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Streptomycetes as a potential biocontrol agent

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Abstract

Synthetic fungicides are often able to effectively control plant diseases, but some fungicides result in serious environmental and health problems. Therefore, there is growing interest in discovering and developing new, improved fungicides based on natural products as well as introducing alternative biocontrol agents to manage plant diseases. *Streptomyces* bacteria appear to be promising biocontrol agents against a wide range of phytopathogenic fungi, which is not surprising given their ability to produce various bioactive compounds. This review provides insight into the biocontrol potential of various *Streptomyces* spp. Studies clearly show that *Streptomyces* spp. have the potential to be used as highly effective biocontrol agents against many fungal and bacterial disease.

Keywords: Streptomyces, biocontrol agents, biological control

Introduction

Streptomyces is the largest genus of the phylum *Actinobacteria* which consists of a group of Gram-positive, aerobic, non-motile, catalase positive, and non-acid-fast bacteria with a filamentous form that resembles fungi (Flardh and Buttner, 2009; Hasani *et al.*, 2014) ^[14, 38]. Currently, over 700 species of *Streptomyces* have been identified and these bacteria have relatively large genomes of approximately 8–9 Mbp in size with a high GC content of more than 70% (Wu *et al.*, 2005; Hasani *et al.*, 2014; Ser *et al.*, 2015c) ^[114, 38, 103]. The predominant character of *Streptomyces* morphology is formation of thin strands of mycelium with spiral spore chains. Streptomycetes have a life cycle unique among bacteria. It consists of two phases vegetative and the sporogenous. When these organisms are grown on an adequate solid medium, the spores germinate and grow. Later, the germ tube grows and forms a mat of hyphae firmly attached to the solid surface. This represents the substrate or vegetative growth, specialized aerial hyphae arise on the top of the mycelium; this mycelium forms chains of three to many spores called sporophores at maturity. They are formed by formation of cross-walls in the multinucleate aerial filaments followed by separation of individual cells.

When grown in medium, streptomycete colonies form a discrete and lichenoid, leathery or butyrous colonies. Initially, the colonies are relatively smooth surfaced, but later they develop a weft of aerial mycelium that may appear floccose, granular, powdery, or velvety. Streptomycetes produce a wide variety of pigments responsible for the color of the vegetative and aerial mycelia. Colored diffusible pigments may also be formed. The vegetative mycelium is constituted by thin hyphae (0.5-2 μ m in diameter) that often lack cross-walls and are extensively branched. Depending on the temperature, the pH and the age of culture the substrate mycelium can show numerous colors and soluble pigments: blue, dark green, red, and violet.

Streptomycetes, which are abundant in soil, are believed to play a major role in composting the organic matter. The members of *Streptomyces* are well-known for their ability to produce a variety of bioactive compounds. *Streptomyces* strains also have important applications in the agricultural field through their biological control potential against phytopathogens, particularly phytopathogenic fungi. The production of most antibiotics is species specific, and these secondary metabolites are important for *Streptomyces* species in order to compete with other microorganisms that come in contact.

Streptomycetes in soil and their relationship with plant roots

The advantages of *Streptomyces* spp. include their ability to colonize plant root surfaces,

survive in various types of soil and also produce spores which allow them to survive longer and in various extreme conditions (Gonzalez-Franco and Robles-Hernandez, 2009; Ningthoujam *et al.*, 2009)^[29].

Streptomycetes are found to colonize rhizosphere, enter the root tissues and establish endophytic lifestyle with plants (Cao et al., 2004) [118]. Actinomycetes can occur in the plant rhizosphere soil and exercise an antagonistic and competitive effect on the microbial communities. They have the ability to produce active compounds, such as antifungal and antibacterial antibiotics or plant growth regulators (PGRs), that have been developed for agricultural uses (Suzuki et al. 2000) ^[100]. They have also been used as commercially formulated biocontrol agents of plant diseases such as Streptomyces griseoviridis cells used to protect crops against infections by Fusarium spp. and Alternaria spp. Due to production of a wide number of antifungal compounds and chitinase (Mahadevan and Crawford, 1997; Taechowisan et al., 2003a) ^[119, 101], the ability of some streptomycete strains to inhibit plant pathogens and therefore act as promising biological control agents. Some strains were screened and characterized for their activity against soil-borne pathogens. The mode action of Streptomycetes as a potential biocontrol agent is discussed below

Antibiosis

Streptomycetes are the largest antibiotics-producing genus in the microbial world. Streptomyces species exhibit biocontrol activity that correlates with their production of antibiotics (Rothrock & Gottlieb 1984: Hwang et al., 1994: Raatikainen et al., 1994) ^[84, 40, 74]. Streptothricin, actinomycin and streptomycin were the first discovered antibiotics produced by Streptomyces spp. (Waksman, 1943; Waksman and Tishler, 1942) [111]. From 1950s to 1970s started the screening of streptomycetes for antibiotics production and a wide number of compounds were found and characterized, example novobiocin, vancomycin, tetracycline, nystatin (Hopwood, 2007) ^[39]. They have antibacterial and antifungal activities (Hopwood, 2007)^[39]. Streptomyces violaceusniger YCED9 was an isolate from a British soil, exhibited biocontrol activity against a variety of plant pathogenic fungi. The strain produces three antifungal antibiotics viz., nigericin, geldanamycin and a complex of polyenes that includes guanidylfungin a (Trejo- Estrada et al., 1998) [106.]. Anti-Fusarium Activity (AFA) (Trejo-Estrada et al., 1998) [106]. Growth and pathogenesis of R. solani and S. homeocarpa were reduced by the presence of the nigericin produced by YCED9.

The antifungal potential of extracellular metabolites from *Streptomyces* against some fungi was previously reported (Rothrock and Gottlieb, 1984; El-Abyad *et al.*, 1993; Chamberlain and Crawford, 1999; Joo, 2005; Fguira *et al.*, 2005) ^[84, 19, 26]. It has been reported that *Streptomyces violaceusniger* G10 showed a strong antagonism toward *F. oxysporum* f.sp. *cubense* by producing extracellular antifungal metabolites. Validamycin a (VMA) is an aminoglucoside antibiotic produced by *Streptomyces hygroscopicus* var. *limoneus.* VMA effectively controls rice sheath blight caused by *Rhizoctonia solani* (Wakae and Matsuura, 1975) ^[110].

The antibiotic Oligomycin A was first isolated from *Streptomyces diastatochromogenes* and was found to be active against several other phytopathogenic fungi in such as *Magnoporthe oryzae*, *Botrytis cinerea*, *Cladosporium cucumerinum*, *Colletotrichum lagenarium*, *Phytophthora* *capsici, Alternaria alternata*, and *Aspergillus niger* (Smith *et al.*, 1954; Kim *et al.*, 1999; Yang *et al.*, 2010)^[99, 46, 117]. Oligomycin A's ability to control the development of rice blast was evaluated in the greenhouse and the results showed that rice plants treated with Oligomycin A (50 µg/mL) had reduced lesions. When the concentration of Oligomycin A was increased up to 500 µg/mL, the rice plants did not show any rice blast disease symptoms (Kim *et al.*, 1999)^[46].

Rapamycin also known as Sirolimus was initially isolated from *Streptomyces hygroscopicus* (Sehgal *et al.*, 1975; Sehgal, 1998) ^[88, 89]. Rapamycin and Pyrroles are potent antifungal agent found to be effective against many fungus and are also commonly found in various *Streptomyces* species (Robertson and Stevens, 2014; Ser *et al.*, 2015b, 2016b,c; Tan *et al.*, 2015; Awla *et al.*, 2016) ^[77, 90, 91, 4].

An antifungal antibiotic produced by *Streptomyces koyangensis* inhibited the growth of *Pyricularia oryzae* and *Rhizoctonia solani*. Under greenhouse conditions, the antibiotic suppressed blast disease in rice plants (Lee *et al.*, 2005) ^[56]. VOCs produced by *Streptomyces philanthi* inhibited mycelial growth of rice pathogenic fungi such as *Rhizoctonia solani*, *Pyricularia grisea*, *Bipolaris oryzae* and *Fusarium fujikuroi* (Boukaew *et al.*, 2014) ^[6]. Culture filtrates of UCR3-16 showed significant inhibition against the fungal pathogens. The antifungal compounds present in the culture filtrates must be heat labile as antagonistic activity was lost when filtrates were sterilized. Prapagdee *et al.* (2008) ^[72]

Cell wall-hydrolysing enzymes

It has been reported that antifungal mechanism of Streptomyces has been attributed to the action of hydrolytic enzymes such as chitinase, β -1, 3-glucanase, chitosanase, and protease (De Boer et al., 1998; Wang et al., 1999; Wang et al., 2002; Chang et al., 2007) ^[17, 112, 113]. Streptomyces violaceusniger YCED9 produced the extracellular fungal cell wall-hydrolysing enzymes chitinase and β -1,3-glucanase (Trejo- Estrada et al., 1998) [106]. The antagonistic activity of Streptomyces to fungal pathogens was usually related to the production of antifungal compounds (Trejo-Estrada et al., 1998; Ouhdouch et al., 2001; Fguira et al., 2005; Taechowisan et al., 2005) [106, 26] and extracellular hydrolytic enzymes (Valois, 1996; Trejo-Estrada et al., 1998, Mahadevan and Crawford, 1999; Mukherjee and Sen 2006) ^[64]. Chitinase and β -1,3-glucanase are considered to be important hydrolytic enzymes in the lysis of fungal cell walls of Fusarium oxysporum, Sclerotinia minor, and Sclerotium rolfsii (Singh et al., 1999; El-Tarabily et al., 2000) [98]. The production of chitinase and β -1,3 glucanase enzymes by Streptomyces was related to fungal growth inhibition and the biological control of fungal pathogens was possible because of the ability of Streptomyces to degrade fungal cell walls (Valois, 1996; Mahadevan and Crawford, 1997; El-Tarabily et al.,2000; Mukherjee and Sen 2006) [64].

Hyperparasitism may occur due to the release of extracellular lytic enzymes such as chitinases and glucanases from the biocontrol agent (Gonzalez-Franco and Robles-Hernandez, 2009; Palaniyandi *et al.*, 2013)^[29]. It has also been shown that *Streptomyces* spp. are capable of producing chitinases and glucanases which play important roles in destruction of fungal cell walls (Mahadevan and Crawford, 1997; El-Tarabily *et al.*, 2000; Gonzalez-Franco and Robles-Hernandez, 2009)^[29].

UCR3-16 produced major fungal cell wall degrading enzymes such as chitinase, and glucanase, lipase and pro-tease.

Chitinase producing *Streptomyces vinaceusdrappus* inhibited mycelial growth of rice fungal pathogens, *Curvularia oryzae*, *Pyricularia oryzae*, *Bipolaris oryzae* and *Fusarium oxysporum* (Ningthoujam *et al.*, 2009) ^[66]. Chitinase and β 1,3-glucanase produced by *Streptomyces* sp. 385 lysed cell walls of *Fusarium oxysporum* (Singh *et al.*, 1999) ^[98].

Plant growth promotion by growth regulators

Bacteria of the genus *Streptomyces* are common inhabitants of rhizosphere and act as beneficial microorganisms for plant growth and development (Gopalakrishnan *et al.*, 2014; Tokala *et al.*, 2002a) ^[32, 104]. In addition to their ability to inhibit plant pathogens, some actinomycetes are also known to form close associations with plants, colonize their internal tissues without causing disease symptoms, and promote their growth (Kunoh 2002) ^[50]. Streptomycetes have been little investigated as Plant Growth Promoting Bacteria (PGPB). Some works were carried during the 1980 to 1990 at the University of Milan and only recently, the interest on streptomycete beneficial effects on plant growth is gaining increased attention; their positive effects on root nodulation in Pea plants were observed (Tokala *et al.*, 2002b) ^[104], as well as the increase of fresh and dry weight and length of roots and shoots of bean.

The main modes of action involved in the PGP activity are the synthesis of the hormone indole-3-acetic acid (IAA) and the improvement of iron and phosphate availability for the plant in the rhizosphere. Here, a collection of 200 endophytic streptomycetes was analyzed for these PGP traits. IAA was produced by almost all isolates, as commonly reported for bacteria, which inhabit the rhizosphere (Patten and Glick, 1996). *Streptomyces* have been reported for the PGP activity. Especially, they are known to synthesize the hormone auxin and improve the availability of iron (Imbert *et al.*, 1995) and phosphate in the rhizosphere (Sousa *et al.*, 2008).

Several studies have reported plant growth promoting activities of endophytic actinomycetes on tomato seedlings (Coa et al. 2005; El-Tarabily et al. 2008) [14, 23]. The enhancement of plant growth by the strains Streptomyces sp. CA-2 and AA-2 could contribute to the protection of the plant against pathogenic fungi as previously reported with other Streptomyces spp. by Xiao et al. (2002) [115]. The growth promoting effect of the two isolates of actino-mycetes seemed to be correlated with root enhancement and shoot production. In the same cases, where the strains were strictly endo-phytic, such effects were generally attributed to PGRs production (Shi et al. 2009). El-Tarabily et al. (2008)^[31] reported that the involvement of PGRs could not only help the seedlings to grow better but could also help the host to compensate for tissue damage caused by the pathogen agent. Several endophytic bacteria have been reported to produce PGRs in vitro and to promote the growth of seedlings (Kuklinsky-Sobral et al. 2004; Goudjal et al. 2013) [48, 34].

Actinomycetes have been reported to play an important role in the plant rhizosphere by secreting a wide range of antimicrobial products thus preventing growth of common root pathogens. Actinomycetes, especially *Streptomyces*, are prolific producers of secondary metabolites, and are being used as BCAs to control soil-borne and seed borne diseases of plants (Rosales and Mew, 1997)^[78]. Antagonistic activity may be due to production of antifungal metabolites volatile compounds (Khamna *et al.*, 2010; Boukaew *et al.*, 2014)^[7, 45] and cell wall degrading enzymes such as chitinase, glucanase. Actinomycetes, especially *Streptomyces* spp. accounting for an abundant percentage of the soil microflora, are particularly effective colonizers of plant root systems and are able to endure unfavourable growth conditions by forming spores (Alexander, 1997)^[1]. Despite their preliminary track record as BCAs and plant growth promoting (PGP) activities, *Streptomyces* spp. have been scarcely reported in the literature. Some reports exist for their ability to solubilize phosphate, and production of indole acetic acid (IAA), siderophores, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase and cell wall degrading enzymes such as chitinase, glucanase and protease (Singh *et al.*, 1999; Gopalakrishnan *et al.*, 2011; Jog *et al.*, 2012; Sadeghi *et al.*, 2012; Passari *et al.*, 2015; Qin *et al.*, 2015)^[98, 85, 70].

Siderophores

It is well known that microbial siderophores play an important role in plant growth as demonstrated by the effect on root and shoot biomass and length of rice plants, as consequence of the inoculation of a siderophore-producing streptomycete, the growth promoting effect is widely attributed to factors, such as siderophore production and phosphate solubilization (Hamdali et al. 2008) [37] and nitrogen fixation (Ribbe et al. 1997) ^[76]. Streptomycetes also showed promising PGP activity because of the frequent production of indole-3-acetic acid (IAA) and siderophores, although they only rarely solubilized phosphate. These traits are very common among the microorganisms that inhabit the rhizosphere and in some works the PGP activity showed in vitro was confirmed in planta. For instance, rice plants inoculated with siderophoreproducing Streptomyces sp. enhanced plant growth and significantly increased root and shoot biomass.

Volatile Substances

Streptomyces are able to produce useful volatile substances with molecular weight of <300 Da, low polarity, and high vapor [Pichersky et al., 2006]. Bacterial volatile substances have been successfully recognized by gas chromatography comb with pressure mass spectrometry (GC-MS). More than 120 various substances have been recognized in actinomycetes including Alkanes, Alkenes, Alkens, Alcohols, Ketones, Aldehydes, Acids and Esters. Volatile substances derived from Streptomyces sp. and other species of actinomycetes prevent mycelium growth and inhibit spore germination of different fungi (Kai et al., 2008, Anitha et al., 2010). Cyclohexanol, decanol, 2-ethyl-1-hexanol, nonanol, benzothiazole dimethyl trisulfide are important compounds that inhibit spore germination and mycelium growth of Sclerotinia sclerotiorum (Fernandoa et al., 2005)^[25] Volatile substances of *Streptomyces griseus* reduces spore germination of *Gleosporium aridum* which subsequently lead to faster formation of sclerotinia of R.solani and Sclerotinia cepivorum. Volatile substances of Streptomyces platensis also reduced the growth of R.solani, Sclerotinia sclerotiorum and Botrytis cinerea and reduced the disease level of leaf blight, seedling blight in rice, leaf blight in oilseed rape, and fruit rot in strawberry (McCain., 1966, Wan et al., 2008) [62, 37]. In another research, effects of volatile substances of Streptomyces globisporus were examined on spore germinating and mycelium growth Penicillium italicum and infected fruits. Among 41 volatile substances of this bacterium, Dimethyl disulfide and Dimethyl trisulfide have high inhibiting effects against fungus (Li et al., 2010) [117]. Volatile substances of various species of Streptomyces, have high potential in biological control.

Streptomyces in biological control

Biological control is a nonchemical measure that has been reported in several cases to be as effective as chemical control (Dik and Elad, 1999; Elad and Zimand, 1993) ^[20, 21]. The excessive use of chemical fungicides in agriculture has led to deteriorating human health, environmental pollution and development of pathogen resistance to fungicide. Microbial antagonists are widely used for the biocontrol of fungal plant diseases due to lack of induction of pathogen resistance and reduction of chemical fungicide residues in soil. Mukheriee et al., (1995) has reported Streptomyces spp. are well known biocontrol agents that inhibit several plant pathogenic fungi (El-Tarabily et al., 2000; Errakhi et al., 2007; Joo, 2005; Xiao et al., 2002) [115, 24, 43]. The role of actinomycetes in the biocontrol of soil-borne plant pathogens has been demonstrated against various pathogens such as Fusarium spp. (Sabaou and Bounaga 1987; Gopalakrishnan et al. 2011) ^[82], Phytophthora spp. (Shahidi Bonjar et al. 2006) ^[84], Pythium spp.(Hamdali et al. 2008) ^[36], Rhizoctonia spp. (Sadeghi et al. 2006)^[84], and Verticillium spp. (Meschke and Schrempf 2010) $^{[63]}$. The ability of bacteria, especially actinomycetes, to parasitize and degrade the spores of fungal plant pathogen was well established (El-Tarabily et al., 1997). Biocontrol of Phytophthora cinnamomi and root rot of Banksia grandis Willd. was obtained using a cellulaseproducing isolate of Micromonospora carbonacea (El-Tarabily et al., 1996) and control of Phytophthora fragariae var. rubi causing raspberry root rot was suppressed by the application of actinomycete isolates that were selected for the production of β -1,3, β -1,4 and β -1,6 glucanases (Valois et al., 1996).

The genus Streptomyces was well known as antifungal biocontrol agents that inhibit several plant pathogenic fungi (El-Tarabily et al., 2000; Xiao et al., 2002; Joo, 2005; Errakhi et al., 2007) [115, 43]. Streptomyces was important soil microorganism and well known producers of antibiotics and extracellular enzymes (Crawford et al., 1993) [16]. Streptomyces violaceusniger SRA14 had a strong antagonistic activity to Colletotrichum gloeosporioides. Analysis of the 16S rDNA gene sequences showed that the SRA14 was closely related to Streptomyces hygroscopicus (98 per cent similarity). The non-pathogenic strains of Streptomyces was applied to control scab of potato (Solanum tuberosum L.) caused by Streptomyces scabies (Ryan and Kinkel, 1997; Neeno-Eckwall and Schottel, 1999) damping-off of tomato (Sabaratnam and Traquair, 2002) and Sclerotinia basal drop. Mycoparasitism involves the production of extracellular enzymes that hydrolyse the fungal cell walls, whereas antibiosis involves the production of secondary metabolites in the rhizosphere which inhibits the growth and differentiation of fungal pathogens. Members of the genus Streptomyces strains YCED9 and WYEC108 were antifungal biocontrol agents (Crawford et al., 1993; Crawford 1996)^[15, 16]. You et al., 1996 have observed increases in streptomycetes population in soil after enrichment with organic matter. This might explain the enhanced antagonism or suppressiveness of soil sometimes seen after organic enrichment (Malajczuk 1983; van Driesche and Bellows 1996). The Streptomyces strains have been shown to control in vivo lettuce damping off caused by Pythium ultimum (Crawford et al., 1993)^[16], which might be explained by the fact that the lettuce was grown in a rich potting soil. Streptomyces were also studied against Pythium seed and root rot, Phytophthora root rot (Xiao et al., 2002) [115], Rhizoctonia; El-Tarabily et al., 2000) [21]. Several

studies have reported the use of actinomycete strains for biocontrol of *Rhizoctonia solani* damping-off (Coa *et al.*2004; Chung *et al.* 2005; Sadeghi *et al.* 2006; Patil *et al.* 2010) ^[84]. In addition, commercial products to control crop damping-off, such as Mycostop (*Streptomyces griseovirid* is strain K61) and Actinovate (*Streptomyces lydicus* strain WYEC108), have been registered.

Conclusion

This review explores an implementation of antagonistic actinomycetes as plant growth promoters and biocontrol agents in combined way, which make them competitive compared to other commercial biocontrol agents. They are excellent candidates as biocontrol agents for the biological control of devastating plant disease. In order to establish Streptomyces as biocontrol agents, more field experiments should be conducted to determine their control efficacy under different environmental conditions. Additionally, more work is needed to optimize isolation, formulation and application methods of Streptomyces in order to fully maximize their potential as effective biocontrol agents. As actinomycetes especially Streptomyces spp. produce spores that help dissemination and confer resistance to many adverse conditions, they can be promising agents for development as novel biofertil-izers and biocontrol agents.

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