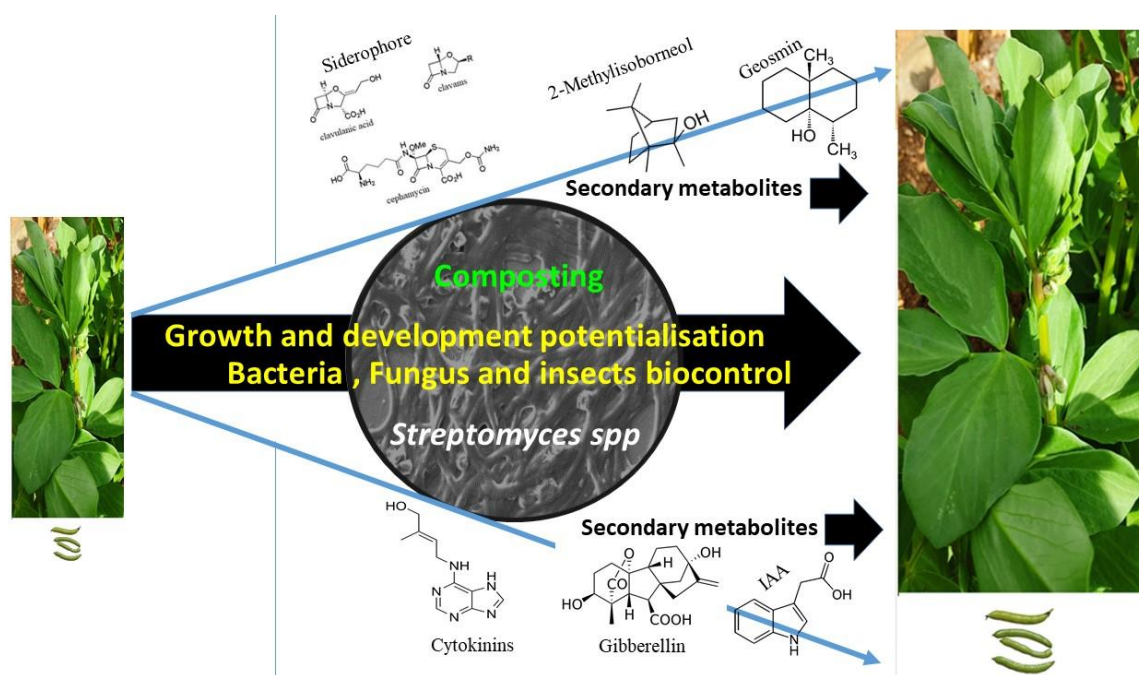


Figure 5. Different roles of secondary metabolites from *Streptomyces spp.* in plant growth stimulation.

In another study done by Pang et al. [231], substances discharged from *Streptomyces coelicolor*, *Streptomyces violaceusniger*, and *Streptomyces violaceusniger* strains, including siderophore, chitinase, antifungal nigericin, and antibiotic geldanamycin [234], regulate stress metabolite and control hyphal development. While *Streptomyces* has been used successfully for biocontrol, one notable case is with rice plants [235]. In this study, two *Streptomyces* strains exhibited biocontrol potential by preventing pathogenic bacteria proliferation through secondary active metabolite production. As a result, the dissemination of *Burkholderia glumae*, a significant bacterial menace that triggers panicle blight in rice plants and poses a serious risk to rice yields, was successfully halted [235].

The fishing and aquaculture industries can benefit from actinobacteria virtues, and *Streptomyces spp.* in particular, and their metabolites can be used to protect marine foodstuffs against *Vibrio*-contamination [236–241]. Morocco, with its highly developed fishing and aquaculture industry, must take this thematic into consideration, as it opens up many routes of research to address the problems associated with serious foodborne infections, especially foodborne illness outbreaks.

7. Role of *Streptomyces* in pesticide degradation

Employing indigenous Streptomycetes for bioremediation in pesticide-contaminated environments proves to be a promising strategy, as these microorganisms are highly suited to thrive in soil and sediment habitats. *Streptomyces* strains have the advantage of potential metabolic diversity, mycelial growth habit, rapid growth rates, semi-selective substrate colonization, and genetic manipulability. *Streptomyces* can differentiate into spores that contribute to their spread and persistence, allowing their survival in soil for long periods, withstanding low nutrient concentrations and water availability [242]. Due to these advantages, different *Streptomyces* strains have been investigated as potential candidates for polluted environments bioremediation with various chemical pesticide families, including organochlorines, organophosphates, pyrethroids, ureas, and chloroacetanilides [242–244]. A study was conducted by Bourguignon et al. [245] have shown that *Streptomyces* strains isolated from sediments contaminated with pesticides are capable of thriving in the presence of methoxychlor. In another field, inoculation of biomixtures with *Streptomyces sp. M7* increased atrazine degradation [246,247]. *Streptomyces sp.* strains demonstrated enhanced propoxur degradation when starch was introduced as a co-substrate, which favored their growth in a liquid medium [248]. *Streptomyces* microorganisms have demonstrated excellent capabilities for the removal or conversion of multiple pollutants simultaneously, with Polti et al. [249] finding, both pure and mixed cultures of *Streptomyces* strains displayed efficient removal of lindane and Cr(VI) from soils contaminated with both substances. Pesticide

degradation by *Streptomyces* has been extensively explored in biotechnological process development aimed at reducing pesticide concentrations in different environmental matrices and preventing their infiltration into the environment, ultimately reducing human exposure.

7.1. *Streptomyces* as biofertilizer

Streptomyces is gaining increasing attention as a commercial biofertilizer among researchers. They possess the ability to biodegrade various agro wastes and produce different enzymes in soil by contributing to plant nutrition and growth [250]. Moreover, actinobacteria have been found to produce plant growth hormones like indole acetic acid (IAA) [251], expanding their potential applications as biofertilizers in agriculture [252]. Also, a study done by Omar et al. [253] have shown that *Streptomyces* sp. HM8, *Streptomyces thinghirensis* HM3, *Streptomyces* sp. HM3, and *Streptomyces tricolor* HM10 produce IAA, siderophore and immobilized inorganic phosphate [253]. Inoculating fields with actinobacteria has been shown to improve plant growth and yield [254], as observed in greenhouse experiments with maize [255]. However, the limited plant development and growth qualities of some actinobacteria species hinder their potential contribution to sustainable horticulture practices. *Streptomyces* offers a valuable benefit through its capacity to enhance phosphate availability in soil [256]. These bacteria can transform bound phosphate into an accessible form by producing various phosphate-solubilizing acids and phytase enzymes. While the exact mechanism of acid-mediated phosphate solubilization is not fully understood [257], certain actinobacteria species like *Streptomyces*, *Micromonospora*, and *Gordonia* have been shown to exhibit phosphate-solubilizing activities [258].

According to recent research [259], biofertilizers made with strains of *Bradyrhizobium* and *Streptomyces griseoflavus* have been found to promote root and shoot growth in mung beans, soybeans, and cowpeas. This study also found that these biofertilizers increase nodulation, nitrogen fixation, phosphorus, and potassium uptake in plants, resulting in higher seed yields. *Streptomyces*, which can establish colonies in the rhizosphere or plant tissue, has been observed to maintain a symbiotic relationship with plants that enhances their growth [233]. A recent study done by Domínguez-González and his collaborators [260] suggests the use of *Streptomyces spp* as a biofertilizer in a biofilm form that uses perlite mineral as a carrier. This approach is recommended as an alternative to enhance crop production over an extended period and to improve plant health owing to its advantages. Notably, research done by Omar et al. [253] demonstrated the efficacy of *Streptomyces* as a biofertilizer in promoting cucumber growth and nutrient uptake under greenhouse conditions. Additionally, Gopalakrishnan et al. [261] found that the usage of *Streptomyces* strains as biofertilizers could improve chickpea crop's yield and growth.

Understanding *Streptomyces*'s potential in agriculture is crucial for sustainable farming practices. Table 10 highlights that the latest strains of *Streptomyces* from research conducted in 2022 and 2023 have shown promising results in disease control, increased plant growth, and yield enhancement.

Table 10. Summary of the latest *Streptomyces* strains and their agricultural significance.

Strains	Crops/ plants	Results	References
<i>Streptomyces chrestomyceticus</i> STR-2	Rice	-Siderophore synthesis, IAA, and phosphate-solubilizing agents, -Plant growth promotion -disease reduction caused by <i>Magnaporthe oryzae Cav</i>	[262]
<i>Streptomyces</i> spp. STRM103 and STRM104, and STRM304	Tomato Banana	-Controlling Fusarium Wilt Disease -Growth Promotion	[263]
<i>Streptomyces griseus</i> KAI-26 and MMA-32 <i>Streptomyces albus</i> KAI-27	Chicpea	-Growth promotion - PGP traits enhancement -Antioxidants and grain nutrients increment	[264]
<i>Streptomyces albus</i> (CAI-24 and KAI-27) <i>Streptomyces griseus</i> MMA-32	Pearl millet	-Improving yield and nutrient content	[265]
<i>Streptomyces tuius</i> AR26	Pepper fruit	-Development of fruit rot symptoms inhibition	[266]
<i>Streptomyces rochei</i> ASH	Sorghum	-Promote plant growth -Inhibition mycelial <i>Rhizoctonia solani</i> and <i>Sclerotinia sclerotiorum</i> growth	[267]
<i>Streptomyces</i> sp. UTM 313	<i>Helianthus annuus</i>	-Growth improvement	[268]
<i>Streptomyces</i> sp. HN6	Cowpea	-Plant growth promotion	[21]
<i>Streptomyces</i> sp HM8 , <i>Streptomyces thinghirensis</i> HM3 , <i>Streptomyces</i> sp HM2, and <i>Streptomyces tricolor</i> HM10	Cucumber	-Production of IAA, siderophore, and immobilized inorganic phosphate -Growth improvement	[253]
<i>Streptomyces chilikensis</i> strain RC1830	Rice	-Preventing the <i>F. oxysporum</i> wilting/root rot disease -Promoting growth	[269]
<i>Streptomyces</i> sp TOR3209	Tobacco	-Development of volatile organic compounds -Growth improvement	[270]
<i>Streptomyces</i> sp. SA5	Tomato plants	-Plant growth-promoting agents production, siderophore, IAA , and ACC deaminase, phosphatase enzymes	[271]

<i>Streptomyces luteogriseus</i> -8	Soybean	Yield improvement -Increase fruit yield	[272]
<i>Streptomyces sp</i> SS12	Bell pepper	-Control plant disease	[273]
<i>Streptomyces sp</i> KS3	Rice	Growth and productivity improvement -Indole-3-acetic acid (IAA) production	[274]
<i>Streptomyces kanamyceticus</i> CIAD-CA45	<i>Phaseolus vulgaris</i>	-Increase hypocotyl diameter and chlorophyll content -Increase biomass accumulation -Indole-3-acetic acid (IAA)	[275]
<i>Streptomyces misionensis</i> CIAD-CA27	<i>Arabidopsis thaliana</i>	-Growth improvement, -Increase biomass accumulation, shoot fresh weights and the root fresh weights -Plant phosphorus uptake increment	[275]
<i>Streptomyces sp</i> UTMC 1478	<i>Zea mays</i>	increased shoot dry weight and leaf chlorophyll content	[276]
<i>Streptomyces tunisiensis</i> AI, <i>Streptomyces enissocaesilis</i> BYC, <i>Streptomyces saprophyticus</i> DE2 and <i>Streptomyces cyaneofuscatus</i> CYM	Sugar beet	-Growth and yield parameters improvement -High protection against root rot disease	[277]

8. *Streptomyces* for boosting the composting process

8.1. Inoculation techniques

Microbial inoculation methods in the composting process involve competent microorganisms in addition to the compost mixture to enhance the waste degradation rate and improve the final quality of compost. These microorganisms can either be isolated from microbial communities according to specific selection pressure or developed through culture mixtures such as soil, manure, and straw [278]. The inoculum can be a single strain or a mixture of efficient microorganisms inoculum [278,279], or matured compost sample [278,280]. Currently, researchers are exploring the use of a combination of microorganisms that work together synergistically, known as a mixed inoculant [281–283]. The addition of microbial inoculants improves temperature profile and ammonia emissions by proliferating mesophilic and thermophilic bacterial populations. It also enhances enzymatic activity and minimizes the initial lag time of biological processes, leading to accelerated composting. Microbial inoculation techniques can efficiently decrease the release of odorous emissions, primarily volatile organic compounds (VOCs), while producing compost with elevated nutritional content [284,285]. Inoculating competent microbes such as *Streptomyces* into compost can significantly improve the resulting compost quality; one effective way is through liquid

culture inoculation. This method involves preculture elaboration, evenly distributing it onto the compost pile, and regularly turning it to ensure microorganisms mixture (Figure 6). Microbial inoculum can be introduced during various stages of the composting process, including single, two-stage, or multi-stage applications. The addition of inoculum at different stages exhibits a notable influence on the physicochemical parameters of the composting process [286].



Figure 6. *Streptomyces* inoculation method.

a): Soil; b): Competent *Streptomyces* strains isolation; c): *Streptomyces* biomass growth ; d): Single or multi-stage garbage inoculation; e): Composting phases and f): Final product (good quality compost)

8.2. *Streptomyces* impact on composting process

Streptomyces are naturally occurring soil-dwelling bacteria. They are well known for their capacity to develop an extensive diversity of enzymes, which makes them an excellent choice for use as additives for solid waste composting [278]. These bacteria can accelerate organic matter breakdown and promote a more effective composting process. One of the key advantages of using *Streptomyces* strains in composting, is their ability to tolerate high temperatures and other drastic conditions. This means they can thrive in the high temperatures that are often present in composting environments, which is essential for rapid organic matter break. As they break down complex organic molecules, they release important nutrients into the soil, improving its quality and promoting other beneficial microorganism's growth [225]. *Streptomyces* are also effective in breaking down a wide range of organic materials, including plant matter, animal waste, and food residues [287]. This makes them an

excellent choice for use in solid waste composting, as they can reduce waste volume and promote more sustainable waste management practices. In addition to their composting benefits, *Streptomyces* can also help to reduce odors and prevent harmful pathogens' growth in composting environment^[288]. This can help to create a protected and more pleasant work setting for those involved in composting process. Overall, the use of *Streptomyces* as additives for solid waste composting can provide a number of benefits, including more efficient and effective composting, leading to improvement of soil quality and a more sustainable waste management solution^[289].

While multiple research projects have investigated the use of various microorganisms as additives in composting problems. The research done on *Streptomyces* bacteria in this application is relatively limited. Numerous studies have examined the impact of microbial inoculation on composting quality and efficiency. In general, a time reduction in the degradation process due to microbial activity is an indicator of good quality compost^[278,279,290]. For example, Wei et al.^[291] studied lignocellulose degradation and found that inoculation with actinobacteria accelerated enzyme production, such as CMCase, xylanase, and lignin peroxidase, leading to increased organic matter degradation rates. Zhao et al.^[292] inoculated a cellulolytic strain of actinobacteria into dairy waste composting, resulting in cellulase activities and humic substance content improvement^[278]. Manu et al.^[293] conducted a decentralized composting of household wet biodegradable waste. The introduction of specific inoculation in the composting process led to a significant reduction in composting time, resulting in a composting period of 30-36 days. Furthermore, the compost produced was free from pathogens. As indicated by a study done by Jusoh et al.^[284], adding microbial agents such as *Streptomyces clavuligerus*, *Aeromonas cavia*, *Corynebacterium pseudotuberculosis*, *Shinella sp* and *Rhizobium*, which were identified from rice straw compost, to the composting pile, resulting in an acceleration of organic matter and insoluble roughage degradation. This was due to an enhancement of key enzymes, such as CMCase and xylanase, as well as core microbial metabolisms. Numerous research studies have been conducted to investigate the impact of introducing various strains of *Streptomyces* bacteria into compost. For example, Shivilata and Satyanarayana^[294] observed that inoculating compost with *Streptomyces spp* and *Micromonospora sp.* resulted in complete degradation of yeast debris and reduced compost odor. In addition, Mansour and Mohamedin^[295] and Abdulla and El-Shatoury^[296] found that cellulolytic actinobacteria such as *Streptomyces thermodiastaticus* produce extracellular enzymes that can improve nutritional characteristics of compost by breaking down pathogenic fungi cells. A study conducted by Chi et al.^[19] found that inoculating cellulolytic *Streptomyces griseorubens* in pig manure and rice straw compost increased temperature, extended thermophilic phase, and improved nutrient content.

Additionally, the use of multiple thermotolerant cellulolytic *Streptomyces spp* and *Actinobacteria* as inocula in different composting stages enriched cellulase activities, enhanced cellulose degradation, and increased humic substances content, thus influencing actinobacteria community structure in dairy manure-corn straw composting [286,292].

The potential of *Streptomyces spp* in pollution degradation in effluent from paper pulp has been proven through the detection of breakdown products observed after incubation period [297]. Furthermore, a recent study done by Kocak et al. [298] found that The introduction of *Streptomyces spp.* to the compost system resulted in significant changes, including the inhibition of other microbiota members. Additionally, the presence of the added strain led to noticeable alterations in organic matter degradation. In addition, Jia et al. [299] noted that the inclusion of a blend of *Aspergillus*, *Penicillium*, *Bacillus*, and *Streptomyces* improved cellulose degradation in mushroom residue and wood chips by enhancing the enzymatic activity of the bacterial community. These studies demonstrate the potential of *Streptomyces spp.* and other microorganisms to enhance organic matter degradation in different composting systems. Overall, results indicate that *Streptomyces* can be used as a potential bio-fertilizer that may replace conventional fertilizer in various situations [21]. Further research is required to develop a formulation that contains these viable strains in combination with other beneficial microorganisms (co-culture) [300] for commercial application.

8.3. Methods of *Streptomyces* inoculation for soil and crop enhancement

The use of beneficial microorganisms for enhancing soil and crop productivity [225] has gained significant attention in recent years as an alternative to conventional chemical fertilizers. Among these beneficial microorganisms, *Streptomyces* species have been found to play a key role in soil health and plant growth promotion. However, there is limited research on the application of *Streptomyces*-enriched compost on soil and crops. Currently, no studies have examined *Streptomyces*-enriched compost application to soil/crop. However, a study on the use of effective microorganisms-enriched manure exists, which could also be applied to compost. Hidalgo et al. [301] suggests various methods for effective microorganisms-enriched manure application, depending on manure type. One method is direct soil inoculation with different effective microorganisms (EM) preparations before sowing or during cultivation. Another method is fertigation, where EM formulations are added to the soil through manure irrigation, with dilutions ranging from 1:1000 to 1:5000 [302]. Spraying EM-enriched liquid manure on plant leaves is also an option for pest control and prophylactic disease treatment. The recommended dilution for spraying is 1:1000, but 1:5000 or 1:2000 dilutions can be used depending on culture type. The required EM dose can

vary based on the amount of manure to be turned into humus, ranging from 20 to 40 liters per hectare for diluted preparations and 1-3 liters per hectare for more concentrated commercial preparations ^[303]. It is advisable to increase the added EM dose if soil contains high levels of undecomposed organic matter and to dose EM in the spring season whenever possible, with increased doses if no autumn treatment has been carried out, to ensure soil proper inoculation with EM. The methods proposed by Hidalgo et al. ^[301] for enriching manure with effective microorganisms may face challenges in terms of reproducibility. The lack of standardized protocols for various application methods and the absence of detailed information on the specific EM formulations used and environmental factors may affect the outcomes, making it difficult for other researchers to replicate the methods accurately and achieve consistent results. It is also important to consider the potential environmental impact of using manure-based products and to follow appropriate management practices to mitigate risks. While these methods may be effective in certain settings, further research is necessary to determine their reproducibility and reliability across different conditions. Alternative approaches such as composting and crop rotation can be used to promote soil health and reduce synthetic fertilizers reliance. Overall, a combination of different soil management techniques, including the use of EM-enriched compost, can help to promote sustainable and resilient agriculture. By carefully considering the potential benefits and limitations of different approaches, farmers and growers can make informed decisions to optimize soil health and productivity while minimizing environmental impact.

8.4. Challenges and recommendations for Streptomyces inoculation in composting

Green Morocco Plan (GMP 2008-2020) is a national strategy launched by the Moroccan government to modernize the agricultural sector and improve its sustainability. One of the key components of this plan is organic agriculture promotion and the use of compost as a natural soil amendment ^[304]. To support this initiative, the Moroccan government has enacted regulations that promote the use of compost in agriculture and encourage farmers to adopt sustainable practices. Morocco passed the Organic Agriculture regulation, which regulates organic production and marketing to promote organic inputs use such as compost. The government also launched the National Compost Strategy, which aims to develop a network of composting facilities across the country and increase compost use in agriculture ^[305]. The strategy includes measures such as providing technical assistance and financial motivation to farmers who adopt compost-based practices, promoting research and development in composting technologies, and improving the quality and consistency of compost through standardization and certification. However, the government's commitment to promoting sustainable agriculture and reducing dependence on synthetic inputs remains

strong. Development of a robust composting industry is seen as a key component for achieving these goals. Despite these efforts, implementation of these regulations has faced several challenges, including the lack of infrastructure for compost production and distribution, limited awareness of farmers to compost, and the high cost of organic inputs. However, to overcome these challenges, the Moroccan government is working to establish a network of composting facilities and promote the application of compost as a cost-effective and environmentally friendly alternative to synthetic fertilizers by adopting compost-based agriculture practices ^[306]. The kingdom of Morocco aims to improve soil health, reduce greenhouse gas emissions, and promote sustainable and inclusive economic growth ^[307]. In the context of the Moroccan government's efforts to promote sustainable agriculture with compost, our study focuses on improving the composting process by employing microorganisms such as *Streptomyces*. The use of *Streptomyces* bacteria in composting is an innovative approach with potential benefits for treating waste. However, several challenges need to be addressed to develop a cost-effective and environmentally sustainable technology ^[308]. One key challenge is determining the appropriate technique and concentration of *Streptomyces* inoculation for optimal composting. Research is necessary to elucidate *Streptomyces* bacteria mechanisms during composting to identify the most suitable inoculants, taking into account their functional, physiological, adaptability, and stability. Moreover, there is a lack of large-scale studies on the use of *Streptomyces* bacteria in composting, and further investigations are needed to confirm the benefits observed in small-scale studies. Furthermore, developing economically viable technological procedures for *Streptomyces* inoculant production is crucial, including the utilization of inexpensive resources such as plant-based substrates or agro-waste for inoculant propagation. Finally, research in modelling and optimizing the composting process by engineering processing techniques is necessary to ensure the composting sustainability process without compromising the quality of the final product ^[309]. By developing more efficient and effective composting practices, we hope to contribute to the broader goal of promoting sustainable agriculture and reducing environmental impact in Morocco and beyond.

9. Conclusion

In conclusion, this review highlights the significant contributions of *Streptomyces* to human well-being and their versatile potential in various sectors. Streptomycetes play a major role in agriculture by replacing chemical fertilizer, enhancing soil health through bioremediation, and acting as biological control agents for pests. Moreover, their role in the production of antibiotics, antioxidants and anticancer agents in the medical and therapeutic sectors opens up new possibilities for high-value molecule creation. Additionally,

actinobacteria contribute to biotechnology by producing valuable enzymes for various industries, leading to considerable profit margins. Finally, we can highlight new trends in nanomedicine, where streptomycetes can contribute to solving the problems of non-solubility of certain active ingredients. This is possible via the contribution of these micro-organisms in the production of active principle shuttle molecules that fail to reach targeted sites by therapeutic activities through the design of nanoparticle-based drug delivery systems (NDDS)^[310]. Overall, the numerous virtues of these microorganisms warrant further research and development to uncover their untapped potential, making them truly magical microorganisms for the betterment of our planet and human life.

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