

REVIEW

Actinomycetes as growth promoters and bioprotectors for plant health improvement

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Actinomycetes enhance plant growth by producing growth regulators and act as potent biocontrol agents against fungal pathogens. Streptomycetes are a group of actinobacteria mainly found in the rhizosphere of plants in association with other microorganisms like rhizobacteria and fungi. They improve plant health by producing plant growth promoting hormones such as IAA and protect the plant against plant pathogenic microorganisms through production of siderophores and mechanisms of induced systemic resistance. Apart from Streptomycetes group, there are endophytic actinomycetes which are as plant growth promoters and biocontrol agents. Many of Non-Streptomyces actinomycetes (NSA) taxa act as biocontrol agents and plant growth promoters through mechanisms like increasing the supply of nutrients, production of IAA, cytokinin and controlling fungal diseases through antibiosis and competition. Non-streptomyces actinomycetes (NSA) have great potential as agents for the biocontrol of soil-borne fungal plant pathogens and also as plant growth promoters. The review depicts the roles of *Streptomyces*, non-streptomyces actinomycetes and endophytic actinobacteria as bioprotectors against fungal pathogens and addresses alternative biological method of improving plant health along with disease resistance capacity.

Keywords: Bioprotectors, bioactive compounds, Endophyte, Non-*Streptomyces* actinomycetes, Plant growth promoters, *Streptomyces*

INTRODUCTION

Extensive use of chemical products in agriculture imparts deleterious effect on environment and on health of human too. Microbial formulation act as better and safer alternative way of chemical pesticides. Formation of Biological pesticides is more sustainable in function as compared to chemical pesticides.

For improvement of plant growth, use of biological pesticides from actinobacteria is considered to be more economical and safe method. The exploration of microbial resources is necessary for plant growth promotion, biological control and to reduce

the use of agrochemicals and fertilizers for sustainable agriculture. Bacteria and fungi are distributed in the biosphere including the rhizosphere and help the host plants by alleviating biotic and abiotic stress through different mechanisms and can be used as bioinoculants for biocontrol and plant growth promotion. Actinobacteria are among the most abundant groups of soil microorganisms. They are known to produce secondary metabolites, antimicrobial compounds and have been explored for their utilization in plant growth promotion and biological control of plant pathogens (Barea *et al.* 2005; Khamna *et al.* 2009; Franco-Correa *et al.* 2010). Diversity, distribution, economic importance of Actinomycetes and their role in plant protection has been extensively reviewed by Krishnaraj *et al.* (2014). Chaurasia *et al.* (2018) have found another way to obtain large vigor in vegetables with safety

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by applying the group of actinobacteria to avoid chemical fertilizers. Plant growth promoting microbes are approved as safe substitute of chemical pesticides in agricultural field (Chakraborty *et al.*, 2014; Chakraborty, 2016; Vurukonda *et al.*, 2018). Several microorganisms are known to act as plant growth promoter and they have the capability to suppress plant diseases (El-Tarabily *et al.* 2009; Sadeghi *et al.* 2012; Nimaichand *et al.* 2013; Chakraborty, 2019a, 2019b).

Actinomycetes are prolific producers of thousands of biologically active natural compounds with diverse activities, and they are behind the discovery of a substantial number of antibiotics that help to treat deadly infections. More than half of these bioactive compounds have been isolated from members belonging to the dominant genus *Streptomyces* (Fig. 1) which acts as both plant growth promoter and plant disease suppressor by various mechanisms which include increase in the supply of nutrients such as phosphorus, iron, production of IAA and siderophore production. In recent decades, non-*Streptomyces* actinomycetes (NSA) have received considerable research attention, and there have been numerous advancements in the discovery of natural products. Several promising compounds with versatile bioactivities have been reported from non-*Streptomyces* actinomycetes (Jose *et al.* 2019). In addition, modern genome mining and metabolomics tools have widened the promise of discovery of novel bioactive compound from non-*Streptomyces* actinomycetes. Besides, endophytic actinobacteria also help in plant growth promotion through multiple way by producing plant hormones; controlling fungal disease through antibiosis and competition. This review briefly summarizes the effects of actinobacteria on biocontrol, plant growth promotion and association with plants as endophytes.

The rate of discovery of naturally antibiotics derived from the actinobacteria is increasing continuously (Qin *et al.* 2010). Almost 80% drugs of the world are known to come from the species of actinobacteria like *Streptomyces* and *Micromonospora* (Pandey *et al.* 2011). The antagonistic activity of *Streptomyces* is due to the production of antifungal compound, antibacterial compound and extra cellular enzymes (Srividhya *et al.* 2012). They have been reported to be

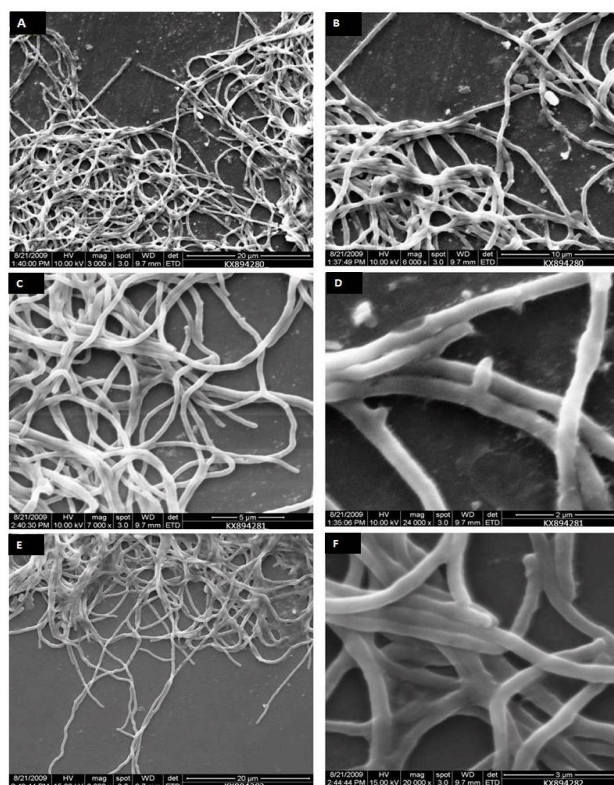


Fig. 1. (A-E): Scanning Electron Micrograph of (A & B) *Streptomyces tricolor*; (C & D) *Streptomyces flavogriseus* (E & D) *Streptomyces griseus*

important producers of phytohormone (Jog *et al.* 2014) and secondary metabolites (Tyc *et al.* 2017) which are utilized for different biological activities such as antibacterial, antifungal, insecticidal activities. These genera have been found to show a great potential to improve the future of agriculture (Olanrewaju and Babalola, 2019).

Endophytic bacteria (including actinomycetes) or endophytic fungi spends the whole or part of its life cycle inside the healthy tissues of the host plant by colonizing inter- or intracellularly, typically without causing any harm to host plant (Sturz *et al.* 2000). Host plant become benefited by entophytic actinobacteria which can inhibit the other harmful microbes and helps the host plants by increasing the nutrient uptake like iron, phosphorus etc. (Singh *et al.* 2015).

They colonize the internal tissue of the plants and accelerate physiological plant responses (Hardoim *et al.* 2008; Van Wees *et al.* 2008) and can produce different types of metabolites in the plant which are used for different applications, such as, antimicrobials (Yan *et al.* 2010; Igarashi *et al.* 2011; Ding *et al.* 2013), plant growth promotion

(Shutrirung *et al.* 2013; Borah and Thakur, 2020), stress tolerance and biocontrol agents for reduction in disease symptoms (Dudeja *et al.* 2012; Li *et al.* 2014; Alblooshi *et al.* 2022). For pharmaceutical industries and agricultural applications endophytic actinobacteria could be a potential source of novel antimicrobial compound (Castillo *et al.* 2007; Chen *et al.* 2009; Qin *et al.* 2010; Shen *et al.* 2014; Rachnyom *et al.* 2015).

DISTRIBUTION OF ACTINOBACTERIA

Actinobacteria are a heterogeneous and globally distributed soil inhabiting microorganisms which includes *Streptomyces*, *Micromonospora*, *Nocardia*, *Actinoplanes* and *Streptosporangium* (Basilio *et al.* 2003; Oskay *et al.* 2004). They grow as hyphae like fungi which are for the characteristically “earthy odor of freshly turned healthy soil (Sprusansky *et al.* 2005). Actinobacteria are found to survive in soil inhabitants (George *et al.* 2012) as well as in extreme environments. *Microbispora*, *Nocardia*, *Microtetraspora*, *Amycolaptosis*, *Actinomadura* and *Saccharothrix* are thermo-tolerant (up to 50°C) actinobacteria.

Endophytic Actinobacteria

The word endophyte means “in the plant” (endon Gr. = within, phyton = plant). Endophytes are the microorganisms, which reside inside the plant tissues without causing any harmful effect on their host and have proven to be the richest source of bioactive natural products. Normally the endophytes without subjecting the plant to any disadvantage complete their life cycle within the host plants. When groups of actinobacteria reside within living plant cells cooperatively is called endophytic actinobacteria, such as nitrogen fixing endophytes *Frankia* producing actinorrhiza. It is reported that endophytic actinobacteria help to promote the growth of host plants and can reduce disease symptoms. Endophytes are ubiquitous in nature and they produce phytohormones and other growth promoting factors to enhance the growth of the host plants. In return, the host plant helps the endophytes with nutrients and shelter. The endophytic actinobacteria form one of the interesting groups of microorganisms which is associated with a wide range of plant species. Endophytic actinobacteria may be of two types ‘obligate’ and ‘facultative’. The growth of obligate endophytes depend on the host plant . Facultative

endophytes can exist outside the host plant (Hardoim *et al.* 2008). Endophytic actinobacteria have been isolated from different plant parts, such as root (Indananda *et al.* 2011; Shen *et al.* 2014), stem (Gu *et al.* 2007), leaves (Kafur and Khan, 2011), fruits (Du *et al.* 2013). Endophytic actinobacteria in plants are found to produce different types of metabolites that can be used for different applications, such as, antimicrobials (Ding *et al.* 2013), plant growth promoters (Shutrirung *et al.* 2013), biocontrol agents (Li *et al.* 2014). Presence of PKS/ NRPS gene clusters in endophytic actinobacteria are responsible for secondary metabolite biosynthesis (Passari *et al.* 2016). Endophytic actinobacteria are reported to produce several plant growth promotion compounds such as auxins, cytokinins and gibberellins or producing siderophore to improve nutrient uptake (Compant *et al.* 2005; Nimnoi *et al.* 2010). Coombs and Franco (2003) reported that different strains of actinobacteria including *Microbispora*, *Nocardia*, *Streptomyces* were recognized from the tissues of vigorous wheat plants. *Streptomyces aureofaciens* is one of the endophytic actinobacteria which were obtained from the root of *Zingiber officinale* and that endophyte was found to inhibit the growth of *Candida albicans* (Taechowisan *et al.* 2005). By secreting phytohormones they help the plants in nutrition improvement and enhancement of the growth of plants by protecting them against phytopathogens (Shen *et al.* 2019).

PLANT GROWTH PROMOTING ACTIVITIES BY ACTINOBACTERIA

Colonization of actinobacteria is influenced by different climatic conditions and rate of colonization is high in summer than in winter. The genera *Microbispora*, *Micromonospora*, *Saccharopolyspora*, *Micrococcus*, *Amycolatopsis*, *Microbacterium* and *Nocardia* were isolated only in summer (Gohain *et al.* 2015). However, the genus *Streptomyces* was often isolated in both the seasons. Stimulation of plant growth by actinobacteria are of two types, direct and indirect. In direct method, phytohormones such as IAA and cytokinins are produced along with solubilization of minerals like iron and phosphorus by the production of siderophores for enhancing plant nutrition and 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase (Tamreihao *et al.* 2016). In direct method actinobacteria help the plants as

biocontrol agents. They can increase plant growth promotion and destroy the harmful phytopathogen by stimulating the resistance system of plant. They are able to produce phytohormones, fix nitrogen and can also prevent the growth of phytopathogen by their antagonistic activity and they help in the solubilization of phosphate (Podile and Kishore, 2006). Numerous actinobacterial species as endophytes with plants have been reported to have various plant growth-promoting properties (Nimaichand *et al.* 2016). They have also been found to show antagonistic properties against many root-borne and disease-causing plant pathogens (Jacob *et al.* 2016). Plant growth-promoting actinobacteria have been listed in Table 1 and their plant growth promoting attributes have been presented in Figure 1.

Production of plant growth hormone- indole acetic acid (IAA)

Species of *Streptomyces* such as *S. olivaceoviridis*, *S. rimosus*, *S. rochei* and *Streptomyces* spp. from tomato rhizosphere have been reported to have the ability to produce indole-3-acetic acid (IAA) and promote growth (Tokala *et al.* 2002). The primary form of auxin is IAA which has an important contribution to control different cellular process of plants including cell elongation and cell division (Hardoim *et al.* 2008) which can determine the nature of the resulting plant-microbe interactions. To form the root hair and to make short root length IAA perform very important functions. IAA helps to increase the nutrient absorption ability of the plant. Some strains of endophytic actinobacteria were reported to produce IAA to enhance the growth of cucumber plants (El-Tarabily *et al.*, 2009). The naturally-occurring auxin, IAA is produced by plants through different tryptophan-dependent IAA production pathways and also by *Streptomyces* sp (Khamna *et al.* 2010; Palaniyandi *et al.* 2013; Madhurama *et al.* 2014) and fungi (Duca *et al.* 2014). *Streptomyces* strains obtained from eglewood (*Aquilaria crassna*), *Azadirachta indica*, tomato plants and *Arabidopsis* plantlets were found to produce IAA and to stimulate the plant growth (Nimnoi *et al.* 2010; Verma *et al.* 2011; Lin and Xu, 2013). Several endophytic actinobacteria including *Streptomyces viridis*, *S. rimosus*, *S. olivaceoviridis*, *S. atrovirens* and *S. rochei* have exhibited improved germination as well as root and shoot elongation (Abdallah *et al.* 2013). In cereals and

leguminous plant, endophytic actinobacteria function as plant growth promoter; as a result they have the capacity to influence plant growth and can increase the ability of nutrition absorption by plants (Nimaichand *et al.* 2016). IAA and siderophore producing actinobacteria that colonize the root in the rhizosphere are studied to promote the root elongation and plant growth (Sreevidya *et al.* 2016). Various strains of actinobacteria including *Micromonospora*, *Streptomyces*, *Microbacterium*, *Pseudonocardia* can produce plant growth phytohormone IAA (Vijayabharathi *et al.* 2016; Passari *et al.* 2017).

Phosphate solubilization

Phosphorus (P) is an important component which is involved in wide range of cellular process by developing plant organs, increasing cell enlargement in plants. Phosphorus (P) content is generally very low in soil and it is available in the form of insoluble metallic complexes (Ezawa *et al.* 2002). For that reason, plants can absorb little amount of phosphorus for its growth (Hamdali *et al.* 2008). Actinobacteria support the plants to get phosphorus from soil in soluble form through acidification and mineralization of insoluble soil phosphorus to increase the growth of plants (van der Hiejden *et al.* 2008). *Streptomyces griseus*, *Micromonospora aurantiaceae* has been reported to help in P-solubilisation and growth promotion of wheat crop (Hamdali *et al.* 2008a). Various genera of actinobacteria such as *Streptomyces*, *Rhodococcus*, *Arthrobacter*, *Micromonospora* were reported to have P-solubilization potential under *in vivo* as well as *in vitro* (Jog *et al.* 2014; Ahemad and Kibret, 2014). *Nocardia* sp. TP1BA1B and *Streptomyces* sp. UKCW/B isolated from native medicinal plant *Pseudowintera colorata* (Horopito) were also found to solubilise phosphate (Purushotham *et al.* 2018).

Production of siderophore and enhanced iron availability

Siderophores are iron chelating secondary metabolites produced by various microorganisms in order to scavenge iron from their surrounding environment to make this essential element available to cell. Due to high affinity for ferric iron, siderophores are secreted out to form soluble ferric complexes that can be taken up by the organisms. Iron plays an important role in the

physiological processes of plants. It is available in soil as insoluble Fe^{3+} form and plants need soluble Fe^{2+} form to uptake from soil (Francis *et al.* 2010). Actinobacteria can convert iron from Fe^{3+} to Fe^{2+} form and it can increase the bioavailability of iron in the plant rhizosphere by production of siderophores and help the plant by iron uptake. Siderophore production by endophytic actinobacteria to stimulate the plant growth have been demonstrated (de Oliveira *et al.* 2010; Ghodhbane-Gtari *et al.* 2010; Verma *et al.* 2011). High amount of siderophore production by *Streptomyces* CMU-SK 126 isolated from *Curcuma mangga* in rhizospheric soil have been reported (Khamna *et al.* 2010). *S. acidiscabies* E13 is an excellent example of siderophore producer that promotes the growth of *Vigna unguiculata* under abiotic stress conditions (Sessitsch *et al.* 2013).

ACC deaminase production

The enzyme ACC deaminase can cleave the plant ethylene precursor ACC, and thereby lower the

level of ethylene in a developing or stressed plant. Actinobacteria including *Mycobacterium*, *Streptomyces*, *Rhodococcus* were found to contain ACC deaminase producing genes (Nascimento *et al.* 2014). Under unfavourable condition plant growth becomes reduced and in that condition, bacterial ACC deaminase performs important function to increase the plant growth (Nascimento *et al.* 2016). ACC deaminase producing strain *Streptomyces* sp. GMKU 336, following inoculation in Thai jasmine rice Khao Dok Mali 105 cultivar (*Oryza sativa* L. cv. KDML105), significantly increased plant growth and decreased ethylene under salt stress (150mM NaCl) conditions (Jaemsaeng *et al.* 2018).

ACTINOBACTERIA AS BIOCONTROL AGENTS

Powerful activity of actinobacteria as biocontrol agent to decrease the foliar disease was first reported by Shimizu *et al.* (2001). The strain MBR-5 identified as *Streptomyces galbus*, among ten actinobacterial strains, isolated from field-grown

Table 1: Plant growth promotion by actinobacteria

Plant growth promoting attributes	Actinobacteria	Isolated from	References
IAA, siderophore	<i>Streptomyces</i> sp. CMU PA 101	<i>Curcuma mangga</i>	Khamna <i>et al.</i> (2009)
IAA, hydroxymate and catechol type siderophore, protease	<i>Streptomyces</i> sp. S4202, <i>Nonomuraea</i> sp. S3304, <i>Actinomadura</i> sp.S4215	<i>Aquilaria crassna</i>	Nimnoi <i>et al.</i> (2010)
Solubilization of phosphate	<i>Streptomyces</i> sp. Nhcr0816	<i>Triticum aestivum</i>	El-Tarabily <i>et al.</i> (2010)
Production of IAA and ACC deaminase	<i>Actinoplanes campanulatus</i> , <i>Streptomyces spirilis</i>	<i>Cucumis sativus</i>	El-Tarabily <i>et al.</i> (2010)
Production of chitinase, phosphatase activity and siderophore	<i>Streptomyces</i> sp AB131-1, LBRO2	Isolates of microbiology laboratory, Bogal Agricultural University	Hastuti <i>et al.</i> (2012)
Siderophore production	<i>Streptomyces</i> sp. GMKU3100	<i>Oryza sativa</i> L.cv.KDML 105	Rungin <i>et al.</i> (2012)
Production of IAA	<i>Streptomyces</i> sp PT2	Plants of Algerian Sahara	Goudjal <i>et al.</i> (2013)
IAA production	<i>Streptomyces</i> sp. <i>Nocardia</i> sp.	<i>Citrus reticulata</i>	Shutsrirung <i>et al.</i> (2013)
Solubilization of phosphate, production of siderophores	<i>Streptomyces</i> sp. BPSAC34	Medicinal plants	Passari <i>et al.</i> (2015)
Phosphate solubilisation, siderophore production	<i>Streptomyces</i> sp. UKCW/B, <i>Nocardia</i> sp. TP1BA1B	<i>Pseudowintera colorata</i>	Purushotham <i>et al.</i> (2018)

Rhododendron plants showed significant antagonistic activities against *Phytophthora cinnamomi* and *Pestalotiopsis sydowiana*. Actinobacteria such as *Streptomyces spiralis*, *Micromonospora chalcea* isolated from cucumber root were found to promote plant growth by decreasing damping off, crown rot disease incidence of cucumber roots (Cao *et al.* 2004). They were identified as biocontrol agent due to formation of enzymes which can destroy the cell wall of fungal phytopathogen. Endophytic actinobacteria as biocontrol agent against *Gaeumannomyces graminis var. tritici* of wheat (Coombs *et al.*, 2004), disease suppression of leaf blight of rice by *Streptomyces platensis* (Wan *et al.*, 2008) and *Pythium aphanidermatum* in cucumber (El-Tarabily *et al.* 2009) have been demonstrated. *Microbispora rosea*, *Streptomyces olivochromogenes* prevented the growth of phytopathogen of clubroot of Chinese cabbage effectively (Lee *et al.*, 2008). *Streptomyces*, *Streptosporangium*, *Microbispora*, *Streptovetrucillium*, *Saccharomonospora* and *Nocardia* isolated from *Azadirachta indica* showed antagonistic activities against root pathogens *Pythium* and *Phytophthora* sp. (Verma *et al.*, 2009). Prominent antagonistic potential against *Rhizoctonia solani* was found by *Streptomyces avidinii* vh32, *S. toxybicini* vh22 and *S. tricolor* vh85 that also induced the accumulation of phenolic compounds in tomato (Patil *et al.* 2011). Most of the endophytic actinobacteria were seen to protect the hosts from diseases by inhibiting plant pathogens (Palaniyandi *et al.* 2013). *Streptomyces griseus* and *Streptomyces griseolus* could inhibit 68% and 59.7% growth of *Sclerotium rolfsii* *in vitro*. Biochemical and molecular characterization of *Streptomyces* species isolated from agricultural field of North Bengal were done and these isolates were evaluated for growth improvement and suppression of sclerotial blight diseases of *Vigna radiata* (Ray *et al.*, 2016a). *In vivo* evaluation of these isolates showed maximum growth promotion on *Vigna radiata* by enhancing key defense enzymes like chitinase, α -1,3-glucanase, phenylalanine ammonia lyase and peroxidase (Ray *et al.* 2016b). Growth of various phytopathogens including *Fusarium oxysporum*, *Fusarium graminearum*, *Rhizoctonia solani*, *Colletotrichum capsici* were inhibited by *Nocardiaopsis* sp., *Streptomyces* sp. DBT204, *Streptomyces* sp. DBT 207 by the formation of cell wall degrading enzymes and HCN (Passari *et al.* 2016). Some species of *Streptomyces* exhibit

biological control activity by stimulating the plant resistance system or by the formation of secondary metabolites like antibiotics particularly against *Fusarium oxysporum*, *Pythium ultimum* and *Phytophthora* sp. (Tamreihao *et al.* 2016).

The growth of *Alternaria alternata* was inhibited by endophytic actinobacteria isolated from medicinal plant *Ferula sinkiangensis* (Liu *et al.* 2017), while isolates from *Rhynchotoechum ellipticum*, were found to inhibit the growth of *Fusarium proliferatum* and *F. oxysporum*. Endophytic *Streptomyces* sp. showed antifungal activity against *Geotrichum candidum*, *F. oxysporum* and *Alternaria* sp. (Perez-Rosales *et al.* 2017). Different strains of *Streptomyces* sp. such as *Streptomyces olivaceus*, *Streptomyces* sp. BPSAC121, *Streptomyces* sp. BPSAC101 showed antifungal activities. Antifungal antibiotics, fluconazole, ketoconazole and miconazole are produced from *Streptomyces olivaceus* and *Streptomyces* sp. BPSA 121 (Passari *et al.* 2017). Relationship between actinobacteria and their host plants has been discussed by Maggini *et al.* (2017) with special reference to secondary metabolites and their role to protect the host from diseases caused by phytopathogens. *Streptomyces* sp. PRY2RB2 inhibited various phytopathogens such as *Neonectria ditissima* ICMP 14417, *Ilyonectria liriodendri* WPA1C, *Neofusicoccum luteum* ICMP 16678 (Purushotham *et al.* 2018). Stem rot caused by *Sclerotinia sclerotiorum* is a very harmful disease for economically important crops like soybean, sunflower worldwide (Arfaoui *et al.* 2018). *Streptomyces* sp. NEAU-S7GS2 isolated from soybean root could inhibit (99.1%) mycelial growth and germination of *S. sclerotiorum* (Liu *et al.* 2019). In pot experiments, it was observed that the extract of *Streptomyces* sp. MR14 cells significantly suppressed *Fusarium moniliforme* (Kaur *et al.* 2019). Actinobacteria as biocontrol agents have been listed in Table 2.

Streptomyces sp. showed antagonistic activities against *Rhizoctonia solani*, *Alternaria tenuissima*, *Aspergillus niger* and *Penicillium expansum* (Javorekova *et al.* 2021). Competition for space and nutrients, production of antibiotics, secretion of iron chelating agent- siderophores, production of lytic enzymes and induction of resistance mechanism in host plants through induced systemic resistance are the main mechanisms exhibited by actinomycetes which are

Table 2: Actinobacteria as potential biocontrol agents

Actinobacteria	Host plant	Pathogen	References
<i>Streptomyces</i> sp. S30 <i>Streptomyces halstedii</i> <i>Microbispora</i> sp. A004 and A011	<i>Solanum lycopersicum</i> <i>Capsicum</i> sp <i>Brassica rapa</i>	<i>Rhizoctonia solani</i> <i>Phytophthora capsica</i> <i>Plasmophora brassicae</i>	Cao <i>et al.</i> (2004) Liang <i>et al.</i> (2005) Lee <i>et al.</i> (2008)
<i>Streptomyces</i> sp. S30 <i>Streptomyces</i> sp. R18(6) <i>Streptomyces spiralis</i> <i>Microsmonopora chalcea</i> <i>Streptomyces</i> sp.	<i>Lycopersicon esculentum</i> <i>Cucumis</i> sp. <i>Cicer arietinum</i>	<i>Rhizoctonia solani</i> <i>Pythium aphanidermatum</i> <i>Fusarium oxysporum</i> f. sp. <i>ciceri</i> <i>Alternaria alternata</i>	de Olivera <i>et al.</i> (2010) El- Tarabily <i>et al.</i> (2010) Gopalakrishnan <i>et al.</i> (2011) Verma <i>et al.</i> (2011)
<i>Streptomyces</i> sp. AzR-051, AzR – 049 <i>Streptomyces</i> sp.	<i>Azadirachta indica</i> A. Juss <i>Capsicum frutescens</i>	<i>Alternaria brassicae</i> , <i>Colletotrichum gloeosporioides</i> <i>Xanthomonas campestris</i> pv. <i>glycines</i> <i>Fusarium oxysporum</i>	Srividya <i>et al.</i> (2012)
<i>Streptomyces</i> sp.	<i>Glycine max</i>	<i>Xanthomonas campestris</i> pv. <i>glycines</i>	Mingma <i>et al.</i> (2014)
<i>Streptomyces indiaensis</i> KJ872546	<i>Capsium</i> sp	<i>Fusarium oxysporum</i>	Jalaluldeen <i>et al.</i> (2014)
Actinobacteria strains OUA3, OUA5, OUA18, and OUA40 <i>Streptomyces felleus</i> YJ1	<i>Capsicum annum</i> <i>Brassica napus</i>	<i>Colletotrichum capsici</i> and <i>Fusarium oxysporum</i> <i>Sclerotinia sclerotiorum</i>	Ashokvardhan <i>et al.</i> (2014) Cheng <i>et al.</i> (2014)
<i>Streptomyces cyaneus</i> ZEA171 <i>Streptomyces diastaticus</i> , <i>Streptomyces fradiae</i> , <i>Streptomyces collinus</i> <i>Streptomyces</i> sp. DBT204 <i>Streptomyces griseus</i> and <i>Streptomyces griseolus</i>	<i>Lactuca sativa</i> Medicinal plants <i>Solanum lycopersicum</i> <i>Vigna radiata</i>	<i>Sclerotinia sclerotiorum</i> FW361 <i>Sclerotium rolfsii</i> , <i>Rhizoctonia solani</i> , <i>Fusarium oxysporum</i> <i>Fusarium proliferatum</i> <i>Sclerotium rolfsii</i>	Kunova <i>et al.</i> (2016) Singh and Gaur (2016) Passari <i>et al.</i> (2016) Ray <i>et al.</i> (2016a)
<i>Streptomyces humidus</i>	<i>Brassica oleracea</i>	<i>Alternaria brassicicola</i>	Hassan <i>et al.</i> (2017)
<i>Saccharothrix algeriensis</i> NRRL B-24137 <i>Streptomyces</i> sp. PRY2RB2	<i>Solanum lycopersicum</i> <i>Pseudowintera colorata</i>	<i>Fusarium oxysporum</i> <i>Neofusicoccum luteum</i> ICMP 16678	Merrouche <i>et al.</i> (2017) Purushotham <i>et al.</i> (2018)

responsible for antagonistic potentials of actinobacteria (Li *et al.* 2021). *Streptomyces sichuanensis* showed cell death of *Fusarium oxysporum* through the production of siderophores (Qi *et al.* 2022). *Streptomyces* sp. AN090126 was also reported as a potent bioprotector against *Sclerotinia homoeocarpa* (Le *et al.* 2022). Antagonism of *Streptomyces* sp. CACIS-2.15CA strain against *Phytophthora* and *Fusarium oxysporum* was evident (Rios-Muniz *et al.* 2022). *Streptomyces gelaticus* inhibited the growth of *Ganoderma boninense* and reduced the palm stem rot disease to some extent (Budi *et al.* 2022; Silva *et al.* 2022). Wilt disease in tomato and banana plants by *Fusarium* sp. was controlled by the application of two strains- STRM103 and STRM104 of *Streptomyces* sp. (Kawicha *et al.*

2023). Similar biocontrol potentiality of *Streptomyces* spp. against fungal pathogens causing plant diseases were reported by several investigating groups (Zhang *et al.* 2020; Zou *et al.* 2021; Gebily *et al.* 2021; Torres-Rodriguez *et al.* 2022; Zhou *et al.* 2022; Kaari *et al.* 2023). Biocontrol potentials of actinobacteria against different phytopathogens have been presented schematically in Fig. 2.

Non-Streptomyces Actinomycetes (NSA)

The majority of actinomycetes survive in environments such as the soil, rhizosphere, pond and lake sediments as saprophytes by degrading organic materials for nutrition. However there are

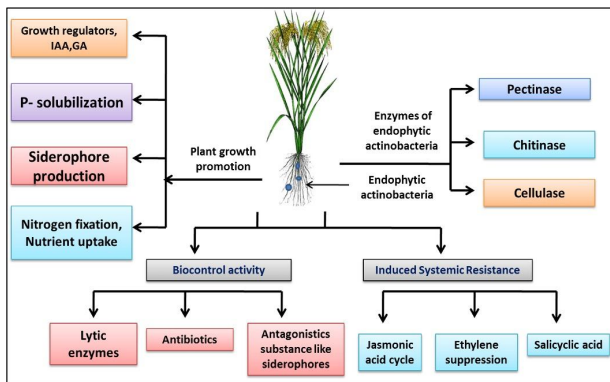


Fig.2. Plant-endophytic actinobacteria interactions favouring plant growth and suppression of phytopathogens (Vardharajula *et.al.*, 2017)

some non-streptomyces actinomycetes (NSA), associated with living plants. Non-Streptomyces are non-taxonomic term also known as rare actinomycetes. Non-Streptomyces defined as actinomycetes other than *Streptomyces* sp., which are less frequent in terrestrial soil (Okazaki, 2006). They grow slowly, and most of them require a distinctive procedure for isolation, preservation and cultivation (Lazzarini *et al.* 2000). These relatively rare actinomycetes inhabit diverse environments and have been proposed as a storehouse of bioactive natural products. NSA produce antibiotics, plant growth promoters with auxin like activity (Igarashi, 2002) and herbicidal antibiotics (Okazaki, 2003).

NSA colonizing inside plants usually get nutrition and protection from the host plants. In return, they confer profoundly enhanced fitness to the host plants by producing a variety of bioactive metabolites. Growth stimulation of plants by NSA can be result of nitrogen fixation or the production of phytohormones, biocontrol of phytopathogens through production of antibiotics or siderophores, nutrient competition, and induction of systemic disease resistance. Although the activity of antagonistic endophytic NSA was reported nearly 50 years ago, it is only recently that interest has been shown in the behavior and activity of these antagonists as endophytes. Application of antagonistic endophytic NSA as biocontrol agents is highly desirable because the antagonist applications targeting the rhizosphere have to be large for effective establishment and operation in the competitive environment of the rhizosphere and the spermosphere. In addition, these endophytes are able to occupy the cortical tissues of roots and have been very effective in the defences against

infection processes of invading pathogens. The cortex or the root tissues occupied by the antagonistic endophytes clearly confers protection to these antagonists from the harsh environment of the bulk soil (Sivasithamparam, 2002). NSA such as *Actinoplanes*, *Micromonospora*, *Microbispora*, *Nocardia*, *Nocardiosis*, *Nocardioides* and *Streptosporangium* have been isolated from inside live tissues of various plant species (Coombes and Franco, 2003; Coombes *et al.* 2004) and they have been shown to protect plants against different soil-borne fungal plant pathogens including *F. oxysporum*, *P. tabacinum* (El-Tarabily, 2003), *G. graminis* var. *tritici* and *R. solani* (Coombes *et al.* 2004). NSA inhibit the growth of soil-borne fungal plant pathogens through the production of inhibitory antifungal metabolites Coombes *et al.* 2004; Tian *et al.* 2004), and cell wall degrading enzymes such as chitinase (El-Tarabily, 2003). NSA was used as pruned root dip method (El-Tarabily, 2003), while Coombes *et al.* (2004) employed the seed coating technique. NSA were recoverable from surface-sterilized roots 8 weeks after inoculation of lupin seedlings.

Two NSA isolates (ARHS/Mn3 and ARHS/Mn7) obtained from the rhizosphere soil of *Solanum tuberosum* and *Mangifera indica* were found to be phosphate solubilizers and showed antagonistic activity against *Sclerotium rolfsii*. *In vivo* evaluation of NSA isolate- ARHS/Mn 3 showed maximum growth promotion on *Vigna radiata* by enhancing key defense enzymes like chitinase, β -1,3-glucanase, phenylalanine ammonia lyase and peroxidase. The results emphasize the fact that NSA could be used as potential biocontrol agents (Ray *et al.* 2016 a). Recent updates on Non-Streptomyces actinomycetes and their natural products have been documented (Jose *et.al.* 2019)

INDUCTION OF RESISTANCE IN HOST

Production of chitinase from *Streptomyces aureofaciens* CMUAC130 has been reported (Taechowisan *et al.* 2003, 2004). *Streptomyces* sp. showed hyperparasitic activity and antimicrobial activity of strain NRRL 30562 obtained from *Kennedia nigriscansin* to prevent the growth of *Fusarium oxysporum*, *Pythium ultimum* by producing an antibiotic munumbicin have also been elucidated (Compant *et al.* 2005). Hydrolytic enzymes degrade fungal cell wall, cell membrane, extracellular virulence factors to control the plant

Table 3: Non-Streptomyces Actinomycetes (NSA) as biocontrol agents

Non-Streptomyces Actinomycetes as biocontrol agents	Diseases	Fungal pathogens	References
<i>Actinoplanes missouriensis</i>	Root rot	<i>Plectosporium tabacinum</i>	El-Tarabily (2003)
<i>Nocardioides</i> sp.	Tale-all	<i>Gaeumannomyces graminis</i> var. <i>tritici</i>	Coombes <i>et al.</i> (2004)
<i>Actinoplanes philippinensis</i>	Damping off	<i>Pythium aphanidermatum</i>	El-Tarabily (2006)
<i>Microbispora rosea</i>	Damping off	<i>P. Aphanidermatum</i>	El-Tarabily (2006)
<i>Nocardia</i> sp. AzL025	Root rot	<i>Pythium, Phytophthora</i> sp	Verma <i>et al.</i> (2009)
<i>Nocardioopsis gilva</i> YIM 90087	Fusarium head blight	<i>Fusarium avenaceum, F. Graminearum, F. culmorum</i>	Tian <i>et al.</i> (2013)
<i>Micromonospora</i> sp. ALFpr18c, ALFb5	Leaf disease	<i>Botrytis cinerea</i>	Martínez-Hidalgo <i>et al.</i> (2015)
<i>Amycolatopsis</i> sp. 521	Bitter rot	<i>Colletotrichum gloeosporioides</i>	Sadeghian <i>et al.</i> (2016)
<i>Actinoallomurus</i>	Leaf and shoot blight	<i>Cryptosporiopsis eucalypti</i> <i>Cylindrocladium</i> sp. <i>Teratosphaeria destructans</i>	Himaman <i>et al.</i> (2016)
<i>Actinomadura</i>			
<i>Amycolatopsis</i>			
<i>Cryptosporangium</i>	Leaf blight	<i>Cryptosporiopsis eucalypti</i> <i>Cylindrocladium</i> sp.	Himaman <i>et al.</i> (2016)
<i>Microbispora</i>			
<i>Micromonospora</i>			
<i>Nocardia</i>	Leaf and shoot blight	<i>Cryptosporiopsis eucalypti</i> <i>Teratosphaeria destructans</i>	Himaman <i>et al.</i> (2016)
<i>Nonomuraea, Pseudonocardia</i>	Fruit disease	<i>Phytophthora capsici</i>	Kafi <i>et al.</i> (2021)
<i>Amycolatopsis</i> strains (3513 and 1119)	Damping-off		

diseases (Pal and Gardener, 2006). A large number of antimicrobial compounds belonging to the classes like alkaloids, peptides, steroids, terpenoids, phenols, quinines and flavonoids were found to produced from actinobacteria (Zhang *et al.* 2006). The extracellular antifungal metabolites especially chitinase and β -1,3 glucanase; produced by actinobacteria inhibited the growth of fungi through hyphal swelling, lysis of cell walls in *Fusarium oxysporum* and *Sclerotium rolfsii* (Prapagdee *et al.* 2008). Growth inhibition of *Botrytis cinerea* by *Streptomyces* sp. GB4-2 has been correlated with stimulation of SAR pathways (Conn *et al.* 2008). Enhanced chitinase and glucanase activities of *Streptomyces* sp. to suppress the growth of fungal phytopathogen have been discussed (Srividya *et al.*2012). The extracellular enzymes- β -1,3-glucosidase, cellulase and protease produced by endophytic actinobacteria cause the lysis of hyphae to inhibit the growth of phytopathogens (Priya, 2012; Xue *et al.* 2013). *Streptomyces* has been found to induce host plant resistance on various crops such as vegetables, oak (Kurth *et al.* 2014), forages (Yandigeri *et al.*2015), *Eucalyptus* (Salla *et al.* 2016). Actinobacteria can act as antagonist against pathogens due to production of lytic enzymes that are capable of destroying fungal cell wall. Many researchers have reported the enzyme activity of

actinobacteria can prevent the growth of fungus by destroying the cell wall with their extracellular enzymes like cellulase, chitinase and amylase. Following application of *Streptomyces* spp. on *Phaseolus vulgaris*, growth promotion was enhanced and induced resistance against *Fusarium solani* (Ray and Chakraborty, 2021).

CONCLUSION

Actinobacteria can enhance plant growth by producing growth regulators and other compounds and also act as biocontrol agent by production of antibiotics. Other properties like production of cell wall degrading enzymes and induced systemic resistance can inhibit the growth of plant pathogens. This review has focused on the importance of actinobacteria as they are widely regarded as excellent biological resource for plant growth promotion and biocontrol agents which act by various mechanisms such as increasing the supply of nutrients, production of IAA, cytokinin, controlling fungal diseases through antibiosis and competition. The excessive use of agrochemical is harmful for environment and use of biocontrol agents for management of plant disease becomes very important. It is very important to review and highlight the previous achievements in such research in order to draw the attention of research

community towards this emerging field. Utilization of actinobacteria can be developed as another way for suitable organic and environmental friendly agricultural crop production.

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