

Review Article

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Actinomycetes: A Promising Tool for Plant Growth Promotion and Disease Control

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ABSTRACT

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Plant growth promotion and biological control without deteriorating the environment and soil for sustainable agriculture has necessitated the exploration for microbial resources to replace the agrochemicals and fertilizers. Bacteria and fungi are widely distributed in the biosphere including the rhizosphere and help the plants by alleviating biotic and abiotic stress through diverse mechanisms and can be developed as bioinoculants for biocontrol and plant growth promoting activities. Actinomycetes are one of the most abundant group of soil microorganisms and well known for their antibiotics production to control the microorganisms. They are well studied for their role in biological control of plant pathogens, interactions with plants and plant growth promotion. This review briefly summarizes the effects of actinomycetes on biocontrol, plant growth promotion and association with plants as endophytes.

Introduction

Green revolution in India made a paradigm shift in agriculture from being a food grain importer to an exporter. This was achieved by consuming huge amount of chemical pesticides and fertilizers which was initially boosted the agricultural yields but became stagnant in the later years. This intensive use of chemical pesticides not only resulted in deterioration of soil health but also affected adversely the microbial diversity and population in the soil. In recent years, there is growing concern towards the utilization of

microbial inoculants as a replacement for the chemical pesticides and fertilizers for achieving the sustainable agriculture. In this perspective, microorganisms with the potential of producing plant growth-promoting substances, antimicrobial compounds seem to be the better alternative to the chemicals (Dhanasekaran *et al.*, 2005). Actinomycetes are Gram-positive, aerobic, filamentous bacteria present in diverse ecological niche such as soil fresh water, back water, lakes, compost, marine environment etc. As most of them are filamentous and sporulating in nature they strongly adhere to the soil particles and

establish intimate contact (endophytic association) with the plants (Cao *et al.*, 2004). They grow abundantly in soil with rich in organic matter and composing approximately 10% - 50% of the soil microflora community over a broad range of soil types and conditions.

The genus, *Streptomyces*, is the largest representative of actinomycetes, as it comprises huge number of species and varieties producing the majority of known antibiotics. Besides acting as agent for organic matter decomposition, actinomycetes play a vital role in control of plant pathogens (Hoster *et al.*, 2005) and plant growth promotion (Nassar *et al.*, 2003). This is due to their capability to act and exhibit production of antibiotics, siderophores, antimicrobial enzymes, plant growth promoting substances, phosphate solubilization, and competition with plant pathogens for food and space. The PGP microbes provide the additional benefit of being a biofungicides with inorganic or as a replacement to manage the fungicide resistance among plant pathogens and to reduce the number of fungicide applications per year (Gopalakrishnan *et al.*, 2013) which may otherwise cause serious deterioration of soil health.

The role of actinomycetes in the plant growth promotion like siderophore production, indole acetic acid (IAA) production, P-solubilization and biocontrol activity against various pathogens such as *Fusarium* sp. (Lu *et al.*, 2008; Gopalakrishnan *et al.*, 2013; Sreevidya *et al.*, 2016), *Rhizoctonia* sp. (Goudjal *et al.*, 2014), *Pythium* sp. (Hamdali *et al.*, 2008), *Sclerotium* sp. (Prapagdee *et al.*, 2008; Pattanapipitsai and Kamlandharn, 2012) and *Colletotrichum* sp. (Prapagdee *et al.*, 2008; Palaniyandi *et al.*, 2011) have been reported. Further, they also exhibit an endophytic association with the plant and benefits for growth and development of the host. These

properties of actinomycetes make them suitable bio-inoculant for the sustainable agriculture and soil health improvement.

Role in plant growth promotion

Plant growth regulators

Plant growth promoting (PGP) microbes are rhizosphere associated organisms that colonize the rhizosphere and rhizoplane which enhances the plant growth when artificially inoculated into the soil directly or through seed coating (Gopalakrishnan *et al.*, 2013& 2015). Root exudates play a vital role in PGP as being a major source for natural tryptophan, which may enhance the microbial biosynthesis of IAA and other auxins in rhizosphere region (Khamna *et al.*, 2009). Many endophytic as well as rhizospheric actinobacteria possess the ability to produce IAA, cytokinins and GA₃ (El-Tarabily and Sivasithamparam, 2006; Vijayabharathi *et al.*, 2016). Nimnoi *et al.*, (2010) reported the production of indole-3-acetic acid (IAA) and ammonia, a trait of plant growth promotion by endophytic actinomycetes from eaglewood (*Aquilaria crassna*). These isolates were found producing different types of siderophores and protease as biocontrol agents. The siderophores secreted by microbes increase the iron supply to plants and microbes; in addition to that they also inhibit the growth of plant pathogens. Hence, IAA and siderophore producing actinomycetes that colonize the root in the rhizosphere are known to promote the root elongation and plant growth (Khamna *et al.*, 2009; El-Tarabily *et al.*, 2009; Sreevidya *et al.*, 2016). They also benefit the plant by increasing the availability of trace elements such as iron, zinc etc., in the rhizosphere (Cakmakci *et al.*, 2006). Gopalakrishnan *et al.*, (2013) evaluated five strains of *Streptomyces* sp. which were proved as biocontrol agent against *F. oxysporum* f.sp. *ciceri* (Gopalakrishnan *et al.*, 2011) in green house and field for their plant

growth promoting ability in sorghum and rice. Several endophytic actinobacteria including *Streptomyces viridis*, *S. rimosus*, *S. olivaceoviridis*, *S. atrovirens* and *S. rochei* exhibited improved germination as well as root and shoot elongation (Abdallah *et al.*, 2013).

P-solubilization

Phosphorus is an important element for the plant growth and agricultural yields and the availability of soluble N and P nutrients are often limiting in agricultural soils due to the extensive cropping pattern and they are supplemented as chemical fertilizers. Though the soluble chemical fertilizers are readily available to the plants, most of them (70-80%) are quickly immobilized in soil and washed away by the raining waters, ground waters and make them unavailable for the plant growth (Shigaki *et al.*, 2006). This indulges the farmers to repeatedly amend their fields with these chemical fertilizers that pose a threat for human life as well as environment which urges the replacement of this expensive soluble chemical P by novel, cheaper and more environment friendly but nevertheless be a efficient P fertilizers.

The natural rock phosphate (RP) seems to be a promising alternative source of P fertilizers if a natural and non-polluting mechanism for its solubilization is found. Several microorganisms generally known as phosphate solubilizing microorganisms (PSM) have been reported to solubilize RP by using different strategies that include acidification, ion chelation or ion exchange. Among the PSM, the strains of *Pseudomonas* and *Bacillus* are the most powerful phosphate solubilizing bacteria. In addition to that, actinomycetes are of special interest since these filamentous bacteria are capable of forming colonization in the root tissue and producing spores for its survival in the agricultural soil and play a key

role by releasing a soluble phosphate from insoluble rock phosphate (Hamdali *et al.*, 2008). Various genera of actinomycetes such as *Rhodococcus*, *Arthrobacter*, *Streptomyces*, *Gordonia* and *Micromonospora* were reported to have P-solubilization potential under laboratory and glasshouse conditions (Jog *et al.*, 2014). Under P-deficient soils, *Streptomyces griseus*, *Streptomyces* spp, *Micromonospora aurantiaceae* performed in terms of P-solubilisation under wheat crop (Hamdali *et al.*, 2008; Jog *et al.*, 2014). Productions of various organic acids such as gluconic acid, citric acid, malic acid, lactic acid, propionic acid, oxalic and succinic acids by actinomycetes are believed to be the mechanism of their phosphate solubilization (Hamdali *et al.*, 2010; Jog *et al.*, 2014). The root exudates represent the major source of nutrients, such as carbohydrates, organic acids, amino acids and they influence the diversity of phosphate solubilizing microbes and their capacity with respect to different rhizosphere of plant.

Actinomycetes in plant-AM fungal and plant-rhizobium association

The Arbuscular Mycorrhiza (AM) fungi represent the key group of soil-borne microbes and known to play an important role in agriculture sustainability. Mycorrhiza, a symbiotic relationship between plant roots and fungi, is a dominating plant symbiosis in terrestrial ecosystem and helps in nutrient uptake by the plants. The formation of mycorrhizal symbiosis is promoted by so-called “mycorrhization helper bacteria (MHB)” (Garbaye *et al.*, 1994) and the possible mechanism underlying the helper effect is the direct effect exerted on mycorrhizal fungi for their pre-symbiotic survival and growth in the soil (Frey-Klett *et al.*, 2007). Inoculation of actinomycetes has significant effect on the enhancement of mycorrhizal colonization. It has been observed

that the occurrence of mycorrhizal colonization and formation of arbuscules, the nutrient transfer site, were significantly higher in roots of plants grown in soil inoculated with *Streptomyces coelicolor* compared with untreated mycorrhizal plants (Abdel-Fattah and Mohamedin, 2000). Inoculation of *Streptomyces* sp. has significantly promoted mycelial extension, growth and mycorrhization rate of *Amanita muscaria* in spruce, *Suillus bovinus* in pine and *Glomus mosseae* in cloves (Schrey *et al.*, 2005; Franco-Correa *et al.*, 2010). The compatibility of inoculated actinomycetes with survival, formation and functioning of AM symbiosis has received interest among researchers and it has been found that certain *Streptomyces* capable of producing antimicrobial compounds (El-Tarabily and Sivasithamparan, 2006) do not exhibit inhibitory effects on AM fungi, but some others reported to be inhibitory.

Actinobacteria when co-inoculated with nitrogen fixing organisms such as *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Sinorhizobium* has shown improved nodulation and nitrogen fixation by the N₂ fixing organism. *Streptomyces*, *Actinoplanes* and *Micromonospora* are the promising actinobacteria for the role of helper bacterial (Gregor *et al.*, 2003; Solans *et al.*, 2009; 2015). Studies conducted by Soe and Yamakawa (2013) showed that the coinoculation of *Streptomyces griseoflavus* P4 and *Bradyrhizobium yuanmingense* MAS34 on soybean resulted in enhanced nodulation, nitrogen fixation and seed in various varieties of soybean. This result emphasizes the importance of inoculation of actinobacteria with nitrogen fixers in leguminous crops.

Role in disease control

The plant system possesses its own resistance mechanism against plant pathogens but the

rhizosphere microorganisms contribute to this resistance additionally by excreting substances or metabolites limiting the growth of phytopathogenic fungi or by stimulating natural defense mechanism of the plant (Lehr *et al.*, 2008).

A greenhouse investigation was carried out with three endophytic actinomycetes *Actinoplanes campanulatus*, *Micromonospora chalcea* and *Streptomyces spiralis* for their potential to promote plant growth and to protect cucumber from pathogen *Pythium aphanidermatum* causing damping-off, crown and root rot. It can be used in the nutrient poor soils for crop production as it has good potential to perform as plant growth promoter. As a mechanism of plant growth promotion these organisms found producing plant growth regulators i.e. auxins indole-3-acetic acid (IAA) and indole-3-pyruvic acid (IPYA), gibberellic acid (GA3) and cytokinins isopentenyl adenine (iPa) and isopentenyl adenosine (iPA). These three endophytic isolates screened on the basis of their ability to produce β -1,3, β -1,4 and β -1,6-glucanases to antagonize *P. aphanidermatum*. These endophytes found producing glucanase especially in a consortial treatment which can be used in place of metalaxyl, a fungicide recommended for *Pythium* diseases in the area. Consortium of these three was proven better for plant growth promotion and biocontrol as compared to the respective individuals (El-Tarabily *et al.*, 2009).

Many workers have been reporting the biocontrol activities of endophytic actinomycetes by secretion of antimicrobials, enzymes, competition for food, etc. establishing a thrust area of research. Dhankar *et al.*, (2005) mentioned several mechanisms of endophytic actinomycetes to protect the plant which involves the production of antifungal compounds, chitinolytic activities and competition for

nutrients through siderophore production. Antibiosis is likely to be the important mechanism for biocontrol activity of actinomycetes as most of the isolates which shown antagonism *in-vitro* was also shown its effect *in vivo* (Trejo-Estrads *et al.*, 1998).

Verma *et al.*, (2009) isolated endophytic actinomycetes from neem (*Azadirachta indica*). Most common genus found was *Streptomyces*. Few other genus isolated were belong to *Streptosporangium*, *Microbispora*, *Streptoverticillium*, *Sacchromonospora* and *Nocardia* were also isolated. These isolates had shown antagonistic activity against root pathogens *Pythium* and *Phytophthora* sp. and can be developed into biocontrol agents against these fungal pathogens.

Rice endophytes were examined for their biocontrol potential by Tian *et al.*, (2004). Biocontrol potential of endophytic fungi and actinomycetes were assessed. In dual culture with pathogens, 41.2% of endophytic fungi and 50% of endophytic actinomycetes were found antagonistic to fungal pathogens. The major genera in endophytic actinomycetes were found to be *Streptomyces griseofuscus* and *hygroscopicus*. More diversity of endophytic actinomycetes was found in roots of rice plant and in alkaline soil.

Antimicrobial activity of endophytic actinomycetes was also studied in *Rhododendron* (Shimizu *et al.*, 2000) and found effective against Gram-positive bacteria, yeast and filamentous fungi. Cao *et al.*, (2004) deciphered biocontrol activity of endophytic actinomycetes against panama wilt of banana. Few of the strains, like *Streptomyces griseorubiginosus* were described as potential biocontrol agents against panama wilt pathogen *Fusarium oxysporum* f. sp. *cubense*. Siderophore-producing *Streptomyces* endophytes were suggested as biological control agent of

fusarium wilt of banana (Cao *et al.*, 2004). Tan *et al.*, (2006) assessed the biocontrol potential of endophytic actinomycetes against bacterial wilt of tomato caused by *Ralstonia solanacearum* and tested different isolates for their potential for production of siderophores. It is a serious pathogen of tomato and very difficult to control. In such cases use of endophytic actinomycetes may be a better candidate as biocontrol agent.

Production of antimicrobials

Actinomycetes are abundant producers of antibiotics, which produces about 45% of the total antibiotics currently in use and they produces diverse natural products that would be approx. 10,000 compounds (Liu *et al.*, 2012). In soil, the production of antibiotic metabolites (Hyang *et al.*, 2005) and antimicrobial compounds (Sabaratnam and Traquair, 2002; Lehman *et al.*, 2005) facilitate actinomycetes to restrict the invasion of plant pathogens to the habitats. The structure of the active metabolite from *Nocardia levis* MK-VL_113 was elucidated using ¹H NMR and ¹³C NMR spectra and identified as 1-phenylbut-3-ene-2-ol which was reported first time as a natural product (Kavitha *et al.*, 2010). In the study of *Streptomyces lydicus* strain A01, the main antifungal compound (antagonist to *Fusarium oxysporum*, *Botrytis cinerea*, *Monilinia laxa* etc.) was obtained using column chromatography and HPLC. Further, the structural analysis revealed that the produced compound is natamycin, a potential polyene antibiotic widely used as a natural bio-preservative for food (Lu *et al.*, 2008).

Streptomyces sp. is the most widely studied biocontrol agent among actinomycetes and they have the essential characteristics that make them suitable as a biocontrol agent against soil borne pathogens. Streptomycin and cycloheximide are the first antibiotics

applied for the control of fungal and bacterial pathogens in plants, which are produced by *Streptomyces griseus*. The potential to produce multiple antibiotics or a antibiotic with diverse mechanism by the biocontrol agent is desirable for the suppression of diverse pathogenic microbes. Further, the antibiotics of actinomycetes have application as a broad range soil fungicide alternative to the use of chemical fungicides such as methyl bromide and metalaxyl (Jinhua *et al.*, 2010). Azalomycin, an antibiotic, when treated with soil as culture filtrate resulted in more than 80% decrease in fungal population after 14 days of treatment and found to be stable over a broad range of pH and temperatre and exhibited antagonism against *Fusarium oxysporum*, *Rhizoctonia solani*, *Sladosporium cladosporioides*, *F. chlamydosporum*, *Alternaria solani* and *Colletotrichum gloeosporioides* (Jinhua *et al.*, 2010). Few of the isolates from medicinal plants of Panxi plateau in China were found to harbour genes for antibiotics production. PCR amplification for genes coding for polyketide synthetase (PKS-I, PKS-II) and nonribosomal peptide synthetase (NRPS) exhibited broad-spectrum antimicrobial activity of endophytic actinomycetes. Predominant genera were *Streptomyces*, while the remainder belonged to genera *Micromonospora*, *Oerskovia*, *Nonomurea*, *Promicromonospora* and *Rhodococcus* (Zhao *et al.*, 2011).

Sreevidya *et al.*, (2016) reported the antagonistic effect of actinomycetes that were isolated from vermicompost and soils against *Macrophomina phaseolina* and *Sclerotium rolfsii* in chickpea crop. Similarly, the antagonistic activity of actinomycetes from wheat Rhizosphere was shown by Jog *et al.*, (2014). The main mechanism involved in biocontrol of pathogens are secretion of bioactive compounds such as antibiotics and cell wall degrading enzymes, competition for space and nutrients , mycoparasitism and

induction of plant defensive mechanism (Bakker *et al.*, 2007). Endophytic actinomycetes are being reported continuously as potential agent for secreting novel antimicrobial compounds. The use of endophyte actinomycetes as a potential biocontrol agent is having great possibility as they can colonize interior of the host plant avoiding competition by the other microbes. The establishment of natural regeneration from seeds to uniformly grown plants under harsh conditions indicates the contribution of endophytic microbes for the bio-protection of germinated seeds against soil borne pathogens and plant growth promotion (Goudjal *et al.*, 2014).

Volatile antibiotics

The actinomycetes especially the genus *Streptomyces* have been reported to produce volatile antifungal substances which inhibit the growth of plant pathogens by causing morphological abnormalities like inhibition of spore and conidial germination, appressorial formation etc. in fungi such as *Aspergillus* sp., *Magnaporthe oryzae*, *Trichoderma viride* and *F. oxysporum* (Herrington *et al.*, 1987). GC-MS analysis of culture filtrate of *Streptomyces alboflavus* revealed 27 different compounds, among which dimethyl disulfide was proved to have inhibitory effect against *F. moniliforme* in vitro (Wang *et al.*, 2013).

Cell wall degrading enzymes

Biocontrol agents produce hydrolytic enzymes which degrade fungal and bacterial cell wall, cell membrane, membrane proteins and extracellular virulence factors in controlling the plant diseases (Pal and Gardener, 2006). Abd-Allah (2001) had reported production of chitinase by endophytic actinomycetes as a biocontrol trait. In this study, 372 strains were screened for the production of this enzyme

and isolate *Streptomyces plicatus* was found better. Chitinase from *Streptomyces plicatus* had a significant inhibition for *Fusarium oxysporum* f.sp. *lycopersici* and *Verticillium albo-atrum*. *Streptomyces plicatus* found affecting spore germination, germ tube elongation and radial growth of wilt pathogens of tomato and protected the plants *in vivo* when applied to the root system of tomato plants before transplantation.

Endophytic actinomycetes have been studied in many plants species. *Streptomyces* sp. is the most extensively studied organisms in actinomycetes for the production of cell wall-degrading extracellular enzymes, their expression, substrate recognition and their involvement in growth and development (Charter *et al.*, 2010). Among cell wall degrading enzymes, the chitinolytic enzyme plays a vital role in exhibiting antagonism by degrading the chitin, which is a major structural component of cell wall. The other extracellular enzymes are β -1,3-glucosidase, cellulase and protease which are also causing the lysis of hyphae and inhibit the growth of phytopathogens (Xue *et al.*, 2013). Actinobacteria produces chitinases which is their main action against fungal pathogens (Yandigeri *et al.*, 2015). The extracellular antifungal metabolites especially chitinase and β -1,3 glucanase produced by actinomycetes inhibit the growth of fungi through hyphal swelling, abnormal shapes and lysis of cell walls in *F. oxysporum* and *S. rolfsii* (Prapagdee *et al.*, 2008; El-Katatny *et al.*, 2001).

Induction of host resistance

Plants exhibit its own defense mechanism that provides resistance against diverse plant pathogens. This defense mechanism is of two types: induced systemic resistance (ISR) and systemic acquired resistance (SAR). The ISR mechanism is induced by the rhizobacteria

and SAR is induced by pathogen and salicylic acid (Schuhegger *et al.*, 2006). Conn *et al.*, (2008) reported that the endophytic actinomycetes were able to induce the SAR and jasmonic acid (JA) / ethylene (ET) pathways which gave the resistance against the fungal pathogen, *F. oxysporum* and bacterial pathogen, *Erwinia carotovora* subsp. *carotovora*, respectively. The culture filtrate of an endophytic *Micromonospora* sp. strain EN43, *Streptomyces* sp. strain EN27 against *E. carotovora* ssp. *carotovora* in *Arabidopsis thaliana*, *Streptomyces bikiniensis* HD-087 against *F. oxysporum* f.sp. *cucumerinum* in cucumber and *Streptomyces* sp. GB4-2 against *Botrytis cinerea* in Norway spruce induced the SAR and JA/ET pathways (Conn *et al.*, 2008; Lehr *et al.*, 2008; Zhao *et al.*, 2012). Dual-culture assay is the most commonly used method for evaluating the antagonistic activity of organisms against plant pathogenic fungi *in vitro* (Khamna *et al.*, 2009; Baz *et al.*, 2012). Actinomycetes has been reported to exhibit antagonistic activity against *Erwinia carotovora* subsp. *carotovaora* and *Burkholderia cepacia* in biological control of onion rot (Abdallah *et al.*, 2013), *Streptomyces avidinii* vh32, *S. toxybicini* vh22 and *S. tricolor* vh85 showed prominent antagonistic potential against *Rhizoctonia solani* and induced the accumulation of phenolic compounds in tomato (Patil *et al.*, 2011) particularly gallic, ferulic, cinnamic, genticic, chlorogenic and salicylic acids by which the bioagents immunize the plants against biotic stresses (Jones and Dangal, 2006). In the recent times, host plant resistance induced by *Streptomyces* had been studied on various crops including vegetables, forages and economically important woody plants like potato (Arseneault *et al.*, 2014), eucalyptus (Salla *et al.*, 2016) and oak (Kurth *et al.*, 2014).

In conclusion, actinomycetes have a great potential to be utilized in the bioinoculant

industry apart from its use in pharmaceuticals. It can enhance the plant growth by producing growth regulators and other compounds and it is well known for production of antibiotics which add to its quality as biocontrol agent. Other features like production of cell wall degrading enzymes and induced systemic resistance can also be useful in targeting new plant pathogens and will add to the campaign of green and sustainable agriculture. Many novel compounds can act as boon in problem of developing resistance among agro-pests. At the last, a much larger effort is being needed in future to explore the ocean of potential of actinomycetes.

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