An overview on Actinomycetes: A source of antimicrobial compounds

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Abstract: Actinomycetes are aerobic, spore forming Gram positive bacteria. Their structure has substrate and aerial mycelium. They are the most abundant microorganisms in the soil, producing earthy smell in ploughed soil. Actinomycetes were explored because they produce important secondary metabolites that plays important roles in many physiological, cellular and biological processes. For example, antibiotics, biopesticide agents, plant growth hormones, antitumor compound, antiviral agents, pharmacological compounds, pigments, enzymes, etc. Among many, *Streptomyces* sps. was the most explored and useful soil actinomycetes. In recent time, new strains of actinomycetes were isolated from extreme environment because of their wide range of application in pharmaceutical, food, agriculture and environmental industries. Therefore, this review is aimed on the use of Actinomycetes as a potential source for novel antimicrobial compounds and highlight on its application in various sectors like medicine, biotechnology, industries, agriculture and research.

Keywords: Actinomycetes; Antibiotics; Streptomycetes; Bioremidation; Enzymes.

Introduction

Antimicrobial compounds are those chemical agents produced by microorganisms as secondary metabolites. They are widely available in nature and they play a role to regulate microbial population in soil, water, etc[1]. Those compounds can be categorized as antibacterial (or antibiotics) that act against bacteria and antifungal which act against fungi. Antimicrobial substances are produced by many microbes, higher plants and animals[2]. A number of antimicrobials currently used in medicine are derived from the microbial origin.

The discovery of Penicillin by Alexander Fleming in 1828 was considered to be golden era of medicine. Antibiotics have saved many lives from bacterial infections. Most of the antibiotics till date are produced by Actinomycetes followed by other bacteria such as Bacillus. They are considered as one of the important class of microbes that can produce different classes of antibiotics. They are also a good resource for many natural compounds which had a great potential uses in diverse purposes[3]. Around 80% of antibiotics are derived from the genus *Streptomyces* and rare actinomycetes, such as *Actinomadura*, and only the 20% is produced by fungal species.

Actinomycetes are the prokaryotic organism and represent one of the largest taxonomic units among the 18 major lineages currently recognized within the domain bacteria. They are generally anaerobic and have mycelium in a filamentous and branching growth pattern. They are soil organism[3]. They are Gram positive bacteria which can form rod or coccoid shape, while some can form spores on aerial hyphae[4]. Gentamycin, Kanamycin, Streptomycin, Tobramycin, etc are some examples of antibiotics produced by Actinomycetes[5].

The use and misuse of antibiotics had resulted in emergence of resistant strains. For example, methicillin resistant *S. aureus* (MRSA). Then after, vancomycin was used to treat infections due to methicillin resistant *S.*

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Email: shradhabc@hotmail.com; https://orchid.org/0009-0006-5023-1917
Received: 22 July, 2025; Received in revised form: 26 Dec, 2025; Accepted: 3 Jan, 2026.
Doi: https://doi.org/10.3126/sw.v19i19.95594

aureus, the most common cause of hospital acquired infections, developed resistance to methicillin and several other antibiotics. The over use of vancomycin to treat MRSA, vancomycin resistant *Enterococcus faecium* (VRE) appeared. In addition, there are many Gram negative pathogens such as *Pseudomonas aeruginosa*, *Acinetobacter baumanii* and Enterobacteriaceae which are resistant to many antibiotics[7]. Although there are many antibiotics available, there is still a need for discovery of new types of antibiotics to solve the problem of multi drug resistant (MDR) among pathogenic bacteria. There are a few antimicrobial compounds, such as antimicrobial peptides, probiotic bacteria, and bacteriophages which are now considered as alternatives to antibiotics. Thus, this review is aimed to explore Actinomycetes as a producer of antimicrobial compounds.

Actinomycetes

Actinomycetes are most widely distributed microorganisms in nature and constitute significant component of microbial population in soil and are important source of antibiotics, enzymes and bioactive products[8]. *Actinomycetes* belong to the order of Actinomycetales, whose phylum is Actinobacteria, which is the largest taxonomic unit within the bacteria domain. This phylum comprises Gram positive bacteria with high guanine-cytosine (G + C) content in their DNA, such as 51% in some Corynebacteria and more than 70% in Streptomyces and Frankia[9]. According to Bergey's manual of Determinative Bacteriology, the order Actinomycetales are divided into eight diverse families: Actinomycetaceae, Mycobacteriaceae, Frankiaceae, Actinoplanaceae, Dermatophilaceae, Nocardiaceae, Streptomycetaceae, and Micromonosporaceae[10]. While, the latest edition of Bergey's Manual, from 1994 has divided the order actinomycetales into three families, as, Mycobacteriaceae, Actinomycetacea and Streptomycetacea. The first family comprise of the genus Mycobacterium, which is beyond the scope of this treatise. The second and third family comprises the true Actinomycetes. The genera Nocardia and Actinomyces fall into second family, and the genera Streptomyces and Micromonospora belong to the third. Another genus has been recently added, Thermoactinomyces, which include certain thermophilic forms.

Actinomycetes are heterotrophic organisms and thus, they depend on various organic materials for their source of energy or food. They decompose various organic materials in their surroundings. To break down these complex compounds they produce a number of enzymes including cellulases and keratinases. They participate in turn-over of soil components, especially in the transformation of organic compounds[11],[12],[13],[14]. Since they can decompose complex mixtures of polymers in dead plants, animals and fungal material[15], [16], [17], they have important role in soil degradation.

Secondary metabolites obtained from Actinomycetes provide a potential source of many novel compounds with antibacterial, antitumour (doxorubicin and bleomycin), antifungal (e.g., amphotericin B and nystatin), antiviral, antiparasitic and other properties viz. immunosuppressives (FK-506 and rapamycin), insecticides (spinosyn A and avermectin B), herbicides (phosphinotricin)[18,19, 20]. Antibiotics are the best-known products of Actinomycetes[21], [22]. It is known that the actinomycetes are the source of some 61% of all microorganism-derived bioactive substances discovered so far [23]. Around two-thirds of all known antibiotics are produced by actinomycetes, Streptomyces being the predominant one [9]. Some examples of antimicrobial compounds produced by actinomycetes are streptomycin (*Streptomyces griseus*), chloramphenicol (*S. venezuelae*), tetracycline (*S. rimosus*), erythromycin (*Saccharopolyspora erythraea*), leucomycin (*S. kitasatoensis*), vancomycin (*S. orientales)*, and gentamicin (from *M. purpurea)* [24].

Antimicrobial compounds from Actinomycetes

Actinomycetes have played a significant role in producing variety of antibiotics[25]. Approximately 80% of antibiotics till date are form Actinomycetes, especially from genera Streptomyces and Micromonospora [26, 27]. A total of 10,100 different bioactive metabolites have been derived from Actinomycetes[28, 29]. Among them, most of the secondary

metabolites are potent antibiotics[30]. The antibiotics produced from Actinomycetes are classified into several classes on the basis of chemical structure: i) beta-lactams (eg. Cephalosporins)[31], ii) macrolides (eg. Erythromycin) and tetracyclines[32], iii) aminoglycosides (eg. Streptomycin)[33], iv) ansamycins (eg. Rifampin)[34], v) anthracyclines (eg. Doxorubicin)[35]. Some of the antibiotics produced by Actinomycetes are described below:

Cephalosporins

Cephalosporins are beta lactam antibiotics produced by *Streptomyces clavuligerus*[31], and are one of the most widely prescribed antibiotic clinically[36]. It is a semisynthetic bactericidal drug which disrupts the synthesis of peptidoglycan layer of bacterial cell wall. It is active against both Gram positive and Gram negative bacteria. Cephalosporin is used to treat bacterial infections caused by bacteria like *Escherichia coli*, *Klebsiella sp*., *Proteus sp*., etc.[37, 38].

Tetracyclines

The tetracycline was first derived as natural product from actinomycetes by fermentation process. Chlortetracycline was produced by *Streptomyces aureofaciens* [39] which was available in market as Aureomycin. In late 1980s, a semisynthetic derivative of tetracycline was discovered with improved activity against emerging multidrug resistant (MDR) Gram positive and Gram negative pathogens[40]. Lately, there are two new tetracycline derivatives have been discovered, eravacycline[41,42] and omadacycline[43] respectively at Tetraphase Pharmaceuticals and Paratek Pharmaceuticals.

Macrolides

Macrolide antibiotics are compounds that occur naturally (Erythromycin), later they are modified to make semisynthetic and synthetic (Azithromycin, clarithromycin, dirithromycin, roxithromycin, josamycin, kitasamysin, spiramycin, flurithromycin, rokitamycin, mycinamycin, mirosamycin, oleandomycin and tylomysin)[44]. Macrolides are made of large macrocyclic lactone ring with 12 to 16 atoms attached to one or more sugar moieties by glycosidic bonds [45]. Most of the macrolides are produced from various species of Streptomyces. They inhibit bacterial growth by targeting on protein synthesis[46].

Streptomycin

Streptomycin is the first discovered aminoglycoside antibiotic which was isolated from *Streptomyces griseus*[44]. It is used to treat aerobic Gram negative bacterial infections such as brucellosis, tularemia, plague, tuberculosis (with isoniazid, pyrazinamide and rifampin) and endocarditis (with beta-lactam antibiotics)[45]. For pulmonary tuberculosis, streptomycin is an alternative therapy, second to RIPE (rifampin, isoniazid, pyrazinamide and ethambutol) therapy[46]. The wide spectrum of activity of streptomycin against Gram negative and Gram positive bacteria is diminished due to the development of antibiotic resistance. Enterobacteriaceae and most Streptococci are generally resistant of streptomycin.

Rifampicin

It is a group of semisynthetic derivatives of an antibiotic produced by *Nocardia mediterranea*. Rifampin is used to treat diverse mycobacterial infections and Gram positive bacterial infections. Rifampin inhibits DNA-dependent RNA polymerase (RNAP). The U.S. Food and Drug Administration (FDA) approved rifampin to treat active and latent tuberculosis (TB)[47] and to eliminate asymptomatic carriers of *N. meningitides*[48]. To reduce the development of resistant strains, rifampin is combined with other antimicrobial agents to treat infections caused by *S. aureus* and for cerebrospinal fluids (CF) shunts and drains[49].

Anthracycline

Anthracyclines are the most effective chemotherapeutic agents for the treatment of various types of cancers. For example: leukemia, lymphomas, breast, stomach, uterine, ovarian, bladder and lung cancers[50]. Anthracyclines are extracted naturally from *Streptomyces peucetius*. and consist of different types like, daunorubicin, doxorubicin, epirubicin, idarubicin, mitoxantrone and valrubicin[51]. The action of anthracyclines is due to their interaction with

topoisomerase-II. The complex formed prevents the relegation of the ds-DNA breaks which causes apoptotic cell death.

Applications of Actinomycetes and its product

1. Application in pharmaceuticals

Actinomycetes produce about 45% of bioactive compounds having antagonistic activity which have application in the food, agriculture, medicine, pharmacy, etc. [52]. Among them, 34% compounds were produced by Streptomyces and 11% compounds were produced by other acinomycetes [53]. The scientific community and public-private partnerships should discover new sources of antimicrobial agents to control pathogens [53].

i. Antibacterial compounds:

Streptomyces sp. XMA39 produced four medermycin-type naphthoquinones, strepoxepinmycins A-D (1-4), and medermycin [5]. *Streptomyces* sp. SM01 produced novel antimicrobials, picolinamycin (SM1). It is more active against Gram positive bacteria than Gram negative bacteria. Also, it is effective against many multidrug resistance (MDR) strains, like methicillin-resistant strains of Staphylococci and Enterococci and MDR strains of *S. aureus*[54].

Streptomyces sp. SNO280 produced various important compound, such as indole derivative chloroindole, diketone streptoone A, ketonic acids streptoones B and C, and a macrolide antibiotic X-14952B. Streptoone A showed antibacterial activity against *Clavibacter michiganinsis*. Streptoone B showed antifungal activity against *Phytophthora capsici*. These molecules helped in the treatment and management of the phytopathogens [55].

ii. Antifungal compounds:

Streptomyces species are the most important genus because they produce about 75% bioactive microbial metabolites[56]. Guan and coworkers in 2016 showed that *Streptomyces songpinggouensis* was active against the fungi *S. sclerotiorum*, *C. cassiicola*, *A. solani*, *C. lunata*, *S. turcicaf*, *H. maydis*, *F. oxysporum*, *C. orbiculare* and *P. infestans* [57].

Streptomyces albus strain CAI-21 and its active metabolite organophosphate can control charcoal rot disease in sorghum caused by *Macrophomina phaseolina* [58].

Streptomyces morookaense AM25 produced a novel peptide gloeosporiocide, having cyclized cysteins to form three thiazoles. It can be used as biocontrol agent and producers of antifungal activity [59].

iii. Antitumor compounds:

Marine actinomycetes are good source of antitumor drugs. For example, *Micromonospora*, *Salinispora* and *Verrucosispora*. The marine *Streptomyces* sp. shell-016 was isolated from a shell sediment sample. It produced four novel bioactive tetrahydroanthra-gama-pyrone compounds called shellmycin A-D (1-4)[60]. These compounds exhibited cytotoxic activity against five cancer cell lines. Also, the putative biosynthetic pathways of these compounds were discussed according to their structure-activity relationship [63].

Bioactive compounds with binding affinity to DNA as a target molecule to fight against cancer cell is very important. *Microbacterium* sp. RP581 produced Microindoline 581 which can cause double-strand breaks through binding to the DNA[62]. The selective action of Microindoline 581 in killing HepG2 cells might be due to specific metabolism in the cells as a precursor [62].

iv. Antiviral compounds:

Moreover, actinomycetes inhibit many viruses like hepatic C virus (HCV), influenza A virus (IAV), human immunodeficiency virus (HIV), herpes simplex virus (HSV) and epidemic diarrhea virus (EDV). The antiviral compounds are labyrinthine, chartreusin, xiamycin, butanolides and antimycins[62].

Streptomyces sp. CPCC 200267 produced two cyclic thiopeptides, geninthiocins E and F, four geninthiocin derivatives, geninthiocins A, B, C and val-geninthiocin. Geninthiocin E, val-geninthiocin, geninthiocin A and B exhibited anti-influenza A virus activities with the IC_{50} values of 28.7, 15.3, 7.3 and 18.3μM, respectively [63].

Streptomyces sp. AM-2504 produced two new antibiotics, called virantmycin B and C. They contain a terahydroquinoline and an indoline, respectively and also a hydroxycyclopentenone moiety. Both compounds showed a weak antibacterial and antifungal activities. Virantmycin B showed antiviral activity against the dengue virus [64].

v. Other compounds:

Actinomycetes also produce antiparasitic agents like valinomycin, butanolides, avermectins and milbemycins which inhibit *Leishmania* sp., *Trypanosoma* sp. and helminths[65].

Actinomycetes also produce therapeutic immune-suppressants or drug immunoconjugates such as rapamycin, tacrolimus and sirolimus[66]. Actinomycetes also produce antioxidant compounds like hexaricins, polyketides, pyrazolofluostatins and agelolines, protecting from infections and degenerative diseases[67].

Furthermore, actinomycetes produce antioxidant, anti-inflammatory, immunosuppressive, antiparasitic and cytotoxic compounds. Anticancer drugs like anthracyclines, bleomycin, mitosanes, enediynes, etc are also produced from actinomycetes[59].

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2. Applications in food and other industries

Streptomyces sps are the most important enzyme producer actinomycetes. They produce enzymes such as chitinase, proteases, cellulases, pectinases, L-glutaminase, amylases, etc [68]. Microbial enzymes are generally safe, stable and functional at different temperature, pH and salinity[69].

Heat stable enzymes are very useful because they reduce the contamination by mesophilic microorganisms and they also improve the efficiency of substrate degradation[70]. Wu and colleagues (2018) showed that *Streptomyces thermo-alkaliphilus* produce alkaline cellulose with potential carb-oxymethyl cellulose degrading activity [71].

Lipases are useful in processing of oils and fats, cosmetics and detergents because lipases catalyse the hydrolysis of lipids[72]. Keratinases are useful in the recycle of chicken feathers and nails because keratinases catalyse the hydrolysis of keratin[69]. Keretinases are produced by *Streptomyces* sp, *Saccharomonospora* sp, *Nocardioides* sp, *Nocardiopsis* sp and *Nonomuraea* sp. Proteases have application in milk coagulation, clarification of fruit juices, paper industry[73]. Pectinases are used in fruit-based foods and beverages, textile, paper and pulp industry, agriculture sector, etc.[74]. L-asparaginase enzyme is produced by soil actinomycetes such as *Streptomyces griseus*, *S. karnatakensis*, *S. albidoflavus* and *Nocardia* sp.[75] and are used not only in food industry but are used for bone marrow treatment and stem cell transplant as well (Table 1). Important antibiotic and enzyme producers are *Streptomyces scabrisporus*, *S. sparsogenes*, *S. misakiensis*, *S. cirratus*, *S. lincolnensis*, *S. endophyticus*, *S. chartreusis* and *S. alboniger*[76,77].

3. Application in Agricultural sector

Actinomycetes are used for sustainable agriculture to produce biofertilizers and biocontrol agents[78]. Biofertilizer is a substance that contains living microorganisms, which colonize the rhizosphere or plant interior and helps to release nutrients to the host plant[79]. Biocontrol agents are used to control plant diseases by releasing secondary release nutrients to the host plant[79]. Biocontrol agents are used to control plant diseases by releasing secondary metabolites[80]. For example, *Streptomyces griseoviridis* is a biocontrol agent. It is effective against plant pathogens together with *Alternaria brassicola* Wiltsh., *Botrytis cinerea* Pers., *Fusarium avenaceum* Sacs., *F. culmorum* [80]. Actinomycetes are very beneficial for soil and plant health, because they produce enzymes, increases soil fertility, fix nitrogen, degrade organic matter, kill pests and bioremediate soils[78].

Streptomyces is the most useful actinomycetes in soil. These fix nitrogen and solubilize phosphate, excrete secondary metabolites like antioxidants, antimicrobials and enzymes in soil[78,81]. *Frankia* family of actinomycetes makes symbiotic relation with nonleguminous plants to fix

Table 1: The applications of enzymes produced from actinomycetes[77] (modified from Sharma, 2014).

Enzymes	Applications
Amylase	Used in fermentation, in food industry, in textile and paper industry
Catalase	Used as an antioxidant, in cold sterilization of beer, in dairy industry
Cellulase	Used in biomechanical pulping, in laundry, in animal feed industry
L-asparaginase	Used in bone marrow treatment, in stem cell transplant, in treatment of acute leukemia
Lipase	Used in oleochemical, in detergent industries, in diagnostic settings, in pharmaceutical industries
Urease	Used in wine industry, in analysis in blood and urine, in analysis of heavy metal content in waste water and soil
Protease	Used as antiinflammation, to protect against clot, in cancer treatment
Chitinase	Used in plant resistant against fungal pathogen, in drug delivery and wound healing, in biochemical industry
Keratinase	Used in poultry industry

nitrogen which is used by the host and other nearby plants[82]. Actinomycetes from the genus *Micromonospora*, *Nocardia*, *Actinomadura* sp, *Rhodococcuss sp*, *Actinoplanes*, *Microbiospora* sp and *Streptosporangium* sp produce phosphatase enzymes. They mineralize organic phosphate which will be available for plants[83]. Actinomycetes are characterized by plant growth-promoting rhizobacteria (PGPR) in rhizosphere[84]. Acinomycetes improve nutrients and minerals, synthesize plant growth regulators and inhibit pathogens. Actinomycetes are important microorganisms in producing siderophores in soil (Table 2). Siderophores are chelate agents of ferric ion and reduce ferric ions to ferrous ions which are easily absorbed by microorganisms[85]. Actinomycetes produce plant growth hormone indole-3-acetic acid (IAA). It is an important auxin which helps in basic cellular processes such as cell division, elongation and differentiation. It also decreases the root length and increases the root hair to enhance nutrient absorption[86]. Actinomycetes produce insecticidal compounds which control housefly *Musca domestica* and kill mosquito *Culex quinquefascietus*[87]. They also act against the fungus *Phytophthora* sp,[88]. *Streptomyces indiaensis* showed antifungal activity against *F. oxysporum*, *A. fumigatus*, *A. flavus*, *A. niger* and *H. graminum*[89]. The antifungal activity of *Streptomyces* is due to the production of enzyme chitinase (Table 2)[90].

4. Environmental purposes and other uses

Actinomycetes are the predominant microorganisms in soil that recycle organic matter[91]. They decompose the cellulose and lignin of wood and paper and the chitin of the exoskeletons of insects. In composting, thermophilic and thermotolerant actinomycetes cause decomposition of organic matter.

They are used for soil bioremediation (Table 3) because it is environment friendly and cheap[92]. In bioaugmentation, microorganisms are used to reduce, remove or transform contaminants present in the soil[93]. *Promicromonospora* sp. UTMC 2243 removed 96.5% residual cadmium[94]. The actinomycetes *Rhodococcus* removed 93% of the fungicide carbendazim from soils in 14 days as shown in table 4[95]. Different strains of actinomycetes produce different and new useful antibiotics so new stains are isolated and screened[30].

Actinomycetes produce pigments such as blue, violet, red, yellow, green, brown and black[96]. A blue pigment actinorhodin was produced by *Streptomyces coelicolor*, *S. violaceusruber* and *S. lividans*. It is applied as an antibiotic

against Gram positive bacteria, as a pH indicator and in food industry for making beverages, desserts, etc and in cosmetic industries[97]. *Streptomyces* species produced yellow antibiotic called 4-hydroxynitrobenzene which was active against *Bacillus subtilis* and *Shigella shiga*. These pigments are safe for human utilization and easy to produce[98]. El-Sheekh colleagues reported the production of biodiesel from *Streptomyces coelicolor* (Table 3) which had higher heating value than algal biodiesel[99].

Table 2: The uses of actinomycetes in agriculture[68] (modified from Nazari et al., 2022).

Actinomycetes	Applications
Streptomyces sp.	Inhibited the mycelial growth of the fungus *Phytophthora infestants* that causes late blight in potato cultivation.
Streptomyces sp.	Increased minerals, vitamins and antioxidants in seeds and increased nitrogen and nutrients in the soil
Streptomyces sp., *Nocardiopsis* sp.	High production of ammonia and indole acetic acid, and inorganic phosphate was dissolved
Streptomyces sp.	Production of chitinase and pest control
Streptomyces sp.	Antifungal potential and better crop quality
Streptomyces sp.	All isolates produced siderophore, and two novel *Streptomyces* produced enterobactin and heterobactin.

Conclusion

The actinomycetes are immensely used in various fields. It has been an important source of biologically active secondary metabolites. Actinomycetes produce industriall -y valuable compounds. Studies have focused on antimicrobial potential, enzymes production, agricultural uses, bioremediation, biofuels and pesticides degradation

Table 3: The environmental applications of soil actinomycetes [68] (modified from Nazari et al., 2022).

Actinomycetes	Applications
Streptomyces coelicolor	Bioethanol production
Rhodococcus qingshengii	Carbendazim bioremediation
Streptomyces coelicolor	Biodiesel production
Streptomyces torulosus	Natural dyes
Streptomyces, Saccharothrix, Streptosporangium, Nonomuraea, Promicromonospora	Heavy metal bioremediation

Streptomyces was the genus with the highest incidence among soil actinomycetes and the most exploited for different uses. Actinomycetes are the most promising industrial microorganisms because they are found in large numbers and can tolerate many substances and environments.

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