Streptomyces for Sustainability

12

Patricia Vaz Jauri, Nora Altier, and Linda L. Kinkel

Abstract

Streptomyces is a genus of gram-positive bacteria with a mycelial growth habit and the ability to produce spores. Due to their unparalleled ability to produce antibiotics, most of the early research carried out on *Streptomyces* was antibiotic discovery-driven, with over two thirds of antibiotics used for medical purposes originally isolated from *Streptomyces*. However, their ubiquity, high capacity of adaptation to different niches and rich secondary metabolite production, make them an invaluable source of solutions in diverse human activities, including medicine, agriculture, industry and toxic waste remotion. In addition to the ability to culture and produce *Streptomyces* and *Streptomyces*-derived metabolites, knowledge on how to manipulate natural populations of *Streptomyces* will likely improve our ability to make environmentally sustainable decisions.

12.1 Introduction

The *Streptomyces* are a large and diverse group of microorganisms that have long captured the attention of researchers. They have been studied for diverse reasons, including their unique morphology; their apparently endless source of secondary metabolites, especially antibiotics and other chemicals for medical use; their pathogenicity; and their symbiotic associations with other organisms, including insects and plants. There is substantial literature on *Streptomyces*, and, overall, research on

P.V. Jauri (✉) • N. Altier
Plataforma de Bioinsumos, INIA-Las Brujas, Canelones, Uruguay
e-mail: pativaz@inia.org.uy

L.L. Kinkel
Department of Plant Pathology, University of Minnesota, Minneapolis, MN, USA

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S. Castro-Sowinski (ed.), *Microbial Models: From Environmental to Industrial Sustainability*, Microorganisms for Sustainability 1,
DOI 10.1007/978-981-10-2555-6_12

Streptomyces has been extremely fruitful, especially in relation to clinical applications of *Streptomyces* secondary metabolites. In this chapter, we aim to present an up-to-date overview of this genus, with an emphasis on their use in agricultural settings.

12.1.1 Life History Traits

The *Streptomyces* are filamentous, spore-forming bacteria. They are ubiquitous in soil and have been more recently recognized to be common and widespread in marine and freshwater sediments (Maldonado et al. 2005; You et al. 2005; Jensen et al. 2005). Most species are mesophilic, aerobic, and saprophytic organisms (Kieser and John Innes Foundation 2000). However, some isolates have been found in extreme environments (Pathom-Aree et al. 2006; Ribbe et al. 1997). Beyond their roles as saprophytes, some *Streptomyces* live as endophytes (Cao et al. 2005; Misk and Franco 2011; Gangwar et al. 2014; Qin et al. 2015), as pathogens of plants (Takeuchi et al. 1996; Hiltunen et al. 2005) or immunocompromised humans (Dunne et al. 1998), and as beneficial symbionts with a wide variety of higher organisms, including insects, plants, and sponges (Haeder et al. 2009; Loria et al. 2006; Kaltenpoth 2009; Kaltenpoth and Engl 2014; Khan et al. 2011; Hulcr et al. 2011; Seipke et al. 2012; Book et al. 2014). *Streptomyces* are gram positive, and their genomes have high G + C content, typically above 70 %. *Streptomyces* genomes are generally large compared to other actinobacteria and eubacteria in general (Gao and Gupta 2012; Myronovskyi et al. 2013; Rückert et al. 2013). However, their genome size is variable (~5.2–12.7 Mbp) and is thought to be related to their life history. Species that have a restricted or highly circumscribed niche width, such as within a host, have a tendency to have smaller genomes than those that are free living and coexist with high densities of other bacteria (Kirchman 2012). *Streptomyces* possess a linear chromosome, which has been observed in only three other actinobacterial genera (*Rhodococcus*, *Gordonibacter*, and *Kineococcus*; Gao and Gupta 2012). Transposons, or highly mobile elements, have also been found in *Streptomyces* genomes (Kieser and John Innes Foundation 2000).

One striking feature of this genus is their mycelial growth, which is uncommon among bacteria. When grown in solid medium in the laboratory, *Streptomyces* form an aerial mycelium after vegetative growth, which is followed by spore formation at the hyphal tips. Spores are resistant to desiccation and heat (Flärdh and Buttner 2009) and are pigmented, which provides protection against UV radiation (Funa et al. 2005). These characteristics are believed key for dispersal in wind and water as well as for survival in natural environments.

Streptomyces are especially notable as antibiotic producers. Secondary metabolites produced by *Streptomyces* have been used in medicine and agriculture for over 60 years. Production of diverse bioactive compounds is perceived to be crucial to *Streptomyces* life history in soil and in symbiotic associations, where antibiotics as weapons or signaling molecules are believed to provide a fitness advantage (Linares et al. 2006; Martínez 2008; Fischbach 2009; Vaz et al. 2013).

12.1.2 Taxonomy and Phylogeny

The genus *Streptomyces* lies within the family *Streptomycetaceae*, order *Actinomycetales* and class *Actinobacteria* (http://www.bacterio.net/-classifphyla.html). *Streptomyces* spp. have been identified based on their cultural and physiological characteristics, including spore and hyphal shapes, and by cell-wall fatty acid content (Wellington et al. 1992). More recently, ribosomal RNA sequences, specifically partial or total 16S rRNA sequences, have become the most common means of identification (Takeuchi et al. 1996; Davelos et al. 2004; Anzai et al. 2008; Kanini et al. 2013; Schlatter and Kinkel 2014; Qin et al. 2015). However, high numbers of 16S rRNA gene copies may be present in each genome and difficulties in distinguishing among closely related isolates based on 16S gene sequence have driven researchers to evaluate phylogenetic relationships using other genes. For example, substantial variation in sporulation-associated genes within the *Streptomyces* (Hsiao and Kirby 2007) led Girard et al. (2013) to propose to classify actinomycetes based on sporulation-associated Ssg-A and Ssg-B. Another strategy involves the sequencing of several conserved or "housekeeping" genes or multilocus sequencing analysis (MLSA) (Guo et al. 2008; Rong et al. 2009). This approach gives more detailed information but is highly demanding in effort and resources. Within the last decade, with the advent of new sequencing technologies, entire genomes have become available, allowing whole-genome comparisons. Thus, phylogenetic studies of *Streptomyces* and, more broadly, of actinobacteria have been based on 16S rRNA, individual or multiple genes, concatenated sequences of several proteins, Ssg-A and Ssg-B, and whole-genome comparisons, depending on the availability of technology and the goals of the study (Takeuchi et al. 1996; Egan et al. 2001; Kim et al. 2004; Guo et al. 2008; Gao and Gupta 2005, 2012; Chater and Chandra 2006; Manteca et al. 2006).

Although there have been changes throughout the years (Anderson and Wellington 2001), as of December 2015, the family *Streptomycetaceae* has a total of ten genera (http://www.bacterio.net/), many of which have been occasionally considered within the genus *Streptomyces*. Genera closely related to *Streptomyces* include *Frankia*, *Kitasatospora*, and *Thermobifida*, which are organisms present within a wide range of habitats and exhibiting diverse functions. Studies based on morphology, chemical taxonomy, and 16S rRNA support the idea that *Kitasatospora* is closely related to *Streptomyces*, sharing characteristics such as excellent soil colonization, mycelial growth habit, and secondary metabolite production with the *Streptomyces* (Chung et al. 1999; Groth et al. 2004; Hsiao and Kirby 2007). In addition, combined approaches using whole genomes and several conserved gene sequences (Alam et al. 2010) showed that the *Streptomyces* spp. group was closest to *Frankia* spp. and also to *Thermobifida fusca* YX, a moderately thermophilic soil bacterium that belongs to the order *Streptosporangiales*. It is likely that future whole-genome sequencing will bring substantial modifications to the taxonomy of members of the *Streptomyces* and related genera and will enhance our understanding of the ecological and evolutionary relationships among these taxa.

12.1.3 Sequenced Genomes: What We Have Learned

New technologies have reduced the costs of sequencing, and thus the number of fully sequenced *Streptomyces* genomes has increased dramatically in recent years (Davis et al. 2013; Tarkka et al. 2015; Gomez-Escribano et al. 2015; Zhai et al. 2015; Deng et al. 2015; Rückert et al. 2013; Ortseifen et al. 2015; Tian et al. 2015; Thibessard et al. 2015; Nanthini et al. 2015). As of December 2015, over 250 *Streptomyces* spp. genome sequencing projects are underway in the GenBank (http://www.ncbi.nlm.nih.gov/bioproject/browse). Much has been learned from the assembly and annotation of the genomes.

Among *Streptomyces* genomes found in the GenBank, the median genome size is 8.2 Mb with 72 % GC content. A few species have particularly small genomes compared to others within the genus [e.g., *S. somaliensis* 5.2 Mb (Kirby et al. 2012), *S. violaceusniger* 6.4 Mb (Chen et al. 2013)]. Most *Streptomyces* carry one or two plasmids, either linear or circular (Gomez-Escribano et al. 2015; Myronovskyi et al. 2013).

Whole-genome sequence data has revealed a wealth of secondary metabolites beyond expected. Work by Zhou et al. (2012) comparing genomes of five *Streptomyces* spp. found 3096 gene families in all 5 genomes, which represented 18 % of the pangenome or the total complement of genes in the group. These may represent a possible "core genome" for this group. All of the fully sequenced *Streptomyces* genomes (n > 20 to date) have genes that confer the potential to produce bioactive secondary metabolites, with more than thirty distinct pathways evident in some isolates. For example, bioinformatic analyses reveal 22 gene clusters predicted to be involved in the synthesis of secondary metabolites in the genome of *S. coelicolor* (Bentley et al. 2002), 30 in the genome of *S. avermitilis* (Ikeda et al. 2003), 32 in the genome of *S. fulvissimus* (Myronovskyi et al. 2013), and 35 in the genome of *S. leeuwenhoekii* (Gomez-Escribano et al. 2015). Such analyses highlight the potential of finding new compounds from organisms, even those that have been thoroughly studied, bringing optimism to the natural products community. Identifying the conditions for expression of such genes and their roles in nature provides important challenges for researchers to solve.

12.2 Plant-Associated *Streptomyces*

Bacteria are commonly associated with plants in all natural settings, composing a portion of what is known as the microbiome (Berendsen et al. 2012). These associations vary in specificity and in relative cost or benefit to the plant. For this reason, plants in natural settings have been seen as part of a holobiont (Hartmann et al. 2014; Lebeis 2015; Smith et al. 2015). While it seems obvious that a diseased plant is infected by microorganisms (bacterium, virus, or fungus), it is still not widely recognized that a healthy, vigorous plant may owe its splendor to the activities of microorganisms. These beneficial associations, just like detrimental ones, vary in specificity. Some associations occur in the rhizosphere, others in the phyllosphere,

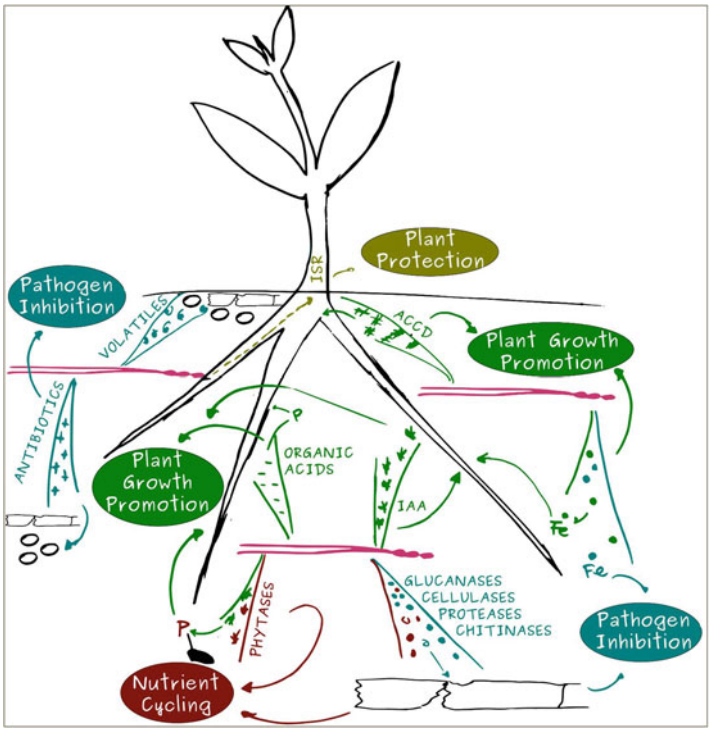

Fig. 12.1 Secondary metabolites produced by *Streptomyces* spp. and processes in which they participate in soil and plants

or even in the inside of the plants (endophytic microorganisms). These interactions have been explored from many standpoints, but of most interest is the potential to utilize these naturally occurring relationships as alternatives to the use of chemicals in crop production.

12.2.1 Plant Growth Promotion

One of the many types of interactions *Streptomyces* spp. may have with plants is as growth-promoting bacteria (Gopalakrishnan et al. 2014, 2015; Jog et al. 2014). *Streptomyces* spp. found in the rhizosphere, on plant surfaces, and living endophytically have traits that are characteristic of plant growth-promoting bacteria (Noumavo et al. 2015; Vorholt 2012; Rungin et al. 2012). Among plant growth-promoting endophytic actinobacteria, most isolates have been reported to belong to the genus *Streptomyces* (Qin et al. 2011, 2015; Kim et al. 2012). Colonizing *Streptomyces* may promote growth in the plant host through direct or indirect mechanisms (Fig. 12.1). The production of hormones and enzymes that interact with plant molecules is an example of a direct mechanism of plant growth promotion by *Streptomyces*, while indirect mechanisms are those involved in nutrient acquisition.

12.2.1.1 Hormones and Enzymes

Some *Streptomyces* have been shown to produce the auxin indole-acetic acid (IAA). Auxins are plant hormones involved in cell division and elongation, whose general effect on plants is the stimulation of growth. Thus, IAA-producing bacteria, including *Streptomyces*, are thought to induce growth through the direct effect of IAA (Barbieri and Galli 1993; Shao et al. 2014). Several studies suggest IAA-producing *Streptomyces* are relatively common among rhizospheric strains (Palaniyandi et al. 2013a, 2014; Qin et al. 2015; Jog et al. 2014), which has been suggested to be a consequence of their potential signaling activity among bacteria (Spaepen et al. 2007). However, Palaniyandi et al. (2013a) showed that IAA production is not always accompanied with plant growth promotion. The influence of IAA production on growth promotion for each plant-microbe pair is difficult to predict, due to potentially different gene expression among isolates in culture vs. *in planta*, variation in microbial colonizing abilities, the potential for IAA metabolism by microbial competitors, and the likelihood of other molecules acting in the process of growth promotion observed in the experiments.

Ethylene is another plant hormone which participates in stress signaling and decreases in production or availability to enhance plant growth. The enzyme 1-ami nocyclopropane-1-carboxylate (ACC) deaminase degrades the precursor of ethylene in plants, ACC, into ammonia and α-ketobutyrate, thereby preventing ethylene production. In a screening of rhizospheric actinobacteria isolated from yam roots, Palaniyandi et al. (2013a) found that of 24 *Streptomyces* spp. isolates, six produced ACC deaminase. These six isolates producing ACC deaminase were subsequently tested for plant growth promotion by inoculation onto *Arabidopsis* plants, but only four increased root biomass. Among these, three *Streptomyces* inoculants induced greater seedling and root length, seedling fresh weight, and leaf total area than non-inoculated plants. In another report, screening endophytic bacteria from *Jatropha curcas*, Qin et al. (2015) found that 19 of 257 (7.4 %) of isolated endophytes were positive for ACC deaminase, 16 of which were *Streptomyces* spp. Similarly to results with IAA-producing strains, plant growth promotion activity was not necessarily found in strains which produced both ACC deaminase and IAA. Instead, plant growth seemed to be stimulated by a variety of factors, including ACC deaminase, IAA, phosphate solubilization, and probably others not evaluated. Information on the identity of these additional factors, as well as understanding the elements that trigger their expression, will aid the achievement of consistent results with PGP bacteria.

12.2.1.2 Facilitation of Nutrient Uptake

An alternative mechanism of plant growth promotion is based on facilitation of nutrient uptake. Bacteria may increase plant nutrient uptake indirectly through the stimulation of root growth or by modifying root architecture and increasing root hair formation. These modifications are driven by hormones and enzymes, including those mentioned above. The increased root surface area can enable higher

efficiency of water and ion uptake into the root system. Alternatively, bacteria may facilitate phosphorus (P) uptake, mediating phosphate solubilization or mineralization through modifications of P-containing molecules in the rhizosphere (Rodríguez et al. 2006 and Richardson and Simpson 2011). Similarly, iron (Fe) acquisition by plants may be mediated through the activities of bacterial siderophores. Both P and Fe are highly abundant in soil but are often found in chemicals that plants cannot access, and bacterial activities can make these more accessible to the host plant.

Inorganic phosphorus in soil is generally bound to calcium, iron, or aluminum [$Ca_3(PO_4)_2$, $FePO_4$ and $AlPO_4$, respectively], and none of these are easily accessible for plant use. Although P is added to soil in fertilizers in soluble forms, it becomes rapidly insoluble. Inorganic P may subsequently be solubilized by rhizospheric bacteria through the secretion of organic acids. Tricalcium phosphate solubilization has been observed in *Streptomyces* spp. (Oliveira et al. 2009; Jog et al. 2014; Qin et al. 2015), and such activity has been associated with promotion of growth of several plant species (Guiñazú et al. 2009; Mamta et al. 2010; Shahid et al. 2012). Secretion of malic acid and a derivative of gluconic acid has also been associated with the mobilization of inorganic P by *Streptomyces* (Jog et al. 2014). Phosphorus mineralization, the process of separating P from larger, organic molecules, is dependent on enzymes (phosphatases and phytases) which have been found in several *Streptomyces* spp. and other microorganisms (Richardson and Simpson 2011; Jog et al. 2014).

Despite the fact that Fe is the second most abundant metal on Earth, both plants and microorganisms must find ways to acquire it from soil. Among *Streptomyces*, siderophore production is one of the most widely distributed plant growth-promoting traits (Jog et al. 2014). Siderophores are typically non-ribosomally produced small peptides that are secreted to the outside of the cell and later reintroduced back to the bacterial cell when bound to an Fe molecule, thus introducing Fe by highly specific transport systems. Plants have been shown to utilize iron from microbially produced siderophores (Crowley et al. 1988; Bar-Ness et al. 1992). Thus, the proliferation in the rhizosphere of bacteria that produce siderophores which may be taken up by the host plant increases the ability of the plant to utilize Fe. Siderophores have diverse chemical structures, and *Streptomyces* may produce more than one type; Gangwar et al. (2014) found siderophores of both catechol and hydroxamate types being produced by single *Streptomyces* isolates. Genome analyses support these observations, revealing that more than one gene associated to the synthesis of siderophores are commonly found in individual strains (Chen et al. 2013; Tarkka et al. 2015; Zhai et al. 2015), suggesting the potential significance of the trait to the ecology of the genus. Lautru et al. (2005), using a genome-mining approach, found a tris-hydroxamate tetrapeptide siderophore coelichelin in the genome of *S. coelicolor*. Information on phylogenetic, niche, and functional variation in the presence and utilization of siderophores is needed.

12.2.2 Plant Protection

Biological control may be used as alternative to pesticides, a complement to existing disease management, or a solution when there is no other type of available control. The management of soils to control plant diseases by addition of green manures or crop rotation may be considered one form of biological control, but here we focus first on "traditional" or inundative biological control. There are several mechanisms by which *Streptomyces* protect plants from pathogens, which include direct growth inhibition through production of antibiotics or cell-wall-degrading enzymes, indirect inhibition through competition for nutrients, and induced systemic resistance (ISR) in the plant (Mandeel and Baker 1991; van Loon et al. 1998; Pieterse et al. 2014).

12.2.2.1 Antibiotics

The capacity of *Streptomyces* to suppress other microbes was first noted nearly a century ago by Greig-Smith (1917). Since then, their extraordinary capacity to produce antibiotics has captured the attention of a broad range of scientists, including natural products chemists, pharmaceutical researchers, plant pathologists, and biochemists. The widespread ability among *Streptomyces* to produce pathogen-inhibiting secondary metabolites (Watve et al. 2001; Kim et al. 2012; Palaniyandi et al. 2013b) makes them well suited to protect crops from pathogens. In fact, soil *Streptomyces* with plant protection capacities have been reported in diverse settings. Among the best studied are antibiotic-producing *Streptomyces* spp. that act as antagonists of bacterial pathogens such as *S. scabies* and *S. turgidiscabies*, causal agents of potato scab, which have been found on potato tubers (Liu et al. 1995) and in soil (Hiltunen et al. 2009; Kobayashi et al. 2015). Soil *Streptomyces* isolates have been shown to protect alfalfa and soybean plants from oomycete infections, such as root rot caused by *Phytophthora medicaginis* and *P. sojae*, respectively (Fig. 12.2; Xiao et al. 2002). Even *Streptomyces* isolated from desert soils have shown antagonism toward soil phytopathogens, such as the nematode *Meloidogyne incognita* and the bacterium *Ralstonia solanacearum* (Köberl et al. 2013).

Endophytic *Streptomyces* with the ability to inhibit pathogens have been found surprisingly often. *Streptomyces* endophytes from cucumber protected the plants from *Colletotrichum orbiculare* (Shimizu et al. 2009). Nematicidal activity has also been reported in *Streptomyces* spp. by production of inhibitory compounds (Kun et al. 2011; Ruanpanun et al. 2011; Ruanpanun and Chamswarng 2016). Abundance, distribution, and ecology of these activities have not been widely studied and would be greatly valued.

Antibiotics are usually produced at the onset of the stationary growth phase when grown in liquid culture and are often associated with aerial hyphae and spore formation on solid medium (Bibb 2005). The biochemical pathways and genes involved in the synthesis of many antibiotics have been studied thoroughly, and polyketide synthases (PKS) and non-ribosomal peptide synthases (NRPS) are often involved (Núñez et al. 2003; Karray et al. 2007; Pulsawat et al. 2007; Laureti et al. 2011). As an example, virginiamycin M is an antibiotic produced by a PKS-NRPS

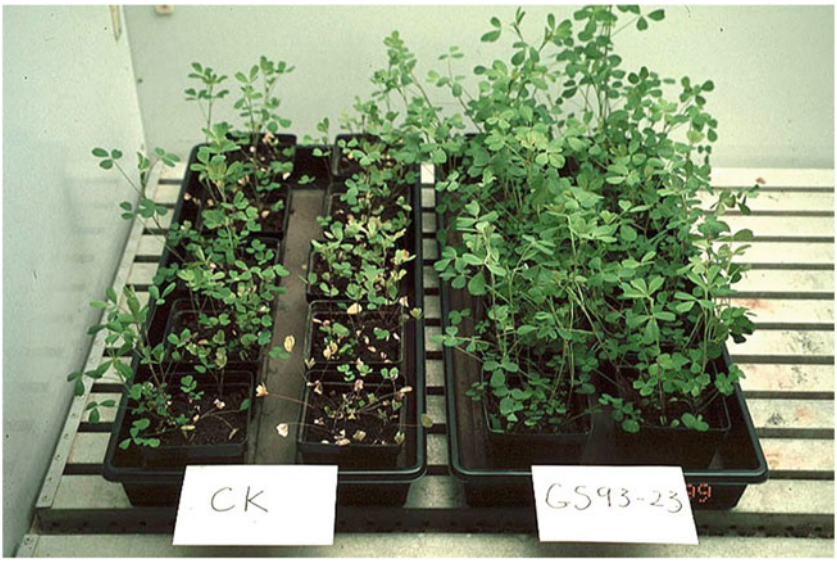

Fig. 12.2 Alfalfa plants grown in field soil naturally infested with *Phytophthora*. Plants on the *left* are non-inoculated; plants on the *right* are inoculated with a single pathogen-suppressive *Streptomyces* isolate (Xiao and Kinkel unpublished)

hybrid by *S. virginiae*, and has inhibitory activity against gram-positive bacteria (Pulsawat et al. 2007). The production of more than one antibiotic substance by *Streptomyces* is also commonly found, leading to a broad range of inhibited targets and in some cases greater inhibition due to the synergistic effect of multiple antibiotics. Production of multiple antibiotics is also desirable in order to minimize the development of resistance in the pathogens.

12.2.2.2 Volatile Compounds

Streptomyces produce many volatile compounds that inhibit growth of potential competitors (Audrain et al. 2015). These compounds are believed to be particularly important in soil settings, where diffusion through a liquid phase may sometimes be impaired.

A compound of 27 volatiles produced by *Streptomyces alboflavus* TD-1 inhibits growth of several plant pathogens, including *Fusarium moniliforme*, *Penicillium citrinum*, and several *Aspergillus* species in vitro (Wang et al. 2013). Volatile-producing *Streptomyces* spp. have the potential to be used as biocontrol agents, for instance, of *Botrytis* postharvest infections (Li et al. 2012) and fruit rot of strawberry (Wan et al. 2008). *S. platensis* F-1 produces volatiles that protect rice from leaf and seedling blight caused by *Rhizoctonia solani* and leaf blight of oilseed rape caused by *Sclerotinia sclerotiorum* (Wan et al. 2008). Further researches on bioactive volatiles from *Streptomyces* are likely to provide compounds with potential applications in medicine and agriculture.

12.2.2.3 Cell-Wall-Degrading Enzymes

Fungal and oomycete plant pathogens have cell walls made of chitin, glucans, and cellulose, respectively. These structures may be subject to degradation by lytic enzymes, such as chitinases, glucanases, and cellulases. Most terrestrial *Streptomyces* species are prolific producers of such extracellular enzymes (Chater et al. 2010), contributing to growth inhibition of fungal and oomycete pathogens.

Anthracnose biocontrol in pepper by *S. cavourensis* SY224 has been associated with glucanase production (Lee et al. 2012). Glucanases were also found responsible for the protection of several plant species from oomycete-caused diseases. As an example, *Streptomyces* spp.-derived reduction of root rot in raspberry caused by *Phytophthora* (Valois et al. 1996), and infection of cucumber by *Pythium aphanidermatum* (El-Tarabily et al. 2009), was dependent on the production of glucanases. Thus, glucanase production is one phenotypic trait worth evaluating while searching for biological control by *Streptomyces*.

Chitinase production and biocontrol potential of endophytic *Streptomyces* isolates were positively correlated, as determined in in vitro inhibition of fungal growth (Quecine et al. 2008). Furthermore, endochitinase production by *S. violaceusniger* XL-2 inhibits the growth of several wood-rotting fungi (Shekhar et al. 2006). In both studies, the *Streptomyces* isolates had to be incubated in chitin-containing medium in order to induce chitinase synthesis, indicating that enzyme production is a tightly regulated process. Chitinase production is apparently widespread among this genus (Kim et al. 2012; Jog et al. 2014), which is in accordance with the ability of *Streptomyces* to colonize varied habitats, such as insects, compost, and soil.

Extracellular proteases are another group of enzymes produced by *Streptomyces* that have been shown to inhibit plant pathogens. Secretion of proteases gives *Streptomyces* the ability to incorporate N from proteinaceous sources, some of which may be quite recalcitrant. Several *Streptomyces* isolates with protease activity have been studied (Chater et al. 2010; Kim et al. 2012). The isolate ExPro138 produces several proteases that inhibit the pathogen *Colletotrichum coccodes* at several stages of development (Palaniyandi et al. 2013c), and another isolate, *Streptomyces* sp. A6, produces a protease which inhibits the wilt-causing pathogen *Fusarium udum* (Singh and Chhatpar 2011).

In plant litter, cellulose is the most abundant organic molecule, making cellulose-degrading enzymes, or cellulases, fundamental for nutrient cycling in soil. *Streptomyces* produce both endo- and exo-cellulases (Book et al. 2014), which have been mostly associated with the turnover of plant material. However, the secretion of cellulases by *Streptomyces* spp. has also been associated with their ability to inhibit some plant pathogens, particularly those with cellulose-containing cell walls, such as *Oomycetes* (van Bruggen and Semenov 2000).

The widespread ability of *Streptomyces* spp. to degrade large organic molecules through the activity of extracellular enzymes provides them with the possibility of colonizing diverse habitats. In addition, these enzymatic activities make them good antagonists of plant pathogens. The ample diversity of enzymes with similar activities that are present in each genome needs to be further studied in order to understand their role in nature and their possibilities as tools for agronomic and industrial purposes.

12.2.2.4 Competition

Niche competition is another potential mechanism of pathogen control. *Streptomyces* spp. have the ability to utilize a broad range of nutrients, which likely contribute to their success in soil (Kieser and John Innes Foundation 2000). Their diverse arsenal of hydrolytic enzymes and siderophores likely make them superb competitors. Iron competition acting as a mechanism of biocontrol by endophytic *Streptomyces* has been suggested against *Fusarium* wilt on banana roots (Cao et al. 2005). It is likely that in many cases, competition acts as a combined factor in disease suppression, and the extent of the importance of competition on antagonistic interactions should be evaluated for each system.

12.2.2.5 Induced Systemic Resistance

Induced systemic resistance (ISR) is another mechanism of plant protection from pathogens. One striking feature about this process is that the beneficial microorganism does not need to be in indirect physical contact with the pathogen for successful disease suppression. ISR is characterized by the readiness with which the plant responds to a pathogen attack. After being exposed to an ISR-inducing microorganism, a latent state of resistance is acquired, which is expressed upon exposure to a pathogen. Generally, the range of pathogens to which the ISR will bring protection is quite broad, although that is specific for each plant-microbe interaction (van Loon et al. 1998; Pieterse et al. 2014).

Most of the research on ISR has been carried out on *Pseudomonas* and *Arabidopsis thaliana* systems; however, other microorganisms including *Streptomyces* have been shown to induce ISR. Induction of systemic resistance on *A. thaliana* by an endophytic *Streptomyces* sp. strain was demonstrated, shifting in gene expression profiles upon exposure to the pathogens *Erwinia carotovora* and *Fusarium oxysporum* with respect to non-primed plants (Conn et al. 2008).

Rhododendron plants were protected from *Pestalotiopsis sydowiana* by endophytic *Streptomyces*. The isolates showed no in vitro antagonism to the pathogen but induced systemic resistance in the plants (Shimizu et al. 2006). More recently, RNA sequence analyses of oak responses to *Streptomyces* priming showed a variety of defense mechanisms being activated by the resistance-inducing isolate; these mechanisms were different from those reported for *Pseudomonas* (Kurth et al. 2014).

Streptomyces isolates with antibiotic production, but also with plant growth-promoting traits or ISR-inducing activity, are currently sought. Table 12.1 shows a list of currently available commercial *Streptomyces*-based inoculants, in which most of the products are based on the antagonistic activity of the isolates. In agronomic settings, where the biotic and abiotic conditions are diverse and vary over time, a combination of plant protection and growth promotion is likely to give *Streptomyces*-based inoculants better chances of success. Combinations of strains in one formulation are also likely to provide enhanced disease protection. In addition, inconsistencies in the efficacy of biological control applications may be improved through a better understanding of the microbial dynamics and species interactions in soil.

Table 12.1 List of *Streptomyces*-containing products for plant care

Product name	Active ingredient	Use (reference)
Actinovate® AG Actinovate® SP	*S. lydicus* WYEC108	Root rot, damping off, foliar and turf diseases (*Fusarium*, *Rhizoctonia*, *Pythium*, *Phytophtora*, *Aphanomyces*, *Armillaria*, *Botrytis*, *Monilinia*, *Xanthomonas perforans*, *X. arboricola* pv. *A. juglandis*, *Gaeumannomyces graminis*, *Lanzia* spp., *Mollerodiscus* spp., *Erysiphe graminis*, *Puccinia* spp., *Colletotrichum graminicola*, *Pynculana grisea*, *Musilaga*, *Physarum*, *Typhula* spp., *Microdochium nivale*) (http://www.monsanto.com/products/pages/actinovate-us.aspx)
Actino Iron®	*S. lydicus* WYEC108	Root rot and damping off fungi (*Pythium*, *Rhizoctonia*, *Phytophthora*, *Fusarium*) (http://www.evergreengrowers.com/actino-iron.html)
Thatch control	*S. violaceusniger* YCED9	Thatch decomposer, prevents turf diseases (http://www.amazon.com/Natural-Industries-LGTC02-Control-Microbes/dp/B0044EK7G0)
Mycostop®	*S. griseoviridis* K61	Root and seed rots, root and stem wilt (*Botrytis*, *Pythium*, *Phytophtora*, *Rhizoctonia*, *Fusarium*, *Alternaria*, *Phomopsis*) (http://www.planetnatural.com/product/mycostop/)
YAN TEN	*S. saraceticus* KH400	Root rots and root-knot nematode (*P. aphanidermatum*, *R. solani* AG-4, *Meloidogyne* sp.) (http://www.yanten.com.tw/products-3_30633-english.html)

Modified from Palaniyandi et al. (2013b). All websites were accessed on January 28, 2016

12.3 Soil Health and *Streptomyces*

The concept of soil health has been evolving in the past few years (van Bruggen and Semenov 2000; Garbeva et al. 2004; Chaparro et al. 2012). Soil health was originally focused on one service of soil, plant productivity, and consequently, was mostly based on soil fertility measurements. However, interest has arisen more recently in a broader range of soil characteristics including sustainability of crop production and human health, adding new factors to the idea of soil health. Recent definitions of soil health involve the idea of soil as a living system that, in addition of enabling productivity, maintains environmental quality and promotes plant, animal, and human health (Larkin 2015). Thus, promoting crop management practices that consider this broader concept of plant health is highly desirable. Some factors, such as soil texture and depth, play a significant role in soil health, but such factors are not within what can be usually managed. Instead, practices that increase organic carbon in soil seem to generally enhance other characteristics related to comprehensive soil health metrics, such as higher water retention and higher microbial activity and density, which comes along with higher pathogen suppression (Altier and Zerbino 2012; Kinkel et al. 2012; Larkin 2015). Managing agronomic soils to increase beneficial *Streptomyces* communities could enhance nutrient cycling in soil, increase crop productivity, and protect crops from disease while reducing chemical inputs.

12.3.1 Nutrient Cycling

A healthy soil may be seen as a stable system in which high internal nutrient cycling is a key factor. Nutrient cycling depends on a microbial community with the ability to metabolize what is being introduced into the soil. Thus, communities with a wide range of nutrient use capacity, and thus able to utilize the diversity of nutrients available in such a complex medium, are desirable. As mentioned previously, most species of the genus *Streptomyces* are saprophytic and have the ability to metabolize a variety of compounds. Their diverse arsenal of secreted molecules includes enzymes that allow the degradation and later utilization of cellulose, chitin, lignin, melanin, and others (Schlatter et al. 2009; Kim et al. 2012), making breakdown products broadly available, which will likely increase total bacterial biomass.

The potential for managing *Streptomyces* antagonistic activities in soil to increase pathogen suppression was explored in a recent study. Following nutrient amendments, *Streptomyces* isolated from soils exposed to different nutrient amendments varied in their antagonistic activity, and populations from soils amended with high doses of nutrients (glucose or lignin) were more inhibitory than isolates from soils with low nutrient doses (Schlatter et al. 2009). Thus, both the type of nutrient and the amount of available nutrients shape *Streptomyces* communities in traits that are particularly important for pathogen suppression and sustainability. In related work, variation in resource use phenotypes within *Streptomyces* genetic groups was significantly associated with the location from which *Streptomyces* were isolated, suggesting that resource use is adapted to local environments (Schlatter et al. 2013). Local adaptation of *Streptomyces* to local nutrient sources highlights once more the relevance of this group in nutrient cycling in diverse environments and the potential for active management of soil populations to achieve specific agronomic goals (pathogen suppression, nutrient cycling).

12.3.2 Suppressive Soils

Suppressive soils are soils in which diseases do not develop on susceptible host plants or do so to a lesser extent than in conducive soils, although the pathogens may be present. Soils showing suppressiveness to several diseases have been reported, including *Fusarium* wilt in carnation and other crops (Cugudda and Garibaldi 1981; Alabouvette et al. 2009), take-all on wheat (Landa et al. 2002), *Phytophthora* on apple (Mazzola et al. 2002), black rot of tobacco (Kyselková et al. 2009), club root disease of Chinese cabbage (Murakami et al. 2000), and scab on potato (Liu et al. 1995). Using metagenomic approaches, *Streptomyces* spp. have been found more abundantly in suppressive than in conducive soils. Furthermore, when suppressive soils were added with *Rhizoctonia solani*, the abundance of *Streptomyces* spp. increased (Mendes et al. 2011), suggesting an important role in the suppressiveness against the pathogen.

In some cases, suppressiveness is achieved through competition for niche use, as was suggested for some *Fusarium* diseases (Alabouvette et al. 2009). Other times, suppressiveness is due to the presence of antibiotic-producing bacteria. In the case of suppressiveness to potato scab, disease reduction was correlated with the presence of high densities of antibiotic-producing, nonpathogenic *Streptomyces* spp. (Liu et al. 1995). However, the fact that antagonists and pathogens share the habitat and nutrients is a key factor in the effectiveness of the suppression of this disease.

12.3.3 Managing Soils for Suppression

In 1926, Sanford investigated the mechanisms by which rye green manure reduced potato scab and noted that *Actinomyces scabies* (now *Streptomyces scabies*) was "very sensitive to the secreted products of many molds and bacteria, some of which prevent its growth." He further suggested green manures favored the antagonistic bacteria that inhibited the pathogen. Subsequently, Millard and Taylor (1927) took the next step in showing that inoculating soil with a saprophytic (nonpathogenic) *Actinomyces* isolate could significantly reduce both disease and pathogen populations. Millard and Taylor concluded that the saprophytic inoculated strain outcompeted the pathogen in soil, thereby reducing plant disease.

It has been widely documented that plants (Micallef et al. 2009; Bakker et al. 2010, 2012) and soil management shape the underground microbial communities (Mazzola 2007; Chaparro et al. 2012; Bakker et al. 2013; Fraser et al. 2015). For instance, the use of green manures has been reported to be beneficial in many cropping systems (Hoagland et al. 2008; Weerakoon et al. 2012). In potato, *Verticillium* wilt was significantly reduced with corn and alfalfa used as green manures. Furthermore, in that experiment, streptomycete inhibitory activity was frequently negatively correlated with plant disease and positively correlated with potato yield (Wiggins and Kinkel 2005). Substantial work has been carried out to find management practices that increase soil health and reduce disease. However, a global understanding of the interactions and dynamics belowground is still evolving.

12.4 Other Notable Lines of Research in *Streptomyces*

The genus *Streptomyces* has been the focus of attention in many and diverse lines of research. Some of these may seem at a first glance to be completely unrelated to their agricultural or sustainability facet. However, the research in signaling among *Streptomyces* within and among strains and species is likely to influence their potential use in agricultural settings. Bioremediation may be a major industrial use for *Streptomyces*, since the accumulation of toxic materials derived from anthropic activities is ubiquitous.

12.4.1 Signaling

Although bacteria are mostly unicellular organisms, they are never alone in natural conditions and have developed the ability to sense signals from others. *Streptomyces* produce signaling molecules that participate in quorum sensing, the gamma-butyrolactones (GBLs) (Takano 2006; Morin et al. 2012). In addition to GBLs, other signaling molecules have been found in *Streptomyces*, such as furans (Corre et al. 2008). The biosynthetic routes for signal production and the receptors involved are well studied for many strains (Kato et al. 2007; Hsiao et al. 2007; Nishida et al. 2007; Sello and Buttner 2008; O'Rourke et al. 2009; Corre et al. 2010). Signaling among kin organisms modulates activities as diverse as sporulation, antibiotic production, entrance to a competent state, biofilm production, and expression of pathogenesis-related molecules (Weinrauch et al. 1991; Kato et al. 2007; Williams 2007).

In nature, the produced signals are likely to participate in sensing the presence of others, integrating information about the outside and the inside and thus synchronize specific activities (Camilli and Bassler 2006; Kato et al. 2007). Eavesdropping, a process in which signals that modulate activities within kin organisms are detected and induce a response by non-intended recipients, may alter the timing or quantity of antibiotic production by the eavesdropper, potentially enhancing the fitness benefit of antibiotic production in the presence of a competitor (Duan et al. 2003; Chandler et al. 2012). Chemical manipulation, when one organism secretes chemicals that modify the metabolism of the target population, usually to benefit the signal emitter (Keller and Surette 2006; Egland et al. 2004), could also significantly alter the phenotype of a *Streptomyces*. Interspecies interactions among *Streptomyces* within a community may shape the phenotype of the coexisting isolates (Vaz Jauri and Kinkel 2014). The compounds mediating such interactions may or may not have evolved for such purposes, as is the case of antibiotics at subinhibitory concentrations (Vaz Jauri et al. 2013, Yim et al. 2006). Nonetheless, these interactions may influence the fitness of the interacting species, and the sum of these and other chemical interactions are likely to shape the structure and function of natural microbial communities.

12.4.2 Bioremediation

Soils and water can be contaminated with a number of substances, ranging from heavy metals, petroleum derivatives, pesticides, and industry effluents. Organisms belonging to the genus *Streptomyces* are valuable also in this area, due to their great metabolic diversity and production of secondary metabolites.

12.4.2.1 Heavy Metals

Soils contaminated with heavy metals are often a consequence of mining activities. However, soils with high concentrations of heavy metals can also be found naturally, due to geogenic activities. These soils may explain the initial existence of

plants and microbes that are able to survive in such extreme conditions, which would be toxic to nonadapted individuals (Kothe et al. 2010). Bacteria cope with heavy metal contamination through adsorption, mineralization, accumulation, chelation, chemical reduction, or simply remotion from the intracellular space through efflux transporters (Schütze and Kothe 2012). Studies on the microbial communities of soils highly contaminated from mining activities have shown that higher proportions of *Streptomyces* and *Bacillus* are found in contaminated soils than in non-contaminated soils, revealing that these organisms are better adapted to contaminated soils than other common inhabitants of soils, such as gram-negative bacteria (Kothe et al. 2010).

The action of siderophores by soil bacteria may protect other organisms, e.g., plants and other microorganisms, by reducing the oxidative damage caused by the presence of heavy metals. Furthermore, secretion of siderophores may reduce the damage to plants by reducing the negative effects of cations on auxin production (Dimkpa et al. 2008). In addition, the presence of heavy metals has been observed to induce the synthesis of siderophores in heavy metal-resistant *Streptomyces* (Schütze et al. 2014).

12.4.2.2 Pesticides

Insecticide, herbicide, and fungicide applications are commonplace in agricultural settings. Some of these compounds are recalcitrant to degradation, leaving a long-lasting toxicity on soils and watercourses where they are drained. In some cases, the compounds are partially degraded, but the degraded products may also have an impact on the health of a plethora of organisms. Thus, finding enzymes and/or organisms that will degrade these compounds is highly valued.

Streptomyces with the ability to degrade insecticides of diverse chemical nature have been found (Fuentes et al. 2010; Chen et al. 2012; Cuozzo et al. 2012; Saez et al. 2012). Furthermore, *Streptomyces* have been found to act as bioremediators in soils with mixed contaminants, such as heavy metals and pesticides (Polti et al. 2014). Given their ability to degrade contaminants and their plant-association capacities, methods have been developed for the combined use of *Streptomyces* and host plants (maize) for the removal of pesticide accumulation (Benimeli et al. 2008; Alvarez et al. 2005).

12.4.2.3 Other Sources of Contamination

Contamination of soil and water with oil is sadly common. Numerous ways to deal with this problem have been searched and are still a matter of concern. As an example, in a work by van Gestel et al. (2003), diesel-contaminated soil was mixed with compost and tested for its capacity to maintain microbial life. Numerous microorganisms were able to live in such conditions, including *Streptomyces* spp., which are common inhabitants of compost. Using another strategy, a strain of *Streptomyces rochei* has been isolated from heavy crude oil with the ability to degrade three- and four-ring compounds (anthracene, fluorene, phenanthrene, and pyrene) (Chaudhary et al. 2011). This finding is encouraging for further efforts to use *Streptomyces* as one more strategy to deal with oil spills.

Although not intuitive, the use of bacteria from sites drastically different from where they will be used is also possible. *S. indianensis* and *S. hygroscopicus* isolated from marine sediments have been tested with enormous success on dairy industry sludge. Effluents treated with each isolate tested alone or a combination of both had improved all the parameters tested, which included chloride and oil content and germination and shoot length of *Vigna radiata* (Sathya Priya et al. 2014). In a similar example, a *Streptomyces* isolated from marine sediments was used to treat soils contaminated with vinase, a waste product in the generation of bioethanol. In this case, the remediation process is not due to the metabolization of a toxic compound, but rather by the production of an emulsifier that reduces the concentration of the waste product (Colin et al. 2016).

12.5 Conclusions

Streptomyces are abundant, diverse, and ubiquitous. Across their evolution, they have developed a number of characteristics that are highly valuable for industry, medicine, and sustainability. The use of *Streptomyces* for industrial and medical purposes has been widely explored, although their high diversity allows for further exploration. The use of *Streptomyces* for sustainable crop production has been less exploited. However, the research already carried out on secondary metabolites production and regulation and signaling should be incorporated to that of their PGP activities and behavior under different environments. Thoughtful analysis of the information rendered by new tools that provide large amounts of information, such as high-throughput sequencing, among others, will greatly accelerate the development of this much-needed area of research. Big companies dedicated to the production of inputs for agriculture have turned to explore this area, carrying out gigantic experiments with over 2000 seed microbial coatings and close to 500,000 field trials (http://www.scientificamerican.com/article/microbes-added-to-seeds-could-boost-crop-production/). This new attitude toward the use of microorganisms reflects the global demand for a more sustainable agriculture but also the great potential microbial-based technologies possess.

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