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Actinomycetes benefaction role in soil and plant health

Asma Absar Bhatti, Shamsul Haq, Rouf Ahmad Bhat*

Division of Environmental Sciences, Sher-e-Kashmir University of Agricultural Sciences and Technology, Kashmir, 190025, India

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A B S T R A C T

Actinomycetes are aerobic, spore forming gram-positive bacteria, belonging to the order actinomycetales characterized with substrate and aerial mycelium growth. They are the most abundant organisms that form thread-like filaments in the soil and are responsible for characteristically "earthy" smell of freshly turned healthy soil. They play major roles in the cycling of organic matter; inhibit the growth of several plant pathogens in the rhizosphere and decompose complex mixtures of polymer in dead plant, animal and fungal material results in production of many extracellular enzymes which are conductive to crop production. The major contribution in biological buffering of soils, biological control of soil environments by nitrogen fixation and degradation of high molecular weight compounds like hydrocarbons in the polluted soils are remarkable characteristics of actinomycetes. Besides this, they are known to improve the availability of nutrients, minerals, enhance the production of metabolites and promote plant growth regulators. Furthermore, actinobacteria do not contaminate the environment instead, they help sustainably in improving soil health by formation and stabilization of compost piles, formation of stable humus and combine with other soil microorganisms in breaking down the tough plant residues such as cellulose and animal residues to maintain the biotic equilibrium of soil by cooperating with nutrient cycling.

Contents

* Corresponding author.
E-mail address: rufi.bhat@gmail.com (R.A. Bhat).

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1. Introduction

The word “Actinomycetes” is derived from Greek word “atkis” (a ray) and “mykes” (fungus), having characteristics of both bacteria and fungi [18] but yet possess sufficient distinctive features to delimit them into kingdom bacteria. Actinomycetes are aerobic spore forming gram-positive bacteria; containing high guanine-cytosine (57–75%) in their genome, and belong to the order *Actinomycetales* characterized with substrate and aerial mycelium growth. They are filamentous like fungi and possess true aerial hyphae. Actinomycetes are ubiquitous and form a stable and persistent population in various ecosystems especially in soil, where they are predominant in dry alkaline soil. They unveil an array of life cycles which are unique among the prokaryotes and seem to play a vital role in the cycling of organic matter in the soil ecosystem [111]. Actinomycetes are economically and biotechnologically most worthwhile microorganisms. Actinomycetes are well known for the production of wide range of secondary metabolites of various medical values like antibiotics, antifungal, antiprotozoal, antiviral, anticholesterol, antihelminth, anticancer and immunosuppressant. Antibiotics such as streptomycin, gentamicin, rifamycin and erythromycin which are used presently are the product of actinomycetes only. They are important not just to the pharmaceutical industries but to the agriculture as well. Actinomycetes have the potential to inhibit the growth of several plant pathogens [44,98]. It also reported that the ability of actinomycetes the ability to inhibit *Erwinia amylovora* a bacteria that cause fireblight to apple and *Agrobacterium tumefaciens* a causal agent of Crown Gall disease [80]. Most of the Actinomycetes feed on protein or non-protein organic matter. Some Actinomycetes are autotrophs as well while as some use waxes, resins, paraffins and petroleum as source of carbon. For them nitrates, ammonium salts, urea, amino acids and other substances can be used as the source of nitrogen. Actinomycetes live under the most diverse conditions, aerobic and anaerobic, at temperatures of 5–7° C and 45–70 °C. They indulge in diverse soil processes (ammonium fixation, decomposition of cellular tissue and the synthesis and decomposition of humus). Many Actinomycetes are used to produce antibiotics, vitamins, amino acids and other biologically active substances.

2. Nature and habitat

Actinomycetes are predominantly found in soil, in the silt of water bodies, in the air and in plant remains. They are the most abundant organisms that form thread-like filaments in the soil. They grow as hyphae like fungi responsible for the characteristically “earthy” smell of freshly turned healthy soil [89]. The actinomycetes exist in various habitats in nature [30] and represent a ubiquitous group of microbes widely distributed in natural ecosystems around the world [99]. They are primarily soil inhabitants [55]but have been found widely distributed in a diverse range of aquatic ecosystem, including sediments obtained from deep sea [14,114] even from greatest depth Mariana Trench [84,106]. They may be present in extreme environments especially at cryophilic region Antarctica [72,87] and even in desert soil [21].

2.1. Terrestrial habitat

Actinomycete population is largest in surface layer of soils and gradually decreases with the depth; individual actinomycete strains are present in all soil layers [104]. Actinomycetes are numerous and widely distributed in soil and are next to bacteria in abundance. They are widely distributed in the soil, compost etc with estimated values ranging from 10^4 to 10^8 per gram of soil. They are sensitive to acidity/low pH (optimum pH range 6.5–8.0) and waterlogged soil conditions. They are mesophilic (25–30 °C) organisms and some species commonly present in compost and manures are thermophilic growing at 55–65 °C temperature (e.g. *Thermoatinomycetes, Streptomyces*).

2.2. Aquatic habitat

2.2.1. Fresh water habitat

Actinomycetes are abundant in fresh water lakes. They are also found in sewage and grew well at 60 °C. Various members of genera *Actinoplanes, Micromonospora, Rhodococcus, Streptomyces* and the endospore-forming *Thermoactinomycetes* have been isolated from freshwater habitats [15]. Majority of these actinomycetes most probably are wash-in from land and accumulated in freshwater habitats [34]. Sporangia of *Actinoplanes* could withstand prolonged desiccation and release motile spores when rehydrated [63]. *Actinoplanes* are mainly discovered on allochthonous leaf litter washed to lake shore and twigs submerged in streams. Members of the genus *Micromonospora* represent a truly indigenous group of microbial inhabitants of waters and bottom deposits of inland lakes. *Micromonospora* spores can survive as dormant propagules as they washed into streams, rivers and lakes [89]. The presence of *Rhodococcus coprophilus* a coprophilic species in lakes is believed due to wash in of contaminated herbivore dung. The presence of *Streptomyces* in freshwater habitat is because of their spores being continuously washed into rivers and lakes [47]. *Streptomyces* are dominant in water samples while great numbers of *Micromonospora* were found in sediments [108].

2.2.2. Marine habitat

The existence of actinomycetes in marine environment was believed because of soil contamination, or to their presence on algal material floating on the surface of the sea, or to the fact that the samples of water were obtained near the docks. Based on absence of apparent morphological and biochemical differences between both marine and terrestrial isolates, actinomycetes might be originated from terrestrial but adapted to salinity level of sea water [37]. The spores of actinomycetes could be transferred from land to the sea by rain or river [78]. However, certain indigenous actinomycetes have been isolated from deep sediments [115]. Besides, a bimodal distribution in relation to depth had also been reported in maximum numbers of actinomycetes from near-shore sediments in both shallow and deep sampling sites showed [46]. It is therefore indicated that the marine-derived actinomycetes are originated from terrestrial ecosystems. Actinomycetes isolated from marine environment are metabolically active and have adapted to life in the sea [46]. Furthermore, studies on isolation of actinomycetes from marine sediments suggested that they are able to survive under marine conditions due to their salt tolerance. In fact they are able to endure for considerable periods of time under marine environment.

2.3. Extreme environments

Actinomycetes are also present in extreme type of habitats. Alkalophilic actinomycetes (*Streptomyces* and *Nocardiopsis* are the dominant genera) are present in alkaline soils (pH 10–12) surrounding mineral springs [48]. A new genus and species of alkalophilic actinomycetes also described as *Bogoriella caseilytica* was isolated from a soda lake soil (pH 10) [38]. [1] isolated *Saccharomonospora halophila*, a halophilic actinomycete with optimum growth at 10% NaCl from marsh soil. *Modestobacter multiseptatus*, a psychrophilic strains with optimum growth at temperature 11–13 °C was isolated from transantarctic mountain soils [70]. An obligate psychrophilic actinomycetes, *Cryobacterium psychrophilum*, with optimum growth temperature 9–12 °C and did not grow at temperature higher than 18 °C was isolated from Antartica soil [100]. Other than that, acidophilic actinomycetes have also been isolated from acidic forest and peat soils, mainly *Streptomyces* and *Micromonospora*. Thermophilic *Streptomyces* spp. isolated from silt and water samples of meteoritic crater [13]. Few rare thermotolerant actinomycetes isolated from desert soils of Mojave Desert, California belonged to genera *Microbispora, Nocardia, Microtetraspora, Amycolaptosis, Actinomadura* and *Saccharothrix* were reported [105].

3. Structure

Actinomycetes are a group of branching unicellular filamentous bacteria, so called because of a fancied resemblance to the radiating rays of the sun when seen in tissue lesions. Actinomycetes reproduce either by fission or by means of special spores or conidia and are characterized by the formation of normally branching threads or rods. The hyphae are generally nonseptate; under certain special conditions, septa may be observed in some forms. The sporulating mycelium may be branching or non branching, straight or spiral shaped. The spores are spherical, cylindrical or oval. They produce initial microcolonies composed of branching system filaments that after 24–48 h fragment into diptheroids, short chain and coccobacillary forms [66]. The cell wall of actinomycetes is a rigid structure that maintains the shape of the cell and prevents bursting of the cell due to high osmotic pressure [35,66]. The wall consists of a large variety of complex compounds including peptidoglycan, teichoic and teichuronic acid and polysaccharides. The peptidoglycan consists of glycan (polysaccharides) chains of alternating N-acetyl-*d*-glucosamine (NAG) and N-acetyl-*d*-muramic acid (NAM) and diaminopimelic acid (DAP), which is unique in prokaryotic cell walls. Teichoic and teichuronic acid are chemically bonded to peptidoglycan [19,66]. The chemical composition of their cell wall is similar to that of gram positive bacteria but because of their well-developed morphological (hyphae) and cultural characteristics, actinomycetes have been considered as a group, well separated from other common bacteria [16,18]. The actinomycetes were called historically as the ray fungi and was thought that they are be related to the true fungi, such as bread molds, because they formed mats (mycelia) of branching filaments (hyphae). However, unlike the true fungi, the actinomycetes have thin hyphae (0.5 1.5 μm in diameter) with genetic material coiled inside as free DNA. The cell wall of the hyphae is made up of a cross linked polymer containing short chains of amino acids and long chains of amino sugars. In general, actinomycetes do not have membrane bound cell organelles. The actinomycetes are characterized by a filamentous or rod- and coccus structure and the presence of lateral protuberances.

Actinomycetes contain a cell wall. The composition of cell wall in actinomycetes varies greatly among different groups and is of considerable taxonomic significance. Four major cell wall types are distinguished in these filamentous bacteria on the basis of the three features of peptidoglycan composition and structure. These features are (i) diaminopimelic acid isomer on tetrapeptide side chain position 3, (ii) sugar content of peptidoglycan, and (iii) the presence of glycine in interpeptide bridges. As is evident in, characteristic sugar patterns are present only in cell wall types II-IV of those actinomycetes with meso-diaminopimelic acid. Flagella grows in and on the substrate. The internal structures are thallus (a tissue like mass that grows in cultures) is mycelium (tangled mass of hyphae that is found in nature).

4. Role of actinomycetes in soil and plant health

Soils on earth differ from a heap of inert rock particles in many ways, but one of the more important is that they have a population of microorganisms living in them, which derives its energy by oxidizing organic residues left behind by the plants growing on the soil or by the animals feeding on these plants. In the final analysis, the plants growing on the soil subsist on the products of microbial activity, for the microorganisms are continually oxidizing the dead plant remains and leaving behind, in a form available to the plant, the nitrogenous and mineral compounds needed by the plants for their growth. The soil microorganisms can be classified into major divisions, such as the bacteria, actinomycetes, fungi and algae. The typical filamentous actinomycetes belong predominantly to the *Streptomyces* and *Micromonospora* groups. They form very find often much branched hyphae when growing, which break up into spores, either by the tip of the hyphae producing one or two spores. They use carbon and nitrogen compound such as cellulose, hemicelluloses, proteins and lignin. Most members are aerobic and some may have a limited ability to reduce nitrates. They also appear to be active under pastures and may be the dominant microorganisms in the surface layers of grass lands and thatch surfaces. Organic residues added to soil are first attacked by bacteria and fungi and later by actinomycetes, because they are slow in activity and growth than bacteria and fungi. They decompose the more resistant and indecomposable organic substance/matter and produce a number of dark black to brown pigments which contribute to the dark colour of soil humus. They are also responsible for subsequent further decomposition of humus (resistant material) in soil.

4.1. Mechanism of organic acid production

Metabolism and physiology of phosphate-solubilizing microorganisms (PSMs) is also one of the important factors that can regulate their mineral phosphate solubilization (MPS) phenotype, as the carbon source availability and metabolism of carbon source will decide the organic acid to be produced. As an example, several Gram-negative bacteria oxidize peripheral glucose via pyrroloquinoline quinone-dependent glucose dehydrogenase (PQQ-GDH) to produce gluconic acid [137,138] which on further oxidation is converted to 2-ketogluconic acid. However, except few Streptomyces strains, actinomycetes lack PQQ cluster and subsequent dehydratase enzyme comprising Entner-Doudoroff oxidation pathway. The mechanism involvement of glyoxylate bypass in high phosphate-solubilizing *Streptomyces* sp. for production of malic acid [137,138] as shown in Fig. 1.

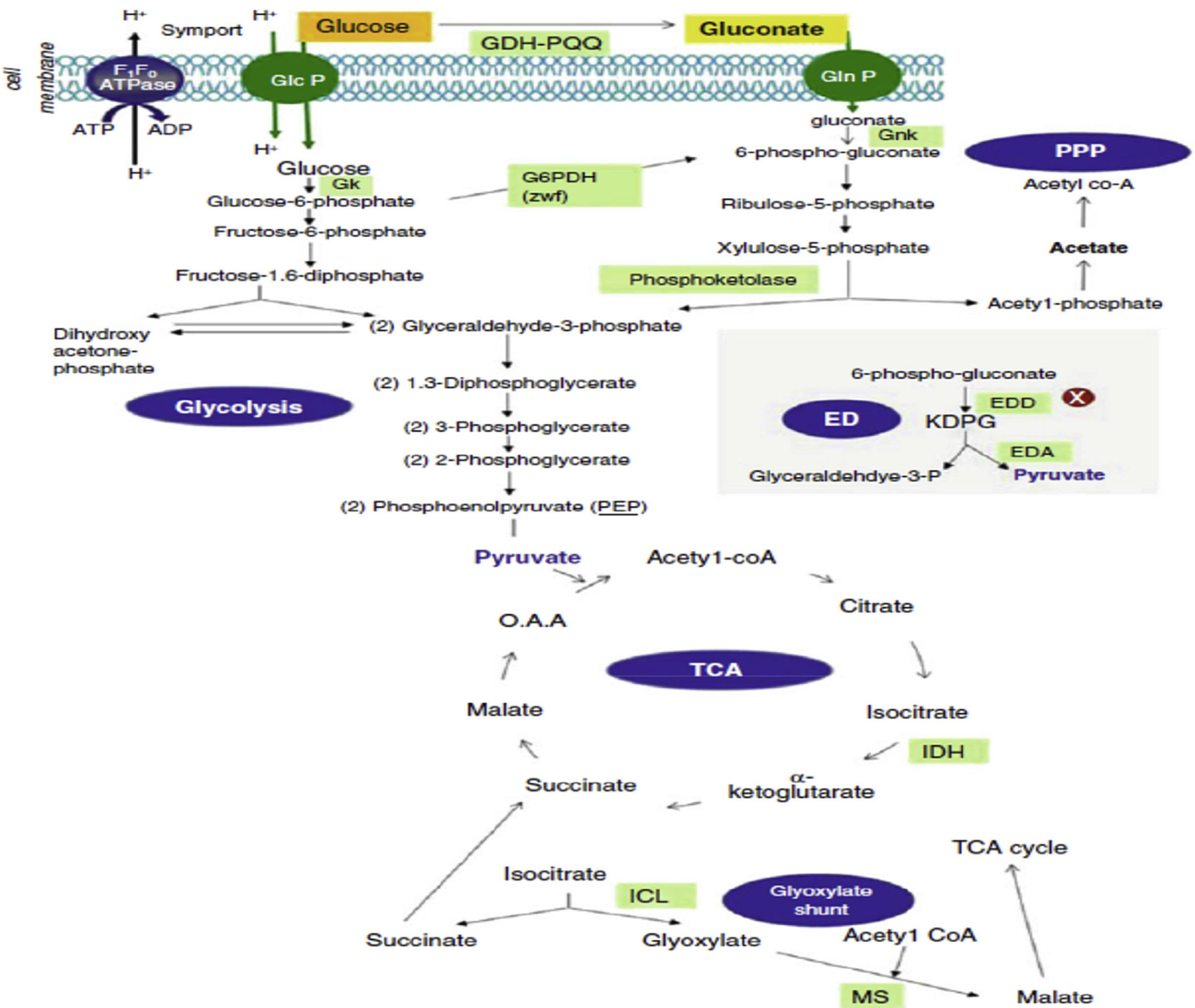

Fig. 1. Overview of central and peripheral carbo metabolism pathways in actinomycetes. GDH glucose dehydrogenase, GK glucokinase, Gnk gluconate dehydrogenase, G6PDH glucose-6-phosphate dehydrogenase, EDD 2-keto-3-deoxy-6-phosphogluconate dehydratase, EDA 2-keto-3-deoxy-6-phosphogluconate aldolase, IDH isocitrate dehydrogenase, ICL isocitrate lyase, MS malate synthase, PQQ pyrroloquinoline quinone, OAA oxaloacetate, KDPG 2-keto-3-deoxy-6-phosphogluconate [137,138].

4.2. Nitrogen fixation

Microorganisms play an important role in the recycling of agricultural wastes [121]. Bacteria are important in agricultural soils because they contribute to the carbon cycle by fixation (photosynthesis) and decomposition. Some bacteria are important decomposers and others such as actinomycetes are particularly effective at breaking down tough substances. Land management has an influence on the structure of bacterial communities as it affects nutrient levels and hence can shift the dominance of decomposers from bacterial to fungal. Actinomycetes form associations with some non-leguminous plants and fix N, which is then available to both the host and other plants in the near vicinity. The natural nitrogen cycle relies on nitrogen fixing bacteria like those found in the *Frankia* family of actinobacteria, to supply the fixed nitrogen. Fixed nitrogen is often the limiting factor for growth, both in your garden and in the general environment. About 15% of the world's nitrogen fixed naturally is from symbiotic relationships between various species of the *Frankia* family of actinobacteria and their host plants. The plants that form symbiotic relationships with *Frankia* are called actinorhizal plants. The *Frankia* is able to provide most or all of the host plant's nitrogen needs. It is believed that much of the new nitrogen in temperate forests, dry chaparral, sand dunes, moraines, and mine waste tailings is thanks to the mutualism of *Frankia* and host plants. They are the main nitrogen fixing relationships in large parts of the world and will only become more important as we adjust to climate change.

4.3. Decomposition of organic matters

Actinomycetes are the main group of soil microorganisms that play a major role in recycling of organic matters in environment by production of hydrolytic enzymes [71]. As a decomposer the actinomycetes specialize in breaking down tough cellulose and lignin found in wood and paper and the chitin found in the exoskeletons of insects. The breakdown of these materials makes nutrients once again available to plants. During the process of composting mainly thermophilic (adapted to high temperatures) and thermo tolerant actinomycetes are responsible for decomposition of the organic matter at elevated temperatures. In the initial phase of composting the intensive increase of microbial activity leads to a self heating of the organic material. High temperatures in composting help to kill viruses, pathogenic bacteria, e.g. coliforms, and weed seeds present. Actinomycetes live predominantly aerobically, i.e. they need oxygen for their metabolism. The compost material should therefore be well aerated. Generally, actinomycetes grow on fresh substrates more slowly than other bacteria and fungi. Natural habitats of thermophilic actinomycetes are silos, corn mills, air conditioning systems and closed stables.

4.4. Actinomycetes as plant growth promoting bacteria

Actinobacteria commonly inhabit the rhizosphere, being an essential part of this environment due to their interactions with plants. Such interactions have made possible to characterize them as plant growth-promoting rhizobacteria (PGPR). As PGPR, they possess direct or indirect mechanisms that favor plant growth. Actinobacteria improve the availability of nutrients and minerals, synthesized plant growth regulators, and specially, they are capable of inhibiting phytopathogens [141]. Different activities that are performed by actinobacteria have been studied, such as phosphate solubilization, siderophores production, and nitrogen fixation. Furthermore, actinobacteria do not contaminate the environment; instead, they help to maintain the biotic equilibrium of soil by cooperating with nutrients cycling. The aforementioned is directly related to the quality and productivity of crops. Moreover, different aspects of these microorganisms have been studied [139,140], such as production of metabolites that improve plant growth, resilience against unfavorable environmental conditions, and beneficial and synergic interactions with arbuscular mycorrhizal fungi. Taking into account the above-mentioned activities, actinobacteria can be considered as possible plant fertilizers.

4.5. Production of plant growth regulators

Growth regulators in plants PGR (Plant Growth Regulators) are known as plants hormones. PGR are small molecules that affect plant growth and development at very low concentrations [27]. One of the parameters used to determine the effectiveness of certain rhizosphere bacteria is the ability to promote the development of characteristic root system of this type of plant growth regulators [26,109].

4.6. Siderophores production

Siderophores are compounds produced by various microorganisms in soil. These organisms rely on chelation phenomena to support their biological activity. Siderophores are extracellular fluorescent pigments that possess affinity to iron (III), they are water-soluble and have low molecular weight (500–1000 Da) [76]. Furthermore, siderophores are produced by a great variety of microorganisms that grow in scarce iron conditions [50,92]. These compounds act as specific chelate agents of ferric ion, leaving available the ionic form (Fe^{+2}), which is easily absorbed by microorganisms [10]. When siderophores form a complex with Fe^{+3}, these are recognized by cell membrane receptors [88]. This facilitates the inclusion of the formed complex to cell. Once in the cell, Fe^{+3} ions are reduced to a Fe^{+2} becoming available to be used in different biological processes. Finally, the siderophore is released again [42]. Actinobacteria is one the most important groups in terms of siderophores production.

4.7. Actinomycetes as plant growth promoting agents

In attempts to develop commercial biocontrol and plant growth promoting products using rhizobacteria, it is important to recognize the specific challenges they present. The interaction between PGPR species and their plant symbionts appears to be specific, even within a crop or cultivar [12,33,51,57]. While a rhizobacterium screened for growth promotion may reveal the positive effects on one crop, it may have no effect, or even retard growth of another crop [28,79]. Although rhizobacteria may present unique challenges to our attempts to harness their beneficial attributes, the prospects for improved agriculture by the use of biocontrol-PGPR seem excellent. PGPR can affect plant growth in two general ways, either directly or indirectly. Indirect promotion occurs when PGPR lessen or prevent the harmful effects of one or more deleterious microorganisms. This is mainly attained through biocontrol, or the antagonism of pathogens of soil plant. Specifically, colonization or the biosynthesis of antibiotics [25] and other secondary metabolites can prevent pathogen establishment and invasion. Direct promotion of plant growth by PGPR occurs when the plant is supplied with a compound that is synthesized by the bacteria, or when PGPR or else facilitates plant uptake of soil nutrients. Possibilities include siderophore synthesis, nitrogen fixation, solubilization and phytohormone synthesis, of minerals to make them available for plant uptake and use [33]. *Streptomyces* spp. produces at least one class of compounds that directly influence plant growth. Direct and indirect interactions between actinomycetes and other nonpathogenic soil microorganisms also influence plant growth. Actinomycetes stimulated the intensity of mycorrhizal formation and that resulted in improved plant growth [85].

4.8. Actinomycetes as biocontrol tools

A prime example of *Streptomyces* biocontrol agent is *Streptomyces griseoviridis*. This is, originally isolated from light coloured *Sphagnum* peat [102,103], has been reported to be antagonistic to a variety of plant pathogens together with *Alternaria brassicola* (Schw.) Wiltsh., *Botrytis cinerea* Pers., *Fusarium avenaceum* Sacc, *F. culmorum* [102,103]. *Streptomyces griseoviridis* is used in root dipping or growth nutrient treatment of cut flowers, potted plants, greenhouse cucumbers, and varied alternative vegetables [85]. Mycostop is a biofungicide that contains *S. griseoviridis* as the active ingrédient. Many properties related to actinomycetes may justify the ability of sereval of them to act as biocontrol tools. Some typical actinomycetes and their major role as biocontrol agent are depicted in Table 1.

4.9. Actinomycetes as production of plant growth hormone (indole-3-acetic acid)

Indole-3-acetic acid (IAA) is the principal form of auxin, which regulates many basic cellular processes including cell division, elongation and differentiation. It also leads to decrease in root length andincrease in root hair formation, so enhancing the potential of the plant to absorb soil nutrients. Besides, there are several developmental processes in which auxin plays a role, together with embryo and fruit development, organogenesis, vascular tissue differentiation, root patterning, elongation and tropistic growth, apical hook formation and apical dominance [9,22,82]. It was observed that synthesis of IAA is induced by six diverse *Streptomyces* species in the presence of tryptophan and recommended indole-3-acetamide as the main pathway, as *S. violaceus* and *S. exfolitus* catabolized indole-3- acetamide (IAM), indole-3-lactic acid (ILA), indole- 3- ethanol (IEt) and indole-3-acetaldehyde(IAAld) into IAA, besides attainable presence of different pathways for IAA biosynthesis. Encapsulation of microbial cells for soil application provides a variety of benefits like application to the soil, reduced off-site drifting, and protection of cells from environmental stress [7,58]. Additionally, they possess high cell loading capability, high retention of cell viability, increased rate of production of microbial products and also act as a reservoir, which releases the bacteria at a slow and constant rate [62]. Actinomycetes are known to be durable organisms and thus appropriate for soil applications. The spores of most actinomycetes

Table 1
Some clinically important antibiotics from actinomycetes and their bio-control role.

S NO.	Antibiotic	Produced by	Activity	Reference
1	Lomofungin	*Streptomyces lomondensis*	Antifungal	[18]
2	Sclerothricin	*Streptomyces scleogranulatus*	Antifungal	[123]
3	Spoxamicin	*Streptosporangium oxazolinicum*	Antitrypanosomal	[124]
4	Avermectin	*S. avermitilis*	Antiparasitic	[125]
5	Antimycin	*Streptomyces lucitanusus*	Antifungal	[126]
6	Rosamicin	*Micromonospora rosaria*	Antibacterial	[127]
7	Validamycin	*Streptomyces hygroscopicus*	Antifugal	[128]
8	Azalomycin	*Streptomyces malaysiensis*	Antifungal	[129]
9	Roseoflavin	*Streptomyces davawensis*	Antibacterial	[130,131]
10	Rifamycin	*Micromonospora rifamycinica*	Antibacterial	[132,133]
11	Salinomycin	*Streptomyces albus*	Antiparasite	[134]

endure desiccation and show slightly higher resistance to dry or wet heat than vegetative cells. Actinomycetes will colonize dry soil owing to their filamentous nature and exist in soil for extended periods as resting arthrospores that germinate in the occasional presence of exogenous substrates. So far, the potential of filamentous actinomycetes in encapsulated state for the assembly of IAA has neither been completely examined nor used in field conditions to any noticeable extent. They additionally act indirectly, by affecting the activity of the indigenous soil microflora [110]. Typical environmental stresses faced by the organisms in the soil may include salinity, unfavourable soil pH, extremes in temperature, inadequate or excessive soil moisture, significant metal toxicity and biocides [65,68,97]. Indole acetic acid (IAA) is a plant growth regulator and active form of auxins. It plays an important role in plant development through its life cycle [81]. IAA stimulates the growth of the radicular system [59,60,101] thanks to the development of lateral roots and divisions of the apical meristem that derives in roots elongation [29,60]. This increases the access of soil nutrients to the plant [66]. IAA has proved to be the main one responsible for plant growth promotion over the nitrogen fixation related to diazotrophic bacteria activity [64]. The production of IAA has been widely studied in actinobacteria [17,23]. IAA can act as endogen regulator of spore germination of *Streptomyces atroolivacezlz* and can be involved in the differentiation of actinobacteria (Manulis et al., 1994). *Streptomyces* genus [17,23], *Frankia* sp. [85,96], *Nocardia* sp. [23,96], *Kitasatospora* sp. [95] have been widely studied as IAA producers.

4.10. Actinomycetes in biocorrosion

Corrosion is a prime reason of pipe failure and high preservation costs in gas pipelines [116]. Biocorrosion is defined as a caustic harm initiated by the direct or indirect activities of microorganisms [117]. A wide range of bacteria is present in most if not all areas of oil production and have been described from water injection plants, drilling mud, and live reservoir cores [24,61]. Primarily found in the Americas, leaf-cutter ants (including the genera *Atta* and *Acromyrmex*) maintain a delicately balanced net work that includes their fungal food source, *Leucoagaricus gongylophorus*, and actinomycetes, which produce antimicrobials to protect the fungal gardens against pathogen invasion [118–120]. Antimicrobial substance (AMS) formed by a Streptomycetes strain having its activity against an aerobic bacterium *B. pumilus*, and sulfate-reducing bacterium *D. alaskensis* known to be involved in biofilm formation and biocorrosion. *S. lunalinharesii* was previously recognized as producer of bioactive compounds against phytopathogenic bacteria and fungi. The antimicrobial activity has been seen over a broad range of pH, and after treatment with several chemicals and heat but not with Proteinase K and trypsin. The AMS, of proteic nature, has publicized to be promising for use in oil making plants, given its stability in the presence of several chemicals and solvents, and over a broad range of temperature and pH values.

4.11. Actinomycetes enzymes

Actinomycetes produce several enzymes (Fig. 1), degrading complex organic materials in soil or sediments such as protease, cellulases, amylase, gelatinase, lectinases, catalase, chitinase and ureases [39]. Amylases secreted to the exterior of the cells used to carry out extracellular digestion. Amylase starch degrading amylolytic enzymes is of great significance in biotechnological applications such as food industry, fermentation and textile to paper industries [83,142]. Actinomycetes are one of the known cellulose producers [2,43]. Lipase is produced from a variety of actinomycetes [54]. Lipases have broad applications in the detergent industries, foodstuff, oleochemical, diagnostic settings and also in industries of pharmaceutical fields [93]. Actinomycetes are of enormous importance since they possess a capacity to produce and secrete a variety of extracellular hydrolytic enzymes [90,107]. Many actinomycetes have been isolated from various natural sources, as well as in plant tissues and rhizospheric soil. Microbial alkaline proteases for manufacturing uses are produced mostly from *Streptomyces* and *Bacillus*. Actinomycetes, particularly *Streptomycetes* are known to secrete multiple proteases in culture medium [94]. Actinomycetes have been revealed to be an excellent resource for L-asparaginase. A range of actinomycetes, mainly those isolated from soils such as *Streptomycesgriseus, S. karnatakensis*, *S. albidoflavus* and *Nocardia* sp. have abilities to produce L-asparaginase enzyme [20,74,75]. L asparaginase has been generally used as a therapeutic agent in the cure of certain human cancers, mostly in acute lymphoblastic leukemia (Verma et al., 2007[112]). Keratin-degrading and antibiotic producing actinomycetes such as *Streptomyces, Saccharomonospora, Nocardioides, Nocardiopsis* and *Nonomuraea* have potentials in turning poultry farm feather waste by composting into odourless and complete biological degradation in pathogen-free biofertilizer. Actinomycete cellulases are inducible extracellular enzymes [41]that can be produced during their growth on cellulosic materials. Thus, introduction of cellulolytic microorganisms is a beneficial microbiological tool for recovery of bioenergy from degraded cellulose [5] and have gained significant attention due to their wide applicability in various industrial processes including pulp and paper, textile, laundry, biofuel production, food and feed industry, brewing and agriculture. *Streptomyces scabrisporus*, *Streptomyces sparsogenes*, *Streptomyces misakiensis*, *Streptomyces cirratus*, *Streptomyces lincolnensis*, *Streptomyces endophyticus*, *Streptomyces chartreusis*, and *Streptomyces alboniger* showed a broad spectrum of enzymatic activities and these isolates may serve as antibiotic and enzyme-producing microbes [136] (see Fig. 2).

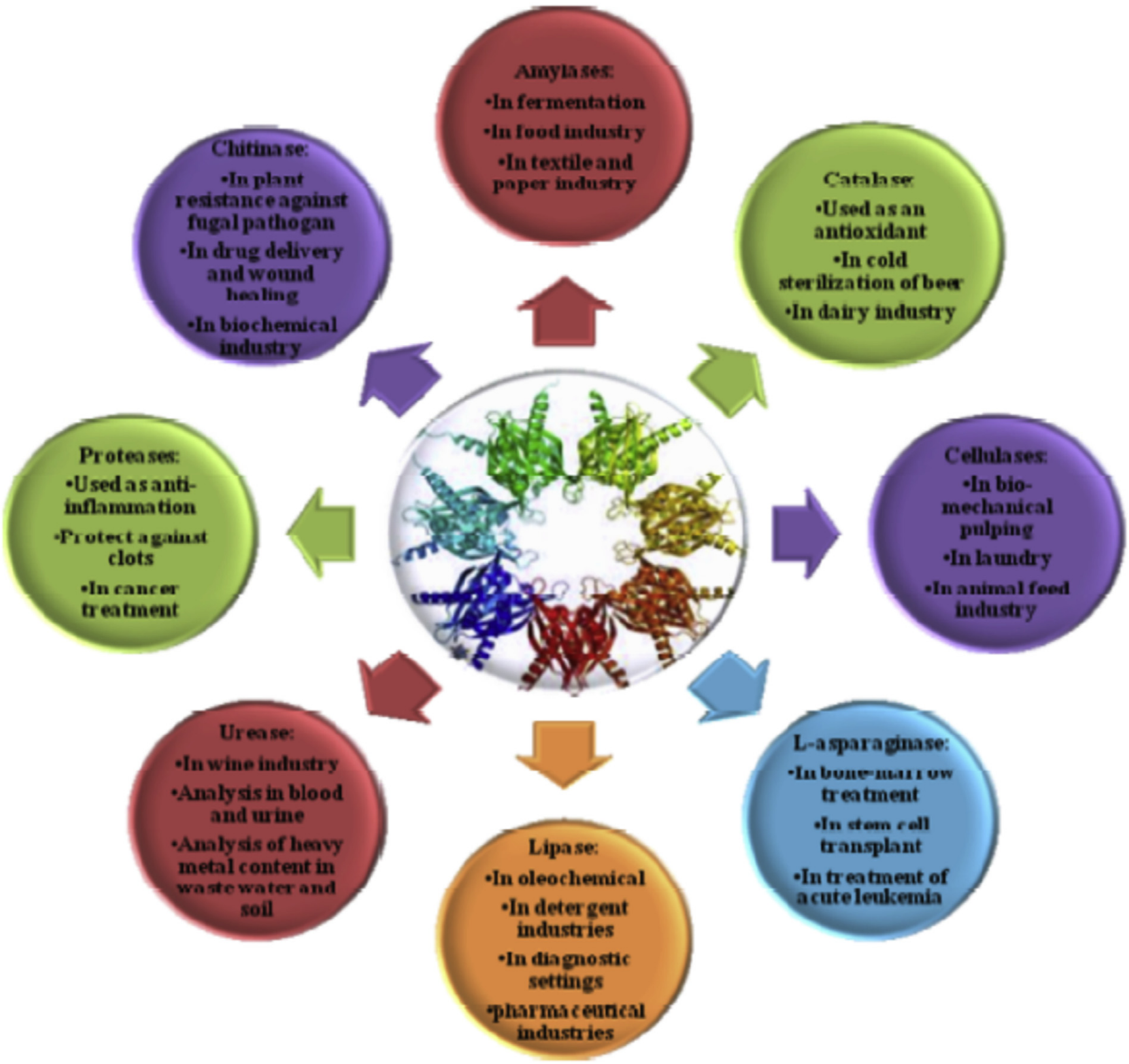

Fig. 2. Application of enzymes produced from actinomycetes [135].

5. Actinomycetes as agents of biodegradation/bioremediation

Actinomycetes are also responsible in pesticides degradation with various different chemical structures, including organochlorines, s-triazines, triazinones, carbamates, organophosphates, organophosphonates, acetanilides, and sulfonylureas [16,29,52,91]. Indigenous soil actinomycetes had been reported to degrade the herbicide Diuron in soil [16]. Diuron, a kind of phenylurea is widely used as weed biocontrol on non-crop areas and certainly on crops like cotton, pineapple, citrus and sugar-cane at low concentration. *In vitro,* by applying Diuron, the selected actinomycetes exhibited up to 37% level of herbicide degradation in seven days. Rubber-degrading actinomycetes are widespread in nature due to natural rubber degradation as sole carbon source is actinomycetes privilege [45]. Actinomycetes possess many properties that make them good contenders for application in bioremediation of soils contaminated with organic pollutants. They play an important role in the recycling of organic carbon and are able to degrade complex polymers [36]. *Streptomyces* play a very important role in degradation of hydrocarbons [6,86]. Many strains have the ability to solubilize lignin and degrade lignin-related compounds by producing cellulose- and hemicellulose-degrading enzymes and extracellular peroxidase [67]. Different strains of actinomycetes generally produce different compounds that help in increasing isolation and screening of new strains to discover new compounds [122]. In some contaminated sites Actinomycetes represent the dominant group among the degraders [49]. These species have the capability to live in an oily environment. So these microorganisms can be applied in bioremediation to deduct oil pollutants. Around 23,000 bioactive secondary metabolites produced by microorganisms have been reported and over 10,000 of these compounds are produced by actinomycetes. Several pharmaceutical companies used microbial natural products as one of the major source of novel drugs.

6. Phosphate solubilization

Organic phosphate is mineralized by the phosphatase enzyme, which is excreted by some microorganisms, and is released [31,53]. Actinobacteria related to genus *Saccharopolyspora, Thermobifida* and *Thermonospora*. Actinobacteria from the genus

Micromonospora sp., *Nocardia* sp., *Actinomadura* , sp.*Rhodococcus* , sp.*Actinoplanes* , sp.*Microbispora* sp. and *Streptosporangium* sp. produce phosphatase enzymes which have been classified according to their alkaline or acid activity, depending on reaction conditions [8].

6.1. Antagonistic activity against phytopathogenic fungi

Antagonism is defined as a mechanism of action based primarily on the direct inhibitory activity between two microorganisms [77] that have opposite actions within the same system. Actinobacteria that belong to *Streptomyces* genus have been commercially used to control plant damages. This genus has demonstrated antagonistic activity against *Alternaria* sp., *Pythium aphanidermatum, Colletotrichum higginsianum, Acremonium lactucum*, and *Fusarium oxysporum* [40,56].

6.2. Mycorrhiza helper bacteria

The ability of certain microorganisms to influence the formation and functioning of the symbiosis MA through various kinds of activities, such as activation in fungal propagules infective presymbiotic stages [3,32], facilitate formation of inputs point into the root [4,113] and increase the growth rate [11,73]. *Streptomyces* cause a stimulation of spores germination of the fungus MA, while *Thermobifida* reduces significantly the germination of spores. *Streptomyces* and *Thermobifida* improve the growth of the mycelium of *Glomus* sp. [69]. Actinobacteria such as *Streptomyces orientalis* have a beneficial effect on spores of *Gigaspora margarita.* The amount of volatile compounds produced has good correlation with the germination of MA spores. Moreover, some mycorrhizosphere bacteria were capable of promoting the MA settle. This improves germination of spores [73].

7. Conclusion

Actinomycetes form associations with some non-leguminous plants and fix N, which is then available to both the host and other plants in the near vicinity. These are the main group of soil microorganisms that play a major role in recycling of organic matters in environment by production of hydrolytic enzymes. These improve the availability of nutrients and minerals, synthesized plant growth regulators, and specially, they are capable of inhibiting phytopathogens. They perform the functions like phosphate solubilization, siderophores production, and nitrogen fixation. Furthermore, actinomycetes do not contaminate the environment; instead, they help to maintain the biotic equilibrium of soil by cooperating with nutrients cycling. Actinomycetes are also responsible in pesticides degradation with various different chemical structures, including organochlorines, s-triazines, triazinones, carbamates, organophosphates, organophosphonates, acetanilides, and sulfonylureas. Actinomycetes possess many properties that make them good contenders for application in bioremediation of soils contaminated with organic pollutants. They play an important role in the recycling of organic carbon and are able to degrade complex polymers.

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