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Chapter 14

Actinomycetes in Environmental Applications

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Abstract

The presence of soil actinomycetes induces plant health by persuading plant growth and development by producing phytohormones. Endophytic actinobacteria such as Actinoplanes, Micromonospora, and Nocardiopsis are the major producers of important phytohormones like indole-3-pyruvic acid (IPYA) and indole-3-acetic acid, whose main function lies in controlling gene regulation and in coordinating cell growth. Describing the microbially produced phytohormone is extremely difficult compared to the phytohormones produced by the host organisms. However, in vitro produced compounds by root colonizing actinobacteria dictate which microorganism is suitable to maintain plant health. Soil actinomycetes, especially Streptomyces, usually enhance the nutrient absorption capabilities of plants along with the growth of rhizobia provided with the soil nutrients. Composting with biomass enzymatic hydrolysis may help to alter the physicochemical and biological properties of the soil's nature. This compost can be easily prepared using consortia of microorganisms, and the process involves rapid mixing of different groups of organisms, especially bacteria belonging to actinomycetes. Other unique environments where actinobacteria occur include fungus-farming ants, beewolf wasps offspring protection, and bioweathering of rock minerals. The examples presented illustrate how diverse actinobacteria can occur in different environments. Genetic methods have also revealed that only a small fraction of these actinbacterial functions are known.

Keywords Environmental applications · Composting · Gene regulation · Root colonization · Indole acetic acid

14.1 Introduction (Theory of Composting, Wastewater, and Enzymes)

The aerobic waste treatment called composting supports the organic material modification towards a fertilizer that improves the biological, physical, and chemical properties of the soil. It is the usual process that could be bioaugmented for enhancement using the consortia of microorganisms with biological activity e.g. from old compost (Barthod et al. 2018; Velasco et al. 2004; Sulochana et al. 2014a, b; Yaradoddi et al. 2020a, b; Yaradoddi and Sulochana 2020). This process contains a quick succession of the mixed group of microbial populations. With respect to the dominant processes, the foremost important community of microorganisms majorly belong to bacteria, including actinobacteria, and also fungi (Ryckeboer et al. 2003; Partanen et al. 2010; Yu et al. 2007; Jayachandra et al. 2012a, b; Mohan Reddy et al. 2015a, b; Yaradoddi et al. 2018). The process of composting is generally divided into three or four different phases. In the beginning mesophilic phase, simple organic molecules, such as proteins and carbohydrates, are degraded that results in the decrease in pH due to organic acid production along with the increase of temperature. Thermophilic or thermotolerant organisms are dominated during the middle thermophilic phase through the production of enzymes that are involved in the degradation of complex organic biopolymers, leading to an increase in temperature. The ultimate phase of the composting process could be characterized by analyzing the growth of actinobacteria and also fungal cultures that degrade the majority of composite organic material in higher pH and decreasing temperature conditions. This third stage can also be divided into two different stages, the cooling phase and the maturation phase (Atchley and Clark 1979; Reyes-Torres et al. 2018; Sundberg et al. 2013; Wei et al. 2017).

The raw materials utilized in composting contain lignocellulosic biomass. These lignocellulosic biomasses mainly consist of hemicellulose (15–35%), cellulose (35–50%), and lignin (10–35%) (Karimi 2015). All these three fractions are very closely connected among each other. The composting process proceeds by disintegrating the three constituents with the help of degradative enzymes. A group of enzymes that are essential during the process belong to cellulases, xylanases, and laccases. The hemicellulose constituent holds the cellulose fibers together, whereas the xylanase enzyme acts upon the xylan; and the enzyme laccase eliminates reinforced material through the lignin disintegration process. As soon as hemicellulose and lignin get eliminated, the cellulosic fibers are readily available for the cellulase enzyme and, therefore, degradation of the lignocellulose constituents proceeds throughout the composting. All these enzymes can act in an associated manner as well as in sequence to yield matured compost. The fertilizer formed serves as a dual application, on the one hand, as a product in solid waste management and, on the other hand, as a fertilizer in the modification of soil properties (Ma et al. 2020; Reyes-Torres et al. 2018; Tuomela et al. 2000; Yu et al. 2007).

Composting as the bioremediation method is also the most emerging research field due to the increased amount of hazardous materials disposed to the environment. Because of several serious issues raised by accumulations of waste, released by industries, a number of nations around the world have adapted limits for the amount of unprocessed fluids being disposed to lakes, rivers, and oceans. Numerous remedial methods have been published, which, however, have been inadequately implemented due to their costs. The biological as well as physiochemical actions were considered to reduce the working capital and increase operational expenses. The biotechnology-based process aimed at reducing the release of toxicants into the environment may be promising in finding inexpensive solutions with respect to thermal issues, increased COD/BOD, or other environmental concerns in the future (Imam et al. 2021; Sayara and Sánchez 2020; Aguelmous et al. 2019; Ventorino et al. 2019).

In addition to municipal wastewater, the major risks exhibited by water bodies are currently formed by the paper and pulp industries. This hazard is directly correlated to the dark-colored effluents (either black or brown), which is the principal outcome of the important stages among the production process, specifically bleaching, pulping, and paper manufacturing. The dark color of fluid

waste hinders the light entering into the water system, which lowers the respiration process and the photosynthesis. Discharge from the paper and pulp industries has direct as well as indirect harmful effects on the environment, and they are also threat to human beings. The passage of such polluted water through drinking or cooking may be headed for enhanced chances of getting hazardous diseases. An additional path of imparting major damage to health can be seen by consuming the fishes thriving within such contaminated environments (Kumar et al. 2021; Haq et al. 2020; Viswanath et al. 2014).

Among the enzymes used for the composting process, the laccase enzyme has a huge potential in the bioremediation process; however, it is yet limitedly explored. Laccase is a multicopper enzyme that belongs to a group of blue oxidases. This enzyme can be designated as oxidoreductases as described by Enzyme Commission (EC). The laccase enzyme catalyzes the monoelectronic oxidation of a comprehensive variety of substrates. These substrates consist of polyphenols, ortho- and paradiphenols, aromatic or aliphatic amines, and aminophenols. The oxidation of the substrates is associated with the four-electron reduction in HO and O. Laccase enzymes are recognized for their capacity to counteract phenolic constituents in lignin, and other common dangerous constituents in effluent PAH (polycyclic aromatic hydrocarbons). Consequently, the laccase enzyme also plays a vital function during the bioremediation process mediated by actinobacteria; bacteria that are generally growing in the form of filaments are filled along with enzymes that are essential for the composting process as well as bioremediation. The filaments produced by the actinobacteria mediate the penetration and also distribution throughout machinery of the organism during their growth, that leads to effective disintegration of these substrate materials. Besides the above, the complex carbohydrates of the compost can stimulate the microbes to discharge extracellular enzymes that degrade the hemicellulose, cellulose, and lignin (Kumar et al. 2021; Haq et al. 2020; Viswanath et al. 2014).

14.2 Actinomycetes and Biomass Hydrolyzing Enzymes

The sediment samples were used in the isolation of actinomycete strains by a very typical method, which is described below. The sampling sites were divided into various categories: mangroves, marine, compost, water spring, lakes sediments, rivers, and soil. The sample collection was carried out by using the sterile spatula, and later these samples were stored in sterilized clean bottles with caps. The sample was treated through an air-drying process for about 48 h, homogenization using pestle and mortar, and it was further sieved. Subsequently, treated samples were properly diluted using saline except for mangrove and marine samples, which were usually diluted using a 1:2 dilution in seawater. Actinobacteria recovering agar at about pH 8 was prepared for isolating the actinobacteria using the sediments. Antibiotics such as streptomycin 100μg/mL and cycloheximide 50μg/mL were added to the media. The inoculated Petri plates were incubated at about 40 °C temperature and further observed for the growth. This incubation time varied between 1 and 3 weeks. The colonies of actinobacteria were recognized based on their phenotypic features using a microscope. The isolation media pH of about 8 and incubation temperature of about 40 °C were maintained in order to obtain a specific class of actinobacterial strains isolated. At this temperature and pH, thermophiles and alkaliphiles normally thrive well. ISP4 medium (International Streptomyces Project medium 4) was utilized for culturing the spore suspension. Spores of about 10^5 spores/mL in saline were prepared for inocula (Limaye et al. 2017).

Isolated cultures can be further screened for cellulase, laccase as well as xylanase activities. During the process, cellulases, laccases, and xylanases producing cultures can be identified and classified, and further explored for their potential other hydrolytic activities. The enzyme production medium of pH about 8 at 40 °C can be maintained to confirm that synthesized enzymes exhibited the alkalitolerant and thermotolerant abilities.

Several different plate assay methods are available for measuring xylanase activity, of which the easy-to-use wheat bran agar method is persented here (Limaye et al. 2017; Nagar et al. 2012; Meddeb-Mouelhi et al. 2014). Qualitative plate assay is involved in the analysis of xylanase activity, and the media used for the test should contain wheat bran agar. The wheat bran agar contains (in g/L) wheat bran, 20; beef extract, 3; peptone, 5; and agar, 20, and about 10 µL spore suspension (105 spores/mL) is added on the media. The medium is incubated for 5 days at 40 °C, and then agar surface is sealed by 1% of Congo red for about 15 min. The overload of Congo red solution is poured off, and the Petri plates are covered by 1 M NaCl for 1 h. The zone of hydrolysis shows the xylanase activity. Further, the microbial strains with the xylanase activity are selected on the basis of the zone produced by them. Typical colonies of xylanase producing *Streptomyces* sp. are shown in Fig. 14.1.

Several different methods are available for screening cellulase-producing microorganisms, one of which is exemplified herein (Kasana et al. 2008; Shanmugapriya et al. 2012; Rasul et al. 2015; Limaye et al. 2017). In analyzing the cellulolytic activity, CMC (carboxy-methyl cellulose) agar medium can be used, which contains (in g/L): CMC, 5; K_2HPO_4, 1; $NaNO_3$, 1; glucose, 1; $MgSO_4$, 0.5; KCl, 1; yeast extract, 0.5; and agar, 20. To the medium, 10 µL (10^5 spores/mL) spore culture was used for inoculation. The inoculated medium was incubated for 5 days at 40 °C temperature; the agar surface was covered by 1% Congo red for about 15 min. The extra solution was removed, and the Petri plates were flooded with 1 M NaCl, kept for 1 h. The hydrolysis zone shows the cellulase enzyme activity. The bacterial cultures with the cellulase activity were selected based on the extent of the zone of clearance.

Various phenolic an non-phenolic compounds have been used to screen laccase enzyme activity, guaiacol being one of the most commonly used substrate in the isolation of actinobacteria, among others (Limaye et al. 2017; Unuofin et al. 2019; Kiiskinen 2004). The qualitative laccase plate assay can be performed using the basal agar medium with the addition of a trace element solution, including 0.01% of guaiacol. The basal agar medium usually consists of (in g/L): $(NH_4)_2SO_4$, 2; KH_2PO_4, 0.5; K_2HPO_4, 1; yeast extract, 1; asparagine, 0.2; maltose, 200 mM; $MgSO_4$, 0.2; and agar, 20. The asparagine amino acid shall be added as a source of nitrogen, and 0.01% guaiacol in ethyl alcohol is added before autoclave, and the sterile trace element containing solution 0.1% v/v can be added to the basal agar after the autoclaving process.

The trace solution composition consists of (in g/L): $ZnSO_4 \cdot 7H_2O$, 0.3; $CuSO_4 \cdot 7H_2O$, 0.025; $MgSO_4 \cdot 7H_2O$, 2.5; $MnCl_2 \cdot 5H_2O$, 0.2; $FeSO_4 \cdot 7H_2O$, 0.25; $COCl_2 \cdot 6H_2O$, 0.05; and $CaCl_2 \cdot 2H_2O$, 1.5, and this solution should be sterilized individually through the autoclaving process. Later on, 10 µL (10^5 spores/mL) of spore suspension can be added on the media, followed by incubation for about 5 days at 40 °C temperature. The positive strains for laccase enzyme are shown by the appearance of a reddish-brown halo around the colonies in the presence of guaiacol in the medium (Limaye et al. 2017).

14.3 Composting Process for Plant Biomass and Forest Industry Effluent

In general, the composting of organic waste, for example source-separated household biowaste, proceeds without any specific additives; only a bulking agent (e.g. wood chips) and proper aeration are required to maintain compost aerobic. Old compost can act as an inoculum (Rainisalo et al. 2011). However, the inoculum can be used in specific applications, such as in the decomposition of organic waste from paper and pulp industry, or in remediation of contaminated material. In the following example by Limaye et al. (2017), eight actinobacterial strains were selected toward the development of compost for enhanced degradation of organic waste from plant material, followed by the composting of effluent from paper and pulp industry.

The selected eight actinobacterial isolates were allowed to grow at a temperature of 40 °C, for about 96 h on ISP medium no. 4 to yield microbial spores. The spore suspension was cultivated for each strain using saline, and 0.01% Tween 80.

The viable counts of spore suspensions were adjusted at 10^9 spores/mL using cultivation on plate count agar. The combined spore suspension was prepared by adding 100 mL of spore suspension of individual strains.

In developing composting, a unit containing dimensions of 35 cm×25 cm×40 cm (length × width × height) was used. About 300 g of organic fruit and vegetable waste was added to individual composter unit. Fifty grams of dehydrated banana peels were poured into the unit, which improves the oxygen supply and circumvents raw material tamping. Three hundred milliliters of spore consortium mixture was added to the composter, and all supplements were mixed thoroughly into a uniform mixture. The negative control of the uninoculated compost was amended 300 mL of saline.

Composting units was kept under the shade. The compost was maintained for about 25 days, and composting could be extended for a longer period. The moisture/available water level was controlled by adding 20 mL water to the heap daily. Furthermore, the compost bin was mixed weekly to confirm the aerobic conditions. After 25 days, the physical and chemical properties of compost were within the desired range.

There are several standard norms laid by the National Centre of Organic Farming (NCOF), Department of Agriculture, Government of India to be followed for the systematic study.

14.3.1 Composting Plant Material

The parameters include (1) moisture, (2) pH, (3) C:N ratio, (4) total nitrogen, (5) organic carbon, and (6) conductivity. In addition, temperature monitoring allows the evaluation of the stage of composting. In the European Union, legislation related to composting is included in the health rules for animal by-products not intended for human consumption, and rules on the making available on the market fertilizing products. A composting plant must be equipped with a closed composting reactor with temperature control without bypass possibility. The maximum particle size of compost is 12 mm and the minimum temperature of compost material is 70 °C for 60 min. Other standardized process parameters are permitted, when the applicant ensures that biological risks are minimized (European Parliament and Council 2009, 2019 and references therein).

As presented above, the potential actinobacterial strains were selected based on enzyme production capacity for the treatment of paper and pulp industry effluent. The selected microbial strains were allowed to grow on nutrient agar (pH about 7.5) in 10% paper and pulp mill effluent supplemented prior to sterilization. This ensures the capacity of strains to grow under rich environments. Especially the paper and pulp effluents can be treated through laccase synthesizing strains of actinobacteria, the specific inoculum being called strain R.

An effluent sample from paper and pulp industries was autoclaved at the beginning of the investigation, and diluted in the ratio of 1:2 using sterilized distilled water. The nitrogen source of 0.1% peptone and carbon source of 0.1% dextrose were supplemented, and the pH was adjuted to 7.5 using sodium hydroxide. To prepare the spore suspension of Streptomyces strain R, saline and 0.01% of Tween 80 were mixed with the spores scrapped from sporulation ISP4 agar medium. Five percent of the spore suspension having density of 105 spores/mL was utilized as the inoculum. The inoculated mixture was continuously aerated using an air pump, and incubated at room temperature. Optical density, chemical oxygen demand, and the degradation of effluent compounds were followed on days 0, 7, and 14. The results showed that the phenolic compounds were cleaved, and various degradation products were formed. The actinobacteria could have potential in the hazardous waste treatment.

14.4 Actinobacterial in Air and Soil

14.4.1 Airborne Actinobacteria

Actinobacterial spores are understood to be significant air contaminants under professional environments, for example, in biowaste composting facilities and agriculture (Nielsen et al. 1997; Lacey and Crook 1988). They have been found to be indicators of mold growth and indoor air problems in buildings. Actinobacteria do not belong to the usual indoor air microbial populations; however, they have been observed in buildings, which suffer from mold and water damage problems (Nevalainen et al. 1991; Suutari et al. 2002; Samson et al. 1994). In particular, *Streptomyces griseus*, *Streptomyces albidoflavus*, and *Streptomyces coelicolor* have been detected in water-damaged buildings, and a real-time PCR test has been developed to detect then (Rintala et al. 2001; Suutari et al. 2002). The spores of numerous actinobacterial taxa, such as *Streptomyces albus*, *Thermoactinomyces vulgaris*, *Micropolyspora faeni*, and *Saccharomonospora viridis*, have been correlated with the occurrence of allergic alveolitis and other serious health illness (Lacey and Crook 1988; Lacey and Dutkiewichz 1976). Investigations have revealed that *Streptomyces* sp., and especially their spores, have the ability to induce lung macrophage reactions that can result in illnesses like tissue injury and inflammation (Hirvonen et al. 1997, 2001).

The spores of actinobacteria are generated via prevailing hyphae subdivision or swelling, or via endogenous spore production. Actinobacterial hyphae are subdivided into spores without or with sheath that are partially left under the spores even after disintegration (Williams et al. 1973). As a result, three major spore types are generated: Aleuriospores (sheathless hypha), arthrospores (sheathed hypha), and the endospores. These variabilities are likely to cause distinction among spore resilience and airborne characters (Williams et al. 1973). In the environment, actinobacterial spores can be converted to airborne by means of mechanical disturbances of the matter they are growing on, for instance, through operating the agricultural tools or by unveiling toward the blustery wind (Lloyd 1969). Laboratory investigations have been conducted using airborne actinobacterial spores, and the impact collection has been found to influence the recovery, injuries, and consequently the colony numbers (Stewart et al. 1995). Lacey and Dutkiewicz (1976) detected the actinobacterial spores in polluted hay by mechanical handling followed by Andersen sampler collection, while Madelin and Johnson (1992) detected these actinomycete spores in culture media through air currents. Due to their smaller size, actinobacterial spores are more difficult to aerosolize than fungal spores (Reponen et al. 1997).

The production of airborne actinomycete spores using general laboratory practices allows the measurement of spore aerodynamic and physical sizes, and the viability of actinobacterial spores. The aerodynamic spore size has been 1.28 μm for *Micromonospora halophytica* aleuriospores, 0.85 μm for *Streptomyces albus* arthrospores, and 0.57 μm for *Thermoactinomyces vulgaris* endospores with the largest size variation. As a result, the spore sizes were close to monodisperse. The physical sizes of the spores were 0.55×0.72 μm for *M. halophytica*, 0.68×0.84 μm for *S. albus*, and 0.66×0.79 μm for *T. vulgaris*. The variations among the spore sizes seem to be connected to the preparation methods for microscopic and aerosol observations. Water will be absorbed by the spores, resulting in extending their diameter. Consequently, the size measurements of dry spores seem to be more suitable for human health-associated studies (Madelin and Johnson 1992; Reponen et al. 1998).

Comparison of the viabilities of spores indicated that spores from *S. albus* had the maximum survival level of 35.3%, whereas that of *M. halophytica* spores was 7.4% and that of *T. vulgaris* spores was 4.6%. These differences seemed to be related to the spore wall structure. The spores of *S. albus* possess the protective outer sheath against physical injury and drying, which is lacking in the spores from *M. halophytica*. The spores from *T. vulgaris* have the dormant or inactive nature that require activation before their germination. In this study, the conventional heat activation was not possible due to the risk of agar melting, and the less effective cold activation at 20 °C for 24 h improved the

recovery of spores 10-fold. The collection of bacterial spores in the filter would enable heat activation (Reponen et al. 1998).

14.4.2 Actinobacteria in Acidic Soil

The words acidophilic and acid-tolerant actinobacteria can be seen in the literature from the end of the last century (Khan and Williams 1975). The research of that time has surprised with the opinion that almost all actinobacteria belong to neutrophilic taxa, with the optimal growth pH range of 6.5-8.0 (Kutzner 1986). However, the particular ecological characters of acidophilic actinobacteria and their influence toward the activity in the soil microbial communities are persisted as unexplored. The most continuously described acidophilic actinobacteria belonged to the genus *Streptomyces*, partly because they are abundant in nearly all soils (Zakalyukina et al. 2002, Kim et al. 2004). Previous reports (Nioh et al. 1995) have shown that within the actinobacteria populations under the acidic soil in tea culture, the acid-tolerant actinobacteria especially belonged to *Streptomycetes*, and to actinobacteria generally associated to *Glycomyces* and *Actinoplanes* genera. It has subsequently been observed that the growth pH ranges of *Streptomyces* spp. are not constant speciesspecific properties, but depend on environmental nutrients. *Streptomyces* spp. were able to growth over a wide pH range in the presence of high organic matter content but not under nutritionally restricted conditions.

Williams et al. (Khan and Williams 1975) isolated acidophilic actinobacteria from pine forests, soils, and mine wastes, i.e. microbes that cannot survive within the neutral medium. Further investigations have indicated that the numbers of acidophilic actinobacteria recovered from various soils can be little or larger based on the soil, or acidity. Within the soils of pine forests, the existence of acidophilic actinobacteria was about 80% of all the recovered actinobacteria, 63% in broadleaved coniferous forest soils, and 33% among the plowed soils (Kim et al. 2004). In later studies, the acidophilic actinobacteria were found to be widespread in acid soils, and an essential mycelial prokaryote component of the soil microbial communities in the soils of the main soil climatic zones, in the intrazonal alluvial soils, and in the anthropogenic substrates in Mongolia and Russia (Zenova et al. 2004, 2006).

Although actinobacteria are clearly widespread in soils, the measured actinobacterial numbers can vary greatly depending on the cultivation conditions. For example, the actinobacterial counts recovered from acid soils using acid cultivation medium exceeded the counts of mycelial prokaryotes isolated on neutral cultivation medium, a phenomenon not observed in chernozems and slightly alkaline soils (Zakalyukina et al. 2002; Selyanin et al. 2005). The dominant actinobacteria recovered on the acid medium belonged to the genera *Micromonospora* and *Streptomyces*, and the quantity of *Micromonospora* spp. isolates on the acid medium was significantly higher than on the neutral medium. The acidophility constant was calculated as actinobacterial counts on acid isolation medium (pH 5.3) divided by the counts on neutral medium (pH 7.0). As a result, among the soils studied, the actinobacteria recovered on the acidic and neutral media varied based on the counts of mycelial prokaryotes, and also concerning to their taxonomic composition. The results revealed that commonly used cultivation on a neutral medium may be a selective factor that distorts actual numbers and may limit the availability of unique isolates (Zakalyukina et al. 2002).

The pH of the cultivation medium also affected the numbers and diversity of the acid soil *Streptomycetes* isolates. However, unlike *Micromonospora* species, the numbers and taxonomic diversity of *Streptomyces* spp. declined in the acid medium in comparison with the neutral medium, when *Streptomycetes* were isolated from acid soils. The taxa of the imperfectus section turn out to dominate within the acidophilic streptomycete complex. In contrast, among the various soil types, taxa from different sections and series prevailed on neutral medium (Zakalyukina et al. 2002). In chernozems with humic substances and buffer capacity, the streptomycete complex tolerated better the acid medium conditions and the numeric and species diversity of the *Streptomycetes* was not

affected. The measured features, for example, the taxonomic arrangements and numbers of soil actinobacteria, and the effects of medium acidity are displaying the processes occurring in the soil. The practical evidence of this is the outcome realized in actinomycetes numbers during the microbial succession in peat soils after fire (Zenova et al. 2008).

The actinobacteria are one of the essential microbial groups in peat soils, and have particular characters discrete from those of mycelial bacteria within the zonal soils. This complex acts as an indicator of variations occurring within the microbial communities of the peatland subsequently to the exclusion of peat for fuel and fertilizer purposes, followed by reconditioning. Fires in peat soils may increase the biophilic element concentration in the burned surface layer, alter the acid-base balance, and modify the hydrothermal regime, followed by the development of particular phytocenoses simultaneously with the evolving actinobacterial succession. The ash consists of only calcium oxalate and calcium carbonate; and the carbon content will range from 0.68 to 0.71%, affecting actinobacterial composition (Zenova et al. 2008).

14.4.3 Actinobacteria in Saline Soil

The physiological adaptation to osmotic stress is of huge importance in the metabolic activities of microbes. Despite the involvement of microbial cells in metabolism, salinity supports the osmotic pressure continuing the dynamic activity of the organisms. The osmotic pressure within the actinobacterial cells is understood to be somewhat higher; it permits them to endure to be in soils within the moisture lagging and higher salt conditions.

Most actinobacterial isolates grow well in the medium having a salt concentration of about 4% (Tresner et al. 1968). The obligatory halophilic *Actinopolyspora halophila* gen. et sp. nov., with a minimum essential salt (NaCl) concentration of about 10% within the solid and 12% in the suspension medium, could be regarded as an extreme halophyte (Gochnauer et al. 1975). The presence of high counts of halotolerant actinobacteria in solonchaks proved the need for high salt tolerance in such extreme conditions (Selyanin et al. 2005). However, actinobacteria isolated from saline soils can vary in the intensity of halophilicity, and many of halophilic mycelial actinobacteria are denoted to rare genera, or they correspond to the novel taxon (Gochnauer et al. 1975). For example, *Microbispora coralline* actinobacteria that have an ability to grow in 3% NaCl under mesophilic conditions were recovered at saline soils (Nakajima et al. 1999). An unique actinobacterium *Actinopolymorpha singaporensis* gen. nov., sp. nov. (Nocardioidacease family) that can grow at 15% of NaCl concentration was recovered from the soil in the tropical forest of Singapore (Wang et al. 2001). Two novel species recovered from the alkaline soils in Korea, *Nocardioides lentus* sp. nov. and *Nocardioides debius* sp. nov., have the potential ability to grow at pH 8.0 in the presence of 0.5% of salts (NaCl) (Yoon et al. 2005, Yoon et al. 2006). The halophiles *Nocardiopsis xinjiagensis* sp. nov. and *Nocariopsis salina* sp. nov. were recovered from soil (Li et al. 2004), and the alkaliphile *Streptomyces sodiiphilus* sp. nov. was identified from the salt lake in China (Li et al. 2005). The novel *Salinispora* genus belonging to the family *Micromonosporaceae* denoted by novel species *Salinispora tropica* and *Salinispora arenicola* is among the group of marine actinobacteria based on investigating their phenotypic properties and genetic features (Maldonado et al. 2005). Saline soils are also often habitually alkaline, specifically, if their salinity is analyzed by the Ca^{2+}, CO_3^{2-}, and Na^{+}, ions. Consequently, the growth is not only limited to halophiles but also alkalophilic in such soils. The ability of the extent of alkalitolerant actinobacteria obtained from different locations is listed in Table 14.1.

14.4.4 Psychrotolerant Actinobacteria in Soil

The psychrotolerant microbes would prefer to grow under lower temperatures, which is associated with the higher specific growth rate (μ) than in mesophiles, the higher concentrations of the unsaturated fatty acids among the membrane lipids, and by means of particular protein conformation supporting low temperature adaptation. The psychrotolerant bacteria play a beneficial role in the organic matter breakdown in the cold terrestrial ecosystems. Bacteria in the cryogenic peatland of the tundra are adjusted to the growth and functioning at low temperatures and do not grow properly at high temperatures (Lipson and Schmidt 2004; Thormann et al. 2004).

The actinobacteria are common within the bacterial communities in the cryogenic soils. The psychrotolerant actinobacteria have been identified from a variety of different environments, including stony rocks, moraine, oceanic water and ice, soil, boreal groundwater, and animal fur. For example, the psychrotolerant actinobacteria of the genera *Micromonospora*, *Promicromonospora*, *Nocardia*, and *Streptomyces* were recovered from the alpine meadow habitats (Wang et al. 2004). The predominant species corresponded to the *streptomycetes* in the cold climate region soils in China (Xu et al. 1996). The species of *Actinosynnema* were detected in the field and forest soils of southeastern Tibet mountains (He et al. 2006). Furthermore, new species have also been described within the psychrophilic actinobacteria. The actinobacterial genus *Frigoribacterium* was recovered from animal shed (Kämpfer et al. 2000). *Pseudonocardia antarctica* sp. nov. was isolated from the Antarctic moraine (Prabahar 2004). The psychrophilic bacteria, *Subtercola frigorans* sp. nov. and *Subtercola boreus* gen. nov., sp. nov., were found the cold boreal groundwater (Männistö et al. 2000). The soil isolate, *Modestobacter multiseptatus* gen. nov., sp. nov. was described from the Antarctic mountains (Mevs et al. 2000).

The occurrence of psychrotolerant actinobacteria in the peat soils of the southern taiga and tundra has been investigated. As the summer temperature in the top layers and litter of such peat soils does not surpass the temperature of 8–10 °C, the conditions are advantageous for the growth and development of the psychrotolerant actinobacteria (Dobrovol'skaya et al. 2014, Zenova et al. 2012). As a result, psychrotolerant and psychrophilic actinobacteria recovered from the soils extended from thousands to several hundred thousands of colony-forming units, depending on the soil horizon layer and type. The numbers of psychrotolerant actinobacterial isolates recovered from the soils were similar to those of mesophilic species. The psychrotolerant actinobacterial counts were highest of hundred thousand in the marshland moss and litter layers, while their number decreased within the deeper deposits due to the shortage of oxygen. The actinobacteria of the genus *Streptomyces* were the most common species (Dobrovol'skaya et al. 2014, Zenova et al. 2012).

14.5 Environmental Actinobacteria in Unique Habitats and Applications

14.5.1 Actinobacterial Natural Products and Fungus-Farming Ants

Among the most widely characterized multiorganism ecosystems with actinobacteria are those associated with the leaf-cutter ants, mostly found in America. The biologically active components produced by actinomycetes regulate the fungal growing leaf-cutter ants, and have vital roles in determining the ecosystem interactions (Currie et al. 1999). The actinobacterial biomolecules are important in maintaining a balanced network especially between the leaf-cutter ants of the genera *Atta* and *Acromyrmex*, their fungal food source *Leucoagaricus gongylophorus*, and the fungal gardens against the attach of pathogens (Andersen et al. 2015). Disruption of this stability would result in the attack by the fungal pathogens of the genus *Escovopsis* ensuing the compact garden biomass and the ultimate demolition of total ant population (Currie et al. 2003). The natural products produced by the

symbiotic actinomycetes are utmost important in the protection of the wellbeing of the leafcutter ant populations by preventing *L. gongylophorus* from pathogenic infection.

Actinobacteria, which belong mainly to the genera *Pseudonocardia* and *Streptomyces*, are in direct connection with the cuticles of leaf-cutter ants. These actinobacteria synthesize a set of antifungal compounds such as candicidin, antimycins, nystatin, and dentigerumycin variations that inhibit Escovopsis and additional potential pathogens by leaving *L. gongylophorus* intact (Dângelo et al. 2016). An antifungal associated to dentigerumycin and known as gerumycins was produced by *Pseudonocardia* spp. related to ants *Trachymyrmex cornetzi* and *Apterostigma dentigerum* (Sit et al. 2015). As part of this complex ecological niche, actinobacteria that live in symbiosis with the leaf-cutter ant produce molecules that help to keep away closely related bacteria that can replace the inhabiting strain. The stronger this antagonism among the various species of ant-associated *Pseudonocardia* was, the greater the phylogenetic distance from the *Pseudonocardia* living in symbiosis with the leaf-cutter ant, suggesting that the differences originally developed from the same evolutionary origin. In fact, *Pseudonocardia* strain is involved in the synthesis of rebeccamycin analog, which inhibits the development of competing *Pseudonocardia* (Van Arnam et al. 2015).

14.5.2 Biomolecules Protecting Beewolf Wasps Offsprings

The streptomycete *Candidatus Streptomyces philanthi* lives in a symbiotic association within the antennal glands of the female beewolf digger wasps (*Philanthus* spp., *Hymenoptera, Crabronidae*) (Kaltenpoth et al. 2005). This bacterial symbiont is stored against the internal walls of the defensive burrows on which they lay eggs. The streptomycetes can be combined with silk while the larvae are spinning the cocoons, which remain fixed within the humid burrows. The streptomycetes protect cocoons by producing nine antimicrobial compounds to the outer surface to protect against the bacterial and fungal pathogens, which live in soil or are carried to the burrow by honeybees bringing food for the larvae.

Three of the important bioactive compounds in situ were piericidin A1, piericidin B1, and streptochlorin, which were uniformly distributed on the cocoon outer surface (Kroiss et al. 2010). The distribution of antimicrobials in higher concentrations outside than inside the cocoon suggests that the bioactive compounds protect from invasive pathogens present in outside environment. Four antimicrobials were inhibitory to the growth of ten soil microorganisms, including fungi M*etarhizium* and *Aspergillus*, which can cause an infection in the cocoons (Kroiss et al. 2010). *In situ* examination indicated that the insect related streptomycetes, and piericidin A1 and B1 were localized together (Kaltenpoth et al. 2016). The streptomycetes protect cocoons by producing nine antimicrobial compounds to the outer surface to protect the beewolf cocoons *in situ* from possible microbial infections, and ensure offspring viability. The unique system is prominent as it is one of the rare instances where the antimicrobials from actinobacteria have been imagined in situ. The chemical and genetic manipulation of the system could be one of the excellent opportunities to assess the direct effect of bioactive compounds produced by the actinobacteria at a natural environment in situ. It will be a challenge to predict what the likely impact of the actinomycetes antimicrobial compounds would be at the ecosystem level.

14.5.3 Specialized Metabolism in Rhizosphere

The remarkably high number of actinobacteria in the rhizosphere can have a huge impact on plant health, as soil actinobacteria synthesize various kinds of natural products that would bring about protection against the pathogenic microorganisms and supports plants in nutrient absorption (Harikrishnan et al. 2014, Hirsch and Mauchline 2012).

Streptomycetes colonizing plant roots are potential producers of antimicrobial compounds, such as 3-acetonylidene-7-prenylindolin-2one, antimycin A18, diastaphenazine, and staurosporine, the in situ investigations of which provide the observation of molecular interactions under natural rhizospheric conditions, as well as the development of plant health and disease resistance through their understanding (Li et al. 2015). Studies have revealed that rhizosphere actinobacteria have a huge impact on health and disease tolerance abilities. For instance, when the endophytic actinobacteria, *Micromonospora chalcea*, *Streptomyces spiralis*, or *Actinoplanes campanulatus* were inoculated alone or in a mixture to cucumber (*Cucumis sativus*), the adverse effects of the soilborne fungal phytopathogen *Pythium aphanidermatum* were attenuated, such as crown and root rot, and the plant was exclusively healthier (El-Tarabily et al. 2009). In another case, the prodiginines produced by *Streptomyces lividans* protected *Arabidopsis thaliana* in the root rhizosphere from the deleterious effects of the pathogen *Verticillium dahlia* fungi (Meschke et al. 2012). Similar results have also been obtained in other different plant systems, where by inoculating actinobacteria into the roots, the plant was protected from the invasion of harmful phytopathogens. Such examples of the ability of rhizosphere actinomycetes to produce metabolites and provide protection against antagonistic phytopathogens emphasis the importance of actinobacteria for plant welfare in primary production.

Soil actinobacteria are also recognized as plant health enhancers through synthesizing the plant phytohormones like IAA (indole-3-acetic acid) and IPYA (indole-3 pyruvic acid), which regulate essential functions while maintaining coordinated cell growth and gene regulation at least in wheat, lettuce, rye and tomato (Subramaniam et al. 2016). These metabolites have been particularly indicated to be produced by endophytic acinomycetes from the genera *Actinoplanes*, *Micromonospora*, and *Nocardiopsis* to promote health plant growth and development (Toumatia et al. 2016). The distinction of microbially and plant produced phytohormones is theoretically challenging, and must be done in in vitro experiments. Both actinobacteria and plants can also produce siderophores, which are important in iron uptake. The siderophores produced by actinobacteria in the rhizosphere or directly in the roots can help the plant to collect iron from the surrounding soil, and thus improve the efficiency of iron-related metabolism. Soil *Streptomyces* species can also promote the growth of critical symbiotic nitrogen fixing bacteria, such as *Rhizobiales,* and aid in root nutrient uptake, thus contributing to the overall efficiency of plants nutrient scavenging activity. The symbiotic *Rhizobiales* clade bacteria can stimulate the production of leguminous plant root nodules, where the bacteria fix atmospheric nitrogen to plants as a nutrient. The inoculation of *Streptomyces* sp. into chickpea plant enhanced nodulation as well as increased nodule size, resulting in an inclusive stimulating effect on plant nitrogen uptake rate (Gopalakrishnan et al. 2015). In general, nitrogen is a nutrient limiting plant growth, emphasing the importance of actinobacteria in the overall efficiently of nutrient uptake.

14.5.4 Plant Growth Promoting Activity

Actinobacteria in symbiosis with plants and rhizosphre bacteria protect against microbial plant pathogens and improve nutrient availability, as described above. Besides these, actinomycetes are also recognized for their insecticidal activities, thereby preventing plant pathogenesis, and improving plant growth. In addition to being involved in the binding of iron by siderophores, actinomycetes regulate the oxidation stage of iron, which is bioavailable to the plant growth in the reduced form of Fe^{2+}, whereas the oxidized form (Fe^{3+}) is common under alkaline soil conditions. The alkaliphilic actinomycetes can reduce the iron from Fe^{3+} to a soluble form of Fe^{2+} that is boavailable to the plant species and microbes (Francis et al. 2010; Valencia-Cantero et al. 2007). For example, *Kocuria rosea* HN01 can reduce Fe^{3+} to the soluble Fe^{2+} form, which is available for plants adapted to alkaline soils (Wu et al. 2014). In addition to iron, actinomycetes are also able to solubilize phosphorus under

alkaline circumstances, the solubility of which reduces in alkaline or acidic soils (Palaniyandi et al. 2013).

14.5.5 Oxido-reduction of Humic Substances

The oxido-reduction of humic substances has a great impact throughout the biotransformation of organic and inorganic pollutants. In humic acids, the quinone moieties act as centers for oxidation and reduction reactions that have a great impact throughout the anaerobic biotransformation of organic and inorganic pollutants. The oxidized humic acids accept electrons released from the organic pollutant mineralization, while the reduced humic acid is involved in biotransformation by reducing insoluble, oxidized pollutants to the soluble, reduced form. The reduced form of humic acid can also reduce the insoluble Fe^{3+} to the soluble Fe^{2+} form that is bioavailable for plant assimilation. *Corynebacterium humireducens* is an alkaliphilic actinobacterium known for its ability to biotransform humic acids into a reduced form, as well as the reduction of quinones to hydroquinones, which improve pollutant mineralization, like that of 2,4-dichlorophenoxy acetic acid (Wu et al. 2011; Wang et al. 2009).

14.5.6 Bioweathering

The process of bioweathering involves the microbially mediated fragmentation of the rock constituents into smaller fragments during decay, decomposition or erosion. These substances are additionally broken into a mobilized form of the elements (e.g., Na, K, Mg, Ca, Mn, Fe, Cu, Zn, Co, and Ni) and essential nutrients (e.g., P and S).

The microbial communities of especially actinobacteria and bacteria survive in the rocks under desiccation, radiation, and nutritional depletion conditions, and particularly the filamentous microorganisms can promote the bioweathering process through invading the rocks by producing mycelia. The *Streptomyces* species with the filamentous structure and anthrospore formation ability can grow under oligotrophic conditions in rocks, utilize recalcitrant organic materials, and release rock contituents for trasport to fields through water or wind. Other sites where actinobacteria have been associated with the bioweathering phenomenon include volcanic rocks, Mediterranean stones and monuments, and soil. *Knoellia*, *Rhodococcus, Arthrobacter, Kribbella*, and *Brevibacterium* species have been isolated from volcanic rocks in Iceland (Cockell et al. 2013). The species from the genera *Blastococcus, Modestobacter*, and *Geodermatophilus* (*Geodermatophilaceae* family) have been involved in the bioweathering of Mediterranean area stones and monuments (Urzì et al. 2001). Other actinomycete species associated with the acceleration of bioweathering are from the genera *Nocardioides*, *Kibdelosporangium* (Abdulla 2009), *Arthrobacter*, and *Leifsonia* (Frey et al. 2010). Besides these, alkalitolerant actinobacterial soil isolates from Nanjing (China), *Arthrobacter nanjingensis* A33T and *Isoptericola nanjingensis* H17T, have potential to carry out biowethering of rocks (Huang et al. 2015, Huang et al. 2012).

14.5.7 Gold Nanoparticle Synthesis

In the gold nanoparticle synthesis, Au3+ is reduced in incubation with gold chloride and microorganisms, either intracellularly of extracellularly (Beveridge and Murray 1980). The prokaryotes are preferred in the nanoparticle sythesis as they tolerate high metal concentrations in producing large quantities of nanopartilces. The synthesis of nanoparticles by actinomycetes has the extra advantage of polydispersity properties that prevents the self-aggregation. Of the actinobacteria

at least *Thermomonospora* sp. (Ahmad et al. 2003a) and alkali-resistant *Rhodococcus* sp. (Ahmad et al. 2003b) have been used in investigations on the gold nanoparticle synthesis. Nonetheless, prokaryotic bacteria and actinobacteria, as well as eukaryotic yeasts, fungi, and algae have all been explored for nanoparticle synthesis. The gold nanoparticles play a vital role in various applications for diagnostic, therapeutic, and catalytic applications. The exploration of actinobacteria is much required for considering their role in creating the sustainable environment (Ahmad et al. 2003b; Prabhu et al. 2015; Khieu et al. 2015; Manikprabhu et al. 2016; Wang et al. 2017).

14.6 Conclusion

In this chapter, environmental actinobacteria were examined in air and in different types of soils, including acidic, saline, and cold soils, as well as in the composting of plant biomass, forest industry waste, and hazardous material. Further, the importance of actinobacterial bioactive compounds in protecting fungus-farming ants, beewolf wasps offspring, and plants in rhizosphere was specifically examined. Actinobacteria with mycelial growth were found to be important in promoting plant growth by enabling nutrient availability, oxidation and reduction reactions of humic substances, dissolution of minerals in bioweathering, and synthesis of gold nanoparticles. Phylogenetic and metagenomic studies have revealed that there are a huge number of poorly characterized environmental actinobacteria with completely unknown sequences in their genomes, indicating that a huge number of completely untapped biological resources are still available. The environmental applications presented are only a small part of the broad potential functions that actinobacteria have as producers of various enzymes and biologically active compounds, as well as biological activity that is beneficial to other living organisms in the environment.

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Fig. 14.1 Potential xylanase enzyme-producing *Streptomyces* sp.

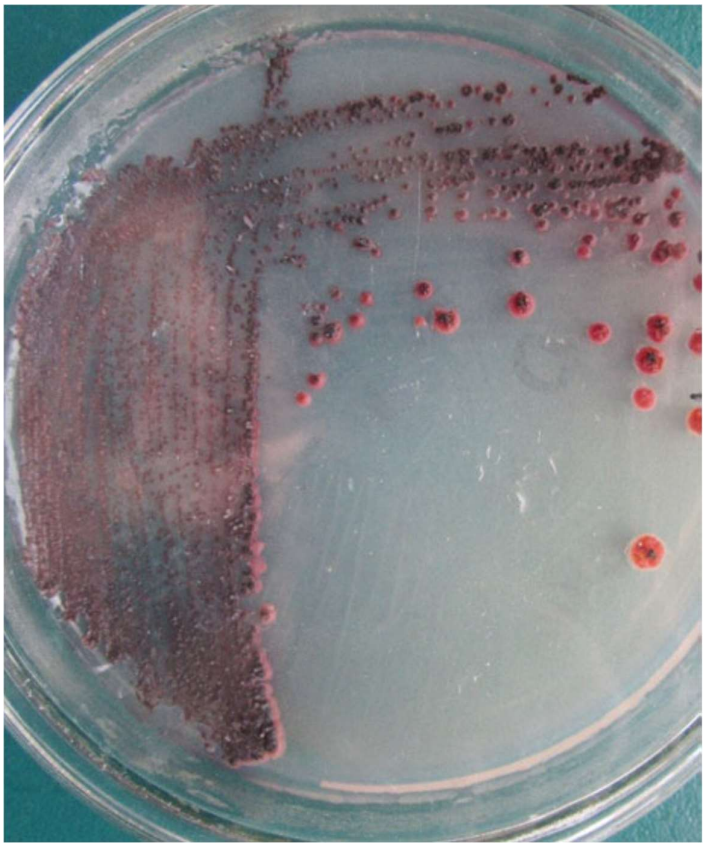

Table 14.1 Extent of alkalitolerance of actinobacteria

Name of the actinobacteria	Location	Extent of pH
Actinopolyspora mortivallis	Saharan soil	5.0–9.0
N. metallicus	Alkaline slag dump	7.0–10.5
N. metallicus	Germany, alkaline conditions of slag dump	8.5–10.5
N. alkaliphila	Desert soil in Egypt	9.5–10.0
Streptomyces sp.	Coastal region of Gujrat	11.0
S. altiplanensis	Sediments from Soda Lake	8.4–10.6
S. deccanensis	Karnataka Province, India	8.0–10.5