PEDOSPHERE（土壤圈英文版）

Pedosphere ISSN 1002-0160/CN 32-1315/P doi:10.1016/S1002-0160(21)60042-5

Running Title: ACTINOBACTERIA FOR SUSTAINABLE AGRICULTURE

Enhanced plant growth, nutrient acquisition, and crop protection by using Actinobacteria: advancements in soil, plant, and microbial multifactorial interactions

Debasis Mitra[1,†], Rittick Mondal[2,†], Bahman Khoshru[3,†], Ansuman Senapati[4], T. K. Radha[5], Bhaswatimayee Mahakur[6], Navendra Uniyal[7], Ei Mon Myo[8], Hanane Boutaj[9], Guerra Sierra B. E.[10], P. Panneerselvam[4,5], A. N. Ganeshamurthy[5], Snežana Anđelković[11], Tanja Vasić[11], Anju Rani[12], Subhadeep Dutta[2] and Pradeep K. Das Mohapatra[1,*]

[1]*Department of Microbiology, Raiganj University, Raiganj 733 134 Uttar Dinajpur, West Bengal (India)*
[2]*Department of Sericulture, Raiganj University, Raiganj, West Bengal 733 134 (India)*
[3]*Department of Soil Science, Faculty of Agriculture, University of Tabriz, Tabriz (Iran)*
[4]*Crop Production Division, ICAR - National Rice Research Institute, Cuttack, Odisha 753 006 (India)*
[5]*Division of Soil Science and Agricultural Chemistry, ICAR - Indian Institute of Horticultural Research, Bengaluru, Karnataka 560 089 (India)*
[6]*Department of Botany and Biotechnology, Ravenshaw University, Cuttack 753 003 Odisha (India)*
[7]*Genetics and Tree Propagation Division, Forest Research Institute, Dehradun, Uttarakhand, 248 003 (India)*
[8]*Biotechnology Research Department, Department of Research and Innovation, Ministry of Education, Kyaukse (Myanmar)*
[9]*Laboratory of Biotechnology and Molecular Bioengineering, Faculty of Sciences and Technology, Cadi Ayyad University, Marrakesh (Morocco)*
[10]*Facultad de Ciencias Exactas Naturales y Agropecuarias, GrupoMicrobiota, Universidad de Santander, UDES Campus Universitario Lagos del Cacique, Bucaramanga (Colombia)*
[11]*Institute for Forage Crops, Kruševac (Republic of Serbia)*
[12]*Department of Life Sciences, Graphic Era (Deemed to be University), Dehradun, Uttarakhand, 248 002 (India)*

[†]These authors contributed equally to this work.

ABSTRACT

Agricultural areas of land are deteriorating every day with population increase, rapid urbanization, and industrialization. To feed today's huge populations, more crop production is

---

[*]Corresponding author. E-mail: pkdmvu@gmail.com.

required from smaller areas, which triggers the continuous application of higher doses of inorganic fertilizers. These cause damage to soil health and therefore, nutrient imbalance conditions arise in arable soil. Under these conditions, the benefits of Actinobacteria as an alternative tool for replacing harmful chemicals with microbial inoculum and promoting eco-friendly sustainable farming practices have been possible through recent technological advances. They are multifunctional traits involved in the production of different types of bioactive compounds responsible for plant growth promotion and biocontrol of phytopathogens have reduced the use of chemical fertilizers and pesticides. There are some well-known groups of nitrogen-fixing Actinobacteria like *Frankia* which undergo mutualism with plants and offer enhanced symbiotic trade-offs. In addition, to nitrogen fixation, increasing availability of major plant nutrients in the soil by solubilization of immobilized forms of phosphorus and potassium compounds in soil, production of phytohormones like indole-3-acetic acid, indole-3-pyruvic acid, gibberellins, and cytokinins, improving organic matter decomposition by releasing cellulases, xylanase, glucanases, lipases and proteases, suppression of soil-borne pathogens by the production of siderophores, ammonia, hydrogen cyanide, and chitinase are some of those important features of Actinobacteria which have been found useful for combating biotic and abiotic stresses in plants. Thus the influence of Actinobacteria on improving soil fertility and plant health has motivated to compile those important findings associated with sustaining plant productivity in the long run.

Key Words: Actinobacteria, plant growth promoters, biocontrol agents, metabolites, sustainable agriculture.

Citation：Mitra D, Mondal R, Khoshru B, Senapati A, Radha T K, Mahakur B, Uniyal N, Myo E M, Boutaj H, Guerra Sierra B E, Panneerselvam P, Ganeshamurthy A N, Anđelković S, Vasić T, Rani A, Dutta S, Das Mohapatra P K. 2021. Enhanced plant growth, nutrient acquisition, and crop protection by using Actinobacteria: advancements in soil, plant, and microbial multifactorial interactions. *Pedosphere*. 2**???**(???): ???--???.

INTRODUCTION

With an increase in the world population, the demand for agricultural productivity is also increasing. To cope with rising food demand, there has been large-scale application of chemically synthesized pesticides and fertilizers to boost agricultural productivity (Zhang *et al.,* 2018). With advances in agricultural equipment and innovative methods of application, traditional methods have reached their limits of efficiency (Pivoto *et al.,* 2018). For HYVs (high yielding varieties), chemical fertilizers are often used conventionally in higher doses to increase productivity. These chemicals not only become accumulated in crop plants and seeds but also cause pollution of soil and water, including groundwater (Kumar *et al.,* 2007, Heidarpour *et al.,*, 2019). In this context, scientists have found several sustainable ways for switching to eco-friendly farming activities (Mishra, 2013, Khoshru *et al.,* 2020a). A number of studies have pointed out different ways to combat this problematic situation of chemical usage in agriculture. Among the solutions, microorganisms with multifunctional traits have been found to reduce the use of chemical fertilizers and pesticides, by producing or releasing different types of bioactive compounds (Janardhan *et al.,* 2014), enzymes (Verbon and Liberman, 2016; Turan *et al.,* 2016, Khoshru *et al.,*, 2020b), antimicrobial substances or biocontrol compounds (Dhanasekaran *et al.,* 2005; Liu *et al.,* 2018), and others are plant growth promoters (Pérez-Montaño *et al.,* 2014; Sarikhani *et al.,* 2016 and 2020; Tang *et al.,* 2016; Gange and Gadhave 2018; Khoshru *et al.,* 2020c). Considering this point, plant growth-promoting rhizobacteria (PGPR) are a good choice since rhizobacteria can demonstrate mutual relationships with plants and share nutrients; these findings have been critically supported by several studies (Tang et al. 2016; Zhang et al. 2016; Rosier et al. 2018; Raklami et al. 2019; Sarikhani et al. 2020; Khoshru et al. 2020a). PGPR are naturally occurring (Rosier *et al.,* 2018), free-living rhizosphere-colonizing bacteria that enhance plant yield, growth and soil fertility and decrease the percentages of pathogens as well as reducing biotic or abiotic stresses (Vessey, 2003; Kumar *et al.,* 2014; Sarikhani *et al.,* 2019; Khoshmanzar *et al.,* 2020). Actinobacteria are among these bacteria equipped with multifunctional plant growth promoting traits and many plant growth beneficial properties (El-Tarabily and Alkhajeh, 2016; Monteiro *et al.,* 2017) (Fig. 1).

Fig. 1 Beneficial impacts and interaction of Actinobacteria with plant and rhizosphere to imply the acquisition of nutrients, growth promotion and plant protection

Today's world requires high output yield and enhanced crop production as well as better soil fertility achieved in an ecofriendly way (Yasari *et al.,* 2009). Actinobacteria as bio-inoculants and bio-pesticides are an alternative to chemical fertilizers, and they can be used for improving crop production under multiple stress conditions such as temperature, pH, salinity and drought (Cheng *et al.,* 2018a). *Streptomyces* represent the most abundantly occurring Actinobacteria genus in the soil (Panneerselvam *et al.,* 2020). First of all, due to their higher growth rate, they achieve efficient colonization with plant root and can withstand adverse growth circumstances through the formation of spores. *Streptomyces* produce many enzymes and organic compounds that are beneficial to plant growth (Vonothini *et al.,* 2008; Syed *et al.,* 2009; Polak *et al.,* 1992). Soil Actinobacteria are known to produce active compounds in the rhizospheric area of plants, many of which are very important in agriculture (Suzuki *et al.,* 2000). Khan *et al.* (2010) reported that phosphorus could be implicated in an assortment of metabolic process of plant hosts, as energy transfer, photosynthesis, macromolecular biosynthesis, signal transduction and respiration. Phosphorus availability to hosts plants is facilitate through soil phosphorus cycle. Richardson and Simpson (2011) noted that Actinobacteria solubilize and mineralize directly inorganic phosphorus or mediate organic phosphorus availability through microorganism turnover and increase the root system. These Actinobacteria lower soil pH through section of different types of organic acids and thus facilitate the phosphorus availability to hosts plants (Kaur *et al.,* 2016). Among all microorganisms, Actinobacteria have also been reported as showing potential for solubilizing the insoluble organic and inorganic phosphorus compounds into simpler forms for the plants to absorb easily. Phosphorus improves plant yield by the establishment and development of the entire root system and consequently improving shoots (Khan *et al.,* 2010). Moreover, solubilization of phosphorus is a common process among microbes involving archaea, bacteria, and fungi. Sahu *et al.* (2007) demonstrated the phosphate-solubilizing potential of Actinobacteria in the estuarine environment. The positive influence of pure Actinobacterial strains on plants through multifunctional attributes such as rock phosphate solubilization has been briefly described by Hamdali *et al.,* (2008a, b). Several reports on plant growth-promoting Actinobacteria with a vast number of phosphate solubilizing microbes have been represented in a number of studies (Dastager *et al.,* 2010; Verma *et al.,* 2013; Singh *et al.,* 2014; Anwar *et al.,* 2016). According to Karlidag *et al.* (2007), plant growth promotion is also improved by K-solubilizing Actinobacteria. Similarly, Iron is a necessary co-factor for numerous enzymatic reactions for virtually all organisms and an essential nutrient. The Fe-chelating compounds producing microbes show both direct and indirect improvement of plant growth by beneficial Actinobacteria, including *Streptomyces*, *Micrococcus*, *Microbacterium*, *Kocuria*, *Corynebacterium* and *Arthrobacter* (Tiwari *et al.,* 2011). There are numerous reports of Actinobacteria involved in nitrogen fixation, such as members of the genus *Frankia*, which are widespread endophytic Actinobacteria symbiotically associated with plant roots and that fix atmospheric nitrogen for host plants. Symbiotic association with Actinobacteria lead legume crops undergo biological nitrogen fixation and meet their own needs without depending external sources. Actinobacteria strains have been proved to be effective in a multidimensional way. They are involved in numerous plant growth promoting activities such as siderophore production, IAA, complementing mycorrhizal fungi and maintaining the ecological balance in the soil system. The ability to produce phytohormones is extensively distributed among IAA-producing Actinobacteria and may potentially be employed to improve plant growth (Tomilova *et al.,* 2016; Sharma *et al.,* 2016). Merckx *et al.* (1987) and Khamna *et al.* (2010) reported that the involvement of Actinobacteria is crucial in plant growth promotion through siderophore as well as IAA production, which resulted in enhanced nutrient uptake. Moreover, metabolites produced by Actinobacteria restricted fungal phytopathogens like *C. gloeosporioides* (potato dry rot), *A. brassicicola* (rose apple anthracnose), *F. oxysporum* (chinese cabbage leaf spot), *S. rolfsii* (damping-off of balsam) and *P. digitatum* (orange green mold), exhibiting reduced disease symptoms. There is much evidence that proves Actinobacteria are potential bio-inoculants and biocontrol agents for plant growth improvement. All these special qualities of this group make them an inevitable tool in this current agricultural practices (Poovarasan *et al.,* 2016; Panneerselvam *et al.,* 2017; Panneerselvam *et al.,* 2020). Given all these special aspects, we concentrate on Actinobacteria as an alternative tool for sustainable farming practices and for reducing harmful chemical usage to promote eco-friendly sustainable agriculture, so that we can reduce some environmental damage and transform chemical farming into organic farming. This review has been focused on the interaction and current situation of Actinobacteria related to plant growth development, secondary metabolite production, biocontrol activity and soil nutrient management for sustaining agricultural productivity.

TAXONOMY, PHYSIOLOGY AND MULTIFUNCTIONAL ACTINOBACTERIA IN SUSTAINABLE AGRICULTURE

The term “Actinobacteria, formerly known as Actinomycetes” was derived from the Greek term *aktis* or *aktin*, representing ‘Ray Fungi’ (Wiliams, 1990). These bacteria are Gram positive, aerobic, spore-forming with a high percentage of guanine (G) and cytosine (C) in their DNA (>55mol %) (Krogius-Kurikka *et al.,* 2009). Members of Actinomycetales are commonly referred to as Actinobacteria (Goodfellow, 2012). Actinobacteria possess both bacterial (cell wall shows peptidoglycan structure) and fungal properties (filamentous appendages). The Actinobacteria phylum is the largest in bacteria classified into 6 classes; namely, *Coriobacteriia, Actinobacteria, Thermoleophilia, Rubrobacteria, Acidimicrobiia* and *Nitriliruptoria* (Goodfellow, 2012). Actinobacteria are categorized with bacteria in the same class as *Schizomycetes* in the strict taxonomic context, but limited to the *Actinomycetales* order (Goodfellow, 2012). The class Actinobacteria is further divided into sixteen orders, which are *Actinopolysporales, Glycomycetales, Actinomycetales, Jiangellales, Streptosporangiales, Micrococcales, Bifidobacteriales, Catenulisporales, Frankiales, Kineosporiales, Micromonosporales, Pseudonocardiales, Propionibacteriales, Streptomycetales, Corynebacteriales* and *Incertae sedis* (Zhi *et al.,* 2009; Goodfellow, 2012). With the recent development of new sequencing technology has allowed a better grading of higher taxa unknown to the vast majority of researchers and has introduced new methods to rebuild phylogeny reconstruction.

Further Nouioui *et al.* (2018) reported twenty orders of Actinobacteria *viz. Actinomycetales, Acidothermales, Micrococcales, Corynebacteriales, Bifidobacteriales, Micromonosporales, Pseudonocardiales, Cryptosporangiales, Sporichthyales, Nitriliruptorales, Streptosporangiales, Catenulisporales, Frankiales, Geodermatophilales, Glycomycetales, Propionibacteriales, Jiangellales, Kineosporiales, Nakamurellales,* and *Streptomycetales* based on the whole-genome sequences in the latest re-classification. Different types of soil Actinobacteria e.g. *Streptomyces, Actinoplanes, Nocardia, micromonospora,* and *Streptosporangium* have been extensively used to enhance the properties of soil and found to increase crop yield (Wahyudi *et al.,* 2019), among which the members of *Streptomyces* sp. have been found to play major role due to higher production of different plant beneficial enzymes and metabolites (Kekuda *et al.,* 2014). Actinobacteria can promote and protect the plant growth by using various enzymes such as cellulose, protease, pectin, α-amylase, xylanase, lipase, chitinase and lignin (Nascimento *et al.,* 2002; Vonothini *et al.,* 2008; Syed *et al.,* 2009; Sreevidya *et al.,* 2016; Zang *et al.,* 2018; Siddharth and Rai, 2019; Sharma and Thakur, 2020), siderophore production (Lee *et al.,* 2012), nitrogen (N) fixation (Prakash and Cummings, 1988), phosphate solubilization (Farhat *et al.,* 2015; Anwar *et al.,* 2016), indole-3-acetic acid (IAA-$C_{10}H_9NO_2$) production (Myo *et al.,* 2019), and plant growth regulators like hormones (Passari *et al.,* 2016). Actinobacteria play an important role in management of phytopathogens by suppressing the growth of several types of plant pathogens e.g. *Fusarium* sp., *Pythium* sp., *Alternaria* sp., *Botrytis* sp., *Rhizoctonia* sp., *Helminthosporium* sp., *Phytophthora* sp., *Phanerochaete* sp., *Aspergillus* sp., *Oidium* sp., *Curvularia* sp., *Sclerotium* sp., *Colletotrichum* sp., and *Pyricularia* sp. by secreting antimicrobial products (Lu *et al.,* 2008; Prapagdee *et al.,* 2008; Hamadali *et al.,* 2008; Gopalakrishnan *et al.,* 2013; Goudjal *et al.,* 2014; Sreevidya *et al.,* 2016). Actinobacteria has a major role in the decomposition of organic materials through which the nutrient recycling process in soil get fastened by virtue of lignocellulotic enzymes released by this group of bacteria (Das *et al.,* 2007). Actinobacteria can adapt more easily to harsh environments than other microorganisms. They can grow in alkaline as well as acidic soil and keep the soil properties in balanced conditions (Phoebe *et al.,* 2001; Trenozhnikova and Azizan, 2018). Hence, to establish sustainable agriculture Actinobacteria are an excellent choice because they can show dual nature, both promoting plant growth and presenting effective biocontrol activity (Coombs *et al.,* 2004; Meguro *et al.,* 2006).

Further insights into the studies conducted on structural community of Actinobacteria in soil using next generation sequencing of 16S amplicons from soil DNA have found a total abundance of 16.68 ± 5.93% Actinobacteria in rice rhizosphere soil (Imchen *et al.,* 2019). Related studies have also found the population of Actinobacteria was 45% higher in rhizosphere as compared to non-rhizospheric soil (Jang *et al.,* 2019). DNA-SIP techniques have found application of biochar to have beneficiary impact on increasing the population of Actinobacteria in the oxisol (Yu *et al.,* 2020). Compared to rice plants, millets rhizosphere has 42.22% total abundance making it the dominating phylum among other bacterial phylum in this crop type (Prabha *et al.,* 2019). Several uncommon actinobacteria related have been found to be associated with the rhizosphere of alpine plants among which *Kitasatospora* genus and certain clades of *Streptomyces* genera including, *Streptomyces subrutilus*, *S. avidinii*, *S. chinensis*, *S. mirabilis*, *S. olivochromogenes*, *S. brevispora*, *S. spororaveus*, *S. anulatus*, *S. camponoticapitis*, *S. erringtonii* and *S. scabrisporus* have been some of the peculiar strains to be identified from rhizosphere soil (Oberhofer *et al.,* 2019). Furthermore in banana endophytes, actinobacteria constituted 9.30% of the total bacteria identified with the population remaining unaffected by infestation of phytopathogenic fungal pathogens (Kaushal *et al.,* 2020). These findings clearly demonstrates the structural diversity of actinobacteria to shift in accordance to the plant type, soil amendments and environment. This demonstrates that actinobacteria have preferences for certain soil and plant types and is a commensal microorganism for plant ecosystem.

BENEFICIAL IMPLICATIONS FOR THE RHIZOSPHERE BY THE INTERACTION OF ACTINOBACTERIA AND ITS MAJOR ATTRIBUTES IN PLANT GROWTH PROMOTION

Plant growth promoting microorganisms (PGPMs) are mainly colonizers of the rhizoplane and rhizosphere region (Gopalakrishnan *et al.,* 2015a and 2013; Sarikhani *et al.,* 2020). Within the phylum Actinobacteria, the genus *Streptomyces* is predominant and present ubiquitously in soil or water, existing both as rhizosphere-colonizing bacteria and plant endophytes. As some of the *Streptomyces* are endophytic, they can easily grow in the host cell without harming the host's internal appearance (Kumar *et al.,* 2014; Marella, 2014). They assist the growth of plant by providing different types of nutrients (e.g. soluble phosphorus), and increases the water uptake as well as the retention capacity of the plant (Schütze *et al.,* 2014). In return, Actinobacteria receives nutrients such as sugars from the plant, which help them proliferate their growth in soil. *Streptomyces* spp. also produce some catalytic enzymes and provides them to the host systems, wherein these enzymes easily breaks down several complex biomolucular compounds into simpler chemical units (Nascimento *et al.,* 2002; Syed *et al.,* 2009). Actinobacteria, mainly *Streptomyces* and some other beneficial strains, possess various plant growth promoting (PGP) attributes (Gopalakrishnan *et al.,* 2013; Anwar *et al.,* 2016). Thus, *Streptomyces* are considered as plant growth-promoting *Streptomyces* (PGPS) which have the ability to increase plant growth by direct or in-direct biosynthetic pathways (Vurukonda *et al.,* 2018). These common PGP attributes are shown in Fig. 2 (Saito *et al.,* 2003; El-Tarabily *et al.,* 2008; Khamna *et al.,* 2010). There are two different ways by which Actinobacteria can influence plant growth. The direct way of influence on plant has been through facilitation of plant growth by releasing microbial metabolites and providing biological nutrients such as phosphorus and nitrogen are ideal than agrochemicals which caused serious environmental damage and also expensive (Tanvir *et al.,* 2018). Whereas indirectly the Actinobacteria influences the plant by minimizing the deleterious effects of pathogenic microbe by production of antagonistic compounds. Table I shows the lists of Actinobacteria that help regarding plant growth promoting attributes in plant growth.

Fig. 2 Major PGP attributes of Actinobacteria

TABLE I

Beneficial effects of Actinobacteria on growth promotion attributes and growth enhancement in different host systems

Actinobacteria name	**Host**	**Major PGP traits**	**Production of growth promoters substance**																**References**
			IAA	**PS**	**SP**	**AD**	**AP**	**HCN**	**CP**	**LP**	**PP**	**β-G**	**ChP**	**PhP**	**GBs**	**CKs**	**NF**	**OA**	
Nocardiopsis dassonvillei subsp. *dassonvillei* D14, *Nocardiopsis aegyptica* H14	*Solanum lycopersicum*	IAA, and PS	21.4 µg/mL	24.84 µg $PO4^{3-}$ mL^{-1} (D14)	-	-	√	√	-	-	-	-	√	-	-	-	-	√	Djebaili *et al.* (2020)
Streptomyces spp. (A20, 5.1, 7.1)	*Oriza sativa*	IAA, SP and PS	7.98 ± 0.87 µg/mL	388.53 ± 43.66 µg/mL	√	√	-	-	-	-	-	-	-	-	-	-	√	√	Suarez Moreno *et al.* (2019)
Streptomyces spp.	*Glycine max*	IAA, PS and NF	2.08 µg/mL to 16.70 µg/mL	2.05±0.06 to 2.72±0.08 µg/mL	-	-	-	-	-	-	-	-	-	-	-	-	√	√	Wahyudi *et al.* (2019)
S. rochei (WZS1-1) and *S. sundarbansensis* (WZS2-1)	*Mikania micrantha*	IAA	absence tryptop- 11.40 ± 0.49 µg/mL (WZS1-1), 19.72 ± 1.56 µg/mL (WZS2-1) presence of tryptophan 7.08 ± 0.32 µg/mL (WZS1-1), 35.76 ± 2.92 µg/mL (WZS2-1)	√	√	-	-	-	-	-	-	-	-	-	-	-	√	√	Han *et al.* (2018)

Streptomyces spp. (SAI-29)	Chickpea	IAA, SP, CP, ChP, LP, PP, β-G and HCN	14.6 µg/mL	-	11–20 mm	-	-	-	31–40 mm	11–20 mm	55 mm	0.32 mg/mL	11–20 mm	-	-	-	-	-	Sreevidya *et al.* (2016)
S. nobilis WA-3, *S. Kunmingenesis* WC-3*, S. enissocaesilis* TA-3*, Streptomyces* spp. WA-1*, S. djakartensis* TB-4 and *S. mutabilis*WD-3	*Triticum aestivum*	IAA, SP, PS, AP and HCN	500µg/ml L-tryptophan)-79.5 µg/mL (WA-3), 79.23µg/mL (WC-3), 69.26µg/mL (TA-3)	√	72.13 mg/100 ml (WA-1), 70.36 mg/100 ml (TB-4), 66.0 ± 0.40 (WA-3), 61.46 ± 0.279 (WC-3), 57.83 ± 0.32 (WD-3), 62.9 ± 0.40 (TA-3)	√	√	√	-	-	-	-	-	-	-	-	-	√	Anwar *et al.* (2016)
Streptomyces spp. HM1	*Zea mays*	IAA	-	-	-	-	-	√	-	-	-	-	√	√	-	-	√	√	El-Sayed *et al.* (2015)
Streptomyces spp.	*O. sativa*	IAA and SP	43.6 g/mL	-	√	-	-	√	-	-	-	√	√	√	-	-	√	√	Gopalakrishnan *et al.* (2014)
Streptomyces spp., *Microbispora* spp., *Actinomadura* spp., *Micromonospora* spp., *Nocardia* spp., and *Actinoplanes* spp.	*G. max*	IAA, GBs, CKs, SP and HCN	√	√	-	-	-	√	-	-	-	√	-	-	√	-	-	√	Dalal and Kulkarni (2014)
Streptomyces spp.	*T. aestivum*	IAA, PS,	136.5 mg/L	1916 mg/L	47.4 mg/L	-	-	-	-	-	-	-	6.2 U/	0.68	-	-	-	√	Jog *et al.* (2014)

		PhP, ChP and SP											mL	U/ mL					
Streptomyces sp VSMGT1014	*O. sativa*	IAA	15.96 µg/ml	-	-	-	-	-	-	-	-	-	-	-	-	-	-	√	Harikrishnan *et al.* (2014)
Streptomyces spp. ASU14	*T. aestivum*	IAA	22 µg/mL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	√	Abd-Alla *et al.* (2013)
S. rochei IDWR19, *S. carpinensis* IDWR53 and *S. thermolilacinus* IDWR81	*T. aestivum*	IAA, SP and PS	17.81±2.1(IDWR19), 13.36±2.3(IDWR53), 11.5±2.1(IDWR81)	√	34.17±0.07 (IDWR19), 27.63 ± 0.08 (IDWR53), 26.9 ± 0.07(IDWR81) PS- 95.40 ± 5.1 (IDWR19), 405.17 ± 6.2 (IDWR53), 911.6 ± 5.3 (IDWR81)	-	-	-	-	-	-	-	-	-	-	-	-	√	Jog *et al.* (2012)
Streptomyces spp.	*T. aestivum*	Increased uptake of N,P,Fe and Mn	2.4 µg/ml	92 mg/l	√	-	-	-	-	-	-	-	-	-	-	-	-	√	Sadeghi *et al.* (2012)
S. hygroscopicus TP-AO451	*Phaseolus vulgaris*	Pteridic acids A and B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Igarashi *et al.* (2002)
Streptomyces spp.	*Z. mays, C. arietinum*	IAA, GA,Phosphatas	-	√	√	√	-	-	-	-	-	-	-	-	-	-	-	√	Radha T.K. (2016)

		e and PS																	
Streptomyces spp.	*Vigna radiata*	SP	√	-	√	√	-	-	-	-	-	-	-	-	-	-	-	√	Rungin *et al.* (2012)
Streptomyces AzR-051	*Azadirachta indica* A. Juss.	IAA, SP	13.73 µmol/mL	√	√	-	-	-	√	-	-	-	-	-	-	-	-	√	Verma *et al.* (2011)
Streptomyces CMU-H009	lemongrass (*Cymbopogon citratus*)	IAA	300 mg/mL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	√	Khamna *et al.* (2010)
N. jiangxiensis	*Aquilaria crassna* Pierre ex Lec (eaglewood)	IAA	15.14 ± 0.22 µg/mL	-	√	-	√	-	-	-	√	-	-	-	-	-	-	-	Nimnoi *et al.* (2010)
Streptomyces ST24	*Heritiera fomes* (mangrove)	PS	-	√	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Gupta *et al.* (2010)
Thermobifida MCR24	*Trifolium repens* L	SP	-	√	√	-	-	-	-	-	√	-	-	-	-	-	√	√	Franco-Correa *et al.* (2010)
Actinomycete LSCH-10C	*O. sativa*	PS and ChP	√	√	-	-	-	-	-	-	-	-	√	-	-	-	-	√	Ningthoujam *et al.* (2009)
Micromonospora endolithica	*Phaseolus vulgaris L.*	PS	-	√	-	-	-	-	-	-	-	-	-	-	-	-	-	√	El-Tarabily *et al.* (2008)
S. aureofaciens CMUAc130	-	ChP	-	-	-	-	-	-	-	-	-	-	0.0833 ± 0.0045 mU/ml	-	-	-	-	√	Taechowisan *et al.* (2003)

S.olivaceoviridis, S.rimnosus, S. rochei	*T. aestivum*	IAA, GBs and CKs	34.19 ± 1.46 µg/mL, 39.04 ±0.61 µg/mL, 32.75 ± 0.23 µg/mL	-	-	-	-	-	-	-	-	-	-	-	5.53±0.16 µg/mL, 8.30 ± 0.87 µg/mL, 5.69±0.09 µg/mL	14.88± 0.26 µg/mL, 4.70 ± 0.08 µg/mL, 6.73 ± 0.37 µg/mL	√	√	Aldesuquy *et al.* (1998)

√: positive findings / tested, IAA: indole-3-acetic acid, PS: phosphate solubilization, SP: siderophore production, AD: ACC deaminase, AP: ammonia production, HCN: hydrogen cyanide production, NF: nitrogen fixation, CP: cellulase production, LP: lipase production, PP: protease production, β-G: β-1, 3-glucanase, ChP: chitinase production, PhP: phytase production, GBs: gibberellins, CKs: cytokinins, OA: others PGP attributes

ACTINOBACTERIA AS BIOCONTROL AGENTS FOR PLANT PROTECTION

There are several studies and trials based on the usage of biological sources of pesticides instead of chemical sources. A good alternative to chemical sources is microbial sources, which have an impact on their multifunctionality and a beneficial effect on plants and ecosystems. Actinobacteria are usually regarded as potent natural biocontrol agents in soil (Gopalakrishnan *et al.,* 2013). Actinobacteria competing with pathogens through the production of different secondary metabolites, enzymes, parasitism, and other biocontroling activities (Hamdali *et al.,* 2008a; Goudjal *et al.,* 2014; Sreevidya *et al.,* 2016). Studies reported that the different types of plant pathogens e.g. *Alternaria* spp*., F. oxysporum, C. higginsianum, P. aphanidermatum, P. capsici*and *A. lactucum*are are very sensitive to the different bioactive compounds produced by *Streptomyces* spp. (Lu *et al.,* 2008; Hamdali *et al.,* 2008a; Goudjal *et al.,* 2014; Sreevidya *et al.,* 2016). Recently, Wu *et al.* (2019) reported that *Streptomyces* spp. produce a novel compound ‘Antifungalmycin N2’ which was effective against *R. solani*. De Oliveira *et al.* (2014) and Kanini *et al.* (2013) reported that *Streptomyces* spp. demonstrated antimicrobial activity against *Xylella fastidiosa* and *R. solani.* Similarly, *S. vinaceusdrappus* showed activity against rice fungal pathogens. *S. violarus* was effective against leaf blight disease pathogens (e.g. *A. alternata*). Furthermore, studies have discovered a metabolite, namely ‘A Factor’, which induced the production of other secondary metabolites in Actinobacteria (Fiebig *et al.,* 2018). Different kinds of antibacterial agents, such as lankacidin C (Lu *et al.,* 2018), lankamycin (Lu *et al.,* 2018), actinorhodin (Čihák *et al.,* 2017) and aureomycin, are synthesized by *Streptomyces* spp., including avermectins (Cheng *et al.,* 2018b). Table II shows the lists of Actinobacteria which suppress plant pathogens and their efficiency in biocontrol activity.

TABLE II

Biocontrol activity of Actinobacteria against pathogens for plant protection and disease management

Actinobacteria name	**Host**	**Pathogen name**	**Biocontrol activity against**	**References**
S. avermitillis, S. cinnamonesis* and *S. canus	*Punica granatum* L.	*Cerotocystis fimbriata, Fusarium oxysporum, Macrophomina* sp. and *Sclerotium* sp.	Suppression level 58.0% to 85.0%	Panneerselvam *et al.* (2020)
***Streptomyces* spp.**	*O. sativa*	*Burkholderia glumae*	Bacterial diseases	Suarez Moreno *et al.* (2019)
S. rochei* and *S. sundarbansensis	*Mikania micrantha*	*Fusarium graminearum*	Inhibit *F. graminearum* by 39.31% and 31.72%, respectively	Han *et al.* (2018)
***Streptomyces* spp. CB-75**	*Musa*	*F. oxysporum* f. sp. *cubense Race 1, F. oxysporum f.* sp. *cubense Race 4, C. gloeosporioides (Penzig), C. fragariae Brooks, C. acutatum Simmonds, Botrytis cinerea Persoon, C. musae; Curvulatia fallax, C. gloeosporioides, A. tenuissima* and *C. gloeosporioides*	Against plant pathogenic fungi and highest antifungal activity against *C. gloeosporioides*	Chen *et al.* (2018b)
S. vinaceusdrappus	*O. sativa*	*Magnaporthe oryzae (Pyricularia oryzae)*	Rice fungal pathogen	Law *et al.* (2017)
S. violarus	*Arachis hypogaea*	*Alternaria alternate*	Biocontrol of leaf blight disease	Chitraselvi and Kalidass (201
S. globosus	*Phoenix dactylifera*	*Thielaviopsis punctulata*	biocontrol of the black scorch disease	Saeed *et al.* (2017)
***Streptomyces* spp.**	*Fragaria × ananassa*	*B. cinerea, Mucor hiemails, Rhizopus stolonifer*, and *S. sclerotiorum*	Suppression of fruit rot pathogen	Lyu *et al.* (2017)
S. rimosus	*Cucumis sativus*	*F. oxysporum* f. sp. cucumerinum	Prevents the development of the disease caused by *F. oxysporum*on *C. sativus*	Lu *et al.* (2016)
***Nonomuraea* spp.**	*O. sativa*	*Xanthomonas oryzae*	Bacterial leaf blight	Ilsan *et al.* (2016)
Micromonospora	*Solanum lycopersicum*	*Fusarium circinatum, Sclerotinia sclerotiorum, R. solani* and *B. cinerea*	Against *B. cinerea* (reduced leaf infection)	Martínez-Hidalgo *et al.* (201
***Streptomyces* sp. UPMRS4**	-	*Pyricularia oryzae*	Highest activity against mycelial growth of *P. oryzae*	Awla *et al.* (2016)
***Amycolatopsis* spp.**	*Malus domestica*	*Colletotrichum gloeosporioides*	Against bitter rot	Sadeghian *et al.* (2016)
***Streptomyces* spp. PM9**	*Eucalyptus globulus*	*Botrytis cinerea*	Establishment of gray mold	Salla *et al.* (2016)
S. vinaceusdrappus	*S. lycopersicum*	*R. solani*	Against *R. solani*	Yandigeri *et al.* (2015)

***Streptomyces* spp.**	*Sorghum bicolor*	*Macrophomina phaseolina*	Control of charcoal rot disease	Gopalakrishnan *et al.* (2015b
S. philanthi	*O. sativa*	*Rhizoctonia solani*	Effectively suppressed	Boukaew and Prasertsan (201
S. flavotricini	*O. sativa*	*Pyricularia grisea*	Antifungal activity	Khalil *et al.* (2014)
S. sindeneusis	*O. sativa*	*Magnaporthe oryzae*	Inhibition - pathogen and suppression - leaf symptoms	Zarandi *et al.* (2009)
***Streptomyces* spp., *Micromonospora* spp., *Nocardia* spp., *Actinomadura* spp., *Microbispora* spp., and *Actinoplanes* spp.**	*Glycine max*	*R. solani, F. oxysporum, S. rolfsii, C. truncatum, M. phseolina* and *A. alternata*	For crop protection and biological control	Dalal and Kulkarni (2014)
***Streptomyces* spp.**	-	*Aspergillus niger, Penicillium chrysogenum* and *Microsporum gypseum*	Antifungal activity	Jog *et al.* (2014)
S. pluripotens	-	*S. aureus*	Exhibited a broad-spectrum bacteriocin	Lee *et al.* (2014)
S. fradiae, S. avermitilis, S. cinnamonensis and S. canus	*Punica granatum* L. cv. Bhagwa	*Xanthomonas axonopodis* pv punicae (Xap)	Controls bacterial blight disease	Poovarasan *et al.* (2013)
***Streptomyces* spp. ASBV-1**	*Arachis hypogaea*	*A. parasiticus*	Inhibits the spore viability of *A. parasiticus*	Zucchi *et al.* (2008)

PLANT GROWTH-PROMOTING TRAITS AND PLANT PROTECTION ABILITIES OF ACTINOBACTERIA

Nitrogen fixation

Nitrogen (N) has been regarded as one of the most important elements for plant and accounts for about 78% of the atmosphere. Due to the presence of stable triple bond, N remains unavailable for most of the organisms (Callaham *et al.,* 1978). N fixing bacteria convert the atmospheric N_2 into ammonical form (NH_4^+) that becomes available for plants (Dudeja *et al.,* 2012). Plants undergoing symbiosis with N fixing bacteria generally do not experience N deficiency and their co-existence in soil decreases the rate of N application (Hurek *et al.,* 2002). Two groups of N-fixing bacteria, rhizobia and *Frankia*, form nodules, which are specialized organs, required for coexistence of microorganisms in roots of the host plant. Diazotrophy in Actinobacteria for long time has been thought to be restricted to the genus *Frankia* (Villegas *et al.,* 1997; Buckley *et al.,* 2007; Trujillo *et al.,* 2010; Gonzalez-Ruiz *et al.,* 2012; Dahal *et al.,* 2017). Molecular studies revealed the existence of *nif*H gene in numerous species of *Frankia* and this observation has bought deep insights into the origin and emergence of bacterial isotrophs among the Actinobacteria phyla (Buckley *et al.,* 2007; Trujillo *et al.,* 2010; Gonzalez-Riz, 2012). These findings on Actinobacteria have stimulated further research and inquiries on the basis of diazotrophy and *nif*H gene transfer. Studies have found *Frankia* establish symbiosis with several non-legume plant species (>200) belonging to 23 genera of 8 families called actinorhizal plants (Normand and Lalonde 1982). Additionally, several studies have been performed on non-*Frankia* N fixing Actinobacteria, and discovered new plant-Actinobacteria associations among which *Micromonospora* based N fixation has been the most prevalent one.Various species beolonging to the genus *Micromonospora* have been obtained in Italy and Brazil from the root surface of plants such as maize (Carro *et al.,* 2012; Martínez-Hidalgo *et al.,* 2015). In recent years *Micromonosporae* have been reported as the major symbiont involved in N fixing in root nodules of both leguminous and actinorhizal plants (Garcia *et al.,* 2010; Carro *et al.,* 2012; Trujillo *et al.,* 2015).

Actinobacteria as a phosphate enhancer

Phosphorus (P) is one of the key plant nutrients responsible for plant growth promotion. In soil, P is mainly present in unavailable form (*i.e.* insoluble, precipitate or immobilized form), constituting 30-65% of organic P present in total soil (Shen *et al.,* 2011). Thus, it is very difficult for plants to utilize this type of P because of their association with different cations present in soil. The availability of P directly affects crop production, if the P level is low. Plant uptake of P is only in the form of soluble organic monobasic ($H_2PO_4^-$) and dibasic (HPO_4^{2-}) ions (Narang *et al.,* 2000). Phosphate solubilizing soil microbes have the ability to release free phosphate by mechanisms including production of organic acids such as commonly succinic acid, gluconic acid, oxalic acid and citric acid which participate in dissociation of chemical bonds of bound phosphates in soil (Verma, 2019; Rajput *et al.,* 2013).Therefore, converting the unavailable forms of P to available state by solubilization and mineralization is one of the basic criteria involved in the selection and introduction of P solubilizing microorganisms (PSM), among which Actinobacteria have been found to be important (Lunggani and Suprihadi, 2019). These bacteria are used to secrete different types of organic acids (e.g. gluconic acid and ketogluconic acid etc.) that decrease the rhizosphere pH, thereby releasing bound forms of P, such as $Ca_3(PO_4)_2$, into calcareous soils (Farhat *et al.,* 2015).

Recent research has established the P-solubilizing activity of Actinobacteria has role in sustainable agriculture (Hozzein *et al.,* 2019). It has been found that about 20% of Actinobacteria, such as *Streptomyces* and *Micromonospora*, have high P solubilization potential (Barreto *et al.,* 2008). Jog *et al.,* (2014) reported that highest malate amount was recorded for a P solubilizing Actinobacteria, *Streptomyces* mhcr0816. Malate synthesis may be performed by glyoxalate by-pass that was proved among relative expression of isocitrate dehydrogenase (IDH), malate synthas (MS) and isocitrate lyase (ICL) using specifically designed enzymes and primers activities. Some studies have shown that N-fixing Actinobacteria also have present P solubilization activity (Sahu *et al.,* 2007; Gangwar *et al.,* 2012; Salcedo *et al.,* 2014). Actinobacteria with P solubilization potential increase plant growth due to their ability to produce active metabolites such as phytohormones, siderophores and antibiotics, as well as their ability to withstand stressful conditions (Hamdali *et al.,* 2008c; Tanvir *et al.,* 2018). A study found that 44% of all Actinobacteria isolated from the rice rhizosphere had P solubilization activity in which the actinobacterium, *S. lavendulae* R22, showed the highest amount of P solubilization (265 mg/l) (Gangwar *et al.,* 2012). In one experiment, it was reported that from all the Actinobacteria isolated from the rhizosphere of *Trifolium repens,* Actinobacteria exhibited 20% inorganic P dissolution activity. In that experiment, all isolates were capable of producing acid phosphatase, and 43% produced alkaline phosphatase, which showed the higher potential of Actinobacteria to mineralize organic P (Richardson *et al.,* 2009). In addition, Actinobacteria have been also reported producing phosphatases (Franco-Correa *et al.,* 2010; Pragya *et al.,* 2012).

The rate of solubilization of P by Actinobacteria depends on: (i) the type of insoluble inorganic phosphorus sources, (ii) the intrinsic phosphorus solubilization ability of the Actinobacteria species and (iii) the amount and types of photosynthetic compounds present in the rhizosphere (Banik and Dey, 1982). It has been observed that a single Actinobacteria species can have the capacity to dissolve both inorganic and organic P (Guang-Can *et al.,* 2008; Asadu *et al.,* 2018). Actinobacteria have also been reported to produce the extracellular enzyme phytase in addition to phosphatase. The phytate mineralized through phytase is known as a predominant form of phosphorus but unavailable to plant hosts. Phytate is produced by sporulating *Streptomyces, Bacillus* and several other Actinobacteria (Richardson and Simpson, 2011; Jog *et al.,* 2012). Ghorbani-Nasrabadi *et al.* (2012) reported the isolation of phytate-degrading Actinobacteria (*S. alboniger* and *S. venezuelae)* from arable soil with the highest activity at 46.30%. In another study, P-soluble Actinobacteria isolated from Moroccan P mines were tested on the wheat crop, and the results implied an increase in wheat plant biomass. The highest P solublizer, which was Actinobacteria strain BH7, produced the highest biomass in wheat under *in-vitro* conditions. An increase in plant yield of 70% was observed in test tubes and of more than 30% in soil with rock P. Similarly, Jog *et al.* (2014) reported Actinobacteria isolated from soil with P solubilization (1.916 mg l^{-1}) and production of phytase (0.68 U ml^{-1}), auxin (136.50 mg l^{-1}), siderophore (47.40 mg l^{-1}) and chitinase (6.20 U ml^{-1}). Inoculation of this Actinobacteria (*Streptomyces* mhcr0816) with the wheat plant not only increased the biomass and yield but also enhanced the contents of potassium, iron and zinc. If applied as bio-fertilizers, efficient strains of Actinobacteria can reduce the use of chemical fertilizers (Sahu *et al.,* 2007; Hozzein *et al.,* 2019). PSM has been found as an alternative biotechnology solution for sustainable agriculture, including the heterogeneous and naturally abundant rhizosphere microbes, whose participation *in-toto* fulfills phosphate demands of the plant (Richardson and Simpson, 2011).

Phytohormone production by Actinobacteria and their role in plant growth

Plant hormones perform an essential role in controlling plant cell physiological processes (Le Bris, 2017) and also in plant-microbial interactions (Solans *et al.,* 2011). The effects of plant hormones (e.g. auxins, abscisic acid, ethylene, cytokines and gibberellins) on plant growth depend upon the hormone levels (Passari *et al.,* 2016). Some microorganisms (including fungi and bacteria) are capable of synthesizing these phytohormones (Shutsrirung *et al.,* 2013). The synthesis of *in vitro* phytohormones including gibberellic acid, auxins and cytokinins from Actinobacteria, which support in plant growth, has been documented by several researchers (Mahadevan and Crawford, 1997; Ghodhbane-Gtari *et al.,* 2010; Gopalakrishnan *et al.,* 2014; Anwar *et al.,* 2016; Solá *et al.,* 2019).

The primary type of auxin is IAA, which controls many fundamental cellular mechanisms including cell division, differentiation and elongation (Le Bris, 2017). It also results in enhanced formation of root hair, which improves the rhizospheric area and nutrient absorption capacity from soil. Auxins also play an integral role in several developmental processes, like the development of embryos and fruit, vascular tissue differentiation, elongation, organogenesis, root patterning, tropic growth, apical dominance and apical hook formation (Dobbelaere *et al.,* 1999). Farina *et al.* (2012) reported that five isolates of Actinobacteria produced high amount of IAA when grown on tryptophan supplemented medium. Several reports have suggested that the application or treatment with Actinobacteria in plant or seeds induces seed germination, seedling growth, rooting and cell elongation etc. (El-Tarabily, 2008 ; Goudjal *et al.,* 2013). Radha T.K. (2016) reported improvement of growth and yield parameters of maize and chickpea with Actinobacterial strains inoculation. Meguro *et al.* (2006) reported that plant inoculated with *Streptomyces* sp. MBR52 (IAA producer), improved emergence and elongation of new roots within a few days. Goudjal *et al.,* (2013) reported *S. rochei* strain PTL2 isolated from Algerian native plants showed IAA was of 127 µg mL^{-1}. Inoculation of this isolate in the tomato plant resulted in a significant increase in seed germination and root elongation rates, respectively. In a similar experiment, inoculation of tomato with auxin phytohormones producing *S. caeruleatus* ZL2 strain significantly increased dry weight and root length of the plant (Zamoum *et al.,* 2017). Inoculation of plants with an auxin and gibberellin-producing actinobacterium, *Streptomyces* sp. IA1, isolated from field soil, was also found to increase both tomato (Goudjal *et al.,* 2016) and wheat growth (Toumatia *et al.,* 2016). El-Tarabily *et al.* (2008) reported that the inoculation of cucumber plants with endophytic Actinobacteria significantly increased growth of the plant due to the production of IAA, indole-3-pyruvic acid, and gibberellic acid. Shutsrirung *et al.* (2013) reported that 64 isolates from mandarin (*Citrus reticulata* L.) were found to belong to *Nocardiopsis, Streptomyces, Spirillospora, Microbispora, Nocardia,* and *Micromonospora* genera, from which 85.3% belonged to the *Streptomyces* genus. From these 64 isolates, the top 12 auxin-producing isolates were inoculated into the mandarin plant, which resulted in increased shoot - root fresh weight and height. Cytokinin production in the rhizosphere has been reported in plant-associated Actinobacteria (Khamna *et al.,*, 2010; Patel and Saraf, 2017), such as *S. flavousare* (Coppola and Giannattasio 1968). Actinobacteria isolated from *Ochetophila trinervis* have been reported to have the potential for auxin (IAA), cytokinin and gibberellic acid production (Solans *et al.,* 2011). Based on reports and reviews, it is seen that the phytohormone-producing Actinobacteria play a superior role in plant-microbe interactions and act as an effective plant growth regulator that can be used for rhizospheric engineering purposes (Khamna *et al.,* 2010; Solans *et al.,* 2011; AbdElgawad *et al.,* 2019).

Siderophore production by Actinobacteria for nutrient acquisition

Actinobacteria are a versatile group of soil bacteria as far as their metabolic activity is concerned. They can produce different types of substances, including siderophores, which are low–molecular-weight iron-chelating [ferric iron {Fe (III)}] compounds (Walsh and Marshall, 2004; Oves-Costales *et al.,* 2009). Siderophores are generally produced by microorganisms under iron-deficient conditions, and they include phenolate hydroxamates, catecholate, salicylates and carboxylates compounds (Kannahi and Senbagam, 2014). Wittenwiler (2007) suggested that iron bioavailability is enhanced by siderophores through influencing the low mobility and solubility of iron. This atom is coordinated in a soluble complex through siderophores which facilitate dissolution and attach on the mineral surface.The main function of these compounds is the utilization and acquisition of the insoluble form of iron (Fe^{+3}) in available form. Siderophores can supply the iron nutrient during iron deficiency periods of plant development, which have generally been observed in alkaline soils with pH >7.5 (Vansuyt *et al.,* 2007). Siderophores have ben referred to as micronutrient fertilizers because they improve nutrient availability of minerals by chelating those which are required in a very small amount (Ahmed and Holmström, 2014). Sathya *et al.* (2017) suggested that the siderophores can also improve rhizosphere colonization of bacteria. *A. madurae, N. asteroids,* and *S. griseus* are among these siderophore-producing Actinobacteria (Kannahi and Senbagam 2014). Actinobacteria produce mainly hydroxymate and salicylate types of siderophores. Desferrioxamine E, a siderophore, has been reported to be produced by *S. griseus* (Yamanaka *et al.,* 2005). Similarly, coelichelin (Lautru *et al.,* 2005; Challis and Ravel, 2000) and griseobactin (Patzer and Braun 2010) are different types of siderophores produced by *Streptomyces* spp. A new class of siderophores such as heterobactin (hydroxamate and catecholate type) have been found to be produced by *Rhodococcus* (Carrano *et al.,* 2001).

1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity

When the plant is under stress, ethylene is a phytohormone that is evolved through its roots, limiting the growth and development of the plant's roots and further decaying the plant's overall growth (Pandey and Gupta, 2019).Under stress conditions, the production of ethylene phytohormone is mediated by the ACC precursor. A wide variety of microbes are able to separate the amine group from the ACC by the enzyme ACC demaminase (ACCd), and convert it into two ammonia (as a source of N) and α-ketobutyrate. Therefore, these bacteria in stressful conditions, by reducing the level of ethylene, lead to increased growth and elongation of the plant root and its development, and therefore these plants will have a better and more favorable general condition under stress situation (Misra *et al.,* 2017). Many bacteria including the genera *Enterobacter* (Sarkar *et al.,* 2018) and *Bacillus* (Ghosh *et al.,* 2003) produced ACCd, and reduce ACC content in plant tissues. It has been reported that in Actinobacteria, the genera *Streptomyces* spp. has the ACCd activity (El-Tarabily, 2008).

Role of Actinobacteria in decomposition by the production of degrading enzymes

Enzymes play a catalytic role in all biosynthetic and decomposition processes. Actinobacteria play a significant role in decomposition (Tiwari *et al.,* 2019), due to their saprophytic nature and production of different types of plant cell wall degrading enzymes (Ramírez and Calzadíaz, 2016). These enzymes can help to degrade various complex polymers, such as lignin, hemicellulose, laccase, xylanase and cellulose. Ventorino *et al.* (2016) reported that important lignocellulose degrading enzymes are produced by *Streptomyces* spp. The degrading enzymes which are produced by Actinobacteria (Gupta *et al.,* 1995; Fodil *et al.,* 2011) for decomposition provide organic nutrients to plants and are shown in Fig. 3. Apart from the lignocellulolytic enzymes, chitinase produced by Actinobacteria has shown potential for biocontrol activity of several phytopathogens, including fungal and insect prests. The fungal cell wall and insect cell wall contain chitin, which can be degraded by chitinase enzyme (Yandigeri *et al.,* 2015). In this way, Actinobacteria (*Streptomyces* spp.) inhibit the growth of phytopathogens and protect the plant.

Fig. 3 Different enzymes produced by Actinobacteria for increased organic matter decomposition and crop productivity

Actinobacteria as metabolite and antibiotic producers for protection

Actinobacteria are known for production of different secondary metabolites like antibiotics (low molecular weight secondary metabolites that can exterminate or inhibit the growth of other organisms) that can indirectly help plant growth by reducing the incidences of phytopathogenic bacteria and fungal species (Table III; Fig. 4). A variety of antibiotics such as polyketides, peptide β-lactams in addition to other secondary metabolites, are responsible for antifungal, immunosuppressive and antitumor activity (Behal, 2000). Liu *et al.* (2012) reported that 45 % of all antibiotics were produced from Actinobacteria. Among these, *Streptomyces* spp. was dominant as it was capable of producing a wide spectrum of antibiotics (Toumatia *et al.,* 2015). Streptomycin, discovered by Selman A. Waksman in 1943 (Woodruff, 2014), was the first antibiotic to be effective against tuberculosis, and it was produced from *S. griseus*. *Streptomyces* spp. are clearly capable of producing bioactive secondary metabolites with antimicrobial (Singh *et al.,* 2016), antifungal and antiviral activities (Maldonado *et al.,* 2010). Molano *et al.,* (2000) reported that the antibiotic actinomycin, produced by *Nocardia* spp., strongly inhibited *Fusarium oxysporum*. Similarly, *S. avermitilis* produced avermectins, which acts as a potent antimicrobial as well as antiparasitic agent (Cheng *et al.,* 2018b). Actinobacteria also produce VOCs (low molecular weight carbon-containing compounds) which are easily evaporated under normal temperature and help to reduces the pathogenic infestation (Wang *et al.,* 2013). In addition, Quecine *et al.* (2008) reported that *Streptomyces* endophytes with chitinolytic activity significantly reduce pathogenic infection besides plant growth promotion.

Secondary metabolites synthesized by Actinobacteria are not only involved in plant growth promotion and control of pathogens but are also effective against major insect pests of agricultural crops and disease treatments or control (Table III; Fig. 4). The antibiotic avermectin produced by *S. avermitilis* was found to stimulate the gamma amino butyric acid (GABA) system and disrupt nicotinic acetylcholine receptors (Adhya *et al.,* 2018) of the parasite. Nikkomycins, a class of nucleoside peptide antibiotics produced by *S. tendae*, inhibit chitin synthesis of fungi and insects. Similarly, milbemycin, a class of macrocyclic lactone derivatives produced by *S. Hygroscopicus,* showed a broad spectrum of activity against agricultural pests such as aphids, mites, caterpillars, intestinal worms and other parasites that prey on crops and livestock. Tetranectin, a pesticidal macrotetrolide antibiotic produced by *S. aureus,* has been used as an agricultural miticide in Japan since 1973. Spinosyn A and Spinosyn D, produced by *Saccharopolyspora spinosa,* were found to be active against lepidopteran and Dipteran pests (Snyder *et al.,* 2007). Chen *et al.* (2018a) isolated 85 actinomycetes strains from the *Azadiachta indica* tree and tested them for their insecticidal action against *Myzus persicae*. The results revealed that crude extracts from 24 strains were highly effective against *M. persicae* with above 60% of insecticidal activity. El-khawaga and Megahed (2012) screened the antibacterial and insecticidal activities of crude extract of 20 actinomycetes isolates from desert soil samples collected from different locations of Cairo, Egypt. *S. bikiniensis* A11 was found to be the most active actinomycetes isolate against Gram positive and negative bacteria as well as against 2nd instar larvae of cotton leaf worm *Spodoptera littoralis*. The Actinobacteria genome sequencing have provided insights into the production of the secondary metabolites found the gene clusters responsible for biosysnthesis of secondary metabolites are arranged as genomic islands and are dynamic entities transferred from one actinomycete to other through horizontal gene transfer (HGT) (Penn *et al.,* 2009). ActDES (Actinobacterial Database for Evolutionary Studies) is a curated database developed using high-quality genetic sequences of 612 genomes of Actinobacteria covering 80 genera, primarily aimed at understanding the genetic architecture of Actinobacteria and designing a metabolic engineering framework (Schniete *et al.,* 2020). HGT has been mainly found in prokaryotes and contributes to the evolution of new metabolites and pathways of degradation, such as the transfer of Nsar (N-succinylamino acid racemization) and osbs (o-succinylbenzoate synthase) from Firmicutes to Actinobacteria using HGT that required for menaquinone biosynthesis (Bar-Even *et al.,* 2011; Odokonyero *et al.,* 2018).

Fig. 4 Actinobacteria: secondary metabolites and antibiotic production for plant protection and disease control

TABLE III

Metabolites and antibiotics produced by Actinobacteria and their activities

Actinobacteria name	Metabolites / Antibiotic names	Mode of action	References
S. avermitilis	Avermectins	Antiparasitic, antimicrobial, pesticide	Rath *et al.* (*2019*); Cheng *et al.* (2018b); Choi *et al.* (2018); Zhang *et al.* (2015)
S. griseus, S. tinghiriensis **and** ***S. rimosus***	-	Antimicrobial	Ouchari *et al.* (2019)
Micromonospora **spp.,** ***Salinispora*** **spp. and** ***Streptomyces*** **spp.**	-	Antimicrobial	Phongsopitanun *et al.* (2019)
S. griseus, S. flavovirens, kocuria kristinae **and** ***K. rósea***	Bioactive substance	Antimicrobial	Elbendary *et al.* (2018)
S. rochei	Lankacidin C and Lankamycin	Antibacterial	Lu *et al.* (2018)
S. clavuligelus	Cephamycin C	-	Romero-Rodríguez *et al.* (2018)
S. coelicolor	Dihydrogranticin	Novel antibiotics	Hasani *et al.* (2014)
S. sannanensis	Bioactive compound	Antimicrobial	Singh *et al.* (2014)
S. coelicolor	Prodiginines	-	Moore *et al.* (2012)
Actinoplanes philippinensis	Chitinase	Pesticidal	Gadelhak *et al.* (2005)
Streptomyces sp. **8E-12**	Methoxyhygromycin	Herbicidal	Lee *et al.* (2003)
Streptomyces spp.	UN	Antiviral	Mohamed and Galal (2005)
Streptomyces avermitilis	Avermectin	Nematicidal	Jayakumar (2009)
Streptomyces spp.	UN	Fungicidal	Baharlouei *et al.* (2011)
Streptomyces **sp RK-1051**	Enopeptin A	Antiviral	Osada (1995)
Streptomyces **AzR-051**	-	Antifungal	Verma *et al.* (2011)
Streptomyces **sp.**	**-**	Antifungal	Sangmanee *et al.* (2009)
Streptomyces sp.	-	Antifungal and Antibacterial	Oskay M (2009)
Streptomyces hygroscopicus	-	Antifungal	Prapagdee *et al.* (2008)
Streptomyces spp.	-	Antifungal	Errakhi *et al.* (2007)
S. sannanensis **RJT-1**	-	Antibacterial	Vasavada *et al.* (2006)
Streptomyces halstedii	-	Antifungal	Joo (2005)
S. rochei **F20**	Streptothricin	-	Anukool *et al.* (2004)
Streptomyces **sp. AP77**	Anti-*Pythium* protein (SAP)	Antifungal	Woo and Kamei (2003)
Streptomyces **sp.**	-	Antifungal	Samac *et al.* (2003)
Streptomyces **sp.KH-614**	cyclo(L-leucyl-L-prolyl)	Antifungal	Rhee (2003)
S. violaceusniger **G10**	-	Antifungal	Getha and Vikineswary (2002)
Streptomyces viridodiasticus	-	Antifungal	El-Tarabily *et al.* (2000)

***S. violaceusniger* YCED-9**	AFA (Anti-Fusarium Activity), Nigericin, Geldanamycin	Antifungal	Trejo-Estrada *et al.* (1998)
S. violaceonige	Tubercidin	Antifungal	Hwang *et al.* (1994)
S. hygroscopicus AM-3672	Herbimycin	Herbicide	Omura *et al.* (1979)

ACTINOBACTERIAL MEDIATED REGULATION OF PLANT STRESS

Achieving the expanding (about 1.05% each year) global food demand is a massive problem for the agriculture sector (World Population Prospects, 2019). Global agricultural productivity, quality has been regulated by biotic (infection of the plant due to various pests and pathogens) and abiotic stress (salt concentration, water content, and nutrient level in soil, etc.) (Atkinson and Urwin 2012, Kumar *et al.,* 2020). Actinobacterial mediated biotic stress regulation in the plant has been fulfilled by the production of different antimicrobial substances. Salinity and drought are the most devastating abiotic stresses that cause a decrease in plant productivity. Salinity stress caused by the high concentrations of mineral elements (such as Na^+, Ca^+, Mg^+, K^+, Cl^-, SO_4^{2-}, CO_3^{2-}, HCO_3^- and 468 NO_3^-) in the soil. Soil salinity resulted in detrimental effects *i.e.* osmotic stress, oxidative stress, nutrient (N, Ca, K, P, Fe, and Zn) deficiency, ion toxicity, etc. in plants (Grover *et al.,* 2016). Drought is another important environmental stress, that happens due to the absence of an adequate level of soil moisture content. In the drought stress conditions, the growing Plants have water limitation and nutrient deficiencies (Grover *et al.,* 2016). To overcome this environmental stress, soil Actinobacteria plays a critical role by synthesizing different phytohormones, siderophores, phosphate solubilization, ACC deaminase activity, secondary metabolites, extracellular polysaccharides (EPS) production, regulation of stress-responsive genes in the plant, etc. (Table IV) (Grover *et al.,* 2016).

TABLE IV

Actinobacterial mediated alleviation of abiotic stress in plant

Actinobacteria name	**Host/Plant**	**Attributes**	**Reference**
		Salinity Stress	
***Nocardioides* sp. NIMMe6**	Wheat	IAA	Meena *et al.* (2020)
***Streptomyces* sp. GMKU 336**	Rice	Reduction of ethylene by the action of ACCd	Jaemsaeng *et al.* (2018)
***Arthrobacter* sp.**	Maize	IAA, ACCd, biofilm formation	Aslam and Ali (2018)
***Arthrobacter protophormiae* (SA3)**	Wheat	Enhancing IAA, reducing ABA/ACC content, modulating expression of a regulatory component (CTR1) of the ethylene signaling pathway and DREB2 transcription factor	Barnawal *et al.* (2017)
A. pascens	Maize	The accumulation of osmolytes, including sugar and proline, and the elevation of antioxidant enzymes activity	Ullah and Bano (2015)
***S. rochei* SM3**	Chickpea	Increased biomass accumulation, antioxidant activities	Srivastava *et al.* (2015)
***Streptomyces* sp. strain PGPA39**	Tomato	IAA, P solubilization, ACCd	Palaniyandi *et al.* (2014)
		Drought Stress	
S. pseudovenezuelae* and *A.arilaitensis	Maize	IAA and ACCd	Chukwuneme *et al.* (2020)
***Streptomyces* sp. Ac3**	Maize	Flavonoid, antioxidant, phytohormones and Siderophores production and	Warrad *et al.* (2020)

		improved the photosynthesis rate	
***Streptomyces* sp. Ac5**	Maize	Flavonoid, phytohormones and siderophores production and improved the photosynthesis rate	Selim *et al.* (2019)
***Citricoccus zhacaiensis* B-4 (MTCC 12119)**	Onion	Increased the germination rate	Selvakumar *et al.* (2015)

ROLE OF ACTINOBACTERIA IN SOIL HEALTH AND NUTRIENT MOBILIZATION

Soils contain a huge population of living microorganisms that derive their energy by oxidizing organic residues (OR) which are generally left behind after harvesting crops, growth on the soil, or by livestock feeding on these crops. Beneficial soil microorganisms can be classified into four major divisions, which are bacteria, fungi, Actinobacteria, and algae. Bacteria and fungi are the first to act upon OR added to the soil, followed by Actinobacteria, because of their slow activity and growth. In soil they decompose the OR which are more resistant and indecomposable and also generate numerous dark brown to black pigments that add to the dark color of soil humus. They are also liable for further decomposition of humus.

Actinobacteria are an intermediate group between bacteria and fungi, and 70% of soil Actinobacteria have been identified as *Streptomyces*. In general, Actinobacteria may have a positive role in nutrition mobilization, which is associated with the capacity to mobilize nitrogen and metal-containing mineral nutrients such as Zn, Fe and Se (Sathya *et al.,* 2017). Actinobacteria such as *Streptomyces* spp. are involved in nutrient management and thus affect soil fertility and serve as nutrient enhancers (Jog *et al.,* 2014). They play a critical role in soil health through many mechanisms, such as organic acid production (Rozycki and Strzelczyk, 1986), P solubilization (Salcedo *et al.,* 2014; Farhat *et al.,* 2015), solubilization of K (Nafis *et al.,* 2019), N_2 fixation (Kucho *et al.,* 2017), decomposition of organic matter (Das *et al.,* 2007), production of plant growth-promoting hormones (Solá *et al.,* 2019), as plant growth regulators, producing siderophores (Lee *et al.,* 2012), plant protection against biotic stress, bio-corrosion, and biodegradation/bioremediation (Limaye *et al.,* 2017). Actinobacteria can also be a source of metabolites that encourage or enhance the growth and development of host plants, as well as decreasing symptoms of disease induced by plant pathogens or many environmental stresses. Radha (2016) reported improvement of soil chemical properties, nutrient mobilization, soil biological activities *i.e.,* beneficial microbial populations and soil enzyme activities (dehydrogenase, acid and alkaline phosphatase) with the inoculation of Actinobacteria on maize and chickpea. Viaene *et al.* (2016) recently emphasized the contribution of *Streptomycetes* to growth and nutrient managnment of plants. In plants, Actinobacteria play a major role in shaping the root micro-biome by modulating the composition of root exudates (chemotaxis) and nutritional exchanges. Plant root exudates are the source of metabolic signals (such as strigolactones, flavonoids and terpenoids) which participate in shaping the rhizosphere microbial communities. The signals that attract *Streptomycetes* into the rhizosphere of plants are not clearly understood. *Streptomycetes* colonize the root tissues by entering the root from the rhizosphere (Coombs and Franco, 2003). Actinobacteria, such as *Streptomyces* spp., influence soil fertility through the involvement of many components and serve as nutrient enhancers. They play a critical role in maintaining soil fertility and make the complex nutrients into simple mineral forms by secreting hydrolytic enzymes-including amylase, chitinase, cellulase, invertase, lipase, keratinase, peroxidase, pectinase, protease, phytase and xylanase (Ramírez and Calzadíaz, 2016).

IMPROVEMENT OF PLANT RESIDUE DECOMPOSITION BY ACTINOBACTERIA

Lignin degradation potential in *Streptomyces* species is higher than any other species of bacteria (Janusz *et al.,* 2017). Molecular insights into the role played by Actinobacteria during plant residues decomposition have found the reason for predominance of actinoobacteria throughout the decomposition process particularly during degradation of crop residues (Wei *et al.,* 2018). Lignocellulose decomposition in soil proceeds through an array of oxidative biochemical reactions caused by series of enzymes secreted by different groups of microorganisms (Kumar and Chandra, 2020), which have definite sucession orders depending upon the type of plant residue as found in wheat crop residue (Zhong *et al.,* 2020) and rice residue decomposition (Bao *et al.,* 2020) in soil. Lignin is an important polymer of lignocellulose present in the plant cell wall, that provides strength to the plant residue requires coordinated actions of different lignin degrading catabolic enzymes. Kraft lignin (KL) decomposition studies using gel permeation chromatography coupled with mass spectrometry, have revealed S*treptomyces* sp. S6 produces an array of lignin degrading enzymes including laccases, lignin peroxidases, dye-decolorizing peroxidases and aryl-alcohol oxidases, resulting in reduction of 2115.7 Da of KL in seven days with release of at least eight types of aromatic compounds (Riyadi *et al.,* 2020). Recent advancements have revealed those cryptic pathways involved in metabolism of aromatic compounds generated as by-products during microbial lignin degradation. Most of the microbial degraded lignin by-products include vanillate, cumarate and other lignin aromatic hydrocarbons which are referred to as protocatechuate and phenylacetate are converted into succinyl-CoA and acetyl-CoA using the β-ketoadipate pathway using *pca* (protocatechuate) and *paa* (phenylacetate) genes, whereas the phenol derivatives of homoprotocatechuate enters the meta-cleavage pathway leading to production of succinyl-CoA regulated by *Gab* (succinate semialdehyde dehydrogenase) gene, which enter the TCA (trichloroacetic acid) cycle completing oxidation of lignin to CO_2 and H_2O as found in the soil Actinobacteria *Kocuria rhizophila* (Takarada *et al.,* 2008). Genome sequencing have revealed the presence of other different catabolic pathways apart from those discussed above *viz.* 2-hydroxypentadienoate pathway, gentisate pathway, homogentisate pathway and hydroxyquinol pathway as found in the nocardioform Actinobacteria *Rhodococcus ruber* strain Chol-4 (Guevara *et al.,* 2019). Further insights into the genome of *Arthrobacter* sp. strain Rue61a revealed presence of meta cleavage pathway wherein 4-hydroxyphenylacetate catabolism was found to support the growth of this Gram positive bacteria, whereas phenylacetate could not, demonstrating presence of incomplete set of *paa* genes (Niewerth *et al.,* 2012). Actinobacteria have a different type of Type VII secretion system known as WXG100 secretion system for secreting larger protein molecules and found to share homology with similar secretion systems found in some members of other phyla including Proteobacteria, Firmicutes, Cyanobacteria and Lentisphaerae (Sutcliffe, 2011). The presence of competent enzymatic machinery and robust secretion system available for complete catabolism of lignin polymers make Actinobacteria as last sucessors during decomposition of plant residues. Among the other lignocellulose degrading enzymes produced by actinomycete are auxiliary members of glycoside hydrolases (GHs) including Lytic polysaccharide monooxygenases (LPMOs) as found in the Actinobacteria *Jonesia denitrificans* (Mekasha *et al.,* 2020), *Kitasatospora papulosa* (Corrêa *et al.,* 2019) which are capable of enhancing the rate of lignocelluloses degradation particularly affecting the crystalline cellulose polymers. The first representative of bacterial LPMO was found in the cellulose binding module CBH1 of Streptomyces olivaceoviridis (Schnellmann *et al.,* 1994). Later AA10 type LPMO such as CelS2 was identified in *S. coelicolor* (Forsberg *et al.,* 2011), *Streptomyces* sp. SirexAA-E (Takasuka *et al.,* 2013), suggesting that the AA10 group of LPMO are predominantly present in the Actinobacteria *Streptomyces* species (Book *et al.,* 2014). Moreover recent genome sequencing of the Actinobacteria *Streptomyces albus* CAS922 provided insights into the vast lignocellulolytic enzymes repertoire including 232 GHs with 3 belonging to AA10 family identified as LPMO (Tippelt *et al.,* 2020). Earlier reports found some members of *Streptomyces* such as *S. flavovirens* produces lignin degrading enzymes and cause decay of thick vascular tissue walls as in Douglas-fir (Sutherland *et al.,* 1979) and *S. viridosporus* T7A which being found as potent lignin depolymeriser due to secretion of higher amount of extracellular esterases was also found to be a potent phytopathogen (Donnelly and Crawford, 1988). Presently, several nonpathogenic beneficial Actinobacteria have been known among which some lignocellulose degrading Actinobacteria species have been classified as probiotic entites for plants which includes *Actinoplanes*, *Agromyces*, *Arthrobacter*, *Curtobacterium*, *Frankia*, *Kocuria*, *Microbacterium*, *Microbispora*, *Micromonospora*, *Nocardia*, *Streptomyces* and *Rhodococcus* through different PGPR traits including as mentioned above through production of phytohormones, P solubilization, siderophore production, antimicrobial and antagonistic activities suggested by Menendez and Carro (2019).

IMPACT OF FARMING PRACTICES ON ACTINOBACTERIA DIVERSITY IN SOIL

Cultural independent studies have revealed the population of Actinobacteria to be higher in non-cultivated soil rather than cultivated soil (Wolińska *et al.,* 2019). The finding suggested, Actinobacteria are sensitive to physical disturbances in soil, which breaks the actinomycetal hyphaes that are difficult to repair. The cell diameter of *S. coelicolor* although less than 1 μm but can reach 100 μm through hyphal extensions occurring at the tips by using membrane vesicles transporter, which can become perturbed by tangential forces in soil acting on the hyphae resulting in mechanical disruption of hyphae (Goriely and Tabor, 2003). Therefore, soil texture plays an important role in determining the dominance of soil bacterial species and such studies have found conservation tillage practices to improve abundance of functional bacteria population in soil (Wang et al. 2016). Actinobacteria plays an important role in carbon biogeochemical cycle, whose cellulose catabolism rate seems to be controlled by the C/N ratio of soil (de Menezes *et al.,* 2015). Although research have found the application of inorganic fertilizers to have impact the spatial community structure of Actinobacteria (Piao *et al.,* 2008), there are evidences which suggests improvement of relative abundances of Actinobacteria population under long term doses of only N fertilization as compared to combination with P and K (Dai *et al.,* 2018). Studies have also found a certain Actinobacteria consortium comprising four *Streptomyces* sp. strains A2, A5, A11, and M7 had demonstrated capability to revove 70.3% of recalcitarce insecticide lindane from contaminated soil, which showed the Actinobacteria to act as promising tools for restoring soil types contaminated with agrochemicals and thereby help in reclamation of soil arability (Raimondo *et al.,* 2019). Moreover, metagenomic studies have confirmed that the Actinobacteria have higher diversity in organic soil as compared to conventional modern agricultural soil (Sharma *et al.,* 2019). The association of Actinobacteria with AM fungi is quite intriguing since the close association of *Arthrobacter* with the arbuscular mycorrhizae fungi (AMF) *Rhizophagus intraradices*, absorbed cadmium from soil, making it unavailable to plants, as reported for reducing the Cd toxicity in rice (Chen *et al.,* 2019). Because of the high price of chemical fertilizers and the widening gap between supply and demand, the solubilization of nutrients by microorganisms has been seen to be useful and economical. Microbial inoculants are eco-friendly and environmentally secure with low-cost technology, so productivity can be enhanced and environmental problems can be decreased. They play a vital role in sustainable development by controlling physical, chemical and biological components (Fig. 5).

Fig. 5 Actinobacteria help to manage the availability of nutrients in plants and rhizosphere.

CONCLUSION

In this highly demanding era, the scarcity of food and scientific ability to face new challenges have led to the introduction of novel agricultural tools and chemicals. Indiscriminate use of various chemicals have decreased soil quality, including soil fertility, texture etc. An alternative way to sustain crop yield is by focusing on some biological sources. Actinobacteria are a special and proven group of bacteria that can easily troubleshoot several soil-related problems. These special bacteria participate in different plant growth promoting activities, such as IAA production, enzyme production, hormone production, P solubilization, siderophore production, N fixation and secretion of other useful metabolites. Moreover, their strong biocontrol activities, such as competition with other microrganisms, parasitism, antibiosis and volatile organic compound production, provide additional traits for Actinobacteria along with plant growth promotion activities, which have made these bacteria a good alternative for replacing chemical fertilizers and pesticides. Therefore, taking into consideration all these factors, we can affirm that Actinobacteria are a very promising group of soil microbes with proven records for agricultural practices and can help to maintain ecofriendly crop outputs.

PROSPECTS AND CHALLENGES FOR THE FUTURE

The large and diverse group of Actinobacteria has become widely known primarily for its contribution to the production of different types of metabolites, which have a tremendous impact on agriculture. However, continuous research allows us to discover more and more properties of Actinobacteria that are useful for improving agricultural productivityand maintaining agricultural sustainability. The findings and discoveries of new members of Actinobacteria will generate new challenges and changes, not only in taxonomic reclassification but also in the potential discoveries of many more plant-beneficial properties that would have important biotechnological applications to meet future needs.

ABBREVIATIONS

PGPMs: Plant growth-promoting microorganisms; PGPR: plant growth-promoting rhizobacteria; HYVs: high yielding varieties; PSM: phosphate-solubilizing microorganisms; PSB: phosphate-solubilizing bacteria; PGPS: plant growth-promoting *Streptomyces*; G: guanine; C: cytosine; CP: cellulase production; LP: lipase production; PP: protease production; β-G: β-1,3-glucanase; ChP: chitinase production; PhP: phytase production; GBs: gibberellins; CKs: cytokinins; IAA: indole-3-acetic acid; PS: phosphate solubilization; SP: siderophore production; AP: ammonia production; GABA: gamma amino butyric acid; HCN: hydrogen cyanide production; NF: nitrogen fixation; VOC: volatile organic compound; OR: organic residues; KL: Kraft lignin; TCA: trichloroacetic acid; GHs: glycoside hydrolases; LPMOs: lytic polysaccharide monooxygenases.

CONTRIBUTION OF AUTHORS

DM, RM and BK contributed equally as first authors. DM, RM, BK, AS, NU, EMM, BM, HB, BEG, TKR was involved in the review writing; PKDM, AR, TV, SA, PP, ANG, SD was involved in manuscript refinement and important intellectual content discussion; BK, DM, NU, RM was involved in manuscript figure and table preparation and DM, RM, BK initiated the idea of the review.

ACKNOWLEDGEMENTS

The authors are thankful to Raiganj University, India; University of Tabriz, Iran; ICAR - National Rice Research Institute, India; ICAR - Indian Institute of Horticultural Research, India; Ravenshaw University, India; Forest Research Institute, India; Ministry of Education, Myanmar; Cadi Ayyad University, Morocco; Universidad de Santander, Colombia; Institute for Forage Crops, Republic of Serbia; University of Niš, Republic of Serbia and Graphic Era (Deemed to be University) India for the support. DM is grateful to the Government of West Bengal, India for Swami Vivekananda Merit Cum Means Ph.D. Scholarship.

REFERENCES

Abd-Alla MH, El-Sayed ESA, Rasmey AHM. 2013. Indole-3-acetic acid (IAA) production by *Streptomyces atrovirens* isolated from rhizospheric soil in Egypt. *J Biol Earth Sci* **3(2):**182-93.

AbdElgawad H., Saleh AM, Al Jaouni S, Selim S, Hassan MO, Wadaan MA, Shuikan AM, Mohamed HS, Hozzein WN. 2019. Utilization of Actinobacteria to enhance the production and quality of date palm (*Phoenix dactylifera* L.) fruits in a semi-arid environment. *Sci Total Environ* **665**:690-697.

Adhya TK, Lal B, Mohapatra B, Paul D, Das S. 2018. Eds. Advances in soil microbiology, recent trends and future prospects. Volume 1: Soil-Microbe Interaction. Springer, Singapore, pp 197.

Ahmed E, Holmström SJ. 2014. Siderophores in environmental research, roles and applications. *Microbial Biotechnol* **7(3)**:196-208.

Aldesuquy HS, Mansour FA, Abo-hamed SA. 1998. Effect of the culture filtrates of *Streptomyces* on growth and productivity of wheat plants. *Folia Microbiol* **43**:465-470.

Al-Dhabi NA, Esmail GA, Ghilan AK, Arasu MV. 2020. Isolation and screening of *Streptomyces* sp. Al-Dhabi-49 from the environment of Saudi Arabia with concomitant production of lipase and protease in submerged fermentation. *Saudi J Biol Sci* **27(1)**:474-479.

Anukool U, Gaze WH, Wellington EM. 2004. *In situ* monitoring of streptothricin production by Streptomyces rochei F20 in soil and rhizosphere. *Appl Environ Microbiol* **70(9)**:5222-5228.

Anwar S, Ali B, Sajid I. 2016. Screening of rhizospheric actinomycetes for various *in-vitro* and *in-vivo* plant growth promoting (PGP) traits and for agro-active compounds. *Front Microbiol* **7**:1334.

Araújo JMD, Silva ACD, Azevedo JL. 2000. Isolation of endophytic *actinomycetes* from roots and leaves of maize (*Zea mays* L.). *Br Arch Biol Technol* **43**:447–451.

Asadu CO, Aneke NG, Egbuna SO, Agulanna AC. 2018. Comparative studies on the impact of bio-fertilizer produced from agro-wastes using thermo-tolerant actinomycetes on the growth performance of Maize (*Zea-mays*) and Okro (*Abelmoschus esculentus*). *Environ Technol Inno* **12**:55-71.

Aslam F, Ali B. 2018. Halotolerant bacterial diversity associated with *Suaeda fruticosa* (L.) forssk. improved growth of maize under salinity stress. *Agronomy* **8(8):**131.

Atkinson NJ, Urwin PE. 2012. The interaction of plant biotic and abiotic stresses: from genes to the field. *J Exp Bot* **63(10):**3523–3543.

Awla HK, Kadir J, Othman R, Rashid TS, Wong MY. 2016. Bioactive compounds produced by *Streptomyces* sp. isolate UPMRS4 and antifungal activity against *Pyricularia oryzae*. *Am J Plant Sci* **7(7)**:1077.

Baharlouei A, Sharifi-Sirchi GR, Bonjar GS. 2011. Biological control of *Sclerotinia sclerotiorum* (oilseed rape isolate) by an effective antagonist *Streptomyces*. *Afr J Biotechnol* **10(30)**:5785-5794.

Banik S, Dey BK. 1982. Available phosphate content of an alluvial soil as influenced by inoculation of some isolated phosphate-solubilizing micro-organisms. *Plant Soil* **69(3)**:353-364.

Bao Y, Feng Y, Stegen JC, Wu M, Chen R, Liu W, Zhang J, Li Z, Lin X. 2020. Straw chemistry links the assembly of bacterial communities to decomposition in paddy soils. *Soil Biol Biochem* pp107866.

Bar-Even A, Noor E, Savir Y, Liebermeister W, Davidi D, Tawfik DS Milo R. 2011. The moderately efficient enzyme, evolutionary and physicochemical trends shaping enzyme parameters. *Biochemistry* **50(21):** 4402-4410.

Barnawal D, Bharti N, Pandey SS, Pandey A, Chanotiya CS, Kalra A. 2017. Plant growth-promoting rhizobacteria enhance wheat salt and drought stress tolerance by altering endogenous phytohormone levels and TaCTR1/TaDREB2 expression. *Physiol Plant*. **161**: 502-14.

Barreto TR, Silva A, Soares ACF, Souza JTD. 2008. Population densities and genetic diversity of actinomycetes associated to the rhizosphere of *Theobroma cacao*. *Braz J Microbiol* **39(3):** 464-470.

Behal V. 2000. Bioactive products from, *Streptomyces*. *Adv Appl Microbiol.* **47**: 113-157.

Berry AM, Harriott OT, Moreau R A, Osman SF, Benson DR, Jones AD. 1993. Hopanoid lipids compose the *Frankia* vesicle envelope, presumptive barrier of oxygen diffusion to nitrogenase. *Proc Natl Acad Sci USA* **90(13):** 6091-6094.

Book AJ, Yennamalli RM, Takasuka TE, Currie CR, Phillips GN, Fox BG. 2014. Evolution of substrate specificity in bacterial AA10 lytic polysaccharide monooxygenases. *Biotechnol Biofuels* **7(1):**109.

Boukaew S, Prasertsan P. 2014. Suppression of rice sheath blight disease using a heat stable culture filtrate from *Streptomyces philanthi* RM-1-138. *Crop Prot* **61:**1-10.

Buckley DH, Huangyutitham V, Hsu SF, Nelson TA. 2007. Stable isotope probing with 15N2 reveals novel non-cultivated diazotrophs in soil. *Appl Environ Microbiol* **73(10):**3196-3204.

Callaham D, Deltredici P, Torrey JG. 1978. Isolation and cultivation in vitro of the *actinomycete* causing root nodulation in Comptonia. *Science* **199:**899–902.

Carrano CJ, Jordan M, Drechsel H, Schmid DG, Winkelmann G. 2001. Heterobactins, a new class of siderophores from *Rhodococcus erythropolis* IGTS8 containing both hydroxamate and catecholate donor groups. *Biomet* **14(2):**119-125.

Carro L, Spröer C, Alonso P, Trujillo ME. 2012. Diversity of *Micromonospora* strains isolated from nitrogen fixing nodules and rhizosphere of *Pisum sativum* analyzed by multilocus sequence analysis. *Syst Appl Microbiol* **35(2):**73-80.

Challis GL, Ravel J. 2000. Coelichelin, a new peptide siderophore encoded by the *Streptomyces coelicolor* genome, structure prediction from the sequence of its non-ribosomal peptide synthetase. *FEMS Microbiol Lett* **187(2):**111-114.

Chen XW, Wu L, Luo N, Mo CH, Wong MH, Li H. 2019. Arbuscular mycorrhizal fungi and the associated bacterial community influence the uptake of cadmium in rice. *Geoderma* **337:**749-757.

Chen Y, Shafi J, Li M, Fu D, Ji M. 2018a. Insecticidal activity of endophytic actinomycetes isolated from *Azadirachta indica* against Myzus persicae. *Arch Biol Sci* **70(2):**349-357.

Chen Y, Zhou D, Qi D, Gao Z, Xie J, Luo Y. 2018b. Growth promotion and disease suppression ability of a *Streptomyces* sp. CB-75 from banana rhizosphere soil. *Front Microbiol* **8:**2704.

Cheng Y, Yang R, Lyu M, Wang S, Liu X, Wen Y, Song Y, Li J, Chen Z. 2018. IdeR, a DtxR family iron response regulator, controls iron homeostasis, morphological differentiation, secondary metabolism, and the oxidative stress response in *Streptomyces avermitilis*. *Appl Environ Microbiol* **84(22):**e01503-18.

Chitraselvi RPE, Kalidass S. 2017. Biocontrol activity of *Streptomyces violarus* bioformulation against leaf blight disease of groundnut. *Trends Bio Sci* **10(39):**8249-8251.

Choi H Y, Van Minh N, Choi JM, Hwang JY, Seo ST, Lee SK, Kim, WG. 2018. Enzymatic synthesis of avermectin B 1a glycosides for the effective prevention of the pine wood nematode *Bursaphelenchus xylophilus*. *Appl Microbiol Biot* **102(5):**2155-2165.

Chukwuneme CF, Babalola OO, Kutu FR, Ojuederie OB. 2020. Characterization of actinomycetes isolates for plant growth promoting traits and their effects on drought tolerance in maize. *J Plant Interact* **15(1)**:93-105.

Čihák M, Kameník Z, Šmídová K, Bergman N, Benada O, Kofroňová O, Petříčková K, Bobek J. 2017. Secondary metabolites produced during the germination of *Streptomyces coelicolor*. *Front Microbiol* **8:**2495.

Coombs JT, Franco CM. 2003. Isolation and identification of Actinobacteria from surface-sterilized wheat roots. *Appl Environ Microbiol* **69(9):**5603-5608.

Coombs JT, Michelsen PP, Franco CMM. 2004. Evaluation of endophytic Actinobacteria as antagonists of *Gaeumannomyces graminis* var. tritici in wheat. *Biol Control* **29:**359–366.

Coppola S, Giannattasio M. 1968. Cytokinin activity in a rhizospheric actinomyces. *Boll Soc Ital Biol Sper* **44(22):** 1913-1915.

Corrêa TLR, Júnior AT, Wolf LD, Buckeridge MS, dos Santos LV, Murakami, MT. 2019. An actinobacteria lytic polysaccharide monooxygenase acts on both cellulose and xylan to boost biomass saccharification. *Biotechnol Biofuels* **12(1):**117.

Dahal B, NandaKafle G, Perkins L, Brözel VS. 2017. Diversity of free-Living nitrogen fixing Streptomyces in soils of the badlands of South Dakota. *Microbiol Res* **195:**31-39.

Dai Z, Su W, Chen H, Barberán A, Zhao H, Yu M, Yu L, Brookes PC, Schadt CW, Chang SX, Xu J. 2018. Long-term nitrogen fertilization decreases bacterial diversity and favors the growth of Actinobacteria and Proteobacteria in agro-ecosystems across the globe. *Glob Chang Biol*. **24**: 3452-3461.

Dalal JM, Kulkarni NS. 2014. Antagonistic and plant growth promoting potentials of indigenous endophytic actinomycetes of soybean (*Glycine max* (L) Merril). *CIB Tech J Microbiol* **3:** 1-12.

Das M, Royer TV, Leff LG. 2007. Diversity of fungi, bacteria, and actinomycetes on leaves decomposing in a stream. *Appl Environ Microbiol* **73(3):**756-767.

Dastager SG, Deepa C, Pandey A. 2010. Isolation and characterization of novel plant growth promoting *Micrococcus* sp. NII-0909 and its interaction with cowpea. *Plant Physiol Biochem* **48(12):**987–992.

de Menezes AB, Prendergast-Miller MT, Poonpatana P, Farrell M, Bissett A, Macdonald LM, Toscas P, Richardson AE, Thrall PH. 2015. C/N ratio drives soil actinobacterial cellobiohydrolase gene diversity. *Appl Environ Microbiol* **81(9):**3016-3028.

De Oliveira LG, Gonzalez GDT, Samborsky M, Marcon J, Araujo WL, de Azevedo JL. 2014. Genome sequence of *Streptomyces wadayamensis* strain A23, an endophytic actinobacterium from *Citrus reticulata*. *Genom Ann* **2(4):**e00625-14.

Delangiz N., Khoshru B., Asgari Lajayer B., Ghorbanpour M., Kazemalilou S. 2020. Molecular Mechanisms of Heavy Metal Tolerance in Plants. In: Faisal M., Saquib Q., Alatar A.A., Al-Khedhairy A.A. (eds) Cellular and Molecular Phytotoxicity of Heavy Metals. Nanotechnology in the Life Sciences. Springer, *Cham*. https://doi.org/10.1007/978-3-030-45975-8_8

Dhanasekaran D, Sivamani P, Pannerselvam A, Thajuddin N, Rajakumar G, Selvamani S. 2005. Biological control of tomato seedling damping off with *Streptomyces* sp. *Plant Pathol J* **4:**91-95.

Djebaili R, Pellegrini M, Smati M, Gallo MD, Kitouni M. 2020. Actinomycete Strains Isolated from Saline Soils, Plant-Growth-Promoting Traits and Inoculation Effects on *Solanum lycopersicum*. *Sustainability* **12:**4617.

Dobbelaere S, Croonenborghs A, Thys A, Broek AV, Vanderleyden J. 1999. Phytostimulatory effect of *Azospirillum brasilense* wild type and mutant strains altered in IAA production on wheat. *Plant soil* **212(2):**153-162.

Donnelly PK, Crawford DL. 1988. Production by *Streptomyces viridosporus* T7A of an enzyme which cleaves aromatic acids from lignocellulose. *Appl Environ Microbiol* **54(9):**2237-2244.

Dudeja SS, Giri R, Saini R, Suneja-Madan P, Kothe E. 2012. Interaction of endophytic microbes with legumes. *J Basic Microbiol* **52:**248–260.

Elbendary AA, Hessain AM, El-Hariri MD, Seida AA, Moussa IM, Mubarak AS, Kabli SA, Hemeg HA, El Jakee JK. 2018. Isolation of antimicrobial producing Actinobacteria from soil samples. *Saudi J Biol Sci* **25(1):**44-46.

El-khawaga MA, Megahed, MMM. 2012. Antibacterial and insecticidal activity of actinomycetes isolated from sandy soil of (Cairo-Egypt). *Egypt Acad J Biol Sci* **4(1):**53-67.

El-Sayed HE, Othaimen HS, Aburas MMA, Jastaniah SD. 2015. Efficiency of an Cd-tolerant actinomycete isolate obtained from wastewater in removal of heavy metals and enhancing plant growth of *Zea mays* L. plant. *Int J Curr Microbiol Appl Sci* **4:**553-565.

El-Tarabily K, Alkhajeh. 2016. A field performance of endophytic actinomycetes in relation to plant growth promotion and biological control of *Fusarium oxysporum* a pathogen of tomato. In., vol. 106. Amer phytopathological soc 3340 pilot knob road, St Paul, MN 55121 USA, pp. 55–55.

El-Tarabily KA, Nassar AH, Hardy GSJ, Sivasithamparam K. 2009. Plant growth promotion and biological control of Pythium aphanidermatum, a pathogen of cucumber, by endophytic actinomycetes. *J Appl Microbiol*. **106**:13-26.

El-Tarabily KA, Nassar AH, Sivasithamparam K. 2008. Promotion of growth of bean (*Phaseolus vulgaris* L.) in a calcareous soil by a phosphate solubilizing, rhizosphere-competent isolate of *Micromonospora endolithica*. *Appl Soil Ecol* **39(2):**161-171.

El-Tarabily KA, Soliman MH, Nassar AH, Al-Hassani HA, Sivasithamparam K, McKenna F, Hardy GSJ. 2000. Biological control of Sclerotinia minor using a chitinolytic bacterium and actinomycetes. *Plant Pathol*. **49**(5): 573-583.

El-Tarabily KA. 2008. Promotion of tomato (*Lycopersicon esculentum* Mill.) plant growth by rhizosphere competent 1-aminocyclopropane-1-carboxylic acid deaminase-producing *streptomycete* actinomycetes. *Plant Soil* **308:**161-174.

Errakhi R, Bouteau F, Lebrihi A, Barakate M. 2007 Evidences of biological control capacities of *Streptomyces* spp. against *Sclerotium rolfsii* responsible for damping-off disease in sugar beet (*Beta vulgaris* L.). *World J Microbiol Biotechnol* **23(11)**: 1503-1509.

Farhat MB, Boukhris I, Houayekh H. 2015. Mineral phosphate solubilization by *Streptomyces* sp. CTM396 involves the excretion of gluconic acid and is stimulated by humic acids. *FEMS Microbiol Lett* **362(5):**fnv008.

Farina R, Beneduzi A, Ambrosini A, de Campos SB, Lisboa BB, Wendisch V, Vargas LK, Passaglia LM. 2012. Diversity of plant growth-promoting rhizobacteria communities associated with the stages of canola growth. *Appl Soil Ecol* **55(1):**44-52.

Fiebig D, Storka J, Roeder M, Meyners C, Schmelz S, Blankenfeldt W, Scrima A, Kolmar H, Fuchsbauer HL. 2018. Destructive twisting of neutral metalloproteases, the catalysis mechanism of the Dispase autolysis-inducing protein from Streptomyces mobaraensis DSM 40487. *FEBS J.* **285**: 4246-4264.

Fodil D, Badis A, Jaouadi B, Zaraî N, Ferradji FZ, Boutoumi H. 2011. Purification and characterization of two extracellular peroxidases from *Streptomyces* sp. strain AM2, a decolorizing actinomycetes responsible for the biodegradation of natural humic acids. *Int Biodeter Biodegr* **65(3):**470-478.

Forsberg Z, Vaaje-Kolstad G, Westereng B, Bunæs AC, Stenstrøm Y, MacKenzie A, Sørlie M, Horn SJ, Eijsink VG. 2011. Cleavage of cellulose by a CBM33 protein. *Protein Sci.* **20**:1479-1483.

Franco-Correa M, Quintana A, Duque C, Suarez C, Rodríguez MX, Barea JM. 2010. Evaluation of actinomycete strains for key traits related with plant growth promotion and mycorrhiza helping activities. *Appl Soil Ecol* **45(3):**209-217.

Gadelhak GG, El-Tarabily KA, Al-Kaabi FK. 2005. Insect control using chitinolytic soil actinomycetes as biocontrol agents. *Int J Agri Biol* **7(4):**627-633.

Gange AC, Gadhave KR. 2018. Plant growth-promoting rhizobacteria promote plant size inequality. *Sci Rep* **8(1):**1-10.

Gangwar M, Rani S, Sharma N (2012) Investigating endophytic actinomycetes diversity from rice for plant growth promoting and antifungal activity. *IJALS* 1.

Garcia LC, Martínez-Molina E, Trujillo ME. 2010. *Micromonospora* pisi sp. nov., isolated from root nodules of *Pisum sativum*. *Int J Syst Evol Microbiol* **60(2):**331-337.

Getha K, Vikineswary S. 2002. Antagonistic effects of *Streptomyces violaceusniger* strain G10 on *Fusarium oxysporum* f. sp. cubense race 4, indirect evidence for the role of antibiosis in the antagonistic process. *J Ind Microbiol Biot* **28(6):**303-310.

Ghodhbane-Gtari F, Essoussi I, Chattaoui M, Chouaia B, Jaouani A, Daffonchio D, Boudabous A, Gtari M. 2010. Isolation and characterization of non-*Frankia* Actinobacteria from root nodules of *Alnus glutinosa, Casuarina glauca* and *Elaeagnus angustifolia*. *Symbiosis* **50(1-2):**51-57.

Ghorbani-Nasrabadi R, Greiner R, Alikhani HA, Hamedi J. 2012. Identification and determinationof extracellular phytate-degrading activity in actinomycetes. *World J Microbiol Biotechnol* **28(7):**2601-2608.

Ghosh S, Penterman JN, Little RD, Chavez R, Glick BR. 2003. Three newly isolated plant growth-promoting bacilli facilitate the seedling growth of canola, *Brassica campestris*. *Plant Physiol Biochem* **41(3):**277-281.

Goodfellow M, Kampfer P, Busse HJ, Trujillo ME, Suzuki K, Ludwig W, Whitman WB. 2012. Taxonomic outline of the phylum Actinobacteria. In,Whitman WB Editor. Bergey's Manual of Systematic Bacteriology, 2nd edition. New York, Springer 1-2024.

Gopalakrishnan S, Srinivas V, Alekhya G, Prakash B, Kudapa H, Rathore A, Varshney RK. 2015b. The extent of grain yield and plant growth enhancement by plant growth-promoting broad-spectrum *Streptomyces* sp. in chickpea. *Springer Plus* **4(1):**31.

Gopalakrishnan S, Srinivas V, Vidya MS, Rathore A. 2013. Plant growth promoting activities of *Streptomyces* spp. in sorghum and rice. *Springer Plus* **2:**574

Gopalakrishnan S, Vadlamudi S, Alekhya G, Prakash B, Kudapa H, Varshney RK. 2015a. Evaluation of *Streptomyces* spp. Obtained from herbal vermicompost for broad spectrum of plant growth promoting activities in Chickpea. *Organ Agricul* **5:**123-133.

Gopalakrishnan S, Vadlamudi S, Bandikinda P, Sathya A, Vijayabharathi R, Rupela O, Kudapa H, Katta K, Varshney RK. 2014. Evaluation of *Streptomyces* strains isolated from herbal vermicompost for their plant growth-promotion traits in rice. *Microbiol Res* **169(1):**40-48.

Goriely A, Tabor M. 2003. Biomechanical models of hyphal growth in actinomycetes. *J Theor Biol* **222(2):**211-218.

Goudjal Y, Toumatia O, Sabaou N, Barakate M, Mathieu F, Zitouni A. 2013. Endophytic actinomycetes from spontaneous plants of Algerian Sahara, indole-3-acetic acid production and tomato plants growth promoting activity. *World J Microbiol Biotechnol* **29(10):**1821-1829.

Goudjal Y, Toumatia O, Yekkour A, Sabaou N, Mathieu F, Zitouni A. 2014. Biocontrol of *Rhizoctonia solani* damping off and promotion of tomato plant growth by endophytic actinomycetes isolated form native plants of Algerian Sahara. *Microbiol Res* **169(1):**59- 65.

Goudjal Y, Zamoum M, Meklat A, Sabaou N, Mathieu F, Zitouni A. 2016. Plant-growthpromoting potential of endosymbiotic Actinobacteria isolated from sand truffles (*Terfezia leonis* Tul.) of the Algerian Sahara. *Ann Microbiol* **66(1):**91-100.

Grover M, Bodhankar S, Maheswari M, Srinivasarao C. 2016. Actinomycetes as mitigators of climate change and abiotic stress. In. Plant Growth Promoting Actinobacteria. Springer, Singapore. pp. 203-212.

Guang-Can TAO, Shu-Jun TIAN, Miao-Ying CAI, Guang-Hui XIE. 2008. Phosphatesolubilizing and-mineralizing abilities of bacteria isolated from soils. *Pedosphere* **18(4):**515-523.

Guevara G, Lopez MC, Alonso S, Perera J, Navarro-Llorens JM. 2019. New insights into the genome of *Rhodococcus ruber* strain Chol-4. *BMC genomics* **20(1):**332.

Gupta N, Sahoo D, Basak UC. 2010. Evaluation of in vitro solubilization potential of phosphate solubilising *Streptomyces* isolated from phyllosphere of Heritiera fomes (mangrove). *Afr J Microbiol Res* **4(3):**136-142.

Gupta R, Saxena RK, Chaturvedi P, Virdi JS. 1995. Chitinase production by *Streptomyces viridificans*, its potential in fungal cell wall lysis. *J Appl Bacteriol* **78(4):**378-383.

Hamdali H, Bouizgarne B, Hafidi M, Lebrihi A, Virolle MJ, Ouhdouch Y. 2008b. Screening for rock phosphate-solubilizing Actinomycetes from Moroccan phosphate mines. *Appl Soil Ecol* **38:**12-19.

Hamdali H, Hafidi M, Virolle MJ, Ouhdouch Y. 2008a. Growth promotion and protection against damping-off of wheat by two rock phosphate solubilizing actinomycetes in a P-deficient soil under greenhouse conditions. *Appl Soil Ecol* **40(3):**510-507.

Hamdali H, Hafidi M, Virolle MJ, Ouhdouch Y. 2008c. Rock phosphate-solubilizing Actinomycetes, screening for plant growth-promoting activities. *World J Microbiol Biotechnol* **24(11):**2565-2575.

Han D, Wang L, Luo Y. 2018. Isolation, identification, and the growth promoting effects of two antagonistic actinomycete strains from the rhizosphere of *Mikania micrantha* Kunth. *Microbiol Res* **208:**1-11.

Harikrishnan H, Shanmugaiah V, Balasubramanian N. 2014. Optimization for production of Indole acetic acid (IAA) by plant growth promoting *Streptomyces* sp VSMGT1014 isolated from rice rhizosphere. *Int J Curr Microbiol Appl Sci* **3(8):**158-71.

Hasani A, Kariminik A, Issazadeh K. 2014. *Streptomycetes*, characteristics and their antimicrobial activities. *IJABBR* **2(1):**63-75.

Heidarpour A, Aliasgharzad N, Khoshmanzar E, Khoshru B, Lajayer BA. 2019. Bio-removal of Zn from contaminated water by using green algae isolates. *Environ Technol Innov* **16**, p.100464.

Hozzein WN, Abuelsoud W, Wadaan MA, Shuikan AM, Selim S, Al Jaouni S, AbdElgawad H. 2019. Exploring the potential of actinomycetes in improving soil fertility and grain quality of economically important cereals. *Sci Total Environ* **651:**2787-2798.

Hurek T, Handley LL, Reinhold-Hurek B, Piché Y. 2002. *Azoarcus* grass endophytes contribute fixed nitrogen to the plant in an unculturable state. *Mol Plant Microbe Interact* **15:**233–242.

Hwang BK, Ahn SJ, Moon SS. 1994. Production, purification, and antifungal activity of the antibiotic nucleoside, tubercidin, produced by Streptomyces violaceoniger. *Can J Bot* **72(4):**480-485.

Igarashi Y, Iida T, Yoshida R, Furumai T. 2002. Pteridic acids A and B, novel plant growth promoters with auxin-like activity from *Streptomyces hygroscopicus* TP-AO451. *J Antibiot* **55(8):**764-767.

Ilsan NA, Nawansih AA, Wahyudi AT. 2016. Rice phyllosphere actinomycetes as biocontrol agent of bacterial leaf blight disease on rice. *Asian J Plant Pathol* **10:**1-8.

Imchen M, Kumavath DR, Vaz A, Góes-Neto A, Barh D, Ghosh P, Kozyrovska NO, Podolich O, Azevedo VADC. 2019. 16S rRNA gene amplicon based metagenomic signatures of rhizobiome community in rice field during various growth stages. *Front. microbiol* **10**, 2103.

Jaemsaeng R, Jantasuriyarat C, Thamchaipenet A. 2018. Molecular interaction of 1-aminocyclopropane-1-carboxylate deaminase (ACCD)-producing endophytic *Streptomyces* sp. GMKU 336 towards salt-stress resistance of *Oryza sativa* L. cv. KDML105. *Sci Rep* **8(1):**1-15.

Jaemsaeng R, Jantasuriyarat C, Thamchaipenet A. 2018. Molecular interaction of 1-aminocyclopropane-1-carboxylate deaminase (ACCD)-producing endophytic *Streptomyces* sp. GMKU 336 towards salt-stress resistance of *Oryza sativa* L. cv. KDML105. *Sci Rep* **8(1):**1-5.

Janardhan A, Kumar AP, Viswanath B, Saigopal DVR, Narasimha G. 2014. Production of bioactive compounds by actinomycetes and their antioxidant properties. *Biotechnol Res Int.* Article ID **217030**, 8.

Jang SW, Yoou MH, Hong WJ, Kim YJ, Lee EJ, Jung KH. 2020. Re-Analysis of 16S Amplicon Sequencing Data Reveals Soil Microbial Population Shifts in Rice Fields under Drought Condition. *Rice* **13(1)**:1-7.

Janusz G, Pawlik A, Sulej J, Świderska-Burek U, Jarosz-Wilkołazka A, Paszczyński A. 2017. Lignin degradation, microorganisms, enzymes involved, genomes analysis and evolution. *FEMS Microbiol Rev* **41(6):**941-962.

Jayakumar J. 2009. *Streptomyces avermitilis* as a biopesticide for the management of humid regions (AER 3 and AER 6) and their effect on growth and yield of Maize (*zea mays* L.) and Chickpea (*cicer arietinum*). Ph.D Thesis, Univ. Agric. Sci GKVK, Bengaluru.

Jog R, Nareshkumar G, Rajkumar S. 2012. Plant growth promoting potential and soil enzyme production of the most abundant *Streptomyces* spp. from wheat rhizosphere. *J Appl Microbiol* **113(5):**1154-1164.

Jog R, Pandya M, Nareshkumar G, Rajkumar S. 2014. Mechanism of phosphate solubilization and antifungal activity of *Streptomyces* spp. isolated from wheat roots and rhizosphere and their application in improving plant growth. *Microbiol* **160(4):**778-788.

Joo GJ (2005) Production of an anti-fungal substance for biological control of *Phytophthora capsici* causing phytophthora blight in red-peppers by *Streptomyces halstedii*. *Biotech Letters* **27(3):**201-205.

Kanini GS, Katsifas EA, Savvides AL, Hatzinikolaou DG, Karagouni AD. 2013. Greek indigenous Streptomycetes as biocontrol agents against the soil-borne fungal plant pathogen Rhizoctonia solani. *J Appl Microbio*. **114**:1468-1479.

Kannahi M, Senbagam N. 2014. Studies on siderophore production by microbial isolates obtained from rhizosphere soil and its antibacterial activity. *J Chem Pharm Res* **6(4):**1142-1145.

Karlidag H, Esitken A, Turan M, Sahin F. 2007. Effects of root inoculation of plant growth promoting rhizobacteria (PGPR) on yield, growth and nutrient element contents of leaves of apple. *Sci Horticul* **114(1):**16-20.

Kaur H, Kaur J, Gera R. 2016. Plant Growth Promoting Rhizobacteria, A Boon to Agriculture. *Int J Cell Sci Biotechnol* **5:**17-22.

Kaushal M, Mahuku G, Swennen R. 2020. Metagenomic insights of the root colonizing microbiome associated with symptomatic and non-symptomatic bananas in fusarium wilt infected fields. *Plants*, **9(2)**:p.263.

Kekuda PTR, Onkarappa R, Jayanna ND. 2014. Characterization and antibacterial activity of a glycoside antibiotic from *Streptomyces variabilis* PO-178. *Sci Technol Arts Res* J **3:**116–121.

Khalil MS, Moubasher H, Hasan FF. 2014. Biological control of rice blast disease by *Streptomyces flavotricini*. *RJPBCS* **5(5):**1453-1461.

Khamna S, Yokota A, Peberdy JF, Lumyong S. 2010. Indole-3-acetic acid production by *Streptomyces* sp. isolated from some Thai medicinal plant rhizosphere soils. *Eurasia J Biosci* **4:**23-32.

Khan MS, Zaidi A, Ahemad M, Oves M, Wani PA. 2010. Plant growth promotion by phosphate solubilizing fungi–current perspective. *Arch Agron Soil* Sci **56(1):**73-98.

Khoshmanzar E, Aliasgharzad N, Neyshabouri MR, Khoshru B, Arzanlou M, Lajayer BA. 2020. Effects of Trichoderma isolates on tomato growth and inducing its tolerance to water-deficit stress. *IJEST* **17(2):**869-878.

Khoshru B, Mitra D, Khoshmanzar E, Myo EM, Uniyal N, Mahakur B, Mohapatra PK, Panneerselvam P, Boutaj H, Alizadeh M, Cely MV. 2020a. Current scenario and future prospects of plant growth-promoting rhizobacteria: an economic valuable resource for the agriculture revival under stressful conditions. *J Plant Nut.* **30:**1-31.

Khoshru B, Mitra D, Mahakur B, Sarikhani M R and Mondal R. 2020b. Role of soil rhizobacteria in utilization of an indispensable micronutrient - zinc for plant growth promotion, *J Natural Remed* **21(6):**239-251

Khoshru B, Moharramnejad S, Gharajeh NH, Asgari Lajayer B, Ghorbanpour M. 2020c. Plant Microbiome and Its Important in Stressful Agriculture. In: Varma A., Tripathi S., Prasad R. (eds) Plant Microbiome Paradigm. Springer, *Cham*. https://doi.org/10.1007/978-3-030-50395-6_2.

Krogius-Kurikka L, Kassinen A, Paulin L, Corander J, Mäkivuokko H, Tuimala J, Palva A. 2009. Sequence analysis of percent G+ C fraction libraries of human faecal bacterial DNA reveals a high number of Actinobacteria. *BMC microbial* **9:**68.

Kucho KI, Tamari D, Matsuyama S, Nabekura T, Tisa LS. 2017. Nitrogen fixation mutants of the actinobacterium *Frankia casuarinae* CcI3. *Microbes Environ* p.ME17099.

Kumar A, Chandra R. 2020. Ligninolytic enzymes and its mechanisms for degradation of lignocellulosic waste in environment. *Heliyon* **6(2):**p.e03170.

Kumar A, Maurya BR, Raghuwanshi R. 2014. Isolation and characterization of PGPR and their effect on growth, yield and nutrient content in wheat (*Triticum aestivum* L.). *Biocatal Agric Biotechnol* **3:**121–128.

Kumar A, Singh S, Gaurav AK, Srivastava S, Verma JP. 2020. Plant Growth-Promoting Bacteria: Biological Tools for the Mitigation of Salinity Stress in Plants. *Front Microbiol* **11**:1216.

Kumar N, Prasad R, Zaman FU. 2007. Relative response of high yielding variety and a hybrid of rice to levels and sources of nitrogen. *Proc. Nat. Acad. Sci. India Sect* **73(1):**1.

Kumar SV, Sahu MK, Kathiresan K. 2005. Isolation and characterization of *Streptomycetes* producing antibiotics from a mangrove environment. Asian Jr. of Microbial. *Biotech Env Sc* **7(3):**457-464.

Lautru S, Deeth RJ, Bailey LM, Challis GL. 2005. Discovery of a new peptide natural product by *Streptomyces coelicolor* genome mining. *Nat Chem Biol* **1(5):**265.

Law JWF, Ser HL, Khan TM, Chuah LH, Pusparajah P, Chan KG, Goh BH, Lee LH. 2017. The potential of *Streptomyces* as biocontrol agents against the rice blast fungus, *Magnaporthe oryzae* (*Pyricularia oryzae*). *Front Microbiol* **8:**3.

Le Bris M. 2017. Hormones in Growth and Development. *Encyclopedia of Rose Science*, **2003:**364-369.

Lee HB, Kim CJ, Kim JS, Hong KS, Cho KY. 2003. A bleaching herbicidal activity of methoxyhygromycin (MHM) produced by an actinomycete strain Streptomyces sp. 8E-12. *Lett Appl Microbiol.* **36**(6):387-391.

Lee J, Postmaster A, Soon HP, Keast D, Carson KC. 2012. Siderophore production by actinomycetes isolates from two soil sites in Western Australia. *Biomet* **25(2):**285-296.

Lee LH, Zainal N, Azman AS, Eng SK, A Mutalib NS, Yin WF, Chan KG. 2014. *Streptomyces pluripotens* sp. nov., a bacteriocin-producing *Streptomycete* that inhibits meticillin-resistant *Staphylococcus aureus*. *Int J Syst Evol Micro* **64(9):**3297-3306.

Limaye L, Patil R, Ranadive P, Kamath G. 2017. Application of potent actinomycete strains for bio-degradation of domestic agro-waste by composting and treatment of pulp-paper mill effluent. *Adv Microbiol* **7(1):**94-108.

Liu K, McInroy JA, Hu CH, Kloepper JW. 2018. Mixtures of plant-growth-promoting rhizobacteria enhance biological control of multiple plant diseases and plant-growth promotion in the presence of pathogens. *Plant Dis* **102(1):**67-72.

Liu X, Bolla K, Ashforth EJ, Zhuo Y, Gao H, Huang P, Stanley SA, Hung DT, Zhang L, (2012) Systematics-guided bioprospecting for bioactive microbial natural products. *Anton Leeuw Int J G* **101(1):**55-66.

Lu C, Li JM, Qi H, Zhang H, Zhang J, Xiang WS, Wang JD, Wang XJ. 2018. Two new lankacidin-related metabolites from *Streptomyces* sp. HS-NF-1178. *J Antibiot* **71(3):**397.

Lu CG, Liu WC, Qiu JY, Wang HM, Liu T, Liu DW. 2008. Identification of an antifungal metabolite produced by a potential biocontrol *Actinomyces* strain A01. *Braz J Microbiol* **39:**701-707.

Lu D, Ma Z, Xu X, Yu X. 2016. Isolation and identification of biocontrol agent *Streptomyces rimosus* M527 against *Fusarium oxysporum* f. sp. cucumerinum. *J Basic Microb* **56(8):**929-933.

Lunggani AT, Suprihadi A. 2019. Characterization phosphate-solubilizing marine actinobacteria associated with Sargassum Sp from Menjangan kecil island, Indonesia. In Journal of Physics, *Conference Series* (Vol. 1217, No. 1, p. 012161). IOP Publishing.

Lyu A, Liu H, Che H, Yan, L, Zhang J, Wu M, Chen W, Li G. 2017. Reveromycins A and B from *Streptomyces* sp. 3–10, antifungal activity against plant pathogenic fungi *in vitro* and in a strawberry food model system. *Front Microbiol* **8:**550.

Mahadevan B, Crawford DL. 1997. Properties of the chitinase of the antifungal biocontrol agent Streptomyces lydicus WYEC108. Enz *Microb Technol* **20(7):**489-493.

Maldonado MC, Orosco CEF, Gordillo M, Navarro AR. 2010. *in vivo* and *in vitro* antagonism of *Streptomyces* sp. RO3 against *Penicillium digitatum* and *Geotrichum candidum*. *Afr J Microbiol Res* **4(22):**2451-2456.

Marella S. 2014. Bacterial endophytes in sustainable crop production, Applications, recent developments and challenges ahead. *Int J Life Sci Res* **2:**46–56.

Martínez-Hidalgo P, García JM, Pozo MJ. 2015. Induced systemic resistance against *Botrytis cinerea* by *Micromonospora* strains isolated from root nodules. *Front Microbiol* **6:**922.

Meena KK, Bitla UM, Sorty AM, Singh DP, Gupta VK, Wakchaure GC, Kumar S. 2020. Mitigation of Salinity Stress in Wheat Seedlings Due to the Application of Phytohormone-Rich Culture Filtrate Extract of Methylotrophic Actinobacterium *Nocardioides* sp. NIMMe6. *Front Microbiol* **11**:2091.

Meguro A, Ohmura Y, Hasegawa S, Shimizu M, Nishimura T, Kunoh H. 2006. An endophytic actinomycete, *Streptomyces* sp. MBR-52, that accelerates emergence and elongation of plant adventitious roots. *Actinomycetologica* **20(1):**1-9.

Mekasha S, Tuveng TR, Askarian F, Choudhary S, Schmidt-Dannert C, Niebisch A, Modregger J, Vaaje-Kolstad G, Eijsink VG. 2020. A tri-modular bacterial enzyme combining hydrolytic activity with oxidative glycosidic bond cleavage efficiently degrades chitin. *J Biol Chem jbc-RA*120.

Menendez E, Carro L. 2019. Actinobacteria and Their Role as Plant Probiotics. In Biofertilizers for Sustainable Agriculture and Environment. Springer, *Cham* 333-351.

Merckx R, Dijkra A, Hartog AD, Veen JAV. 1987. Production of root derived material and associated microbial growth in soil at different nutrient levels. *Biol Fertil Soils* **5:**126-132.

Mishra M (2013) Role of eco-friendly agricultural practices in Indian agriculture development. *Int J Res Agric Food Sci* **4(2):**11-15.

Misra S, Dixit VK, Khan MH, Mishra SK, Dviwedi G, Yadav S, Lehri A, Chauhan PS. 2017. Exploitation of agro-climatic environment for selection of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase producing salt tolerant indigenous plant growth promoting rhizobacteria. *Microbiol Res* 205:25-34.

Mohamed SH, Galal AM. 2005. Identification and antiviral activities of some halotolerant Streptomycetes isolated from Qaroon Lake. *Int J Agric Biol* **7(5):**747-753.

Molano A, Algecira N, Bernal J, Franco-Correa M. 2000. Evaluation and selection of a culture medium from actinomycetes. In, Memories of the 2th International Congress of Industrial Microbiology; May 10-12; Bogotá D.C. Pontifical Javeriana University.

Monteiro P, Borba MP, Van Der Sand ST. 2017. Evaluation of the antifungal activity of *Streptomyces* sp. on *Bipolaris sorokiniana* and the growth promotion of wheat plants. *J Agric Sci* **9(12):**229.

Moore JM, Bradshaw E, Seipke RF, Hutchings MI, Mc Arthur M. 2012. Use and discovery of chemical elicitors that stimulate biosynthetic gene clusters in *Streptomyces* bacteria. In *Methods in Enzymology*. *Academic Press* **517:**367-385.

Myo EM, Ge B, Ma J, Cui H, Liu B, Shi L, Jiang M, Zhang K. 2019. Indole-3-acetic acid production by *Streptomyces fradiae* NKZ-259 and its formulation to enhance plant growth. *BMC microbiology* **19(1):**155.

Nafis A, Raklami A, Bechtaoui N, El Khalloufi F, El Alaoui A, Glick BR, Hafidi M, Kouisni L, Ouhdouch Y, Hassani L. 2019. Actinobacteria from extreme niches in morocco and their plant growth-promoting potentials. *Diversity* **11(8):**139.

Narang RA, Bruene A, Altmann T. 2000. Analysis of phosphate acquisition efficiency in different *Arabidopsis* accessions. *Plant Physiol* **124(4):**1786-1799.

Nascimento RP, Coelho RRR, Marques S, Alves L, Gırio FM, Bon EPS, Amaral-Collaço MT. 2002. Production and partial characterisation of xylanase from *Streptomyces* sp. strain AMT-3 isolated from Brazilian cerrado soil. *Enzyme Microb Technol* **31(4):**549-555.

Nassar AH, El-Tarabily KA, Sivasithamparam K. 2003. Growth promotion of bean (*Phaseolus vulgaris* L.) by a polyamine-producing isolate of *Streptomyces griseoluteus*. *Plant growth Regul* **40(2):**97-106.

Niewerth H, Schuldes J, Parschat K, Kiefer P, Vorholt JA, Daniel R, Fetzner S. 2012. Complete genome sequence and metabolic potential of the quinaldine-degrading bacterium *Arthrobacter* sp. Rue61a. *BMC genomics* **13(1):**534.

Nimnoi P, Pongsilp N, Lumyong S. 2010. Endophytic actinomycetes isolated from *Aquilaria crassna* Pierre ex Lec and screening of plant growth promoters production. *World J Microbiol Biotechnol* **26(2):**193-203.

Ningthoujam DS, Sanasam S, Tamreihao K, Nimaichand S. 2009. Antagonistic activities of local actinomycete isolates against rice fungal pathogens. *Afr J Microbiol Res* **3(11):**737-742.

Normand P, Lalonde M. 1982. Evaluation of *Frankia* strains isolated from provenances of two Alnus species. *Can J Microbiol* **28(10):**1133-1142.

Nouioui I, Carro L, García-López M, Meier-Kolthoff JP, Woyke T, Kyrpides NC, Pukall R, Klenk HP, Goodfellow M, Göker M. 2018. Genome-based taxonomic classification of the phylum Actinobacteria. *Front Microbiol* **9:** p.2007.

Oberhofer M, Hess J, Leutgeb M, Gössnitzer F, Rattei T, Wawrosch C, Zotchev SB. 2019. Exploring Actinobacteria associated with Rhizosphere and Endosphere of the native alpine medicinal plant Leontopodium nivale subspecies alpinum. *Front microbiol* **10**, p.2531.

Odokonyero D, McMillan AW, Ramagopal UA, Toro R, Truong DP, Zhu M, Lopez MS, Somiari B, Herman M, Aziz A, Bonanno JB. 2018. Comparison of *Alicyclobacillus acidocaldarius* o-Succinylbenzoate Synthase to Its Promiscuous N-Succinylamino Acid Racemase/o-Succinylbenzoate Synthase Relatives. *Biochemistry* **57(26):**3676-3689.

Omura S, Iwai Y, Takahashi Y, Sadakane N, Nakagawa A, Oiwa H, Hasegawa Y, Ikai T. 1979. Herbimycin, a new antibiotic produced by a strain of *Streptomyces*. *J Antibiot* **32(4):**255-261.

Osada H. 1995. Fascinating bioactive compounds from actinomycetes. *Actinomycetologica* **9(2):**254-262.

Oskay M. 2009. Antifungal and antibacterial compounds from Streptomyces strains. *Afr J Biotechnol* **8(13)**.

Ouchari L, Boukeskasse A, Bouizgarne B, Ouhdouch Y. 2019. Antimicrobial potential of actinomycetes isolated from the unexplored hot *Merzouga* desert and their taxonomic diversity. *Biol Open* **8(2):** bio035410.

Oves-Costales D, Kadi N, Challis GL. 2009. The long-overlooked enzymology of a nonribosomal peptide synthetase-independent pathway for virulence-conferring siderophore biosynthesis. *Chem Commun* **43:**6530-6541.

Palaniyandi SA, Damodharan K, Yang SH, Suh JW. 2014. *Streptomyces* sp. strain PGPA39 alleviates salt stress and promotes growth of 'Micro Tom'tomato plants. *J Appl Microbiol* **117(3)**:766-73.

Pandey S, Gupta S. 2019. ACC deaminase producing bacteria with multifarious plant growth promoting traits alleviates salinity stress in French bean (*Phaseolus vulgaris*) plants. *Front Microbiol* **10:**1506.

Panneerselvam P, Kumar U, Anandan A, Selvakumar G, Nayak AK. 2017. Arka Microbial Consortium and Arka Actino Plus for sustainable rice production. ICAR-NRRI, Cuttack. https,//krishi.icar.gov.in/jspui/handle/123456789/16304.

Panneerselvam P, Selvakumar G, Ganeshamurthy AN, Mitra D, Senapati A. 2020. Enhancing pomegranate (*Punica granatum* L.) plant health through the intervention of a *Streptomyces* consortium. *Biocontrol Sci Techn.* DOI: 10.1080/09583157.2020.1859095.

Passari AK, Chandra P, Mishra VK, Leo VV, Gupta VK, Kumar B, Singh BP. 2016. Detection of biosynthetic gene and phytohormone production by endophytic Actinobacteria associated with *Solanum lycopersicum* and their plant-growth-promoting effect. *Res Microbial* **167(8):**692-705.

Passari AK, Mishra VK, Gupta VK, Yadav MK, Saikia R, Singh BP. 2015. *in vitro* and *in vivo* plant growth promoting activities and DNA fingerprinting of antagonistic endophytic actinomycetes associates with medicinal plants. *PLoS one* **10(9):**p. e0139468.

Patel T, Saraf M. 2017. Biosynthesis of phytohormones from novel rhizobacterial isolates and their *in vitro* plant growth-promoting efficacy. *J Plant Interact* **12(1):**480-487.

Patzer SI, Braun V. 2010. Gene cluster involved in the biosynthesis of griseobactin, a catechol-peptide siderophore of *Streptomyces* sp. ATCC 700974. *J Bacteriol* **192(2):**426-435.

Penn K, Jenkins C, Nett M, Udwary DW, Gontang EA, McGlinchey RP, Foster B, Lapidus A, Podell S, Allen EE, Moore BS. 2009. Genomic islands link secondary metabolism to functional adaptation in marine Actinobacteria. *The ISME journal* **3(10):**1193-1203.

Pérez-Montaño F, Alías-Villegas C, Bellogín RA, Del Cerro P, Espuny MR, Jiménez-Guerrero I, López-Baena FJ, Ollero FJ, Cubo T. 2014. Plant growth promotion in cereal and leguminous agricultural important plants, from microorganism capacities to crop production. *Microbiol Res* **169(5-6):**325-336.

Phoebe CH, Cambie J, Albert FG, Van Tran K, Cabrera J, Correira HJ, Guo Y, Lindermuth J, Rauert N, Galbraith W, Selitrennikoff CP. 2001. Extremophilic organisms as an unexplored source of antifungal compounds. *J Antibiotics* **54(1):**56-65.

Phongsopitanun W, Suwanborirux K, Tanasupawat S. 2019. Distribution and antimicrobial activity of Thai marine actinomycetes. *J Appl Pharm Sci* **9(02):**129-134.

Piao Z, Yang L, Zhao L, Yin S. 2008. Actinobacterial community structure in soils receiving long-term organic and inorganic amendments. *Appl Environ Microbiol* **74(2):**526-530.

Pii Y, Mimmo T, Tomasi N, Terzano R, Cesco S, Crecchio C. 2015. Microbial interactions in the rhizosphere, beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process A review. *Biol Fert Soils* **51(4):**403-415.

Pivoto D, Waquil PD, Talamini E, Finocchio CPS, Dalla Corte VF, de Vargas Mores G. 2018. Scientific development of smart farming technologies and their application in Brazil. *Inform Proc Agri* **5(1):**21-32.

Polak EH, Provasi J. 1992. Odor sensitivity to geosmin enantiomers. *Chem Sens* **17:**23–26.

Poovarasan S, Mohandas S, Paneerselvam P, Saritha B, Ajay KM (2013) Mycorrhizae colonizing actinomycetes promote plant growth and control bacterial blight disease of pomegranate (*Punica granatum* L. cv Bhagwa). *Crop Prot* **53:**175-181.

Poovarasan S, Mohandas SST, Usharani TR, Paneerselvam P. 2016. Application of Actinomycetes in Nutrients Management of Guava Crop. ICAR-IIHR.

Prabha R, Singh DP, Gupta S, Gupta VK, El-Enshasy HA, Verma MK. 2019. Rhizosphere Metagenomics of *Paspalum scrobiculatum* L.(Kodo Millet) Reveals Rhizobiome Multifunctionalities. *Microorganisms* **7(12):**p.608.

Pragya R, Yasmin A, Anshula J. 2012. An insight into agricultural properties of actinomycetes. *Int J Res Bio Sci* **1:**7-12.

Prakash R K, Cummings B. 1988. Creation of novel nitrogen-fixing actinomycetes by protoplast fusion of *Frankia* with *streptomyces*. *Plant Mol Boil* **10(3)**: 281-289.

Prapagdee B, Kuekulvong C, Mongkolsuk S. 2008. Antifungal potential of extracellular metabolites produced by *Streptomyces hygroscopicus* against phytopathogenic fungi. *Int J Biol Sci* **4:**330-337.

Quecine MC, Araujo WL, Marcon J, Gai CS, Azevedo JLD, Pizzirani-Kleiner AA. 2008. Chitinolytic activity of endophytic Streptomyces and potential for biocontrol. *Lett in appl microbial.* **47**: 486-491.

Radha TK. 2016. Diversity of Actinomycetes in Crop Rhizosphere of Arid, Semi Arid and Humid Regions (AER 3 and AER 6) and Their Effect on Growth and Yield of Maize (*Zea Mays* L.) and Chickpea (*Cicer Arietinum*) (Doctoral dissertation, University Of Agricultural Sciences Gkvk, Bengaluru).

Raimondo EE, Aparicio JD, Briceño GE, Fuentes MS, Benimeli CS. 2019. Lindane Bioremediation in Soils of Different Textural Classes by an Actinobacteria Consortium. *J Soil Sci Plant Nutr* **19(1):**29-41.

Rajput MS, Kumar GN, Rajkumar S. 2013. Repression of oxalic acid-mediated mineral phosphate solubilization in rhizospheric isolates of *Klebsiella pneumoniae* by succinate. *Arch Microbiol* **195(2):**81-88.

Raklami A, Bechtaoui N, Tahiri AI, Anli M, Meddich A, Oufdou K. 2019. Use of rhizobacteria and mycorrhizae consortium in the open field as a strategy for improving crop nutrition, productivity and soil fertility. *Front Microbiol* **10:**1106.

Ramírez MV, Calzadíaz L. 2016. Industrial enzymes and metabolites from Actinobacteria in food and medicine industry. Actinobacteria, Basics and Biotechnological Applications, **315**.

Rath S, Fostier AH, Pereira LA, Dioniso AC, de Oliveira Ferreira F, Doretto KM, Peruchi LM, Viera A, de Oliveira Neto OF, Dal Bosco SM, Martínez-Mejía MJ. 2019. Sorption behaviors of antimicrobial and antiparasitic veterinary drugs on subtropical soils. *Chemosphere* **214:**111-122.

Rhee KH. 2003. Purification and identification of an antifungal agent from *Streptomyces* sp. KH-614 antagonistic to rice blast fungus, *Pyricularia oryzae*. *J Microb Biot* **13(6):**984-988.

Richardson AE, Barea JM, McNeill AM, Prigent-Combaret C. 2009. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant Soil* **321(1-2):**305-339.

Richardson AE, Simpson RJ. 2011. Soil microorganisms mediating phosphorus availability update on microbial phosphorus. *Plant physiol* **156(3):**989-996.

Riyadi FA, Tahir AA, Yusof N, Sabri NSA, Noor MJMM, Akhir FNM, Zakaria Z, Hara H. 2020. enzymatic and genetic characterization of lignin depolymerization by *Streptomyces* sp. S6 isolated from a tropical environment. *Sci Rep* **10(1):**1-9.

Romero-Rodríguez A, Maldonado-Carmona N, Ruiz-Villafán B, Koirala N, Rocha D, Sánchez S. 2018. Interplay between carbon, nitrogen and phosphate utilization in the control of secondary metabolite production in *Streptomyces*. *Anton Leeuw Int J G* **111(5):**761-781.

Rosier A, Medeiros FH, Bais HP. 2018. Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. *Plant soil* **428(1-2):**35-55.

Rozycki H, Strzelczyk E. 1986. Organic acids production by *Streptomyces* spp. isolated from soil, rhizosphere and mycorrhizosphere of pine (*Pinus sylvestris* L.). *Plant soil* **96(3):**337-345.

Rungin S, Indananda C, Suttiviriya P, Kruasuwan W, Jaemsaeng R, Thamchaipenet A. 2012. Plant growth enhancing effects by a siderophore-producing endophytic *Streptomycete* isolated from a Thai jasmine rice plant (*Oryza sativa* L. cv. KDML105). *Anton Leeuw Int J G* **102(3):**463-472.

Sadeghi A, Karimi E, Dahazi PA, Javida MG, Dalvand Y, Askari H. 2012. Plant growth promoting activity of an auxin and siderophore producing isolate of *Streptomyces* under saline soil condition. *World J Microbiol Biotechnol* **28:**1503-1509.

Sadeghian M, Bonjar GHS, Sirchi GRS. 2016. Post-harvest biological control of apple bitter rot by soil-borne Actinomycetes and molecular identification of the active antagonist. *Postharvest Biol Tec* **112:**46-54.

Saeed EE, Sham A, Salmin Z, Abdelmowla Y, Iratni R, El-Tarabily K, Abu Qamar S. 2017. *Streptomyces globosus* UAE1, a potential effective biocontrol agent for black scorch disease in date palm plantations. *Front Microbiol* **8:**1455.

Sahu MK, Sivakumar K, Thangaradjou T, Kannan L. 2007. Phosphate solubilizing actinomycetes in the estuarine environment, An inventory. *J Environ Biol* **28(4):**795-798.

Saito A, Fujii T, Miyashita K. 2003. Distribution and evolution of chitinase genes in *Streptomyces* species, Involvement of gene-duplication and domain-deletion. *Anton Leeuw Int J G* **84:**7-16.

Salcedo LDP, Prieto C, Correa MF. 2014. Screening phosphate solubilizing actinobacteria isolated from the rhizosphere of wild plants from the Eastern Cordillera of the Colombian Andes. *Afr J Microbiol Res* **8(8):**734-742.

Salla TD, Astarita LV, Santarém ER. 2016. Defense responses in plants of Eucalyptus elicited by *Streptomyces* and challenged with *Botrytis cinerea*. *Planta* **243(4):**1055-1070.

Samac DA, Willert AM, McBride MJ, Kinkel LL. 2003. Effects of antibiotic-producing *Streptomyces* on nodulation and leaf spot in alfalfa. *Appl Soil Ecol* **22(1):**55-66.

Sangmanee P, Bhromsiri A, Akarapisan A. 2009. The potential of endophytic actinomycetes, (*Streptomyces* sp.) for the biocontrol of powdery mildew disease in sweet pea (*Pisum sativum*). *As J Food Ag-Ind* **93:**e8.

Sardi P, Saracchi M, Quaroni S, Petrolini B, Borgonovi GE, Merli S. 1992. Isolation of endophytic *Streptomyces* strains from surface-sterilized roots. *Appl Environ Microbiol* **58(8):**2691-2693.

Sarikhani MR, Aliasgharzad N, Khoshru B. 2020. P solubilizing potential of some plant growth promoting bacteria used as ingredient in phosphatic biofertilizers with emphasis on growth promotion of *Zea mays* L. *Geomicrobiol* J **37(4):**327-335.

Sarikhani MR, Khoshru B, Greiner R. 2019. Isolation and identification of temperature tolerant phosphate solubilizing bacteria as a potential microbial fertilizer. *World J Microb Biot* **35(8):**126.

Sarikhani MR, Khoshru B, Oustan S. 2016. Efficiency of some bacterial strains in potassium release from mica and phosphate solubilization under *in vitro* conditions. *Geomicrobiology* J **33(9):**832-838.

Sarkar A, Ghosh PK, Pramanik K, Mitra S, Soren T, Pandey S, Mondal MH, Maiti TK. **2018.** A halotolerant *Enterobacter* sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. *Res Microbiol* **169(1):**20-32.

Sathya A, Vijayabharathim R, Gopalakrishnanm SM. 2017. Plant growth-promoting Actinobacteria, a new strategy for enhancing sustainable production and protection of grain legumes. *Biotech* **7(2):**102.

Schnellmann J, Zeltins A, Blaak H, Schrempf H. 1994. The novel lectin‐like protein CHB1 is encoded by a chitin-inducible Streptomyces olivaceoviridis gene and binds specifically to crystalline α-chitin of fungi and other organisms. *Mol Microbiol.* **13**: 807-819.

Schniete JK, Selem-Mojica N, Birke AS, Cruz-Morales P, Hunter IS, Barona-Gomez F, Hoskisson PA. 2020. ActDES-a Curated Actinobacterial Database for Evolutionary Studies. *bioRxiv*. DOI, 10.1101/2020.05.20.105536.

Schütze E, Klose M, Merten D, Nietzsche S, Senftleben D, Roth M, Kothe E. 2014. Growth of *streptomycetes* in soil and their impact on bioremediation. *J Hazard Mater* **267:**128-135.

Selim S, Hassan YM, Saleh AM, Habeeb TH, AbdElgawad H. 2019. Actinobacterium isolated from a semi-arid environment improves the drought tolerance in maize (*Zea mays* L.). *Plant Physiol Biochem* **142:**15-21.

Selvakumar G, Bhatt RM, Upreti KK, Bindu GH, Shweta K. 2015. *Citricoccus zhacaiensis* B-4 (MTCC 12119) a novel osmotolerant plant growth-promoting actinobacterium enhances onion (*Allium cepa* L.) seed germination under osmotic stress conditions. *World J Microbiol Biotechnol* **31**:833–839.

Selvakumar G, Panneerselvam P, Ganeshamurthy AN. 2014. Diversity utility and potential of Actinobacteria in the agro-ecosystem. In Bacterial Diversity in Sustainable Agriculture. Springer, *Cham.* pp.23-40.

Sharma G, Mehta S. 2016. Trends, Growth and Instability in Area, Production and productivity of Maize crop across regions in India. *Product* **56(4):**368.

Sharma P, Thakur D. 2020. Antimicrobial biosynthetic potential and diversity of culturable soil actinobacteria from forest ecosystems of Northeast India. *Sci Rep* **10(1)**:1-18.

Sharma PK, Sharma V, Sharma S, Bhatia G, Singh K, Sharma R. 2019. Comparative metatranscriptome analysis revealed broad response of microbial communities in two soil types, agriculture versus organic soil. *JGEB* **17(1):**6.

Shen J, Yuan L, Zhang J, Li H, Bai Z, Chen X, Zhang W, Zhang F. 2011. Phosphorus dynamics, from soil to plant. *Plant Physiol* **156(3):**997-1005.

Shutsrirung A, Chromkaew Y, Pathom-Aree W, Choonluchanon S, Boonkerd N. 2013. Diversity of endophytic actinomycetes in mandarin grown in northern Thailand, their phytohormone production potential and plant growth promoting activity. *Soil Sci Plant Nutr* **59(3):**322-330.

Siddharth S, Rai VR. 2019. Isolation and characterization of bioactive compounds with antibacterial, antioxidant and enzyme inhibitory activities from marine-derived rare actinobacteria, *Nocardiopsis* sp. SCA21. *Microb Pathog* **137**:103775.

Singh LS, Sharma H, Talukdar NC. 2014. Production of potent antimicrobial agent by actinomycete, *Streptomyces sannanensis* strain SU118 isolated from phoomdi in Loktak Lake of Manipur, India. *BMC Microbiol* **14(1):**278.

Singh P, Kumar V, Agrawal S. 2014. Evaluation of phytase producing bacteria for their plant growth promoting activities. *Int J Microbiol* 1-7.

Singh V, Haque S, Singh H, Verma J, Vibha K, Singh R, Jawed A, Tripathi CK. 2016. Isolation, screening, and identification of novel isolates of actinomycetes from India for antimicrobial applications. *Front Microbiol* **7:**1-2.

Snyder DE, Meyer J, Zimmermann AG, Qiao M, Gissendanner SJ, Cruthers LR, Slone RL, Young DR. 2007. Preliminary studies on the effectiveness of the novel pulicide, spinosad, for the treatment and control of fleas on dogs. *Vet Parasitol* **150(4):**345-351.

Solá MZ, Lovaisa N, Costa JS, Benimeli CS, Polti MA, Alvarez A. 2019. Multi-resistant plant growth-promoting Actinobacteria and plant root exudates influence Cr (VI) and lindane dissipation. *Chemosphere* **222:**679-687.

Solans M, Vobis G, Cassán F, Luna V, Wall LG. 2011. Production of phytohormones by root-associated saprophytic actinomycetes isolated from the actinorhizal plant *Ochetophila trinervis*. *World J Microbiol Biotechnol* **27(9):**2195-2202.

Sreevidya M, Gopalakrishnan S, Kudapa H, Varshney RK. 2016. Exploring plant growth-promotion actinomycetes from vermicompost and rhizosphere soil for yield enhancement in chickpea. *Braz J Microbiol* **47(1):**85-95.

Srivastava S, Patel JS, Singh HB, Sinha A, Sarma BK. 2015. *Streptomyces rochei* SM3 induces stress tolerance in chickpea against *Sclerotinia sclerotiorum* and NaCl. *J Phytopathol* **163:**583–592.

Suárez-Moreno ZR, Vinchira-Villarraga DM, Vergara-Morales DI, Castellanos L, Ramos FA, Guarnaccia C, Degrassi G, Venturi V, Moreno-Sarmiento N. 2019. Plant-growth promotion and biocontrol properties of three *Streptomyces* spp. isolates to control bacterial rice pathogens. *Front Microbiol* **10:**290.

Sutcliffe IC. 2011. New insights into the distribution of WXG100 protein secretion systems. *Anton Leeuw Int J G* **99(2):**127-131.

Sutherland JB, Blanchette RA, Crawford DL, Pometto A. 1979. Breakdown of Douglas-fir phloem by a lignocellulose-degrading *Streptomyces*. *Curr Microbiol* **2(2):**123-126.

Suzuki SI, Yamamoto K, Okuda T, Nishio M, Nakanishi N, Komatsubara S. 2000. Selective isolation and distribution of *Actinomadura rugatobispora* strains in soil. *Actinomycetologica* **14:**27-33.

Syed DG, Agasar D, Pandey A. 2009. Production and partial purification of α-amylase from a novel isolate *Streptomyces gulbargensis*. *J Ind Microbiol Biotechnol* **36(2):**189-194.

Taechowisan T, Peberdy JF, Lumyong S. 2003. Chitinase production by endophytic *Streptomyces aureofaciens* CMUAc130 and its antagonism against phytopathogenic fungi. *Ann Microbiol* **53(4):**447-462.

Takarada H, Sekine M, Kosugi H, Matsuo Y, Fujisawa T, Omata S, Kishi E, Shimizu A, Tsukatani N, Tanikawa S, Fujita N. 2008. Complete genome sequence of the soil actinomycete Kocuria rhizophila. *J Bacteriol* **190(12):**4139-4146.

Takasuka TE, Book AJ, Lewin GR, Currie CR, Fox BG. 2013. Aerobic deconstruction of cellulosic biomass by an insect-associated *Streptomyces*. *Sci Rep* **3:**1030.

Tang X, Placella SA, Daydé F, Bernard L, Robin A, Journet EP, Justes E, Hinsinger P. 2016. Phosphorus availability and microbial community in the rhizosphere of intercropped cereal and legume along a P-fertilizer gradient. *Plant Soil* **407:**119–134.

Tanvir R, Sheikh AA, Javeed A. 2018. Endophytic actinomycetes in the biosynthesis of bioactive metabolites, chemical diversity and the role of medicinal plants. *Stu Nat Product Chem* **60:**399-424.

Tippelt A, Nett M, Gurovic MS. 2020. Complete Genome Sequence of the Lignocellulose-Degrading Actinomycete *Streptomyces albus* CAS922. *Microbiol Resour Announc* **9(21).**

Tiwari D, Bhati P, Das P, Shouch S. 2019. Potential of actinomycetes as bioremediating and biocontroling agents. *PIJR* **8(1):**36-40.

Tiwari S, Singh P, Tiwari R, Meena KK, Yandigeri M, Singh DP, Arora DK. 2011. Salt-tolerant rhizobacteria-mediated induced tolerance in wheat (*Triticum aestivum*) and chemical diversity in rhizosphere enhance plant growth. *Biol Fertil Soils* **47(8):**907.

Tomilova OG, Kryukov VY, Duisembekov BA, Yaroslavtseva ON, Tyurin MV, Kryukova NA, Skorokhod V, Dubovskiy IM, Glupov VV. 2016. Immune-physiological aspects of synergy between avermectins and the entomopathogenic fungus *Metarhizium robertsii* in Colorado potato beetle larvae. *J Invertebr Pathol* **140:**8-15.

Toumatia O, Compant S, Yekkour A, Goudjal Y, Sabaou N, Mathieu F, Sessitsch A, Zitouni A. 2016. Biocontrol and plant growth promoting properties of *Streptomyces mutabilis* strain IA1 isolated from a Saharan soil on wheat seedlings and visualization of its niches of colonization. *S Afr J Bot* **105:**234-239.

Toumatia O, Yekkour A, Goudjal Y, Riba A, Coppel Y, Mathieu F, Sabaou N, Zitouni A. 2015. Antifungal properties of an actinomycin D-producing strain, Streptomyces sp. IA1, isolated from a Saharan soil. *J Basic Microbiol*. **55**: 221-228.

Trejo-Estrada SR, Paszczynski A, Crawford DL. 1998. Antibiotics and enzymes produced by the biocontrol agent *Streptomyces violaceusniger* YCED-9. *J Ind Microbiol Biotechnol* **21(1-2):**81-90.

Trujillo ME, Alonso-Vega P, Rodríguez R, Carro L, Cerda E, Alonso P, Martínez-Molina E. 2010. The genus *Micromonospora* is widespread in legume root nodules, the example of *Lupinus angustifolius*. *ISME J* **4(10):**1265-1281.

Turan M, Topcuoğlu B, Kıtır N, Alkaya Ü, Erçelik F, Nikerel E, Güneş A. 2016. Plant growth promoting rhizobacteria's (PGPRs) enzyme dynamics in soil remediation. *J Soil Contam* **209**.

Ullah S, Bano A. 2015. Isolation of plant-growth-promoting rhizobacteria from rhizospheric soil of halophytes and their impact on maize (*Zea mays* L.) under induced soil salinity. *Can J Microbiol* **61**:307–313.

Vansuyt G, Robin A, Briat JF, Curie C, Lemanceau P. 2007. Iron acquisition from Fe-pyoverdine by *Arabidopsis thaliana*. *Mol*. Plant. *Microbe Interact* **20(4):**441-447.

Vasavada SH, Thumar JT, Singh SP. 2006. Secretion of a potent antibiotic by salt-tolerant and alkaliphilic actinomycete *Streptomyces sannanensis* strain RJT-1. *Curr Sci* 1393-1397.

Vasconcellos RL, Silva MC, Ribeiro CM, Cardoso EJ. 2010. Isolation and screening for plant growth-promoting (PGP) actinobacteria from *Araucaria angustifolia* rhizosphere soil. *Scientia Agricola* **67(6):**743-746.

Ventorino V, Ionata E, Birolo L, Montella S, Marcolongo L, de Chiaro A, Espresso F, Faraco V, Pepe O. 2016. Lignocellulose-adapted endo-cellulase producing *Streptomyces* strains for bioconversion of cellulose-based materials. *Front Microbiol* **7**:p.2061.

Verbon EH, Liberman LM. 2016. Beneficial microbes affect endogenous mechanisms controlling root development. *Trends Plant Sci* **21:**218–229.

Verma DK. 2019. Ed. Microbiology for Sustainable Agriculture, Soil Health, and Environmental Protection. CRC Press. pp. 408.

Verma P, Yadav AN, Kazy SK, Saxena AK, Suman A. 2013. Elucidating the diversity and plant growth promoting attributes of wheat (*Triticum aestivum*) associated acidotolerant bacteria from southern hills zone of India. *Natl J Life Sci* **10(2):**219-226.

Verma VC, Singh SK, Prakash S. 2011. Bio-control and plant growth promotion potential of siderophore producing endophytic Streptomyces from Azadirachta indica A. Juss. *J Basic Microbiol.* **51**:550-556.

Vessey JK. 2003. Plant growth promoting rhizobacteria as biofertilizers. *Plant Soil* **255:**571–586.

Viaene T, Langendries S, Beirinckx S, Maes M, Goormachtig S. 2016. *Streptomyces* as a plant's best friend? *FEMS Microbiol Ecol* **92.**

Villegas M, Vásquez L, Valdez-Ramirez MD. 1997. Growth and nitrogenase activity conditions of a new diazotrophic group of filamentous bacteria isolated from Casuarina root nodules. *Rev Latinoam Microbiol* **39(1-2):**65-72.

Vonothini G, Murugan M, Sivakumar K, Sudha S. 2008. Optimization of protease production by an actinomycete strain, PS-18A isolated from an estuarine shrimp pond. *Afr J Biotechnol.* **7**.

Vurukonda SS, Giovanardi D, Stefani E. 2018. Plant growth promoting and biocontrol activity of *Streptomyces* spp. as endophytes. *Inter J Mol Sci* **19(4):**952.

Wahyudi AT, Priyanto JA, Afrista R, Kurniati D, Astuti RI, Akhdiya A. 2019. Plant growth promoting activity of actinomycetes isolated from soybean rhizosphere. *Online J Biol Sci* **19(1)**:1-8.

Walsh CT, Marshall CG. 2004. Siderophore biosynthesis in bacteria. In, Crosa JH, Mey AR, Payne SM (eds) Iron transport in bacteria. ASM Press, Washington DC. pp.18–37.

Wang C, Wang Z, Qiao X, Li Z, Li F, Chen M, Wang Y, Huang Y, Cui H. 2013. Antifungal activity of volatile organic compounds from *Streptomyces alboflavus* TD-1. *Fems Microbiol Lett* **341(1):**45-51.

Wang Z, Liu L, Chen Q, Wen X, Liao Y. 2016. Conservation tillage increases soil bacterial diversity in the dryland of northern China. *Agron Sustain Dev* **36(2):**28.

Warrad M, Hassan YM, Mohamed MS, Hagagy N, Al-Maghrabi OA, Selim S, Saleh AM, AbdElgawad H. 2020. A bioactive fraction from *Streptomyces* sp. enhances maize tolerance against drought stress. *J Microbiol Biotechnol* **30(8)**:1156-68.

Wei H, Wang L, Hassan M, Xie B. 2018. Succession of the functional microbial communities and the metabolic functions in maize straw composting process. *Bioresour Technol* **256:**333-341.

Wiliams ST. 1990. Actinomycetes—The ray fungi. *Mycologist* **4(3):**110-114.

Wittenwiler M. 2007. Mechanisms of Iron Mobilization by Siderophores. Master *Studies in Environmental Sciences Master* 1-22.

Wolińska A, Górniak D, Zielenkiewicz U, Kuźniar A, Izak D, Banach A, Błaszczyk M. 2019. Actinobacteria structure in autogenic, hydrogenic and lithogenic cultivated and non-cultivated soils, A culture-independent approach. *Agronomy* **9(10):**598.

Woo JH, Kamei Y. 2003. Antifungal mechanism of an anti-Pythium protein (SAP) from the marine bacterium *Streptomyces* sp. strain AP77 is specific for *Pythium porphyrae*, a causative agent of red rot disease in *Porphyra* spp. *Appl Microbiol Biotechnol* **62(4):**407-413.

Woodruff HB. 2014) Selman A. Waksman, winner of the 1952 Nobel Prize for physiology or medicine. *Appl Environ Microbiol* **80(1):**2-8.

World Population Prospects 2019 (World Bank; 2019): Highlights. Available online at: https://data.worldbank.org/indicator/AG.LND.AGRI.ZS (accessed August 24, 2019).

Wu ZM, Yang Y, Li KT. 2019. Antagonistic activity of a novel antifungalmycin N2 from *Streptomyces* sp. N2 and its biocontrol efficacy against *Rhizoctonia solani*. *Fems Microbiol Lett* **366(3)**, fnz018.

Yamanaka K, Oikawa H, Ogawa HO, Hosono K, Shinmachi F, Takano H, Sakuda S, Beppu T, Ueda K. 2005. Desferrioxamine E produced by *Streptomyces griseus* stimulates growth and development of *Streptomyces tanashiensis*. *Microbiol* **151(9):**2899-2905.

Yandigeri MS, Malviya N, Solanki MK, Shrivastava P, Sivakumar G. 2015. Chitinolytic *Streptomyces vinaceusdrappus* S5MW2 isolated from Chilika lake, India enhances plant growth and biocontrol efficacy through chitin supplementation against *Rhizoctonia solani*. *World J Microbiol Biotechnol* **31(8):**1217-1225.

Yasari E, Azadgoleh ME, Mozafari S, Alashti MR. 2009. Enhancement of growth and nutrient uptake of Rapeseed (*Brassica napus* L.) by applying mineral nutrients and biofertilizers. *Pak J Biol Sc.***12:**127–133.

Yousuf J, Thajudeen J, Aneesa PA, Joseph A, Divya PS, Varghese A, AA MH. 2020. Diversity and activity of culturable nitrogen fixing heterotrophic bacteria from estuarine and coastal environments of Southeastern Arabian Sea (SEAS). *Reg Stud Mar Sci* **33:**100973.

Yu J, Pavia MJ, Deem LM, Crow SE, Deenik JL, Penton CR. 2020. DNA-Stable Isotope Probing Shotgun Metagenomics Reveals the Resilience of Active Microbial Communities to Biochar Amendment in Oxisol Soil. *Front. microbiol*, **11**.

Zamoum M, Goudjal Y, Sabaou N, Mathieu F, Zitouni A. 2017. Development of formulations based on *Streptomyces rochei* strain PTL2 spores for biocontrol of *Rhizoctonia solani* damping-off of tomato seedlings. *Biocontrol Sci Techn* **27(6):**723-738.

Zang X, Liu M, Fan Y, Xu J, Xu X, Li H. 2018. The structural and functional contributions of β-glucosidase-producing microbial communities to cellulose degradation in composting. *Biotechnol Biofuels* **11**(1): p.51.

Zarandi ME, Bonjar GS, Dehkaei FP, Moosavi SA, Farokhi PR, Aghighi S. 2009) Biological control of rice blast (*Magnaporthe oryzae*) by use of *Streptomyces sindeneusis* isolate 263 in greenhouse. *Am J Appl Sci* **6(1):**194-199.

Zhang J, Yan YJ, An J, Huang SX, Wang XJ, Xiang WS. 2015. Designed biosynthesis of 25-methyl and 25-ethyl ivermectin with enhanced insecticidal activity by domain swap of avermectin polyketide synthase. *Microb Cell Fact* **14(1):**152.

Zhang L, Xu M, Liu Y, Zhang F, Hodge A, Feng G. 2016. Carbon and phosphorus exchange may enable cooperation between an arbuscular mycorrhizal fungus and a phosphate-solubilizing bacterium. *New Phytol* **210:**1022–1032.

Zhang L, Yan C, Guo Q, Zhang J, Ruiz-Menjivar J. 2018. The impact of agricultural chemical inputs on environment, global evidence from informetrics analysis and visualization. *IJLCT* **13(4):**338-352.

Zhi XY, Li WJ, Stackebrandt E. 2009. An update of the structure and 16S rRNA gene sequence-based definition of higher ranks of the class Actinobacteria, with the proposal of two new suborders and four new families and emended descriptions of the existing higher taxa. *Int J Syst Evol Microbiol* **59:**589 –608.

Zhong Y, Liu J, Jia X, Shangguan Z, Wang R. Yan W. 2020. Microbial community assembly and metabolic function during wheat straw decomposition under different nitrogen fertilization treatments. *Biol Fertil Soils* 1-14.

Zucchi TD, De Moraes LAB, De Melo IS. 2008. Streptomyces sp. ASBV-1 reduces aflatoxin accumulation by aspergillus parasiticus in peanut grains. *J Appl Microbiol*. **105**(6):2153-2160.

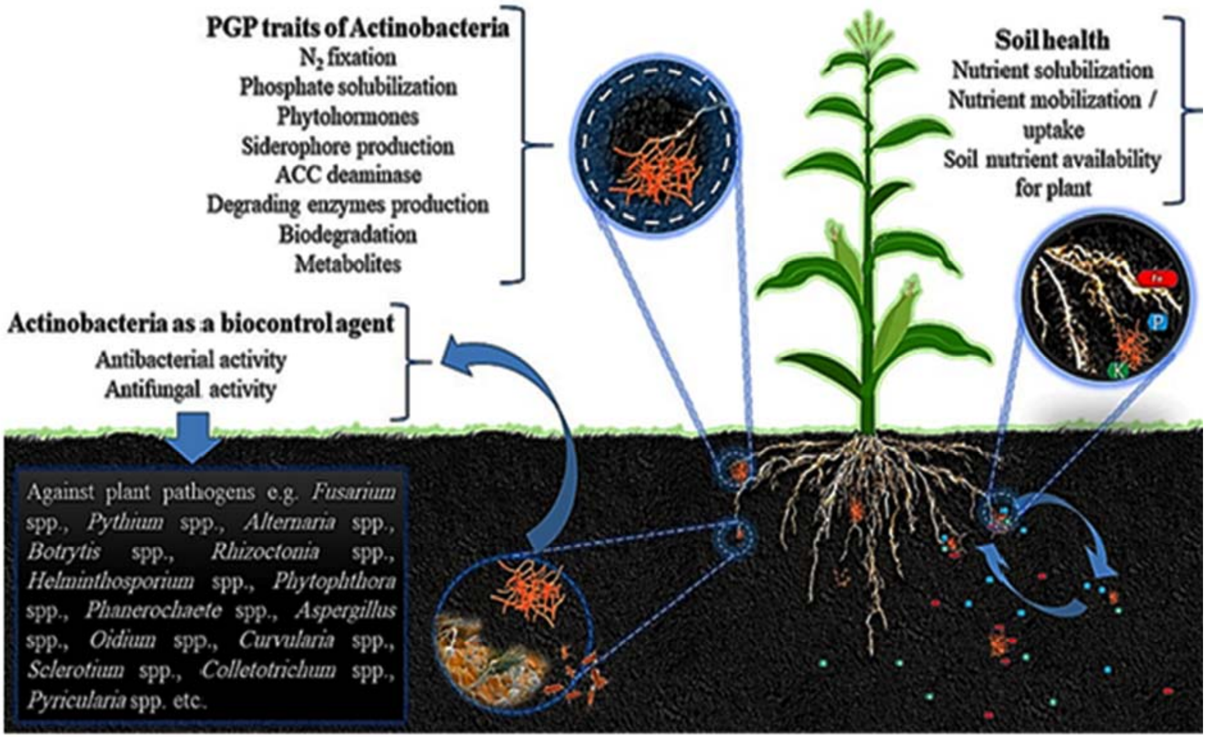

Fig. 1 Beneficial impacts and interaction of Actinobacteria with plant and rhizosphere to imply the acquisition of nutrients, growth promotion and plant protection

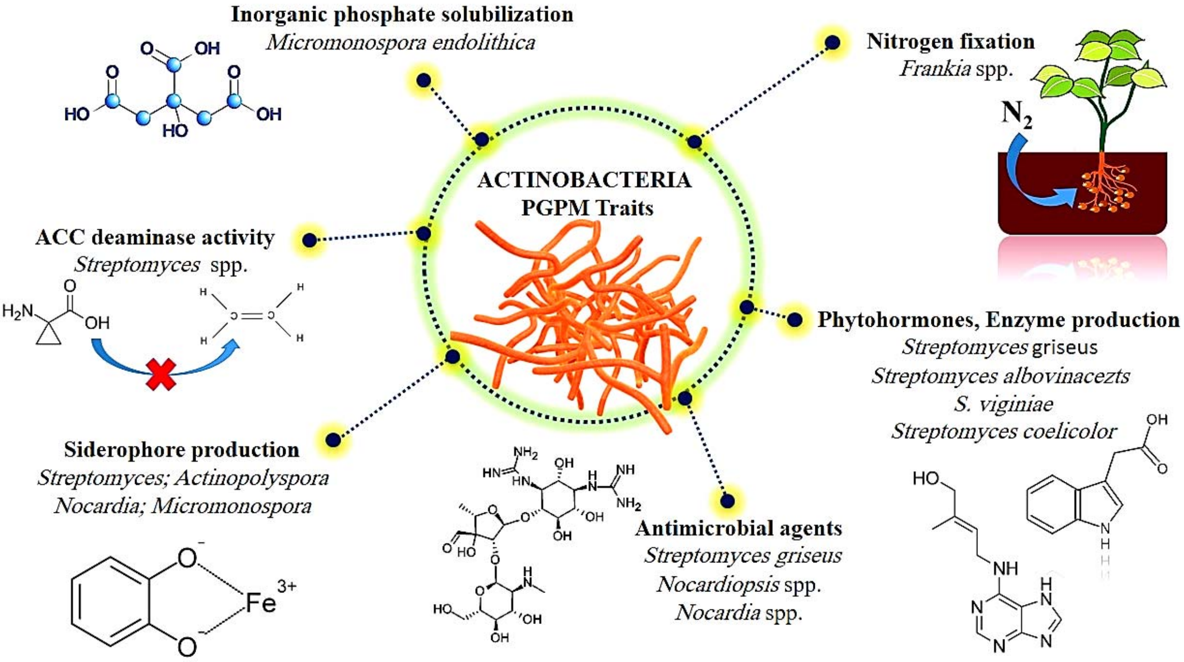

Fig. 2 Major PGP attributes of Actinobacteria.

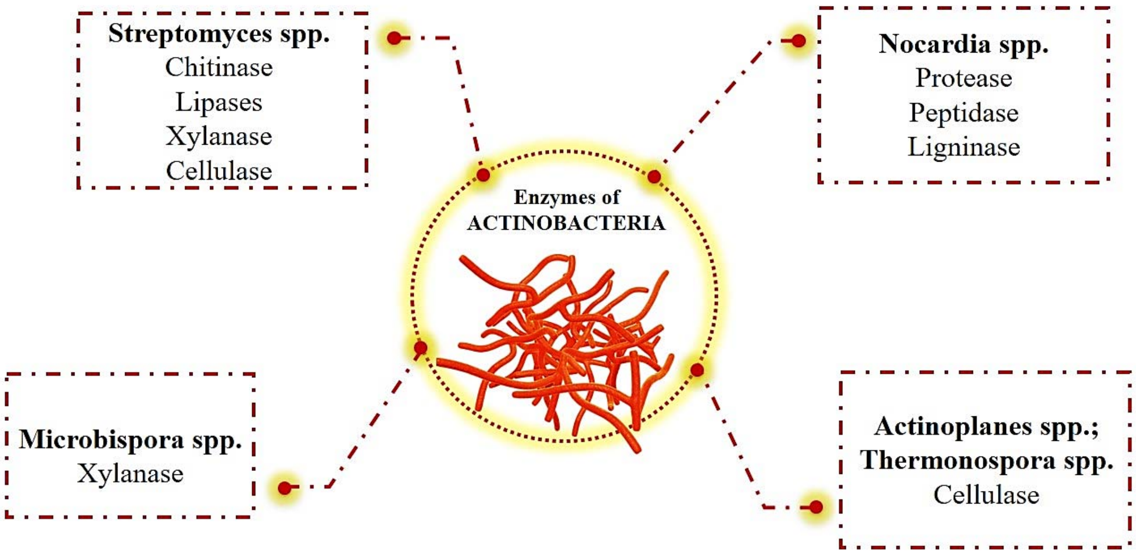

Fig. 3 Different enzymes produced by Actinobacteria for increased organic matter decomposition and crop productivity

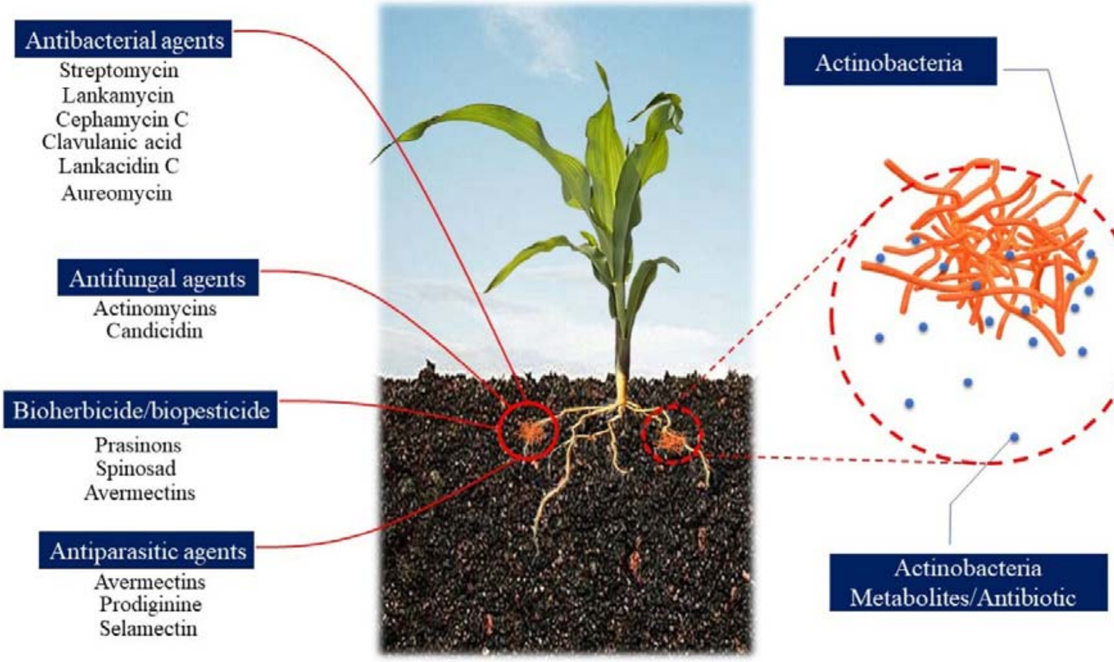

Fig. 4 Actinobacteria: secondary metabolites and antibiotic production for plant protection and disease control.

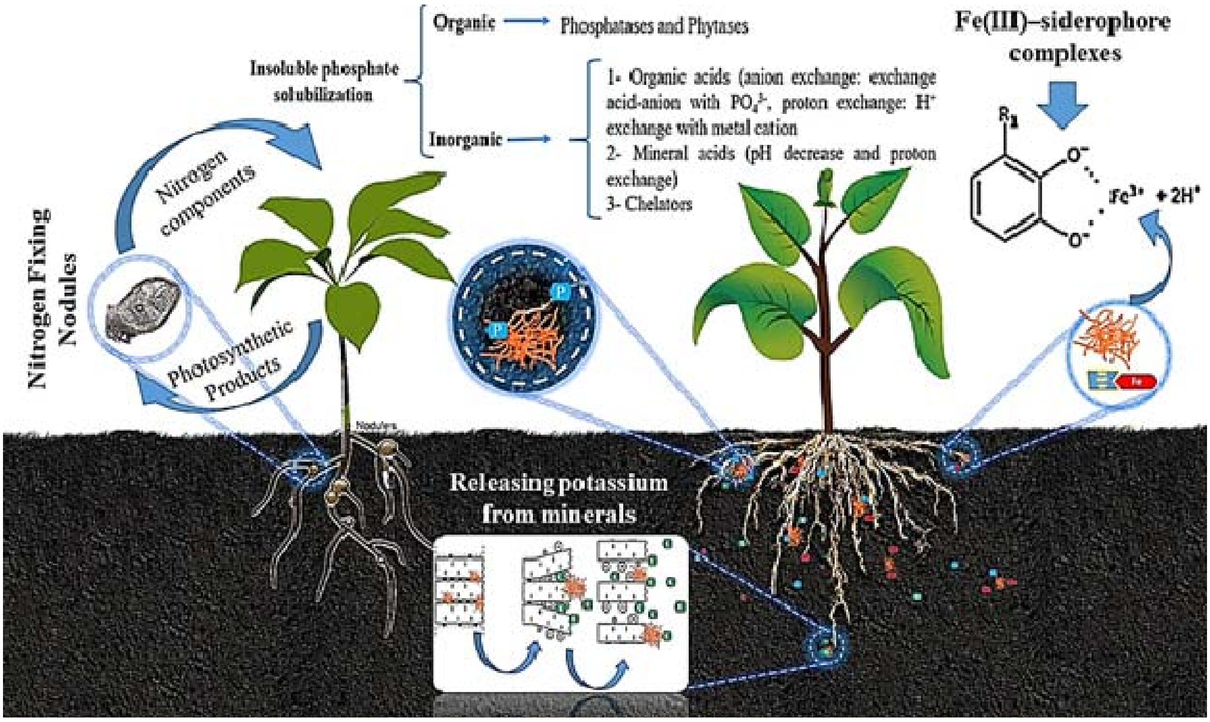

Fig. 5 Actinobacteria help to manage the availability of nutrients in plants and rhizosphere.