

# Actinomycetes as biological control agents of phytopathogenic fungi

## Los actinomicetos como agentes de control biológico de hongos fitopatógenos

ANA CECILIA GONZÁLEZ-FRANCO<sup>1,2</sup> Y LORETO ROBLES HERNÁNDEZ<sup>1</sup>

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### Resumen

Los actinomicetos son un reservorio enorme de antibióticos y metabolitos bioactivos y muchos de ellos son excelentes agentes de biocontrol para proteger a las plantas contra fitopatógenos. Aunque miles de antibióticos y metabolitos bioactivos han sido descritos, se cree que estos representan solo una fracción de los compuestos bioactivos producidos por los actinomicetos. En esta revisión se abordan las características generales y propiedades de los actinomicetos como agentes de control biológico, sus mecanismos a través de los cuales realizan el biocontrol y el impacto de la composición química de la pared celular de los hongos fitopatógenos en el proceso de control.

**Palabras clave:** *Streptomyces*, competencia, parasitismo, antibiosis.

### Abstract

Actinomycetes are an enormous reservoir for antibiotics and bioactive metabolites, and many are excellent biocontrol agents for use in protecting plants against phytopathogens. Although thousands of antibiotics and bioactive metabolites have been described, these are thought to represent only a small fraction of the bioactive compounds produced by actinomycetes. In this review, we summarize the general characteristics and properties of actinomycetes as biocontrol agents, the mechanisms through which the biocontrol occurs, as well as the impact of the phytopathogenic fungal cell wall composition in the control process.

**Keywords:** *Streptomyces*, competition, parasitism, antibiosis.

### Introduction

**A**ctinomycetes are among the most widely distributed group of microorganisms in nature. They are found abundantly in cultivated and uncultivated soils, in various regions throughout the world (Goodfellow and Simpson, 1987; Goodfellow and Williams, 1983).

Actinomycetes, especially streptomycetes, can degrade a wide diversity recalcitrant polymers occurring naturally in plant litter and soil, including hemicelluloses, pectin, keratin, and chitin (Gooday, 1990; Warren, 1996). Actinomycetes also have the genetic capability to synthesize several biologically active

secondary metabolites of which some are antibiotics that are predominant in therapeutic and commercial importance (Alderson *et al.*, 1993). Over one thousand secondary metabolites from actinomycetes were discovered during the years 1988-1992, and approximately 75% of these compounds were

<sup>1</sup> Profesor de la Facultad de Ciencias Agrotecnológicas, Universidad Autónoma de Chihuahua, Ciudad Universitaria S/N Campus 1, Chihuahua, Chih., 31310, México.

<sup>2</sup> Dirección electrónica del autor de correspondencia: [conzalez@uach.mx](mailto:conzalez@uach.mx)

produced by strains of the genus *Streptomyces* (Sanglier *et al.*, 1993). The compounds isolated during this period of time belong to 46 chemical classes, demonstrating the chemical diversity of the secondary metabolites biosynthesized by actinomycetes. Some examples of bioactive compounds include anti-viral and anti-cancer compounds, modulators of immune responses, various enzyme inhibitors, as well as herbicides, insecticides, anti-fungal, and anti-helminthic compounds (Sanglier *et al.*, 1993; Vining, 1990).

### Morphology and taxonomy of actinomycetes

Actinomycetes are Gram-positive bacteria with a high guanine plus cytosine content in

their DNA (> 55 mol%). The group encompasses genera covering a wide range of morphologies extending from the coccus (*Micrococcus*) and rod-coccus cycle bacteria (e.g. *Arthrobacter*), through fragmenting hyphal forms (e.g. *Nocardia*), to genera with a permanent and highly differentiated branched mycelium (*Micromonospora*, *Streptomyces* and others). Some, but not all, genera form spores that range from motile zoospores to specialized propagules that resist desiccation and mild heat, but which do not have the organization and marked resistance properties of the bacterial endospore. The molecular classification of actinomycetes has been examined by Stackebrandt *et al.* (1997). All the actinomycete families were divided into ten suborders (Stackebrandt *et al.*, 1997) (Table 1).

**Table 1.** Hierarchic classification of the actinomycetes based on the phylogenetic analyses of the 16S rDNA sequence data (Stackebrandt *et al.*, 1997).

Class: <i>Actinobacteria</i> ; Subclass: <i>Actinobacteridae</i> ; Order: <i>Actinomycetales</i>	
Suborder	Family
<i>Micrococcineae</i>	<i>Micrococcaceae</i> , <i>Brevibacteriaceae</i> , <i>Cellulomonadaceae</i> , <i>Dermabacteriaceae</i> , <i>Dermatophilaceae</i> , <i>Intrasporangiaceae</i> , <i>Jonesiaceae</i> , <i>Microbacteriaceae</i> , <i>Promicromonosporaceae</i>
<i>Actinomycineae</i>	<i>Actinomycetaceae</i>
<i>Frankineae</i>	<i>Frankiaceae</i> , <i>Acidothermaceae</i> , <i>Geodermatophilaceae</i> , <i>Microsphaeraceae</i> , <i>Sporichthyaceae</i>
<i>Propionibacterineae</i>	<i>Propionibacteriaceae</i> , <i>Nocardioidaceae</i>
<i>Streptomycineae</i>	<i>Streptomycetaceae</i>
<i>Corynebacterineae</i>	<i>Corynebacteriaceae</i> , <i>Dietziaceae</i> , <i>Gordoniaceae</i> , <i>Mycobacteriaceae</i> , <i>Nocardiaceae</i> , <i>Tsukamurellaceae</i>
<i>Micromonosporineae</i>	<i>Micromonosporaceae</i>
<i>Streptosporangineae</i>	<i>Streptosporangiaceae</i> , <i>Nocardiopsaceae</i> , <i>Thermomonosporaceae</i>
<i>Pseudonocardineae</i>	<i>Pseudonocardiaceae</i>
<i>Glycomycineae</i>	<i>Glycomycetaceae</i>

By far, streptomycetes are the most abundant culturable actinomycete (Lee and Hwang, 2002). The genus *Streptomyces* belongs to the family *Streptomycetaceae*, a unique family of the suborder *Streptomycineae*. Streptomycetes grow as mycelial filaments in soil; their mature colonies may contain two types of mycelia, the substrate (vegetative) mycelium, and the aerial mycelium. Each has a different biological role (Hopwood, 1999). Vegetative mycelia absorb nutrients, and are composed of a dense and complex network of hyphae usually embedded in the soil or immobilize substrate. Once the cell culture becomes nutrient-limited, an aerial mycelium develops from the surface of the vegetative mycelium. The role of this type of mycelium is mainly reproductive; indeed, the aerial mycelium develops into spore chains as the mature stage in their life cycle (Hopwood, 1999). Both, reproductive and aerial mycelium along with clearly sporulation of some mesophilic *Streptomyces* strains are shown in Figure 1.

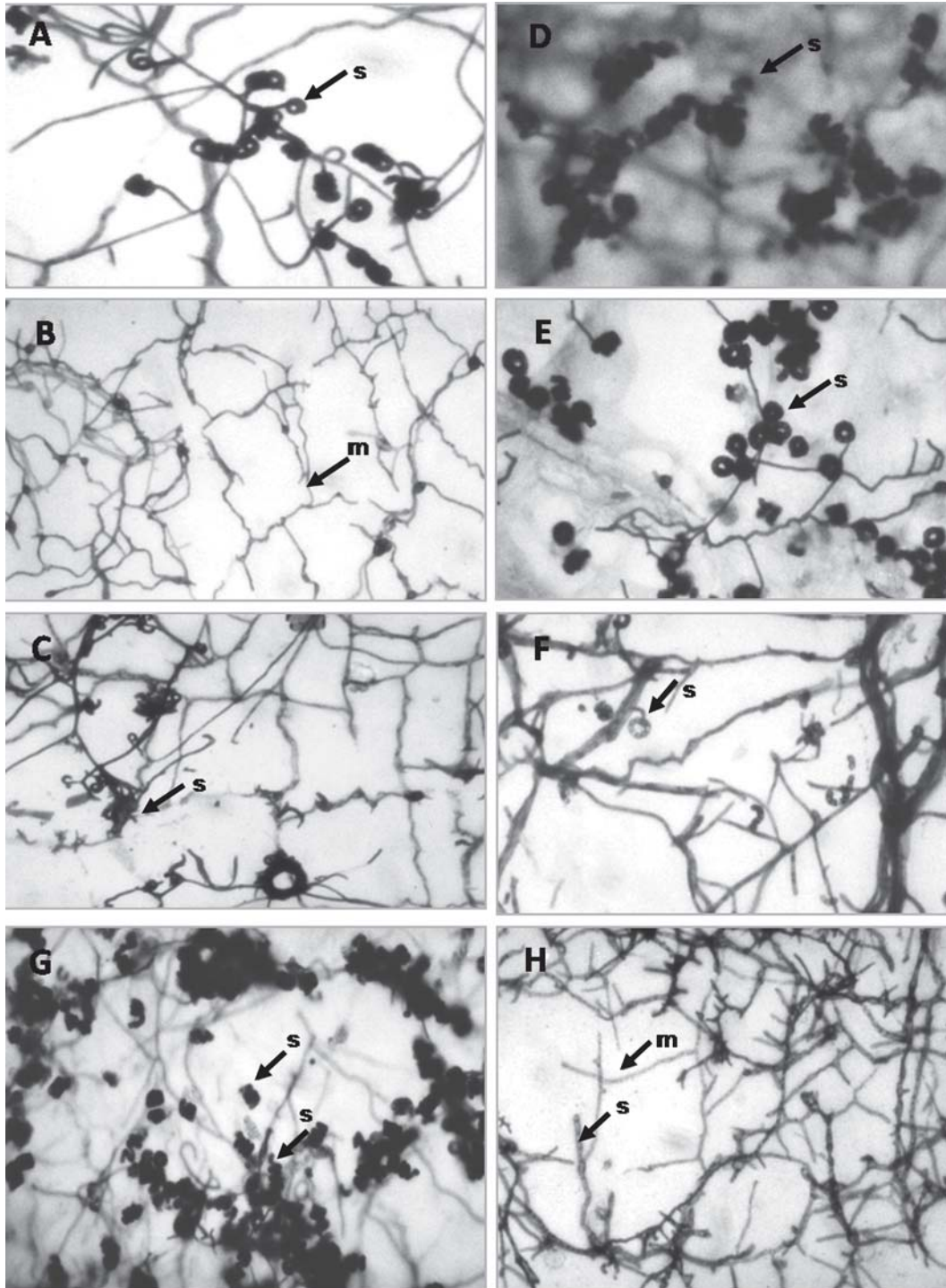
## Actinomycetes as biological control agents

Besides the enormous numbers of agroactive metabolites produced by actinomycetes (Tanaka and Omura, 1993), they also play an important role in agriculture as biocontrol agents. Antagonism against an extensive variety of plant pathogens has been reported (Bressan, 2003; Chamberlain and Crawford, 1999; Doumbou *et al.*, 2002; Tahvonen and Avikainen, 1987; Trejo-Estrada *et al.*, 1998a; Yuan and Crawford, 1995). A microorganism that colonizes roots is ideal for use as a biocontrol agent against soil-borne diseases (Weller, 1988). Actinomycetes, especially *Streptomyces*, are qualitatively and quantitatively important in the rhizosphere where they actively colonize plant root systems (Crawford *et al.*, 1993; Doumbou *et al.*, 2001; Tokala *et al.*, 2002). To better understand how these bacteria may act as biocontrol agents,

we must understand how they colonize the rhizosphere environment, and how they utilize the different mechanisms of biocontrol once they are established there. The rhizosphere is a special environment where the plant is the provider of nutrition to many life forms that are competing for life space. Information on the microflora present in the rhizosphere has been obtained primarily through isolation and cultivation of microorganisms from rhizosphere soils on laboratory media. However, more detailed descriptions of the microbial populations associated with roots are now possible with the use of molecular ecology methods such as repetitive elements-PCR (repPCR) (Schneider and De Bruijn, 1996), denaturing gradient gel electrophoresis (DGGE) (Muyzer and Smalla, 1998; Williamson *et al.*, 2000), and green fluorescent protein (GFP) (Gage *et al.*, 1996). These methods examine unculturable as well as culturable organisms.

Within the rhizosphere, plant roots have a direct effect on the composition and density of the soil microbial populations. Root exudates selectively influence the growth of bacterial and fungal populations by altering the presence of substrates in soil in the vicinity of roots (Grayston *et al.*, 1996; Yang and Crowley, 2000). Plant root exudates contain sugars, amino acids, organic acids, fatty acids, sterols, vitamins, nucleotides, and other compounds (Jaeger *et al.*, 1999; Smucker, 1993). The specific varieties of organic compounds released by different plants have been postulated to be a key factor influencing the diversity of microorganisms in the rhizosphere of different plant species (Buyer *et al.*, 2002; Doumbou *et al.*, 2002; Grayston *et al.*, 1996; Grayston *et al.*, 1998). There is also evidence that production of root exudates can be up regulated in the presence of certain nutrients. For example, citrate, malate, and related organic acids are over excreted by wheat and maize in response to high Al<sup>3+</sup> concentrations (Ma *et al.*, 2001). The microflora present on

**Figure 1.** Microscopic morphological structures of *S. hygrosopicus* strains AZ529 (A-C), AZ541 (D-F), AZ560 (G) and *S. lydicus* WYEC108 (H). All the strains showed the spore chain morphology (s) in compact long spirals, except for *S. lydicus* WYCED-108, which showed flexuous chains of spores. Substrate mycelia is also showed (m).



Photographs by Ana C. Gonzalez-Franco

the roots can also influence the amount of root exudates produced. Rhizosphere-colonizing bacteria referred to as plant growth-promoting rhizobacteria (PGPR) can also influence the nutritional status of the rhizosphere in several ways. For example, many PGPR are able to produce plant growth hormones such as auxins (Brandl *et al.*, 2001). Thus, the rhizosphere is a dynamic habitat rich in microorganisms and in plant microbe interactions, some of which are beneficial to the microbes and plants, and some of which are detrimental to one and/or the other. For example, root exudates from peas susceptible to *Fusarium oxysporum* stimulated the fungus in pure culture, but also caused many rhizosphere isolates to antagonize the pathogen (Rovira, 1965).

## Mechanisms for biological control of plant pathogens

Interest in biocontrol of plant pathogens has increased considerably over the past years, partly as a response to public concern about the use of hazardous chemical fungicides and pesticides such as methyl bromide, but also because it may provide control of diseases that cannot, or can only partially, be managed by other control strategies (Cook, 1993). Many studies on the biocontrol of phytopathogens focus on the suppressive effects of single biocontrol strains on specific fungal pathogens.

Biocontrol of plant diseases, especially of fungal origin, has been achieved using microorganisms such as *Trichoderma* sp., *Pseudomonas* sp., *Bacillus* sp., and *Streptomyces* sp. (Elad *et al.*, 1980; Ligon *et al.*, 2000; Raaijmakers *et al.*, 2002; Trejo-Estrada *et al.*, 1998a). Streptomycetes, along with other bacterial strains belonging to the Actinomycetales, have several properties that give them the ability to act as effective biocontrol agents in the rhizosphere, including the ability to colonize plant root surfaces, antibiosis against plant root pathogens, the

synthesis of particular extracellular enzymes, and the degradation of phytotoxins (Lewis and Starkey, 1969; Tokala *et al.*, 2002; Trejo-Estrada *et al.*, 1998a). There are three mechanisms known to be involved in this disease-suppression phenomenon.

**Antibiosis.** Antibiosis occurs when the antagonist (biocontrol agent) colonizes the rhizosphere and produces one or more substances that inhibits or kills the pathogen. Antibiosis by root-colonizing actinomycetes has been studied in several systems (Chamberlain and Crawford, 1999; Crawford *et al.*, 1993; Rothrock and Gottlieb, 1984; Trejo-Estrada *et al.*, 1998a). There is evidence that antibiotics are indeed produced in soil, and they have been implicated in the biocontrol of pathogens *in situ*. Rothrock and Gottlieb (1984) tested *Streptomyces hygrosopicus* var. *geldanus*, a producer of geldanamycin, in soil pots for its ability to control *Rhizoctonia* root rot of pea. Soil antibiotic extraction was quantified and the presence of antibiotic was correlated with pathogen control. Amended soils with geldanamycin in amounts equivalent to that produced *in vivo* by the streptomycete also controlled the disease (Rothrock and Gottlieb, 1984). Similarly, Trejo-Estrada (1998) tested *Streptomyces violaceusniger* YCED9, producer of nigericin, geldanamycin and a complex of macrocyclic lactone antibiotics, in greenhouse experiments to control *Rhizoctonia solani* and *Sclerotinia homeocarpa* (causative agents of grass seedling and crown-foliar disease, respectively). Partial control of the pathogen was associated with production of antibiotics, one of which (nigericin) could be extracted from the soil (Trejo-Estrada *et al.*, 1998b). Another study in the same *Streptomyces* species showed that a mutant of the strain defective in the production of geldanamycin lost the ability to control the disease (Beausejour *et al.*, 2001).

**Competition for nutrition and space.** There are cases where mutants of biocontrol strains that are deficient in the production of

antimicrobial substances are almost as efficient in biocontrol as the wild type strains (Kempf and Wolf, 1989). This mechanism of biocontrol is related to the colonization ability and other competitive traits of the biocontrol agent. The ability to use a specific compound as an energy source that not all microorganisms are able to use, for example, can provide a competitive advantage to the biocontrol agent. Also, the ability to use and out compete pathogens for inorganic compounds is another important aspect, which would determine whether a potential biocontrol agent will be successful or not in suppressing a pathogen. Iron is one of the resources that can limit growth of plant pathogens and one well-known source for nutrient competition in the rhizosphere (Douling and O'Gara, 1994). By sequestering iron away from invading pathogens, the root-colonizing biocontrol strain prevents it from invading and colonizing the plant roots.

Streptomycetes, along with other bacterial strains belonging to the Actinomycetales have the ability to colonize plant root surfaces (Kortemaa *et al.*, 1994; Tokala *et al.*, 2002). Also, they have the capacity to synthesize extracellular enzymes that allow them to use recalcitrant organic compounds as energy sources and to degrade phytotoxin compounds (Goodfellow and Williams, 1983; Lewis and Starkey, 1969; McCarthy and Williams, 1992). Streptomycetes have the ability to produce iron-chelating compounds, siderophores, that starve pathogens for iron (Tokala *et al.*, 2002). The ability to produce siderophores as a mechanism gives the biocontrol agent a competitive advantage in environments, such as rhizospheres, where soluble iron is scarce (Mullen, 2004).

*Parasitism.* Parasitism is the third mechanism of phytopathogen biocontrol. Mycoparasitism of fungal pathogens can sometimes be attributed to the production of extracellular lytic enzymes such as chitinases (Berg *et al.*, 2002; Chernin *et al.*, 1995; Lorito *et al.*, 1996) and  $\beta$ -1,3 glucanases (Berg *et al.*,

2002; Valois *et al.*, 1996) by a biocontrol agent. These hydrolases initiate the process of physical destruction of the fungal cell walls (FCW) (Adams, 1990). As was mentioned above, actinomycetes have the ability to produce a wide variety of extracellular enzymes that allows them to degrade various biopolymers in soil. Numerous correlations between fungal antagonism and bacterial production of chitinases or glucanases have been noted (Gonzalez-Franco *et al.*, 2003). Also, mature composts amended with chitin residues acquire suppressive properties against fungal plant pathogens. The microbial population of one such suppressive compost was characterized, and mainly Gram-positive bacteria belonging to the actinomycetes were found (Labrie *et al.*, 2001). To have more insight in the correlation of fungal mycoparasitism and bacterial production of lytic enzymes, knowledge of the composition of the FCW is required, and enzymes from known antifungal biocontrol agents need to be isolated and characterized for the mycolytic activities.

## Components of fungal cell walls

Fungal cell walls are made of fibrillar polysaccharides (structural components) including chitin, cellulose or other  $\beta$ -glucans, embedded in a matrix of amorphous components (cementing components) that include polysaccharides, lipids, and proteins that maintain the organization of the whole structure (Ruiz-Herrera, 1992). Some of these components are chemically associated via covalent bonds, although hydrogen bonding and hydrophobic associations are also important in the configuration of the resulting structure (Garret and Grisham, 1998; Gooday, 1990; Ruiz-Herrera, 1992).

Fungal cell walls are made mostly of polysaccharides, which comprise typically about 80-90% of their dry weight (Bartnicki-Garcia, 1968). Proteins, lipids, pigments (e.g. melanins), and inorganic salts are present in smaller amounts (Ruiz-Herrera, 1992).

Bartnicki-Garcia found that cell walls from fungi could be grouped into eight different chemotypes according to their polysaccharide composition (Bartnicki-Garcia, 1968). This author suggested an evolutionary pathway to explain the divergence of the wall chemotypes (Table 2). By far, the most numerous category (including most of the pathogens of plants) is the group V (chitin-glucan), harboring all mycelial forms of the Ascomycetes, Basidiomycetes, and Deuteromycetes. The Chytridiomycetes, are also included (Table 2). Chitin is the most characteristic polysaccharide of the fungal cell walls. It is an unbranched polysaccharide made of N-acetylglucosamine (GlcNAc) joined through  $\beta$ -1,4 bonds. Chitin was once thought to be absent in Oomycetes; however, traces of chitin are actually present in the cell walls of members of this fungal group, including pathogens such as *Phytophthora*, and *Pythium* species (Dietrich, 1973). Differences in the content of chitin between both morphologies of dimorphic fungi have been noticed. However, these differences appear unrelated to either morphology. Some species contain more chitin in the mycelial

form, whereas in others, the opposite occurs. In the case of *Candida albicans*, there is higher amount of chitin present in the cell walls of the mycelial (invasive) form of the fungus that is associated to animal pathogenesis, since data suggest that adhesive properties of invasive mycelial cells are dependent, at least in part, on the chitin present in the cell wall (Lehrer, 1986). The yeast form of *C. albicans* is included in group VI of Bartnicki-Garcia (Table 2), which comprises the yeast forms of the Ascomycetes and Deuteromycetes. Glucans comprise cellulose made of  $\beta$ -1,4 bonded glucose units, and noncellulosic glucans containing variable proportions of  $\beta$ -1,3 and  $\beta$ -1,6 linkages, and  $\alpha$ -1,3 glucans. The noncellulosic glucan type is the most abundant form in fungal cell wall chemotypes (Table 2). Some polysaccharides are characteristic of specific fungal groups, for example chitosan. This deacetylated analog of chitin has been found to be a characteristic component of the cell walls from Zygomycetes (Table 2). Biocontrol agents that have the ability to mycoparasitize fungal pathogens generally produce a variety of hydrolytic enzymes active against multiple cell wall components.

**Table 2.** Chemotypes of fungal cell walls (Bartnicki-Garcia, 1968).

	Chemotype	Taxonomic group
I	Cellulose-glycogen	Acrasiales
II	Cellulose-glucan	Oomycetes
III	Cellulose-chitin	Hyphochytridiomycetes
IV	Chitosan-chitin	Zygomycetes
V	Chitin-glucan	Chytridiomycetes, Euscomycetes, Homobasidiomycetes and Deuteromycetes
VI	Mannan-glucan <sup>b</sup>	Hemiascomycetes
VII	Mannan-chitin	Heterobasidiomycetes
VIII	Polygalactosamine-galactan	Trichomycetes

<sup>a</sup> Incompletely characterized; probably  $\beta$ -1,3- and  $\beta$ -1,6-linked.

<sup>b</sup> Chitin is present in low amounts


## Conclusion remarks

The control of plant diseases is an urgent need for sustainable agriculture. The application of agrochemicals for this purpose, while still an important method in agricultural practices, is not without its problems, such as environmental pollution and detrimental effects on non-target organisms. *Streptomyces* species as biological control agents offer a much needed alternative to the use of synthetic agrochemicals. They produced the natural antibiotics within the microhabitat of the rhizosphere being less polluting and less stressful on indigenous microbes compared with chemical fungicides. They also have the ability to colonize plant root surfaces protecting the plant for pressure of plant pathogens. These biological control agents compete for nutrients and space with plant pathogens; they also synthesize extracellular enzymes that attack the phytopathogenic fungal cell walls and they have the ability to produce descant-resistant spores to survive under water deficiency. All the properties exhibited by actinomycetes, especially those that belong to the genus *Streptomyces* as biological control agents of fungal phytopathogens, not only give us a better understanding in their environmental and ecological benefits, but also in their impact as an attractive alternative for use in agriculture.

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## Resúmenes curriculares de autor y coautores

**ANA CECILIA GONZÁLEZ-FRANCO.** Es profesora-investigadora de la Facultad de Ciencias Agrotecnológicas de la Universidad Autónoma de Chihuahua (UACH). Obtuvo su licenciatura en la Facultad de Ciencias Químicas, su maestría en la Facultad de Ciencias Agrotecnológicas de la Universidad Autónoma de Chihuahua y su doctorado en Microbiología, Biología Molecular y Bioquímica lo obtuvo en la Universidad de Idaho, USA. Su área de investigación se centra en el control biológico de enfermedades y en la interacción-microorganismo-planta. Imparte las cátedras de Interacción Microorganismo Planta, Bioquímica, Química y Biotecnología. Asesora estudiantes de licenciatura y posgrado. Es responsable del área de microbiología aplicada y biología molecular en el Laboratorio de Microbiología Aplicada, Fitopatología y Fisiología Post-cosecha de la Facultad de Ciencias Agrotecnológicas, UACH.

**LORETO ROBLES-HERNÁNDEZ.** Es profesor-investigador de la Facultad de Ciencias Agrotecnológicas de la Universidad Autónoma de Chihuahua. Obtuvo su licenciatura en 1992, su maestría en 1994 en la misma institución y su doctorado en la Universidad de Idaho, USA en 2004. Su investigación se centra en la epidemiología de enfermedades de plantas, con énfasis en aquellas causadas por virus y por bacterias fitopatógenas. Imparte los cursos de Fitopatología, Microbiología, Control Biológico y Fisiología Post-cosecha. Asesora estudiantes de licenciatura y maestría. Está a cargo del área de fitopatología y fisiología post-cosecha en el laboratorio de Microbiología Aplicada, Fitopatología y Fisiología de Post-cosecha de la Facultad de Ciencias Agrotecnológicas, UACH.