

1 Actinobacteria: an underestimated source of potential microbial biocontrol agents against *Fusarium*-
2 related diseases in cultivated crops

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Abstract

Crop infections with *Fusarium* spp. and associated mycotoxins have devastating economic implications and are a significant limitation to fifteen of the seventeen United Nations Sustainable Development Goals. Therefore, it is necessary to develop innovative strategies to reduce or eliminate diseases caused by *Fusarium* spp. in cultivated crops. Management of *Fusarium*-related diseases using beneficial microorganisms is a promising and eco-friendly solution. In this context, actinobacteria are considered one of the best candidates because of their multifunctional properties, which consist in the reduction of *Fusarium* spp. diseases and the promotion of plant growth. Actinobacteria represent a large Gram-positive bacterial phylum that is widespread in different environments, especially in soil. They are principally known for their versatile capacity to produce biologically active molecules with potential applications in different fields, including agriculture. As *Fusarium* species threaten diverse crops worldwide and cause global yield and quality losses that can negatively impact food security, the use of actinobacteria for plant diseases management is gaining interest as a safer and more potent alternative to ineffective synthetic-based pesticides. Thus, this work aims to review and highlight the importance of actinobacteria as microbial biocontrol agents and discuss the current research on *Fusarium* spp. diseases with a focus on species that threaten economically important crops, such as *F. graminearum*, *F. oxysporum*, *F. solani*, and *F. culmorum*. This review also presents actinobacteria-based products that have been patented for *Fusarium* disease control. We aim to provide valuable data, guidance and advancements for future research on microbial biocontrol against *Fusarium*-related diseases. In addition, this review emphasizes the need for further research about the impact of actinobacteria-*Fusarium* interactions on mycotoxin production. It also highlights the need of in-depth understanding microbial biocontrol mechanisms to ensure safe and sustainable crop production worldwide.

Keywords Actinobacteria, Antibiosis, Microbial biological control, *Fusarium* diseases, Mycotoxins

Introduction

Crop production is constantly threatened by a wide range of abiotic and biotic stresses, including inadequate farmland management, climate change and diseases. Around the world, phytopathogenic fungi have been reported in crops, accounting for approximately 70-80% of diseases causing significant losses in agricultural activities and food production (Peng et al. 2021). Among these disease-related phytopathogens, *Fusarium* species are well known for their serious impact on crops worldwide (Arie 2019; Timmusk et al. 2020). Since *Fusarium* species are among the most persistent soil-borne fungal pathogens, they pose a significant threat to cultivated plants and impede management practices (Seepe et al. 2021).

One control strategy is the use of synthetic compounds to combat *Fusarium*-related diseases. Synthetic fungicides such as tebuconazole (Zhao et al. 2022) and carbendazim (Sun et al. 2022) remain the primary products registered for controlling *Fusarium* pathogens. In addition to the limited number of synthetic products available, these compounds often exhibit inconsistent effectiveness, as frequently observed in case for *Fusarium* head blight disease. Furthermore, they may pose potential risks for resistance development and have adverse environmental and health effects (Arie 2019; Seepe et al. 2021). This has led to an increased in the prohibition of synthetic products (Gullino et al. 2015). For example, methyl bromide, which was used to control *Fusarium* species and other soil-borne pests in the early 2000s, is now banned because it is categorized as a substance that causes damage to ozone layer (Ruzo 2006; Land et al. 2022). Moreover fungicides use can lead to increased mycotoxin production, depending on *Fusarium* populations and environmental factors (Kokkonen et al. 2014; Degani et al. 2022).

In an effort to develop eco-friendly approaches, microbial biocontrol strategies are recognized as promising alternatives. Many studies have been published on microbial biocontrol against *Fusarium* disease using various microorganisms, including fungi, bacteria and actinobacteria (Singh et al. 1999; Palazzini et al. 2007; Noumavo et al. 2015; Palazzini et al. 2018; Zhang et al. 2019; Olanrewaju and Babalola 2019; El-Sharkawy et al. 2022). However, despite the increasing number of published studies on microorganisms that suppress *Fusarium* growth, only a small number of bacterial species, including actinobacteria, are currently available on the market (O'Sullivan et al. 2021). Actinobacteria are particularly interesting because they are considered to be potential factories for producing a wide range of bioactive compounds that have industrial, pharmaceutical and agricultural applications (Xie and Pathom-areen 2021). Actinobacteria, which are Gram-positive bacteria, constitute the largest bacterial phylum (Ait Barka et al. 2016). Members of this group, particularly those related

to the genus *Streptomyces*, are considered as the primary producers of biologically active molecules (Solecka et al. 2012; Takahashi and Nakashima 2018).

In recent years, significant progress has been noticed in microbial biological control research. However, there is a lack of retrospective literature discussing the effectiveness of actinobacteria in biocontrol, especially against soil-borne pathogens, such as *Fusarium*. In fact, much attention has been given to reporting the use of non-actinobacteria, such as *Pseudomonas* and *Bacillus*, as biocontrol agents against different pathogenic microorganisms and how these bacteria have shown potential in enhancing plant growth and defences (Nguvo and Gao 2019; Tariq et al. 2020; Lahlali et al. 2022; Elnahal et al. 2022). On the other hand, literature sheds light on the potential use of actinobacteria in agriculture as biopesticides and biofertilizers to enhance plant productivity and promote sustainable agriculture (El-Tarabily and Sivasithamparam 2006; Bhatti et al. 2017; Bubici 2018; Chaurasia et al. 2018; Zhang et al. 2020; Boubekri et al. 2021; Jagannathan et al. 2021; Ebrahimi-Zarandi et al. 2022). Even though there are different reviews on the overall effectiveness of actinobacteria used as biopesticides and biofertilizers (El-Tarabily and Sivasithamparam 2006; Bhatti et al. 2017; Bubici 2018; Chaurasia et al. 2018; Zhang et al. 2020; Boubekri et al. 2021; Jagannathan et al. 2021; Ebrahimi-Zarandi et al. 2022), there is still a need to discuss and focus on specific aspects related to complex pathosystems, especially those threaten cultivated crops.

Considering this, an attempt has been made to examine and gather available information on the use of actinobacteria as anti-*Fusarium* agents and assist researchers in joining forces to develop safer and more effective applications against *Fusarium*-related diseases. Hence, attention has been given to discussing the main implications of *Fusarium* diseases, including the associated mycotoxins and standard management practices. As a whole, this review highlights the need for a fundamental understanding of the molecular mechanisms underpinning plant, *Fusarium* and actinobacteria interactions. Moreover, in the context of evaluating future microbial biocontrol applications against *Fusarium* diseases and climate change, further in-depth studies should also focus on the capacity of *Fusarium* to produce mycotoxins.

The Genus *Fusarium*, a Cosmopolitan Soil-Borne Pathogen

Fusarium (Ascomycota, Hypocreales, Nectriaceae) is one of the most extensively studied fungal genera known for its ability to cause significant damage to wide range of crops, resulting in reduced yield, harvest quality and impacting food safety (Rampersad 2020). The taxonomy of the *Fusarium* genus is not entirely resolved. Thus, the number of species is continuously increasing (with at least 300 phylogenetically distinct species/species complexes listed) (Summerell 2019). The genus *Fusarium* includes many species that cause plant diseases, such as Fusarium head blight (FHB), foot and root rot, crown rot and seedling dumping-off (Summerell 2019; Seepe et al. 2021). Most common species known to infect crops are presented in Table 1. As of December 31st 2022, there were 45,550 articles with “*Fusarium*”, as a keyword, in PubMed database. Most of these investigations focused on plant disease issues in agriculture and horticulture. A survey conducted by Dean et al. (2012) based on the scientific and economic importance of the ten most significant plant pathogens revealed that *Fusarium graminearum* and *F. oxysporum* ranked fourth and fifth respectively, behind *Magnaporthe oryzae*, *Botrytis cinerea* and *Puccinia* spp.

Among the major species causing crop loss, *F. graminearum* and *F. culmorum*, are the main causal agents of FHB in cereals. They account for 10 to 70% of worldwide wheat production loss. These fungi are also reported as a post-harvest pathogen for grains that have not been adequately dried or stored (Magan et al. 2010b). Additionally, *F. oxysporum*, causes wilt and stem rot diseases and can infect over 150 different plant species (Dean et al. 2012; Li et al. 2023; Saad et al. 2023). The generic designation “*F. graminearum*” refers to a species complex that contains at least 15 other phylogenetically distinct species, in addition to *F. graminearum sensu stricto*. It includes *F. acaciae-mearnsii*, *F. aethiopicum*, *F. asiaticum*, *F. austroamericanum*, *F. boothii*, *F. brasiliicum*, *F. cortaderiae*, *F. gerlachii*, *F. louisianense*, *F. meridionale*, *F. mesoamericanum*, *F. nepalense*, *F. ussurianum* and *F. vorosii* (Wang et al. 2020). This species complex causes floral diseases, known as FHB, in small grain cereals including wheat, maize, barley, rice and oats. In addition, members of this complex are known to produce a wide range of trichothecenes-type mycotoxins during plant infection and colonization (Dean et al. 2012; Chen et al. 2019).

F. oxysporum is a common filamentous fungus that causes vascular wilt, and crown, stem and root rot diseases in a variety of host plants. *F. oxysporum* strains are classified based on their host specificity, which are designated as “*formae speciales*” (f. sp.) and referred to as the *F. oxysporum* complex (Li et al. 2020). More than 100 *formae speciales* of *F. oxysporum* have been identified, including the pathogens that infect economically

important crops such as rice, soybean, chickpea, pigeon pea, tomato, cucumber, watermelon, date palm, banana tree, tea and coffee tree. These *Fusarium* pathogens predominantly cause tracheomycosis, which refers to vascular wilting and rotting (Edel-Hermann and Lecomte 2019).

F. solani, which corresponds to a highly diverse assemblage of fungi in terms of morphology, pathogenicity and distribution, is regarded as a species complex that includes at least 60 distinct phylogenetic species (Aoki et al. 2014; Schroe et al. 2016; Summerell 2019). Among *Fusarium*, individuals of this species complex are the most frequently isolated from soil (Homa et al. 2018). *F. solani* can cause a wide range of serious diseases in horticultural and greenhouse-cultivated plants (Coleman 2016). Phytopathogenic members of the *F. solani* species complex include some of the most impactful plant pathogens associated with vascular wilts and root rots of some of the most cultivated crops, especially Solanaceae plants (*F. solani* f. sp. *eumartii*), legumes (*F. solani* f. sp. *pisi*) and cucurbits (*F. solani* f. sp. *cucurbitae*) (Romberg and Davis 2007; Soltanzadeh et al. 2016; Rezaee et al. 2018). As individual species are often associated with only one or a few plant hosts, populations of phytopathogenic *F. solani* have been divided into 12 *formae speciales* (Šišić et al. 2018).

Amongst other serious *Fusarium* pathogen, *F. verticillioides*, *F. proliferatum* and *F. subglutinans* are the primary *Fusarium* species involved in the ear rot disease of cereals (Ferrigo et al. 2016). These fungi are typically found randomly on groups of kernels or on physically injured kernels (Lanubile et al. 2017).

***Fusarium* Mycotoxins and their Regulation in Foodstuffs**

Mycotoxins are secondary metabolites produced by fungi with potentially negative effects on animal and human health (Habschied et al. 2021). Depending on the mycotoxin, its deleterious impact can be mutagenic, carcinogenic, teratogenic and cytotoxic (Harkai et al. 2016).

Fusarium spp. are known to be the main producers of trichothecene, zearalenone and fumonisin families of toxins, each of these toxins is regulated in the European Union (Perincherry et al. 2019). Trichothecenes, which belong to the sesquiterpenoids family, are toxic to plants and mammals, with more than 200 known derivatives to date (Polak-Śliwińska and Paszczyk 2021; Mahato et al. 2022). Trichothecenes are divided into four types (A to D) based on the chemical groups located at five positions of the trichothecene skeleton. The most predominant trichothecenes produced by *Fusarium* spp. include T-2 toxin, HT-2 toxin, NX-2 and neosolaniol (type A), which are mainly produced by *F. langsethiae* and *F. sporotrichioides*. Nivalenol (NIV), DON, and the DON-acetylated derivatives (type B) are primarily produced by *F. graminearum* and *F. culmorum*. Ingestion of trichothecenes can lead to inhibition of RNA synthesis, immunosuppression, nausea, vomiting and anorexia (Stępień et al.

2020). It is hypothesized that some of these mycotoxins provide an ecological advantage in their ecosystem and enhance their fitness in extreme conditions (Kagot et al. 2019). In this context, deoxynivalenol (DON; trichothecene) is identified as a virulence factor in the phytopathogenic process (Yekkour et al. 2015a, b; Zhang and Ma 2017).

Zearalenone, on the other hand, is a macrocyclic β -resorcylic acid lactone mainly produced by *F. graminearum* and *F. culmorum* (Qin et al. 2021; Han et al. 2022). Zearalenone and its associated derivatives (α -zearalenol and β -zearalanol) are among the most effective non-steroidal estrogenic natural compounds thought to act as endocrine disruptors agents in human hormonal balance (Kowalska et al. 2016).

Fumonisin, which are derived from polyketides are mainly produced by *F. verticillioides*, *F. proliferatum* and *F. nygamai* (Zhang and Ma 2017; Perincherry et al. 2019). There are over 28 fumonisin homologues, which have been grouped as fumonisin A, B, C, and P. The two primary mycotoxins produced by *F. verticillioides* are fumonisins B1 and B2 (FB1 and FB2). Fumonisin have been identified as potentially carcinogenic (group 2B; International Agency for Research on Cancer) for the oesophagus (Kamle et al. 2019).

On the other hand, *Fusarium* spp. produced other secondary metabolites with potential toxicity. They constitute a group of emerging and masked mycotoxins, including fusaproliferin, enniatins, beauvericin and moniliformin (Ferrigo et al. 2016; Ekwomadu et al. 2021). These emerging toxins are not yet regulated and are of recent concern in agricultural commodities as they may contribute to adverse health effects (Ekwomadu et al. 2021).

Fusarium mycotoxins are regulated in foodstuffs worldwide, with the European Union leading the regulation as of December 19, 2006 under Commission of the European Communities (EC) No 1881/2006 (consolidated version 2023) (Commission Regulation, 2006). The maximum limits accepted in the European Union are listed in Table 2. The *Fusarium* spp. mycotoxins regulated included deoxynivalenol, zearalenone and fumonisin B1 + fumonisin B2. In addition, T-2 and HT-2 toxins are currently under review for potential regulation starting in July 2024. In the USA, the only regulated mycotoxins of *Fusarium* spp. are deoxynivalenol (at advisory level) and fumonisins (at guidance level) (<https://www.fda.gov/food/natural-toxins-food/mycotoxins>). In African and Asian countries, there is an absence of specific regulations governing the control of *Fusarium* mycotoxins; these countries rely sometimes on the European Union (EU) and sometimes on the Codex Alimentarius Commission (CAC) regulations and guidelines (Anukul et al. 2013; Chilaka et al. 2017).

***Fusarium* and Climate Change**

The relationship between food security and climate change has received significant attention over the past two decades. The effects of interacting abiotic factors such as drought stress, elevated temperatures and increased CO₂ levels in the air, have been studied in fungi, including *Fusarium* species and their associated mycotoxins (Magan et al. 2011; Verheecke-Vaessen et al. 2021).

It has been confirmed that climate influences the growth and spread of *Fusarium* spp. infections worldwide (Parikka et al. 2012; Nnadi and Carter 2021; Zingales et al. 2022; Infantino et al. 2023). It is predicted by Parikka et al. (2012) that the composition of *Fusarium* species in Northern Europe is expected to vary due to climate changes by the year 2050. According to the study of Infantino et al. (2023), climate change conditions are anticipated to increase the prevalence of *Fusarium* species on wheat kernels in Italy. A shift in *Fusarium* communities has been noticed in some temperate regions, with *F. graminearum*, which prefers warmer and humid regions, replacing *F. culmorum* in several temperate zones over the past 20 years. Thus, the severity of FHB is predicted to worsen with future warmer temperatures because *F. graminearum* is more aggressive than *F. culmorum*. The fact that *F. graminearum* produces more mycotoxins than *F. culmorum* makes the situation more problematic (Nnadi and Carter 2021). The modelling studies, within the future decades climate change scenarios, *F. oxysporum* f. spp distribution in Europe, Middle East and North Africa areas were forecasted to be highly favourable for fungal development (Shabani et al. 2014; Alkhalifah et al. 2023).

Furthermore, the adaptability of mycotoxigenic fungi to such environmental factors has been addressed in fungal diseases, such as *Fusarium* related-diseases (Medina et al. 2017; Moretti et al. 2019). The study by Magan et al. (2010a) demonstrated the effects of interactions between *F. culmorum* and other mycobiota on growth and DON production. The authors conclude that changes in water activity and temperature affect the competitiveness of *F. culmorum* and that the presence of other competing fungi can sometimes inhibit *Fusarium* growth. Moreover, the presence of other fungal species has been shown to frequently inhibit DON production, independently of environmental conditions. A study by Medina and Magan (2011), which investigated the effects of interacting ecophysiological parameters on the production of the T-2 and HT-2 toxins produced by strains of *F. langsethiae*, showed that the cited toxins were produced at different temperatures, while water availability appeared to be crucial in determining the level of their production. Verheecke-Vaessen et al. (2019) examined the impact of three leading environmental factors related to climate change; temperature, water activity and CO₂ exposure on growth and mycotoxin production by *F. langsethiae* strains on oat-based media and in stored oats. Interestingly, the authors showed that combining climate change factors significantly affected fungal growth, expression of biosynthetic toxin genes (*Tri5*, *Tri6* and *Tri16*), and the generation of T-2+HT-2

and associated metabolites. Van der Fels-Klerx et al. (2016) investigation showed that the fungal population and the mycotoxin production patterns would shift with climate change. Numerous studies have attempted to understand the possible shift of *Fusarium* species implicated in *Fusarium*-related diseases, notably FHB, in various geographical locations according to future scenarios of environmental changes (Medina et al. 2015; Skelsey and Newton 2015; Moretti et al. 2019; Perrone et al. 2020; Zingales et al. 2022). Medina et al. (2017) highlighted a particular interest in how FHB disease, caused by *F. graminearum*, adapted to elevated CO₂ levels over 10 to 20 generations. However, the authors of this study did not investigate the effects of *Fusarium* mycotoxins. According to Moretti et al. (2019), the incidence and severity of the FHB disease are positively correlated with the levels of *Fusarium* mycotoxins in wheat kernels.

Existing Management Practices

In general, control approaches for soil-borne diseases depend on numerous factors, such as the crop grown, the pathogenic agent, the geographical location and the technique available. Synthetic chemicals in different forms (pesticides and host-immunity inducers) are extensively used in the context of intensive and large-scale agriculture (Nicolopoulou-Stamati et al. 2016; Pathak et al. 2022). In order to suppress pathogenic strains of *Fusarium* and prevent harvest losses, especially those related to FHB, agro-chemists have developed several synthetic fungicides including; benomyl, carbendazim (benzimidazoles, FRAC group code 1), hexaconazole, propiconazole, tebuconazole, triadimenol (triazoles, FRAC group code 3) and mancozeb (dithiocarbamates, FRAC group code M3) (Duke 2018). However, these synthetic fungicides often provide limited or conflicting results in controlling *Fusarium* pathogens due to the complex nature of the disease (the fungal life cycle, the mode of spread and the infection strategy) and the interaction with cultural practices (N-fertilization, irrigation and timing and dose of applications) (Wagacha and Muthomi 2007; Arie 2019). The study by Ramirez et al. (2004) highlighted the interactions between rainfall, temperature and fungicide concentration on the control effectiveness of *F. graminearum*-induced FHB. The authors also showed that in particular conditions of suboptimal fungal growth and low fungicide dose, DON and NIV production could be stimulated in addition to fungicide ineffectiveness against FHB.

An additional determining factor is the frequent involvement of different *Fusarium* species as a pathogenic consortium for the same disease, which is difficult to control (Pathak et al. 2022; Degani et al. 2022). Synthetic chemicals' extensive and widespread use gives rise to the emergence of fungicide-resistant organisms and increase concerns about food safety. Both circumstances lead to limit fungicide residues in food and enhance the restriction of synthetic chemical management options (Nicolopoulou-Stamati et al. 2016; Liu et al. 2019).

The non-chemical control strategies can include agronomic practices to reduce the available inoculum for dispersal, such as crop diversification, crop rotation and tillage practices. Other strategies include regulative measures like quarantine, genetic approaches such as developing disease-resistant/tolerant varieties, and eradication methods like soil solarization, ultraviolet radiation and flooding. These methods can be used alone or in combination with synthetic and biological control agents as an integrated disease management strategy (He et al. 2021).

In general, the integrated management of *Fusarium* diseases, especially those affecting cereals, is recommended as the best short/medium-term strategy for reducing losses at the field level. For example, Willyerd et al. (2012) demonstrated the efficacy and stability of FHB and DON-integrated management strategies, including appropriate tillage, irrigation and timing for the application of fungicides or microbial biocontrol agents, across multiple environments. In contrast, research for less susceptible cultivars of *Fusarium* spp. through the development of continuous breeding programs is seen as a necessary long-term strategy.

Use of Microbial Biocontrol Agents

The use of microbial biocontrol agents remains one of the most promising alternative control strategies to synthetic chemical applications. These agents are considered safe and have minimal adverse effects on the environment (He et al. 2021). Therefore, antagonist bacterial and fungal strains have been used to control plant pathogenic fungi, including *Fusarium* species (Yekkour et al. 2012; Palazzini et al. 2018; Anusha et al. 2019; Wei et al. 2020; Zhang et al. 2020; Babu et al. 2022). These microorganisms include strains of *Pseudomonas* spp., *Bacillus* spp., *Trichoderma* spp., and non-pathogenic isolates of *F. oxysporum*, which have been shown to be effective not only in controlling plant pathogens but also in assisting plants to mobilise and acquire nutrients (Gopalakrishnan et al. 2011). There is also a growing interest in using actinobacteria as biological agents due to their exceptional metabolic properties (Boubekri et al. 2021; Ebrahimi-Zarandi et al. 2022). In addition, the use of actinobacterial strains exhibiting plant growth-promoting properties is also regarded as an emerging approach in mitigating the impact of climate change by triggering plants' defensive mechanisms against various related abiotic stresses, such as drought, salinity, alkalinity and temperature increase (Gasmi et al. 2019; Djebaili et al. 2021; Aallam et al. 2021; Pellegrini et al. 2022).

Actinobacteria: Ubiquitous Bacteria with a Wide Range of Interests

Actinobacteria are a distinct group of bacteria that are widely distributed in nature, including aquatic and terrestrial ecosystems, and can survive in extreme environments (Lewin et al. 2016). It is one of the largest

taxonomic phylum of Gram-positive filamentous bacteria with a high guanine-plus-cytosine (G+C) content in their DNA (Ait Barka et al. 2016). This phylum consists of the following six classes: Actinobacteria, Acidimicrobiia, Coriobacteriia, Nitrospirae, Rubrobacteria and Thermoleophilia. According to Parte et al. (2020), the aforementioned classes contain 443 genera and 73 families that are disproportionately distributed. *Streptomyces* is the predominant genus and the most frequently isolated from different sources. In addition, other less predominant genera, such as *Micromonospora*, *Actinopolyspora*, *Saccharopolyspora*, *Nocardia*, *Oerskovia* and *Nonomuraea*, have been reported (Golinska et al. 2015). Actinobacteria undergo complex morphological differentiation; they exist as dormant spores or actively growing cells, and species can be either unicellular or mycelial structures such as *Micrococcus* and *Streptomyces*, respectively (van Bergeijk et al. 2020).

Among actinobacteria, the genus *Streptomyces* is the most widely documented for its ecological dominance, diverse capabilities and beneficial roles in plant health. Many *Streptomyces* species have been isolated from rhizospheric soils and are considered effective actinobacterial biological control agents that protect against different plant diseases and possess multiple plant growth-promoting traits (Youssef et al. 2001; El-Tarabily et al. 2009, 2020; Kamil et al. 2018; Kaur et al. 2019; Al Hamad et al. 2021; Al Raish et al. 2021; El-Tarabily et al. 2021a, b; Alwahshi et al. 2022; Alblooshi et al. 2022). Furthermore, many researchers have emphasized the prevalence of actinobacteria as plant endophytes (Golinska et al. 2015; Suman et al. 2016; Alkaabi et al. 2022). Different species of *Streptomyces* and non-*Streptomyces* strains have been reported to colonize the internal tissues of plants (El-Tarabily 2003; El-Tarabily et al. 2019, 2021b; Alkaabi et al. 2022; Alblooshi et al. 2022). Many non-*Streptomyces* strains are rare actinobacteria that are of interest for isolation and identification, as they can serve as a novel source of microbial biocontrol agents and/or plant growth promoters (El-Tarabily and Sivasithamparan 2006; Fialho de Oliveira et al. 2010; El-Tarabily et al. 2010; Meliani et al. 2022).

Actinobacteria have attracted much attention because of their diverse physiological and metabolic properties (Zhang et al. 2019). Actinobacteria represent a rich source of various bioactive natural products such as antibacterial (Streptomycin and Tiacumicin B), antifungal (Rapamycin), antiviral (Ivermectin), antiparasitic (Avermectin), antitumor (Doxorubicin), immunosuppressive (Rapamycin) and insecticidal (Avermectin and Spinosad) agents (Arcamone et al. 1969; Vézina et al. 1975; Pitterna et al. 2009; Tao et al. 2019; El-Saber Batiha et al. 2020; Bhakyashree and Kannabiran 2020). Furthermore, actinobacteria can be used in biotechnological applications because they are considered potential factories of many biologically active compounds that can be useful in the industrial, pharmaceutical and agricultural sectors (Xie and Pathom-aree 2021).

Detection of Actinobacteria

The study of microorganisms biodiversity, including actinobacteria has traditionally focused on microbial cultures from different types of sample sources, such as soil (including rhizosphere), plants (endophytes), freshwater and marine ecosystems, and animals (Jose et al. 2021). One strategy for enhancing the likelihood of obtaining particularly interesting isolates is to explore underresearched and unique ecosystems (Yekkour et al. 2021). However, due to the different growth and incubation requirements of a numerous number actinobacterial strains, it is challenging to culture them via the commonly used media in laboratories. Thus, in order to isolate actinobacteria, it is not possible to recommend a single procedure for different samples (Goodfellow, 2014).

A number of well-known selective techniques are used for the targeted isolation of actinobacteria. These techniques include: (I) physical and chemical treatments applied to the samples (e.g. temperature, pH, microwave and irradiation), (II) the use of selective culture media containing specific compounds such as chitin or humic acid as the sole carbon source, (III) the addition of selective agents to the culture medium (e.g. NaCl, phenol, benzoate and antibiotics), and (IV) specific conditions of incubation (e.g. temperature, aeration and duration) (Bouras et al. 2021; Ebrahimi-Zarandi et al. 2022). The combination of these procedures enables easy isolation of actinobacteria (Oberhofer et al. 2019; Ezeobiora et al. 2022). For instance, Świecimska et al. (2023) used a culture-based bioprospecting strategy to isolate and screen filamentous actinobacteria from poorly studied extreme biomes. The authors showed that the strains belonging to the genera *Actinacidiphila*, *Streptacidiphilus* and *Streptomyces*, showed a remarkable ability to inhibit the growth of diverse fungal plant pathogens, including different *Fusarium* species.

Phenotypic features, 16S rRNA gene sequencing, multi-locus sequence analysis (MLSA) and whole genome sequencing (WGS) are frequently used in a polyphasic approach for actinobacterial identification and genomic data are also used for *in silico* exploration of potential properties (Goodfellow et al. 2012; Glaeser and Kämpfer 2015; Rosselló-Móra et al. 2015). For example, the study by Pengproh et al. (2023), which used 16S rRNA gene sequencing, MLSA as well as WGS for strain identification and genome exploration, revealed the presence of biosynthetic gene clusters (BGCs) associated with plant growth promoting and antagonistic properties in *Streptomyces* sp. strain S.PNR29 against *Fusarium oxysporum* f. sp. *lycopersici*.

Nowadays, in addition to culture-dependent methods, researchers are using culture-independent methods (high-throughput sequencing) as integrative approaches to gain a thorough understanding of the actinobacterial communities in the samples analysed (Goodfellow, 2014; Long et al. 2019). These metagenomic approaches provide a broad-spectrum identification of different microbes along with high-resolution profiling of the microbial communities in the analysed samples (Das et al. 2014; Amin et al. 2020). Thus, the analysis of

actinobacterial communities using classical and novel methods has been documented in diverse environments (Gopalakrishnan et al. 2011; Yekkour et al. 2012; Soltanzadeh et al. 2016; Tang et al. 2020; Babu et al. 2022). Amplicon sequencing studies highlight the presence of actinobacteria in soil and plant microbiomes associated with suppression of plant diseases (Ebrahimi-Zarandi et al. 2022). For example, Chang et al. (2022) demonstrated that intercropping maize and soybean could assist the host in withstanding soil-borne *Fusarium* root rot by reshaping the rhizosphere bacterial community and accumulating beneficial microorganisms in the soybean rhizosphere. Cao et al. (2020) suggested that healthy cucumber roots had a higher richness and abundance of actinobacteria compared to the plants infected with *Fusarium oxysporum* f. sp. *Cucumerinum* when using culture-independent analysis.

Actinobacteria as a Source of Biocontrol and Plant Growth-Promoting Agents

Due to their remarkably diverse biosynthetic capabilities, actinobacterial strains are among the fascinating microorganisms investigated for the microbial biocontrol of plant diseases. *In vitro* studies using various methods, including dual culture, agar well diffusion, paper disc diffusion and streak methods, were carried out on different *Fusarium* strains and showed promising results (Table 3). In addition, different strains of actinobacteria have shown positive effects in combating *Fusarium* strains in crops such as wheat, maize, barley, tomato, rice, chickpea, pigeon pea, pea, soybean, cucumber, watermelon and others (Table 4). The efficiency of actinobacteria is mainly due to their beneficial effects on plant growth and health, which are directly or indirectly related to nutrient availability and assimilation as well as phytopathogen suppression (Boukhatem et al. 2022).

Many members of the phylum *Actinobacteria* can stop the growth of a wide range of plant pathogens via the production of antimicrobial molecules and siderophores, giving them ecological advantages in the natural context of competition for limited nutrients and harsh environments (Ait Barka et al. 2016). Actinobacterial strains, particularly *Streptomyces* species, are considered promising sources of antimicrobial molecules that inhibit the growth of plant pathogens. These compounds cause molecular, biochemical, and structural changes in the target organism (Salwan and Sharma 2020). In addition, by forming stable complexes with iron, siderophores also interact with other heavy metals such as aluminum (Al), cadmium (Cd), copper (Cu), and zinc (Zn), as well as radionuclides like uranium (U) and neptunium (Np), which thought to reduce the deleterious effects of heavy metal pollution on plants (Torres-Rodriguez et al. 2022). This property of actinobacteria, which could mitigate heavy metal stress in plants, is worth applying as industrial and agricultural activities have led to soil contamination by heavy metal(s) /metalloid(s) (Hou et al. 2020). Researchers have made significant efforts to isolate actinobacterial strains that possess multifaceted properties, including stimulating plant growth in the

presence of soil pollutants. For example, in the study by Xu et al. (2023), the mixture of soil amendment and actinobacteria inoculant (2% organic fertilizer with 1.5g.kg⁻¹ actinobacteria) was the most effective method to control Cd contamination in soil on wheat plants. Abdelgawad et al. (2021) reported the isolation of an actinobacterial strain named *Nocardiopsis lucentensis* S5 with the capacity to mitigate arsenic-induced growth reduction in barley and maize. The authors hypothesized that *N. lucentensis* S5 treatment could induce arsenic soil retention *via* arsenic-binding siderophores (Abdelgawad et al. 2021). Thus, the capacity of actinobacterial strains to tolerate heavy metal stress as well as their growth-promoting abilities can be advantageous in reducing the effects of pollutants and stress factors on crop plants (Selim et al. 2021).

Actinobacterial strains also produce many other compounds and contribute to the suppression of phytopathogens, including gases such as hydrocyanic acid (HCN) and volatile ammonia. *Streptomyces* strains are able to produce ammonia to alter microbial environments in which they compete (Avalos et al. 2020). In addition, different hydrolytic enzymes like chitinases, cellulases, glucanases, proteases and phospholipases are produced by actinobacteria (Avalos et al. 2020; Boukhatem et al. 2022). The primary role of these lytic enzymes is to breakdown the cell walls of pathogens, resulting in loss of membrane integrity, the release of intracellular substances, and ultimately cell death (Torres-Rodriguez et al. 2022).

Actinobacterial strains are also involved in promoting of plant growth by solubilizing inorganic phosphates and potassium (Tian et al. 2021; Boubekri et al. 2021), fixing atmospheric nitrogen (Gtari et al. 2011), producing phytohormones (auxins, gibberellins, cytokinins, ethylene and abscisic acid), and synthesising the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase which has a vital role in inhibiting the production of stress-induced ethylene in plants (Mulani et al. 2021). These indirect processes impact plant health and consequently prevent opportunistic pathogens (Santoyo et al. 2016). Thus, the development of actinobacteria as biofertilizers, phytostimulants and microbial biocontrol agents can be further exploited in integrated strategies for the management of problematic fungal disease such as *Fusarium*-related disease in order to develop more sustainable agricultural practices (Kaari et al. 2022; Boukhatem et al. 2022).

Mechanisms Potentially Involved in Control of *Fusarium* Disease by Actinobacteria

Actinobacteria members are generally known to involve both direct and indirect mechanisms in the microbial biocontrol of plant pathogens (Figure 1). For example, competition for space and nutrients with other microorganisms, hyperparasitism, predation and antibiosis are among the direct mechanisms that actinobacterial strains use to inhibit the growth of a wide range of phytopathogens. In addition, actinobacterial strains are also

known to induce host resistance via indirect mechanisms that protect the plants from pathogen attack (Ebrahimi-Zarandi et al. 2022). Moreover, by exhibiting plant growth-promoting properties, actinobacterial inoculation can improve the nutritional and overall health status of the plant, thus contributing to the prevention of opportunistic attacks (Kaari et al. 2022).

Actinobacteria are generally regarded as powerful natural biocontrol agents. They compete with pathogens by producing various secondary metabolites, including different antibiotics, and are therefore the preferred candidates for development of microbial biocontrol agents (Gopalakrishnan et al. 2011; Zhang et al. 2020). Many studies have shown the different mechanisms used by actinobacterial strains to successfully control *Fusarium* related-plant diseases, including seedling blight of barley (Yekkour et al. 2012), *Fusarium* root rot disease of tomato (Zamoum et al. 2015; Goudjal et al. 2016b), *Fusarium* seedling blight of wheat (Toumatia et al. 2016) and *Fusarium* wilt disease on date palm (Alblooshi et al. 2022; Alwahshi et al. 2022). In fact, Yekkour et al. (2012, 2015c), Zamoum et al. (2015), Toumatia et al. (2016) and Goudjal et al. (2016b) showed that the *Streptomyces* strains, including *Streptomyces* sp. WAB9, *S. caeruleatus* strain ZL2, *S. mutabilis* strain IA1 and *S. asterosporus* SNL2 exhibited antifungal activities attributed to the bioactive molecules they produce. Furthermore, Yekkour et al. (2015c) found that *Streptomyces* sp. WAB9 produced a novel small hydroxamic acid-containing molecule that showed broad antimicrobial activity against various tested microorganisms, including *Fusarium* species. Qi et al. (2019) speculated that the chemical compounds isolated from *Streptomyces* sp. SCA3-4 may be involved in the antifungal activity and showed evidence of changes in the cell structure of *Fusarium* strains after treatment with the crude extracts of the studied strain. The study by Alblooshi et al. (2022) confirmed that the suppression of disease symptoms caused by *F. solani* resulted from inoculation with *Streptomyces coeruleoprunus*, suggesting that the diffusible antifungal metabolites were responsible for fungal retardation in date palm plants. Similarly, Zou et al. (2021) reported that extracts of the novel strain *Streptomyces* sp. H3-2 suppressed the growth and spore germination of *F. oxyspoum* f. sp. *cubense* (Foc TR4) *in vitro* by destructing cell membrane integrity and mycelial ultrastructure. Furthermore, the authors identified fourteen chemical constituents in strain H3-2 extracts, with most of them exhibiting antimicrobial activity (Zou et al. 2021). Cheng et al. (2010) isolated a *Streptomyces malaysiensis* MJM1968 strain that produced an azalomycin F complex compound with potent *in vitro* antifungal activity against different phytopathogenic fungi, including *F. oxysporum* and *F. chlamydosporum*. The study conducted by Merrouche et al. (2017) showed that the actinobacterial strain *Saccharothrix algeriensis* NRRL b-24137 has strong antifungal activity against many pathogens, including different *Fusarium* species through the synthesis of dithiolopyrrolone derivatives. In

suppressive soils, the abundance of antagonistic microorganisms, particularly actinobacteria may be increased in the presence of a particular pathogen like *Fusarium* (Ebrahimi-Zarandi et al. 2022). Thus, these environments are considered a rich reservoir of actinobacterial strains that can be used as biological control agents. Cha et al. (2016) study highlighted the key role of actinobacteria, including a *Streptomyces* S4-7 strain, in protecting strawberry roots from *F. oxysporum* attack by the production of a novel heat-stable antifungal thiopeptide antibiotic that inhibited *F. oxysporum* development. Cabrera et al. (2020) suggested that the observed protective effect of *Amycolatopsis* BX17 on the maize plants against infection by *F. graminearum* RH might be due to the action of antifungal compounds produced and secreted into the extracellular space by the studied actinobacterial strain. Klein et al. (2013) showed that the relative abundance of the root-associated actinobacteria, including *Streptomyces*, was significantly higher in suppressive soil compared to non-amended soil, with no significant effect of *F. oxysporum* f. sp. *radicis-cucumerinum* inoculation.

Actinobacteria have shown disease suppression properties by employing hyperparasitism, a phenomenon where they attack and parasitise disease-causing fungi and subsequently kill them (El-Tarabily and Sivasithamparam 2006). The early work of Sabaou et al. (1983) showed that *Nocardioopsis dassonvillei* displayed, in addition to antibacterial properties, mycolytic, and parasitic activities on *Fusarium oxysporum* f. sp. *albedinis*. Upadhyay and Rai (1987) state that hyperparasites penetrate fungal hyphae, forming branches and coagulating their cytoplasm before destroying the hyphae.

Actinobacteria have also been shown to produce a wide range of extracellular hydrolytic enzymes such as cellulases, chitinases, proteases, glucanases, lipases, xylanases, amylases, pectinases and keratinases which they are enable them to degrade various polymers. Many of these enzymes contribute to the biocontrol potential of actinobacterial strains against a wide range of plant pathogens, as the cell wall of most fungal pathogens is composed of polymers such as chitin, glucan, cellulose, proteins and lipids (Boukaya et al. 2018; Boubekri et al. 2021; Torres-Rodriguez et al. 2022). Interestingly, extracellular chitinases may inhibit phytopathogenic fungi by destroying the cell wall, which contains between 10 and 30% chitin (Cabrera et al. 2020). In the study by Gopalakrishnan et al. (2011), many *Streptomyces* strains that were able to produce the enzymes cellulases and proteases reduced *Fusarium* wilt in chickpea. In addition, the ability of actinobacteria to produce organic acids, fix atmospheric nitrogen and decompose organic matter is crucial. Actinobacterial strains can improve nutrient availability by influencing the mineralization and mobilization of essential nutrients for plant growth, such as phosphate and potassium. Thus, thanks to their multifunctional enzymatic machinery, actinobacteria are also involved in nutrient cycling and soil quality (Bhatti et al. 2017; Tian et al. 2021; Boubekri et al. 2021).

Iron in the soil is notoriously unavailable to both plants and microbes due to its presence in the form of insoluble hydroxides and oxyhydroxides. It is made available through the synthesis of siderophores, low molecular weight compounds with a high affinity for iron. Actinobacteria can produce siderophores that chelate Fe(III), thus improving iron bioavailability by influencing its mobility and solubility. Siderophores also provide plant protection by controlling phytopathogens as they acquire iron and consequently create a competitive environment for soil microorganisms, including pathogens, near plant roots (Boubekri et al. 2021; Torres-Rodriguez et al. 2022). The production of siderophores has been reported in several actinobacterial genera like *Streptomyces*, *Actinomadura*, *Microbispora* and *Nocardia* (Kawicha et al. 2020). The study by Passari et al. (2015) revealed that 72% of the tested isolates were siderophore producers. Furthermore, siderophore-producing actinobacteria have been reported to enhance plant growth in different crops and exhibit antagonistic activity against plant pathogens (Tamreihao et al. 2016).

Actinobacteria strains are known to produce volatile compounds, small and low molecular weight molecules with high pressure that disperse rapidly in any medium. Volatile compounds like HCN are involved in pathogen inhibition (Gopalakrishnan et al. 2011; Avalos et al. 2020). In the study by Passari et al. (2015), out of the 22 isolates that were tested, 15 were found to be positive for HCN production. The majority of these isolates belonged to *Streptomyces* and *Microbacterium* strains. HCN has also been reported to be produced by the strain *Streptomyces* sp. BTS40, a strain isolated from the rhizosphere soil of *Artemisia herba-alba* Asso (Djemouai et al. 2022a). Anusha et al. (2019) reported that a selection of *Streptomyces* and *Bacillus* isolates produced HCN, which may have played a role in the suppressive capacity of *Fusarium oxysporum* f. sp. *cicero*; while the study by Gopalakrishnan et al. (2011) noted that only five antagonistic isolates against the same disease from a collection of 137 isolates produced HCN.

Priming for the induction of defence in plants by actinobacteria is another mechanism involved in protecting against plant pathogens. Systemic resistance in plants can be divided into Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR), triggered by pathogenic and non-pathogenic microbes, respectively. ISR is dependent on jasmonic acid (JA) and ethylene (ET) pathways and is not involved with pathogenesis-related proteins (PR Protein). On the other hand, the establishment of SAR, requires a certain period of time, which varies depending on the plant and elicitors. During this period specific PR proteins and salicylic acid (SA) are accumulated in plant (Kamle et al. 2020). Some actinobacterial strains induce the expression of plant hormones, such as SA, ET, and JA. They are also known to synthesise and release phytohormones such as the auxin indole acetic acid (IAA), abscisic acid (ABA), gibberellic acid (gibberellin A3 or GA3) and cytokinins, which can

promote plant growth and are implicated in modulating defence responses to stresses (van Bergeijk et al. 2020; Tran et al. 2021). ABA accumulation is known to inhibit the overproduction of ethylene in plants during exposure to stress (Yao et al. 2010). The microbial production of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, which cleaves the ET precursor, ACC, is another interesting mechanism for mitigating plant-induced stress (Mulani et al. 2021).

Indeed, inoculated plants with actinobacteria can quickly and strongly respond to a possible pathogen infection. Depending on the pathogen, priming by actinobacteria is generally associated with the upregulation of genes in the SAR and/or JA and ET pathways (Ebrahimi-Zarandi et al. 2022). ISR was identified by Conn et al. (2008) as a result of inoculations of *Arabidopsis thaliana* with *Micromonospora* or *Streptomyces* strain. Priming with the culture filtrate of *Streptomyces bikiniensis* HD-087 elicited systemic resistance in cucumber against Fusarium wilt caused by *F. oxysporum* f. sp. *cucumerinum* (Zhao et al. 2012). The strains IC10 and Y28, which were closely related to *S. enissocaesilis* and *S. rochei*, demonstrated a significant ability to induce antioxidant enzyme activity and ISR in tomatoes inoculated with *F. oxysporum* f. sp. *lycopersici* (Abbasi et al. 2019). The mechanisms of priming by actinobacteria suggest an important capacity to activate plant defence responses in the absence of a pathogen, while the common determinants of priming seem to be eliciting both JA/ET and SA-related signals (Ebrahimi-Zarandi et al. 2022). In addition, Baz et al. (2012) showed that priming with *Streptomyces* sp. OE7 strain caused defence responses in BY2 tobacco cell suspensions by increasing cytosolic Ca^{2+} and inducing a biphasic oxidative burst in the upstream signalling processes.

During the *Fusarium* infection process, the fungus is known to induce a hypersensitive reaction (HR) in connection with the production of trichothecene toxins, particularly DON (Walter et al. 2010). In fact, the modulation of DON in the host cell during the infection process seems to depend on the trophic stage of pathogen and participates in a sophisticated strategy to circumvent the plant's defence system (Audenaert et al. 2013). At the cellular level, the induction of HR is traduced by a programmed cell death (PCD), which itself depends on the production of reactive oxygen species (ROS) and mitochondrial dysfunction (Yekkour et al. 2015b). Interestingly, actinobacterial strains like *Streptomyces* species have been reported to increase the accumulation of total phenols, flavonoids and defence-related enzymes, such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POD) and ascorbate peroxidase (APX) in host plants (Ebrahimi-Zarandi et al. 2022; Kaur et al. 2019). These enzymes can eliminate free radicals, thereby reducing the production of ROS. For example, *Streptomyces* S-9 was able to activated defence responses, including antioxidant defence enzymes such as CAT and SOD, after infection with *Fusarium udum* (Dave and Ingle 2021). On the other hand, actinobacterial

strains can reduce mycotoxin production through various mechanisms, including detoxification or inhibition of mycotoxin biosynthesis or a combination of several mechanisms (Ji et al. 2016; Danial et al. 2020; Habschied et al. 2021). This was observed by Strub et al. (2021), where the fumonisin-related pathway appears to be underexpressed in the presence of *Streptomyces*, explaining the observed reduction in fumonisin accumulation in the fumonisin-producing strain *F. verticillioides* BRFM2251. Whereas Nguyen et al. (2018) found that the strain *Streptomyces* sp. AV05, which significantly inhibited *Fusarium verticillioides* growth, was able to reduce fumonisin production.

Many of the mechanisms mentioned above have been found in strains *Streptomyces enissocaesilis* (BYC), *S. bellus* (AYD) and *S. saprophyticus* (DE2), which were isolated from sugar beet rhizospheres by Aallam et al. (2021). Therefore, these authors suggested using the selected strains as efficient biofertilizers and microbial biocontrol agents. Similarly, in the study by Djuidje et al. (2022), all the selected *Streptomyces* species were able to produce siderophores, produce IAA, solubilize tricalcium phosphate and have ACC deaminase activity. These results suggest the use of *Streptomyces* strains to protect cocoyam against root rot disease and to promote root growth (Djuidje et al. 2022).

The modes of action of actinobacterial strains outlined in this section are generally related to plant colonization, plant growth promotion, and ISR. Actinobacteria genome-based studies are considered a key technological advance that is expected to rapidly decipher genomic determinants associated with the mechanisms of efficacy of actinobacteria in microbial biocontrol (Malit et al. 2022). Research using integrated omics methods is also needed to confirm how actinobacterial strains inhibit the growth of *Fusarium* pathogens and their mycotoxins.

Overview of Biocontrol Experiments Using Actinobacteria

The scientific literature analysis conducted in this study shows a high number of indexed research articles related to *in vitro* and *in vivo* microbial biocontrol studies using actinobacteria. Therefore, 92 papers dealing with *in vitro* antagonistic tests are presented in Table 3. From this bibliography, 56 investigations show the use of more than one actinobacterial strain for the antagonism tests against a selection of *Fusarium* species, while 34 papers evaluated only one actinobacterial strain. In addition, only two papers tested actinobacteria strains in combination with other biological control agents (bacteria and fungi).

The *in vivo* microbial biocontrol tests using actinobacterial strains against *Fusarium* pathogens have been carried out in various countries around the world (USA, China, Algeria, Australia, Egypt, Italy, India, ... etc.)

(Winter et al. 2019; Zhang et al. 2019; Tlemsani et al. 2020; O’Sullivan et al. 2021; El-Sharkawy et al. 2022; Mattei et al. 2022; Sharma et al. 2023). The bibliographic survey resulted in 69 published works, which are summarized in Table 4. The highest number of papers were published on the microbial biocontrol of tomato and wheat crops (18 and 15 papers, respectively), followed by chickpea and cucumber (9 and 8 papers, respectively). In addition, the actinobacterial strains used in these microbial biocontrol experiments were mostly limited to the genus *Streptomyces* (Cao et al. 2020; Ankati et al. 2021; Mattei et al. 2022; Kawicha et al. 2023; Sharma et al. 2023). For the 69 articles retrieved from the literature, the authors executed *in vivo* biocontrol assays against eight *Fusarium* species, with *F. oxysporum* being the most studied (41 strains), using different actinobacterial strains. Many published works have reported satisfactory results in the microbial biocontrol of *Fusarium* (Yekkour et al. 2012; Zamoum et al. 2015; Toumatia et al. 2016; Merrouche et al. 2017; Palazzini et al. 2017; Winter et al. 2019; Zhang et al. 2019; Cao et al. 2020; Ankati et al. 2021; Tran et al. 2021; El-Sharkawy et al. 2022; Babu et al. 2022; Kawicha et al. 2023).

By far, the most studied genus is *Streptomyces* which has been widely used to manage infections caused by different *Fusarium* species over the past twenty years. In fact, 63 published papers used different *Streptomyces* strains as microbial biocontrol agents. In contrast, only 11 publications included non-*Streptomyces* strains that were used in pot (eight papers) and field (two papers) experiments or in both conditions (one paper) (Merrouche et al. 2017; Boukaya et al. 2018; Cabrera et al. 2020; Upadhyay and Rai 1987; Djebaili et al. 2021; Singh et al. 2022; Zhang et al. 2019; Babu et al. 2022). Strains belonging to the genera *Saccharothrix*, *Streptosporangium*, *Amycolatopsis*, *Micromonospora*, *Nocardiopsis*, *Actinomycete* and *Kitasato* were used in these assays. Some experiments included more than one strain, such as the use of *Streptomyces albidoflavus* H12 and *Nocardiopsis aegyptica* H14 (Djebaili et al. 2021), and *Streptomyces griseus* and *Micromonospora globose* (Upadhyay and Rai 1987). In addition, other authors used not only actinobacterial strains alone but also a combination of actinobacterial strains with other microorganisms such as bacteria (*Paenibacillus*, *Brevibacillus* and *Bacillus*) (Singh et al. 1999; Palazzini et al. 2007, 2018), fungi (*F. oxysporum* and *Rhizophagus irregularis*) (Zhang et al. 2019; El-Sharkawy et al. 2022) as well as synthetic fungicides (Singh and Chhatpar 2011).

Anti-Proliferative and Anti-Mycotoxigenic Activity of Actinobacteria Towards *Fusarium*

The ability of actinobacterial strains to face both phytopathogenic fungi and their toxins in crops could be a promising approach for developing novel eco-friendly methods in agriculture and the food industry. Microbial biocontrol of *Fusarium* diseases in field crop using actinobacteria has attracted substantial interest. However,

few research efforts have focused on the associated mycotoxins. The available literature on mycotoxin reduction by actinobacteria is presented in Table 5.

In fact, eight studies have been published on the topic and all of the strains evaluated were affiliated within the genus *Streptomyces*. These strains were isolated from different sources, including soil, rhizosphere, plant materials and organic amendments. The *in vitro* tests against fungal growth and/or reduction rate of the mycotoxins tested showed promising results for zearalenone, deoxynivalenol, fumonisin and T-2 toxin. For instance, the study by Colombo et al. (2020) revealed that *Streptomyces* strain DEF09 inhibited the growth of *F. graminearum* up to 60%, while the study by Palazzini et al. (2018) showed only 30% growth inhibition against the same phytopathogenic species. The effect of microbial biocontrol agents on zearalenone toxin was studied in three publications by El-Naggar et al. (2012), Harkai et al. (2016) and Qin et al. (2021). The authors highlighted the possible role of degradative enzymes produced by the antagonistic *Streptomyces* strains in the detoxification mechanisms of zearalenone. For the fumonisin mycotoxin produced by *F. verticillioides*, a reduction rate of 50% was obtained by *Streptomyces* ST03 (Tran et al. 2021), while different reduction rates were obtained by Nguyen et al. (2020) depending on the age of the fungal culture (from 3 to 7 days old).

Mycotoxins can be partially degraded through microbial biotransformation; however, microorganisms can also produce more toxic by-products (Ji et al. 2016). Many actinobacterial strains exhibited degradation abilities towards different *Fusarium* mycotoxins, including zearalenone, fumonisin and deoxynivalenol (Harkai et al. 2016; Samsudin and Magan 2016; Colombo et al. 2020).

For example, *Streptomyces rimosus* (NRRL 2234) transformed zearalenone into 8'-hydroxy-zearalenone, while *Streptomyces griseus* (ATTC 13273) and *Streptomyces rutgersensis* (NRRL-B 1256) were capable of degrading zearalenone to form α -zearalenone (El-Sharkawy and Abul-Hajj 1987). The study by Harkai et al. (2016) revealed that two strains of *Streptomyces rimosus* (K145 and K189) were able to degrade almost the entire amount of zearalenone. Krifaton et al. (2013) also stated that the most promising strains for the bio-detoxification of zearalenone are *Streptomyces cavourensis* K14 and *Rhodococcus pyridinivorans* K402. These strains could metabolise zearalenone without producing cytotoxic end-products and with the lowest residual estrogenic effect. On the other hand, Qin et al. (2021) revealed that the novel dye-decolorizing peroxidase (StDyP) from *Streptomyces thermocarboxydus* 41291 could degrade zearalenone using the catalytic properties of manganese peroxidase and laccase.

The study by Colombo et al. (2020) suggested that the tested *Streptomyces* strains produced different secondary metabolites that could potentially regulate deoxynivalenol production by specific mechanisms that are not linked to antibiosis alone. Nguyen et al. (2020) suggested that when *Streptomyces* sp. interacts with *F. verticillioides*, nucleosides and proteinogenic amino acids increase. This implies a slowing in protein synthesis, which might have an impact on the growth and production of mycotoxins via NRPS and PKS (Nguyen et al. 2020).

Challenges, Commercial Products and Patents Related to *Fusarium* Disease Control Using Actinobacteria

As the global demand for microbial biocontrol products continues to grow, in light of the worldwide consensus among public authorities to drastically reduce the use of synthetic chemicals in agriculture, there is a need to carefully select effective microbial inoculants for both crop protection and growth enhancement.

The main issue with using microorganisms, including actinobacteria, to produce commercial products for the control of plant diseases is that experiments, conducted in laboratory, greenhouse and field, show different biocontrol capacities and contrasting results (Clough et al. 2022). Despite the fact that several actinobacterial agents have shown interesting activities against *Fusarium*-related diseases in laboratory or greenhouse experiments (Tables 3 and 4), examples of successful actinobacteria application in field-based crop protection studies are limited (Rashad et al. 2017; Palazzini et al. 2017, 2018; Babu et al. 2022; Singh et al. 2022). Thus, the biocontrol ability of candidate microbial biocontrol agents should be tested, ideally via phenotype-based screening under field conditions for the desired agricultural application, bearing in mind that variable abiotic and biotic parameters may influence the results (Raymaekers et al. 2020). The barriers to the use of microbial biocontrol agents in the field are the inconsistent efficacy of plant protection under field conditions and the fact that the availability of such products is not yet well established on the market. Another issue is related to the limited acceptance of biological control agents by farmers, the difficulties in the implementation of integrated pest management programs focusing on microbial biocontrol agents and their strong confidence in the potential of synthetic-based products (Abdollahzadeh et al. 2015).

Since microbial biocontrol involves the introduction of non-native living microorganisms, it may have adverse ecological effects (Lahlali et al. 2022). Therefore, it would be useful to conduct field studies on the effects and the interactions of the microbial biocontrol agents with the surrounding environment. Also, studies on the colonization of the host rhizosphere and the inhibitory effects on pathogen growth must be conducted in order to ensure their efficacy in these settings (Sharma et al. 2022).

Another concern is that developing a commercial product based on microorganisms is challenging, time-consuming, costly and complex because it involves living propagules (Niu et al. 2020). Formulation of the microbial biocontrol agent is a necessary step in the sustainable management of diseases in agricultural systems. Furthermore, a certain concentration of the bioactive ingredient(s) and the other inert ingredient(s) must be optimized to create a commercial product for use in the field. This product should be able to undergo massive multiplication, be safe to use, and exhibit positive results in different agroecological conditions (Bonaterra et al. 2022). Furthermore, the formulated product should be optimized to ensure persistence and effectiveness over a determined period (Lahlali et al. 2022).

In agricultural applications, the use of fresh microbial cultures is not suitable. This is why various spore formulations based on solid, liquid, and powder states have been developed (conventional formulation) (Tamreihao et al. 2016). In the field, the main obstacles to the efficacy of any formulated product based on an actinobacterial strain are the development of stable formulations and the different modes of their application (Silva et al. 2022). Thus, optimizing the production of spores and cells of actinobacterial strains is an important step in the formulation process. For liquid formulations, whole cultures or microbial suspensions are combined with other ingredients (e.g. water, oil, or polymers). These ingredients, designed as adjuvants, can enhance the adhesion, stability, surfactancy and dispersion of formulated products (Lobo et al. 2019). Furthermore, liquid inoculants are easier to process and have lower costs when compared to solid inoculants (Silva et al. 2022). However, dry formulations are favored due to their many advantages, including ease of use, storage and transport. A suitable formulation in the context of soilborne diseases control is coated seeds as a preventative approach. Indeed, seed coating has been used extensively worldwide for numerous annual crops, such as cereals and pulses (Ren et al. 2019; Rocha et al. 2019). It has been shown that coating seeds with actinobacteria encourages plant growth, increases yield and productivity, and prevents disease infestation (Ebrahimi-Zarandi et al. 2022). Recently, encapsulated formulations and actinobacteria-based synthesis of nanoparticles have received a lot attention because they have a number of advantages over conventional bioformulations. These advantages are related to better shelf life, survival and viability in diverse environments, and rhizospheric colonization abilities (Lobo et al. 2019; Rani et al. 2021; Balla et al. 2022).

When commercializing a microbial biocontrol agent, attention should be paid not only to the disease inhibition aspects but also to the regulatory aspects. For example, the European commission has established necessary rules to homogenize the authorisation of microorganisms for use as active ingredients in crop protection products, which are given in commission implementing regulation (EU) No 1107/2009 (consolidated

version 2022) (Commission Regulation, 2009). The assessment of active substances requires their identification, mode of action and toxicity evaluation. Thus, the microbial biocontrol agents undergo a risk assessment before commercialization approval (Sabbahi et al. 2022). Information about the formulation of the biological control agent and the validation of the efficacy of the formulation are also required (Velivelli et al. 2014). Thus, the commercialization process includes toxicological and environmental testing as well as a validation of the efficacy of the biological control product (Sabbahi et al. 2022).

To date, very few actinobacteria-based products have reached the market as microbial biocontrol agents for *Fusarium*-related diseases. In fact, only two products have been approved for use in field. These products are Mycostop®, based on *Streptomyces griseoviridis* strain K61, (Lahdenperä et al. 1991) and Actinovate®, based on *Streptomyces lydicus* strain WYEC108, (Tian and Zheng 2013), which are marketed by Verdera Oy (Helsinki, Finland) and Natural Industries Inc. (Houston, USA), respectively. These two products are registered in Canada, the European Union, and the USA particularly for the control of damping-off and wilting caused by soilborne *Fusarium*. Different modes of delivery can be used in order to achieve the biocontrol effect, including foliar spray and soil drench for Actinovate® and seed treatment, soil spray or drench applications for Mycostop® (Lahdenperä et al. 1991; Tian and Zheng 2013).

To have a global view of the patents that deal with actinobacterial strains against *Fusarium* diseases, the search included Espacenet and PatentscopWipo sites. The search showed that 75 patents on actinobacteria as microbial biocontrol agents had been published and retained in this study (Supplementary Table).

From 2000 to 2023, microbial biocontrol tests with successful actinobacterial strains against different *Fusarium* species, which were consecutively patented, have been conducted in various countries around the world, including China, Korea, Australia, Morocco, France, Spain and Switzerland and were limited to the use of *Streptomyces* strains. Most of the documented patents highlighted the general role of the actinobacterial strain against several plant pathogens, including members of the *Fusarium* genus. Furthermore, the ability of actinobacterial strains to increase the growth and yield of crops such as wheat, maize, tomato, rice, and chickpea has been highlighted in these patents. Some of the patents addressed and gave details of methods of formulating the microbial biocontrol agent. Of all the patents listed, only one addressed the degradation of *Fusarium* mycotoxins. The patent number CN107058131A showed that the strain *Streptomyces netropsis* controlled *F. graminearum* and reduced deoxynivalenol and zearalenone toxins in wheat.

Conclusions and Future Prospects

Fusarium is one of the most important pathogenic fungal genera, causing a wide range of plant diseases and having a global distribution. As climate is the key factor in shaping fungal community structure and mycotoxin contamination levels, it is important to strengthen the study of the impact of climate change on *Fusarium* species distribution, pathogenesis and mycotoxin production. Current findings imply that future climate change scenarios may result in an even higher incidence of *Fusarium* on different crops, resulting in economic losses as well as potential food security challenges. Throughout the research into the ecology of *Fusarium* species and their interactions with crops, understanding the effects of climate change on *Fusarium* spp. is critical to developing effective management techniques to reduce their effects.

Due to their multifunctional potential, many studies have focused on the selection of actinobacterial strains that can act as microbial biocontrol agents against *Fusarium*-related diseases. Efforts should be directed to further validating the results currently available and increasing knowledge of the most valuable actinobacterial strains that are efficient in combating *Fusarium* pathogens. Modern omics-based approaches, including the screening of biosynthetic gene clusters (BGCs) potentially expressed under different conditions of use, will facilitate the selection of the most appropriate actinobacterial candidate for biocontrol evaluation.

Despite the large number of published papers and available patents on actinobacteria for the control of *Fusarium*-related diseases, only two products have successfully reached the market. Studies should not only focus on *in vitro* and/or *in vivo* experiments in pots, but also in the field, as the information gained can be used to manage disease control efficiently on a large scale. This suggests massive investments in future research programs to extend the agronomic evaluation of formulated products. Moreover, a simplified and harmonized system of regulation in the approval of microbial agents used for biocontrol will encourage all stakeholders (academia, industry and farmers) to increase investments in biocontrol solutions.

Interdisciplinary collaboration is required for the successful development of actinobacteria as microbial biocontrol agents for commercial use. In this context, with next-generation sequencing (NGS) technologies, cost reduction and advances in nano-biotechnology, significant progress is expected in the industrial development of actinobacterial bioinoculants, especially with the actual improvement of accurate microbial genome mining, which should allow for deciphering the target mechanisms of priming putatively involved in beneficial plant-microbe interactions.

Compliance with ethical standards

Conflict of interest: No conflict of interest is to be declared

Ethical Approval: The authors declare that ethical standards have been followed and that no human participants or animals were involved in this research.

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1719 **Figure legend**

1720 **Figure 1.** Main mechanisms putatively involved in control of *Fusarium* disease by actinobacteria and favouring
1721 plant resilience.

1722 Abbreviations: ABA, abscisic acid; ACC, 1-aminocyclopropane-1-carboxylic acid; CAT, catalase; ET, ethylene;
1723 GA3, gibberellin; HR, hypersensitive reaction; IAA, auxin indole acetic acid; ISR, Induced Systemic Resistance;
1724 JA, jasmonic acid; PCD, programmed cell death; POD, peroxidase; PR, pathogenesis-related proteins; ROS,
1725 reactive oxygen species; SA, salicylic acid; SAR, Systemic Acquired Resistance; SOD, superoxide dismutase.

Cultivated plant

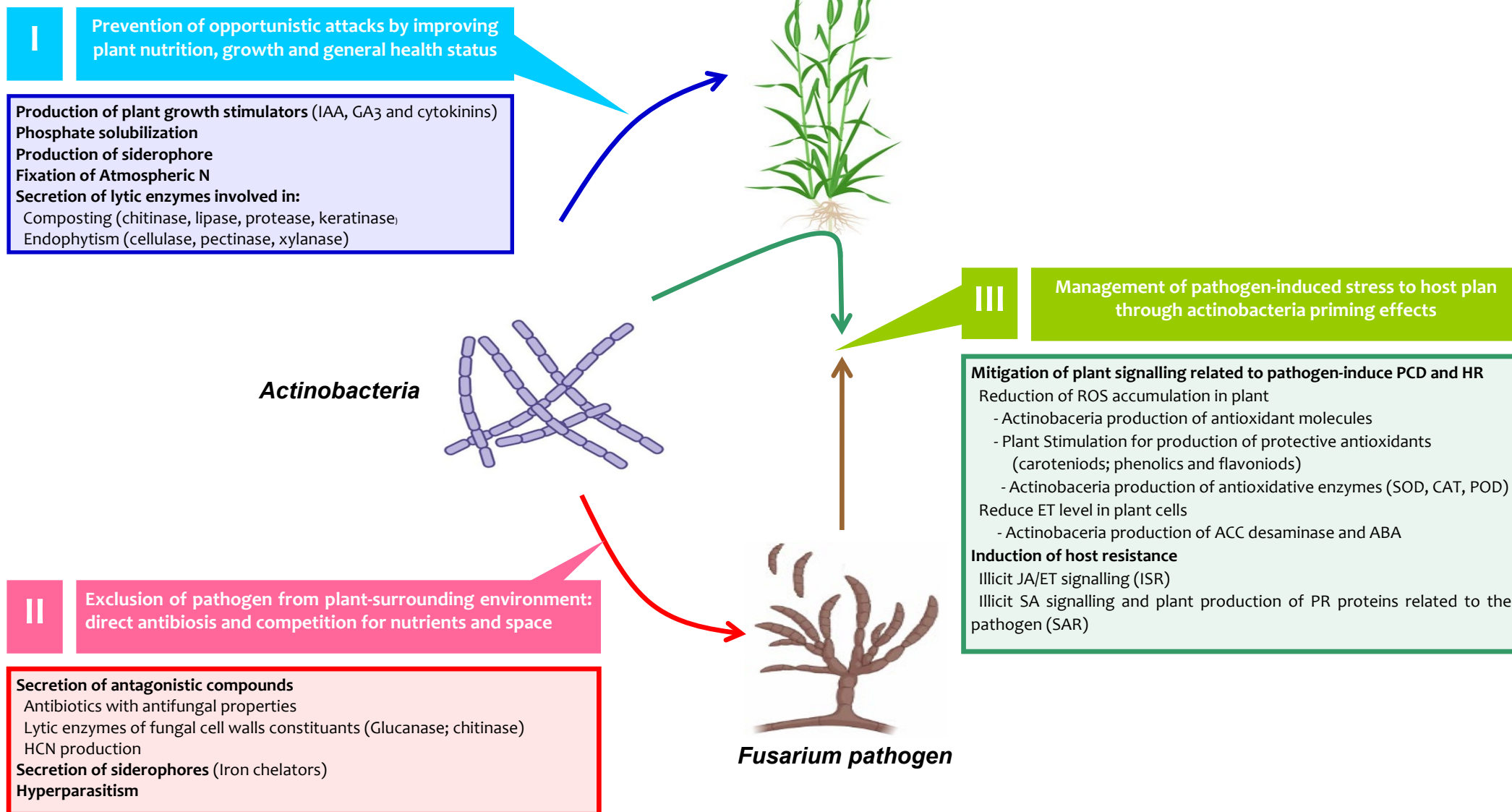


Figure 1

1728 **Table 1** Most common *Fusarium* species known to infect crops and their produced mycotoxins

<i>Fusarium</i> species	Involved crop	Common disease	Produced mycotoxin	Reference
<i>Fusarium fujikuroi</i>	Rice (<i>Oryza sativa</i> L.)	Bakanae disease	Fumonisin	Suga et al. (2018)
<i>Fusarium oxysporum</i> , <i>F. equiseti</i> and <i>F. graminearum</i>	Soybean (<i>Glycine max</i> (L.) and cucumber (<i>Cucumis sativus</i> L.)	Fusarium root rot	Fumonisin, zearalenones and trichothecenes	Żelechowski et al. (2021)
<i>Fusarium graminearum</i>	Bread wheat (<i>Triticum aestivum</i> L.) and durum wheat (<i>Triticum durum</i> L.)	Fusarium head blight/scab disease	Zearalenones and trichothecenes, including type B trichothecenes deoxynivalenol, its 3-acetylated or 15-acetylated derivatives and nivalenol	Chen et al. (2019) Khan et al. (2020)
<i>Fusarium solani</i>	Sugar beat (<i>Beta vulgaris</i>), chickpea (<i>Cicer arietinum</i>) and tomato (<i>Solanum lycopersicum</i> L.)	Fusarium wilt, stem and dry rot	Deoxynivalenol, zearalenones, nivalenol and 15-acetylated derivatives	Moussa and Rizk (2002) Soltanzadeh et al. (2016) Torres-Rodriguez et al. (2022)
<i>Fusarium verticillioides</i>	Maize (<i>Zea mays</i>)	Fusarium ear rot	Fumonisin FB1, FB2 and FB3	Tran et al. (2021)
<i>Fusarium culmorum</i>	Barley (<i>Hordeum vulgare</i>) and wheat (<i>Triticum</i> sp.)	Fusarium head blight and foot and root rot diseases	Type B trichothecenes (nivalenol and deoxynivalenol, as well as zearalenones and fusarenon-X)	Yekkour et al. (2012) Scherer et al. (2013) Ferrigo et al. (2016)
<i>Fusarium equiseti</i>	Potato (<i>Solanum tuberosum</i>)	Fusarium wilt	Zearalenones	Ferrigo et al. (2016)
<i>Fusarium proliferatum</i>	Maize (<i>Zea mays</i>)	Fusarium ear rot	Fumonisin	Ferrigo et al. (2016)

1729

1730 **Table 2** *Fusarium* mycotoxins regulated in the European Union as of December 2022 (European Commission
1731 1881/2006) (Commission Regulation, 2006).

Regulated mycotoxin	Involved foodstuff	Maximum accepted levels ($\mu\text{g.kg}^{-1}$)
Deoxynivalenol	Processed cereal-based foods and baby foods for infants and young children	200
	Bread (including small bakery wares), pastries, biscuits, cereal snacks, and breakfast cereals	500
	Pasta (dry); cereals intended for direct human consumption; cereal flour, bran and germ as end products marketed for direct human consumption, with the exception of processed cereal-based foods and baby foods for infants and young children, milling fractions of maize when not listed elsewhere in the table	750
	Unprocessed cereals other than durum wheat, oat and maize; milling fractions of maize with particle size ≤ 500 micron (with exceptions)	1.250
	Unprocessed durum wheat and oats; unprocessed maize with the exception of unprocessed maize intended to be processed by wet milling	1.750
Zearalenone	Processed cereal-based foods and baby foods for infants and young children	20
	Bread (including small bakery wares), pastries, biscuits, cereal snacks, and breakfast cereals, excluding maize-snacks and maize-based breakfast cereals	50
	Cereals intended for direct human consumption cereal flour, bran and germ as end products marketed for direct human consumption, with the exception listed in this table	75
	Unprocessed cereals other than maize, maize intended for direct human consumption, maize-based snacks and maize-based breakfast cereals	100
	Milling fractions of maize >500 micron/ ≤ 500 micron (with exceptions)	200/300
	Unprocessed maize with the exception of unprocessed maize intended to be processed by wet milling	350
	Refined maize oil	400
Fumonisin (B1 + B2)	Processed maize-based foods and baby foods for infants and young children	200
	Maize-based breakfast cereals and maize-based snacks	800
	Maize-based foods for direct human consumption, with exceptions listed in the table	1000
	Milling fractions of maize >500 micron/ ≤ 500 micron (with exceptions)	1.400/2.000
	Unprocessed maize, with the exception of unprocessed maize intended to be processed by wet milling	4.000
T-2 and HT-2	Unprocessed cereals and cereal products	Excepted in July 2024

1732 **Table 3** *In vitro* antagonistic activity of actinobacteria against different *Fusarium* phytopathogens, referenced in the literature

Evaluated actinobacteria strain	Actinobacteria isolation source	Targeted <i>Fusarium</i> species	Method used for anti- <i>Fusarium</i> activity assessment	Reference
<i>Streptomyces</i> isolates	Rhizosphere soil of white lupine seedlings	<i>Fusarium tabacinum</i> (<i>Cephalosporium tabacinum</i>)	Streak method	Youssef et al. (2001)
<i>Streptomyces aureofaciens</i>	Culture collection	<i>Fusarium solani</i>	Agar well diffusion method	Moussa and Rizk (2002)
Actinomycete isolate	Rhizosphere of healthy sugar beet	<i>Fusarium oxysporum</i>	Dual culture	El-Kazzaz et al. (2002)
21 <i>Streptomyces</i> and 15 non- <i>Streptomyces</i> actinomycetes	Surface-disinfested lupin roots	<i>Fusarium tabacinum</i> (<i>Cephalosporium tabacinum</i>)	Streak method	El-Tarabily (2003)
33 actinobacterial isolates	Agricultural soils, forest soils, caves, salt springs, limestone quarries, lake and river sediments and plants	<i>Fusarium oxysporum</i> MTCC 287	Dual culture	Ningthoujam et al. (2009)
36 strains of actinomycetes	The sea mud of Yellow Sea	<i>Fusarium graminearum</i>	Co-culture plate assay and agar diffusion method	Pei-Sheng et al. (2011)
<i>Streptomyces aureoverticillatus</i> SA74	Tobacco rhizosphere soil sample	<i>Fusarium oxysporum</i>	Plate confrontation	Zhou et al. (2012)
<i>Streptomyces microflavus</i> MSS275	Rhizosphere in fallow lands	<i>Fusarium oxysporum</i>	Plate confrontation	Han et al. (2012)
102 actinobacterial isolates	Rice rhizosphere soil samples	<i>Fusarium oxysporum</i> and <i>F. udum</i>	Dual culture	Harikrishnan and Shanmugaiah (2012)
72 strains of actinobacteria	Rhizospheric semi-arid soil samples	<i>Fusarium culmorum</i> and <i>F. oxysporum</i>	Streak method	Aouar et al. (2012)
33 actinobacterial strains	13 non rhizospheric soil samples	<i>Fusarium culmorum</i> , <i>F. moniliforme</i> , <i>F. sporotrichoides</i> , <i>F. graminearum</i> , <i>F. oxysporum</i> f. sp. lini, <i>F. oxysporum</i> f. sp. albedinis, <i>F. proliferatum</i> and <i>F. equiseti</i>	Streak method	Yekkour et al. (2012)
<i>Streptomyces alboflavus</i> TD-1	Soil sample	<i>Fusarium moniliforme</i>	Volatiles contact	Wang et al. (2013)

<i>Streptomyces aurantiogriseus</i> VSMGT1014	Rice rhizosphere soil samples	<i>Fusarium oxysporum</i> and <i>F. udum</i>	Dual culture	Harikrishnan et al. (2014)
<i>Streptomyces philanthi</i> RM-1-138	Rhizosphere soil of chili pepper	<i>Fusarium fujikuroi</i> PTRRC-36	Dual culture	Boukaew and Prasertsan (2014)
<i>Streptomyces</i> sp. IA1	Soil sample	<i>Fusarium oxysporum</i> f. sp. <i>albedinis</i> , <i>F. oxysporum</i> f. sp. <i>lini</i> , <i>F. oxysporum</i> f. sp. <i>radicis-lycopersici</i> , <i>F. culmorum</i> , <i>F. graminearum</i> , <i>F. sporotrichoides</i> , <i>F. equiseti</i> , <i>F. moniliforme</i> and <i>F. proliferatum</i>	Streak method	Toumatia et al. (2014)
180 actinobacterial isolates	Chinese medicinal plants and rhizosphere soils	<i>Fusarium oxysporum</i> f.sp. <i>cucumerinum</i>	Agar plugs method	Li et al. (2014)
<i>Streptomyces</i> spp. PAL114	Saharan soil	<i>Fusarium culmorum</i> FC200	Disk diffusion method	Aouiche et al. (2014)
<i>Streptomyces hygroscopicus</i> , <i>S. fasciculatus</i> , <i>Pseudomonas aeruginosa</i> , <i>P. putida</i> , <i>P. fluorescens</i> and <i>Azospirillum lipoferum</i>	Maize rhizosphere samples	<i>Fusarium verticillioides</i>	Dual culture	Noumavo et al. (2015)
21 endophytic actinobacteria	Root samples of <i>Aristida pungens</i> , <i>Cleome africana</i> , <i>Astragalus armatus</i> , <i>Peganum harmala</i> , <i>Hammada scoparia</i> and <i>Zizyphus lotus</i>	<i>F. oxysporum</i> f. sp. <i>radicis lycopersici</i> , <i>F. oxysporum</i> f. sp. <i>lycopersici</i> and <i>F. solani</i>	Streak method	Zamoum et al. (2015)
<i>Streptomyces</i> sp. strain WAB9	Soil sample	<i>Fusarium proliferatum</i> , <i>F. oxysporum</i> f. sp. <i>lini</i> , <i>F. culmorum</i> , <i>F. graminearum</i> , <i>F. equiseti</i>	Streak method	Yekkour et al. (2015c)
12 <i>Streptomyces</i> strains	Rhizospheric soil samples of <i>Ononis angustissima</i> and <i>Astragalus gombo</i>	<i>Fusarium oxysporum</i> f. sp. <i>albedinis</i> and <i>F. culmorum</i>	Streak method	Ghadbane et al. (2015a)
42 endophytic actinomycetes	Plant tissues of <i>Eupatorium odoratum</i> , <i>Musa superba</i> , <i>Mirabilis jalapa</i> , <i>Curcuma longa</i> , <i>Clerodendrum colebrookianum</i> , <i>Alstonias cholaris</i> and <i>Centella asiatica</i>	<i>Fusarium oxysporum</i> f. sp. <i>ciceri</i> MTCC-2791, <i>F. proliferatum</i> MTCC-286, <i>F. oxysporum</i> MTCC-284 and <i>F. graminearum</i> MTCC-1893	Dual culture	Passari et al. (2015)
20 presumptive <i>Streptomyces</i>	Arable soil, compost and soil amended with	<i>Fusarium poae</i>	Agar plugs method	Kovácssová et al.

strains	compost			(2015)
16 endophytic actinobacteria	Root samples of <i>Peganum harmala</i> , <i>Stipa tenacissima</i> , <i>Hammada scoparia</i> , <i>Solanum nigrum</i> and <i>Astragalus armatus</i>	<i>Fusarium solani</i> F22 and <i>F. oxysporum</i> f. sp. <i>albedinis</i> F39	Streak method	Goudjal et al. (2016b)
Seven endosymbiotic actinobacteria	Sand truffles (<i>Terfezia leonis</i> Tul.)	<i>Fusarium oxysporum</i> f. sp. <i>radicis lycopersici</i> and <i>F. solani</i>	Streak method	Goudjal et al. (2016a)
122 actinobacterial isolates	Rhizospheric soil samples	<i>Fusarium oxysporum</i> MTCC 287	Dual culture	Ningthoujam et al. (2016)
<i>Streptomyces</i> sp. AS1	Malaysian maize sample	<i>Fusarium verticillioides</i>	Dual culture	Samsudin and Magan (2016)
<i>Streptomyces corchorusii</i> UCR3-16	Rice rhizospheric soil sample	<i>Fusarium oxysporum</i>	Dual culture	Tamreihao et al. (2016)
15 actinobacterial isolates	Endophytes from leaves, stems and roots of <i>Solanum lycopersicum</i>	<i>Fusarium proliferatum</i> MTCC-286, <i>F. graminearum</i> MTCC1893 and <i>F. oxysporum</i> MTCC-284	Dual culture	Passari et al. (2016)
68 chitinolytic endophytic actinomycetes	Plant tissues of <i>Rauvolfia serpentine</i> , <i>Gymnema sylvestre</i> , <i>Stevia crenata</i> , <i>Bacopa monnieri</i> , <i>Andrographis paniculata</i> and <i>Withania somnifera</i>	<i>Fusarium oxysporum</i>	Dual culture	Singh and Gaur (2016)
<i>Streptomyces pluricologrescens</i>	Wheat rhizosphere sample	<i>Fusarium graminearum</i> and <i>F. culmorum</i>	Dual culture	Comby et al. (2017)
<i>Streptomyces</i> spp. isolates bi02, bi21, bi24, bi26 and bi28	Rhizospheric soil samples of <i>Astragalus gombo</i>	<i>Fusarium oxysporum</i> f. sp. <i>albedinis</i>	Cross streak modified method	Ghadbane et al. (2017)
<i>Saccharothrix algeriensis</i> NRRL B-24137	Culture collection	<i>Fusarium oxysporum</i> f. sp. <i>lini</i> , <i>F. oxysporum</i> f. sp. <i>lentis</i> , <i>F. oxysporum</i> f. sp. <i>ciceris</i> and <i>F. oxysporum</i> f. sp. <i>lycopersici</i>	Streak method	Merrouche et al. (2017)
16 actinobacterial strains	Culture collection	<i>Fusarium culmorum</i> , <i>F. graminearum</i> and <i>F. oxysporum</i> f. sp. <i>radicis-lycopersici</i>	Streak method	Boukaya et al. (2018)
13 genera of actinobacteria	19 tea plants	<i>Fusarium graminearum</i> PH-1, <i>F. oxysporum</i> f. sp. <i>lycopersici</i> , <i>F. oxysporum</i> f. sp. <i>cubense</i> and <i>F.</i>	Paper disc diffusion assay	Shan et al. (2018)

		<i>verticillioides</i> 7600		
12 actinobacterial strains	Tomato rhizospheric soil samples	<i>Fusarium oxysporum</i>	Dual culture	Kshetri et al. (2018)
<i>Streptomyces</i> sp. MBRL 10	Soil sample	<i>Fusarium oxysporum</i> MTCC 287	Dual culture	Tamreihao et al. (2018)
191 endophytic actinobacteria	Roots and stems of rice plants	<i>Fusarium moniliforme</i>	Dual culture	Mingma and Duangmal (2018)
59 strains of actinobacteria	Rhizosphere of <i>Mikania micrantha</i>	<i>Fusarium graminearum</i> ATCC 60309, <i>F. oxysporum</i> f. sp. <i>cubense</i> ATCC 38741 and <i>F. oxysporum</i> f. sp. <i>cucumerinum</i>	Crossed method	Han et al. (2018)
14 <i>Streptomyces</i> spp.	Amendments and amended soil	<i>Fusarium verticillioides</i>	Confrontation assay	Nguyen et al. (2018)
<i>Streptomyces</i> sp. AV05	Organic amendment	<i>Fusarium verticillioides</i>	Dual culture	Strub et al. (2019)
<i>Bacillus subtilis</i> , <i>Pseudomonas</i> sp., <i>Streptomyces heliomyces</i> , <i>S. griseoflavus</i> and <i>S. globisporus</i>	Soil rhizosphere samples	<i>Fusarium graminearum</i>	Dual culture	Olanrewaju and Babalola (2019)
20 <i>Streptomyces</i> strains	Collection of endophytic isolates	<i>Fusarium graminearum</i> and <i>F. culmorum</i>	Dual culture	Colombo et al. (2019b)
<i>Streptomyces</i> sp. SCA3-4	Rhizosphere soil sample of <i>Opuntia stricta</i>	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i> Tropical Race 1 ACCC 31271, <i>F. oxysporum</i> f. sp. <i>cucumerinum</i> ATCC 204378 and <i>F. graminearum</i> ATCC MYA-4620	Disc diffusion method	Qi et al. (2019)
126 <i>Streptomyces</i> isolates	Rhizosphere soil samples of cucumber and tomato	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Dual culture	Abbasi et al. (2019)
Three actinobacterial isolates B21, B22 and B37	Soil samples	<i>Fusarium oxysporum</i>	Dual culture	Sánchez-García et al. (2019)
<i>Streptomyces corchorusii</i> stain AUH-1	Soil sample	<i>Fusarium oxysporum</i> f. sp. <i>niveum</i> , <i>F. oxysporum</i> f. sp. <i>vasinfectum</i> and <i>F. oxysporum</i> f. sp. <i>cucumerinum</i>	Dual culture	Yang et al. (2019)
40 actinobacterial isolates	Soil samples	<i>Fusarium oxysporum</i>	Dual culture	Gasmi et al. (2019)
<i>Streptomyces</i> isolate S2-SC16	Mangrove sediments	<i>Fusarium fujikuroi</i>	Dual culture	Pathom-aree et al.

				(2019)
<i>Streptomyces blastmyceticus</i> strain 12-6	Forest soil sample	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Disk diffusion assay	Kim et al. (2019)
<i>Streptomyces</i> sp. MR14	Rhizosphere of mustard plant	<i>Fusarium oxysporum</i> MTCC 284, <i>F. oxysporum</i> f.sp. <i>dianthi</i> MTCC 6659 and <i>F. moniliforme</i>	Agar well diffusion method	Kaur et al. (2019)
<i>Streptomyces</i> sp. WP-1	Endophyte from bark of <i>Pinus dabeshanensis</i>	<i>Fusarium oxysporum</i>	Dual culture	Peng et al. (2020)
<i>Streptomyces</i> sp. strain AV05	Organic amendment	<i>Fusarium verticillioides</i>	Dual culture	Nguyen et al. (2020)
<i>Streptomyces</i> sp. AS1	Egyptian peanuts	<i>Fusarium verticillioides</i>	Dual culture	Danial et al. (2020)
<i>Streptomyces</i> sp. YYS-7	Rhizosphere soil sample	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i> Tropical Race 4ATCC 76255, <i>F. oxysporum</i> f. sp. <i>cucumerinum</i> ATCC 204378 and <i>F. graminearum</i> DSM 21803	Spot inoculation method	Wei et al. (2020)
<i>Streptomyces</i> ACT1, ACT2, ACT3, ACT4, ACT5 and ACT6	Soil samples	<i>Fusarium oxysporum</i> f. sp. <i>ciceri</i>	Direct confrontation, culture filtrate, well and filter paper disc tests	Tlemsani et al. (2020)
<i>Streptomyces netropsis</i> strain A-ICA	Rhizospheric soil sample of <i>Larrea tridentata</i>	<i>Fusarium oxysporum</i> , <i>F. solani</i> and <i>F. equiseti</i>	Dual culture	Abdelmoteleb and Gonzalez-Mendoza (2020)
30 isolates of actinobacteria	Vermicompost soil samples	<i>Fusarium</i> sp. TFPK201 and <i>Fusarium</i> sp. Foc 1699	Dual culture	Kawicha et al. (2020)
<i>Amycolatopsis</i> sp. BX17	Soil sample	<i>Fusarium graminearum</i>	Dual culture	Cabrera et al. (2020)
Eight endophytic actinobacterial isolates	Cucumber root samples	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>	Agar diffusion method	Cao et al. (2020)
14 actinobacterial strains	Culture collection	<i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>	Dual culture	Djebaili et al. (2021)
10 <i>Streptomyces</i> isolates	Sugar beet rhizosphere	<i>Fusarium fujikuroi</i> CHAMP1 and <i>F. equiseti</i> CHAMP2	Plate diffusion method	Aallam et al. (2021)
<i>Streptomyces</i> strains VL 5, VL 18, VL 50 and VL J2	Culture collection	<i>Fusarium verticillioides</i>	Agar well diffusion method	Marathe et al. (2021)

<i>Streptomyces</i> strains ST02, ST03, ST07 and ST08	Soil samples	<i>Fusarium verticillioides</i>	Diffusion and volatile assay	Tran et al. (2021)
20 actinobacterial isolates	Culture collection	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Dual culture	Shahid et al. (2021)
<i>Saccharothrix</i> strain AHO23	Soil sample	<i>Fusarium culmorum</i> and <i>F. proliferatum</i>	Agar plug diffusion method	Saadi et al. (2021)
<i>Streptomyces</i> sp. 135	Soil sample	<i>Fusarium graminearum</i> and <i>F. oxysporum</i>	Agar diffusion method	Li et al. (2021)
<i>Streptomyces</i> spp.	Soil samples	<i>Fusarium oxysporum</i>	Dual culture	Panneerselvam et al. (2021)
<i>Streptomyces rimosus</i> LMG 19352 and <i>Rhodococcus</i> sp. R-43120	Culture collection	<i>F. graminearum</i> and <i>F. poae</i>	Dual culture	Tan et al. (2021)
<i>Streptomyces albireticuli</i> MDJK11 and <i>S. albofavius</i> MDJK44	Rhizosphere soil sample of peony	<i>F. graminearum</i> , <i>F. oxysporum</i> and <i>F. moniliforme</i>	Modified paper diffusion method and microplate spectrophotometer method	Li et al. (2022)
<i>Streptomyces albidoflavus</i> St-220	<i>Salvia miltiorrhiza</i> rhizosphere sample	<i>Fusarium oxysporum</i>	Cross streaking method	Du et al. (2022)
<i>Streptomyces violascens</i> A10	Potato rhizosphere sample	<i>Fusarium oxysporum</i>	Dual culture	Feng et al. (2022)
<i>Streptomyces polychromogenes</i> UAE2 and <i>S. coeruleoprurus</i> UAE1	Endophytes from date palm root tissues	<i>Fusarium solani</i>	Cut-plug and cup plate	Alblooshi et al. (2022)
<i>Streptomyces violaceoruber</i> UAE1	Rhizosphere soils of date palm trees	<i>Fusarium solani</i>	Cut-plug method	Alwahshi et al. (2022)
84 actinomycetes isolates	Body surfaces and guts of <i>Odontotermes formosanus</i> as well as the combs	<i>Fusarium oxysporum</i> f. sp. <i>momordicae</i> , <i>F. oxysporum</i> f. sp. <i>cucumerinum</i> and <i>F. oxysporum</i> f. sp. <i>vasinfectum</i>	Disc diffusion method and growth rate method with slight modifications	Long et al. (2022)
16 actinobacteria	Rhizospheric soil from chickpea plants	<i>Fusarium oxysporum</i>	Dual culture	Singh et al. (2022)
171 actinobacterial isolates	Cocoyam roots (<i>Xanthosoma sagittifolium</i>)	<i>Fusarium oxysporum</i>	Streak method	Djuidje et al. (2022)

13 <i>Streptomyces</i> strains	Rhizospheric soil samples of <i>Artemisia herba-alba</i>	<i>Fusarium graminearum</i> , <i>F. oxysporum</i> f. sp. <i>albedinis</i> , <i>F. oxysporum</i> f. sp. <i>lycopersici</i> and <i>F. culmorum</i>	Agar diffusion method	Djemouai et al. (2022b)
51 endophytic actinobacterial isolates	Roots and leaves of orchids (<i>Dendrobium nobile</i> , <i>D. chrysotoxum</i> , <i>D. moschatum</i> , <i>D. densiflorum</i> , <i>D. fugax</i> , <i>Rhynchostylis retusa</i> , <i>Vanda corulea</i> , <i>Renanthera imschootiana</i> , <i>Micropera obtuse</i> and <i>Cymbidium eburneum</i>)	<i>Fusarium oxysporum</i> MTCC-284 and <i>F. solani</i> MTCC 365	Dual culture spot inoculation	Saikia et al. (2022)
30 actinobacterial isolates	Marine mangrove sediment	<i>Fusarium solani</i>	Dual culture	Torres-Rodriguez et al. (2022)
1763 actinobacterial isolates	Composite soil samples	<i>Fusarium equiseti</i> and <i>F. oxysporum</i>	Plate confrontation	Pérez-Corral et al. (2022)
<i>Saccharothrix</i> sp. COL22 and <i>Actinomadura</i> sp. COL08	Rhizosphere soil samples of the colocynth (<i>Citrullus colocynthis</i>)	<i>Fusarium oxysporum</i> f. sp. <i>albedinis</i>	Agar cylinders method	Meliani et al. (2022)
18 actinobacterial isolates	Tea rhizosphere soil samples	<i>Fusarium solani</i>	Dual culture	Babu et al. (2022)
202 actinomycete strains	Sagebrush rhizosphere soil samples	<i>Fusarium oxysporum</i> ATCC 070233	Dual culture	Gonzalez-Franco and Robles-Hernández (2022)
88 actinobacteria	Surface-sterilized tea plant	<i>Fusarium oxysporum</i> MTCC 284	Conventional spot inoculation method	Hazarika et al. (2022)
<i>Streptomyces</i> sp. isolates STRM103, STRM104, STRM302, STRM304, STRM305, and STRM403	Soil from tomato rhizospheres	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Dual culture	Kawicha et al. (2023)
Nine species of <i>Streptomyces</i> and one of <i>Nocardiopsis</i>	Surface-sterilized seeds of wheat	<i>Fusarium graminearum</i>	Dual culture	Sharma et al. (2023)
86 isolates of <i>Streptomyces</i> -like colonies	Soil	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Dual culture	Pengproh et al. (2023)
<i>Nocardiopsis alba</i> BH35	Rhizospheric sandy soil	<i>Fusarium oxysporum</i> MH105	Dual culture	El-Sayed et al. (2023)

<i>Streptomyces</i> sp. strain YC69	Cave soil sample	<i>Fusarium oxysporum</i>	Agar well diffusion technique and perpendicular streak technique	Bhat and Nayaka. (2023)
69 isolates of <i>Streptomyces</i> and <i>Nocardiopsis</i>	Rhizosphere of different crops and bulk soils	<i>Fusarium udum</i> and <i>F. oxysporum</i> f.sp. <i>ciceris</i>	Dual culture	Kumar et al. (2023)
<i>Streptomyces</i> sp. Act1, <i>Streptomyces atratus</i> Act2 and <i>Arthrobacter humicola</i> Act3	Rhizosphere of black locust (<i>Robinia pseudoacacia</i> L., rosemary (<i>Rosmarinus officinalis</i> L. and olive <i>Olea europaea</i> L.	<i>Fusarium oxysporum</i>	Incorporation method	Elshafie et al. (2023)

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1735 **Table 4** List of actinobacteria reported as microbial biocontrol agent against pathogenic *Fusarium* species in different crops

Actinobacterial strain	Type of Application	Targeted <i>Fusarium</i> species	Host plant	Experimental condition	Disease	Country reported	Key results	Reference
<i>Streptomyces pulcher</i> and <i>S. canescens</i>	Seed coating	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>	Tomato	Pot	Fusarium wilt	Egypt	Infection rate decreased to 42.9% in the soil pre-inoculation treatment	El-Abyad et al. (1993)
<i>Streptomyces corchorusii</i> and/or <i>S. mutabilis</i>	Cultures amended with pendimethalin or metribuzin	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	Egypt	The combination of the two species with pendimethalin was most effective at 2.0 x M and disease incidence was reduced to zero	El-Shanshoury et al. (1996)
<i>Streptomyces griseus</i>	Seed bacterization and chitin amended talc-based formulation	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	India	Low disease severity on treatment of <i>S. griseus</i> suspension (root dipping) and chitin amended <i>S. griseus</i> (root dipping) were recorded	Anitha and Rabeeth (2009)
<i>Streptomyces psammoticus</i> KP1404	Purified strevertenes A and B	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	Korea	Strevertenes A and B strongly inhibited <i>Fusarium</i> wilt development on tomato plants grown at 1 µg/mL and did not show any phytotoxicity toward	Kim et al. (2011)

							tomato plants at a concentration of 500 µg/mL	
<i>Streptomyces miharaensis</i> KPE62302H	Filipin III (purified antibiotic)	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	Korea	Filipin III inhibited the development of Fusarium wilt in tomato plants by treatment with 10 µg ml ⁻¹	Kim et al. (2012)
<i>Streptomyces rochei</i> ACTA1551	Seed bacterization	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	Greece	Tomato seeds treated with ACTA1551 germinated in statistically significant higher rates into infected soil compared to untreated seeds	Kanini et al. (2013)
<i>Streptomyces flavofuscus</i> CPP-53	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	India	Mycelium growth was restricted after application of CPP-53 on tomato seedlings	Ranveer and Sharma (2014)
<i>Streptomyces albidoflavus</i>	Spore suspension	<i>Fusarium oxysporum</i> and <i>F. solani</i>		Pot	/	Egypt	The efficacy of bio-fungicides was more significant to reduce tomato diseases incidence and enhanced plant growth	Haggag et al. (2014)
<i>Streptomyces</i> sp. ZL2	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>radicis lycopersici</i>		pot	Fusarium root rot	Algeria	The four strains decreased the disease incidence in both sterilized and non-sterilized infested	Zamoum et al. (2015)

							soils	
<i>Streptomyces asterosporus</i> SNL2 and <i>Streptomyces</i> sp. SNL1 and AAL2	Seed bacterization	<i>Fusarium oxysporum</i> f. sp. <i>radicis lycopersici</i>		Pot	Fusarium root rot	Algeria	All strains significantly reduced the root rot incidence compared to a positive control (with infested soil), and the strain SNL2 exhibited the highest protective activity with a reduction in disease incidence of 88.5%	Goudjal et al. (2016b)
<i>Streptomyces griseorubens</i> E44G	Spore suspension or culture filtrate	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Field	Fusarium wilt	Egypt	Application of both <i>S. griseorubens</i> E44G treatments significantly increased all tested growth and yield parameters and decreased the disease severity compared with the infected-untreated tomato plants	Rashad et al. (2017)
<i>Saccharothrix algeriensis</i> NRRL B-24137	Solution of antibiotic	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	Algeria	Reduction of the disease incidence by 59.7%	Merrouche et al. (2017)
<i>Streptomyces</i> NSP3	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	Thailand	<i>Streptomyces</i> NSP3 was shown to be a biotic elicitor of priming agents that initiated plant defence responses to	Vilasinee et al. (2019)

							Fusarium wilt disease in tomato	
<i>Streptomyces enissocaesilis</i> strain IC10 and <i>S. rochei</i> strain Y28	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>		Pot	Fusarium wilt	Iran	Disease severity in the plants treated with IC10 was 1.6 and the strain increased control value by 12.5% compared to the chemical fungicide	Abbasi et al. (2019)
<i>Streptomyces</i> sp. MR14	Culture cells, culture supernatant and culture extract	<i>F. moniliforme</i>		Pot	Fusarium wilt	India	The <i>Streptomyces</i> sp. MR14 cells, supernatant and extract significantly suppressed Fusarium wilt caused in tomato plants	Kaur et al. (2019)
<i>Streptomyces albidoflavus</i> H12 and <i>Nocardioopsis aegyptica</i> H14	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>		Pot	Fusarium wilt	Algeria	Cotreatment of plants with fungal infection and actinomycetes consortium improved plant status, allowing normal growth and improving some development parameters	Djebaili et al. (2021)
<i>Streptomyces</i> sp. isolates, STRM103 and STRM104	Culture filtrate	<i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>		Pot	Fusarium wilt	Thailand	The culture filtrate of isolates STRM103 and STRM104 significantly decreased disease severity and symptoms in Fol	Kawicha et al. (2023)

							inoculated plants	
86 isolates of <i>Streptomyces</i> -like colonies	Culture filtrate or cell suspension	<i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>		Pot	Fusarium wilt	Thailand	Isolate S.PNR29 had the best ability to protect the tomato plants from fungal pathogens with low disease severity scores, lowest disease severity index, and highest disease control efficacy	Pengproh et al. (2023)
<i>Streptomyces</i> sp. strain 3	Spore suspension	<i>Fusarium graminearum</i>		Pot	Fusarium head blight	Iran	<i>Streptomyces</i> sp. Strain 3 reduced disease severity of FHB 21 days after inoculation	Nourozian et al. (2006)
<i>Brevibacillus</i> sp. BRC263 and <i>Streptomyces</i> sp. BRC87B	Bacterial suspension	<i>Fusarium graminearum</i>		Pot	Fusarium head blight	Argentina	The strains significantly reduced the disease severity by 49–71%	Palazzini et al. (2007)
<i>Streptomyces luteogriseus</i> A-23, <i>Nostoc linckia</i> , <i>N. commune</i> , and <i>Microchaeta tenera</i>	Spore suspension	<i>Fusarium culmorum</i>	Wheat	Pot	/	Russia	Inhibition of the growth of fungal mycelium in the root zone of wheat seedlings	Domracheva et al. (2010)
<i>Streptomyces</i> sp. 129.01	Seed bacterization	<i>Fusarium graminearum</i> , <i>F. verticilloides</i> and <i>F. culmorum</i>		Pot	Root rot	Turkey	The strain exhibited a high inhibition ratio of more than 60 % against all fungi	Erginbas et al. (2010)
<i>Streptomyces spororaveus</i>	Soaking seeds in culture filtrate	<i>Fusarium udum</i>		Pot	/	Kingdom of Saudi Arabia	The seed coating treatment was the most effective in controlling <i>F. udum</i>	Al Sahli and Abdulkhair (2012)

							at all cultivation periods in all the three-wheat cultivars	
<i>Streptomyces</i> sp. BN1	Spray	<i>Fusarium graminearum</i>		Pot	Fusarium head blight	Korea	spraying of BN1 spores onto wheat heads during the wheat flowering significantly decreased disease severity	Jung et al. (2013)
<i>Streptomyces mutabilis</i> strain IA1	Spore suspension	<i>Fusarium culmorum</i>		Petri dish	Seedling blight	Algeria	Strain IA1 can reduce both disease occurrence (64.7%) and decrease severity (79.6%)	Toumatia et al. (2016)
<i>Streptomyces</i> sp. RC 87B	Spray	<i>Fusarium graminearum</i>		Field	Fusarium head blight	Argentina	Disease severity reduction was observed with the biocontrol treatments during the field trials (29–39%) but no reduction on disease incidence was achieved	Palazzini et al. (2017)
<i>Bacillus velezensis</i> RC 218 and <i>Streptomyces albidoflavus</i> RC 87B	Bacterial and spore suspensions	<i>Fusarium graminearum</i>		Pot and field	Fusarium head blight	Argentina	Both <i>B. velezensis</i> RC 218 and <i>S. albidoflavus</i> RC 87B effectively reduced disease incidence (up to 30%), severity (up to 25%)	Palazzini et al. (2018)
<i>Streptosporangium becharensense</i> strain SG1	Seed bacterization	<i>Fusarium culmorum</i>		Pot	Root rot	Algeria	The highest protective effect was obtained by the	Boukaya et al. (2018)

							strain SG1, which reduced the disease severity index from 77.8% to 16%	
<i>Streptomyces</i> sp. strain DEF09	Spore suspension	<i>Fusarium graminearum</i>		Pot and field	Root rot	Italy	<i>Streptomyces</i> sp. strain, DEF09 was able to inhibit the disease in controlled conditions by blocking the spread of the pathogen at the infection site and in field conditions it decreased disease severity up to 60%	Colombo et al. (2019a)
<i>Streptomyces</i> spp.	Spore suspension	<i>Fusarium graminearum</i> and <i>F. culmorum</i>		Pot	Fusarium crown and root rot	USA	The non-inhibitory (S06) or inhibitory (S05) <i>Streptomyces</i> isolates lowered the mortality rate	Winter et al. (2019)
<i>Streptomyces</i> sp. MH71 and MH243	Seed bacterization	<i>Fusarium pseudograminearum</i>		Pot	Root rot	Australia	Plants treated with seed coatings of either MH71 or MH243 had > 24% lower disease severity than control plants	O'Sullivan et al. (2021)
<i>Streptomyces</i> sp. strain DEF39	Spore suspension	<i>Fusarium graminearum</i>		Pot	Fusarium head blight	Italy	The seed treatment protected the plant from infection by 49%	Mattei et al. (2022)
<i>Streptomyces sampsonii</i> WSA20	Spore suspension	<i>Fusarium graminearum</i>		Pot	Fusarium head	India	Significant protection was	Sharma et al. (2023)

					blight		recorded in microcosm experiment where no symptoms of disease were observed	
<i>Streptomyces tsusimaensis</i> CAI-24, <i>S. caviscabies</i> CAI-121, <i>S. setonii</i> CAI-127, <i>S. africanus</i> KAI-32 and <i>Streptomyces</i> sp. KAI-90	Seed bacterization and culture filtrate	<i>Fusarium oxysporum</i> f. sp. <i>ciceris</i>	Chickpea	Pot and field	Fusarium wilt	India	Reduction of disease incidence of 45–76% and 4–19% were observed	Gopalakrishnan et al. (2011)
<i>Streptomyces</i> spp. 21, 2A26, 1B10 and 2C34	Seed bacterization	<i>Fusarium oxysporum</i>		Pot	Fusarium wilt	Algeria	The <i>Streptomyces</i> strains significantly promoted the growth of the chickpea plants and showed greater suppression of chickpea wilt disease	Ghadbane et al. (2015b)
<i>Streptomyces</i> sp. KS62, KS55, KS112, KS58 and KS31	Seed bacterization	<i>Fusarium oxysporum</i> f. sp. <i>ciceris</i>		Pot	Fusarium wilt	Iran	All biocontrol agents reduced disease severity (ranging from 38.7 to 54.8%) with strain KS62 showed higher control efficacy (54.8%)	Amini et al. (2016)
<i>Streptomyces</i> sp. S3, S12 and S40	Seed bacterization	<i>Fusarium solani</i> f. sp. <i>pisi</i>		Pot	Fusarium wilt	Iran	S12 demonstrated the greatest effect in reducing disease than the other two	Soltanzadeh et al. (2016)
<i>Saccharothrix algeriensis</i> NRRL B-24137	Solution of antibiotic	<i>Fusarium oxysporum</i> f. sp. <i>ciceris</i>		Pot	Fusarium wilt	Algeria	Reduction of the disease incidence by 61.2%	Merrouche et al. (2017)

<i>Streptomyces</i> sp. AC-19 and <i>Bacillus</i> sp. BS-20	Seed bacterization	<i>Fusarium oxysporum</i> f. sp. <i>ciceri</i>		Pot and field	Fusarium wilt	India	The selected <i>Streptomyces</i> and <i>Bacillus</i> isolates reduced disease incidence and delayed expression of symptoms of disease, over the non-inoculated control	Anusha et al. (2019)
<i>Streptomyces</i> sp. ACT2	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>ciceri</i>		Pot	Vascular wilt	Algeria	The degree of suppression of the disease by ACT2 was higher in both the moderately sensitive Col-27 (13.68%) and PPC25 (18.78%) varieties than the sensitive variety ILC-482 (8.76%)	Tlemsani et al. (2019)
<i>Streptomyces griseus</i> CAI-24, <i>S. griseus</i> CAI121, <i>S. griseus</i> CAI-127, <i>S. africanus</i> KAI-32 and <i>S. coelicolor</i> KAI-90	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>ciceri</i>		Pot and field	Vascular wilt	India	Under greenhouse conditions, all the five strains of <i>Streptomyces</i> sp. and strains CAI-127 and KAI-32 were found to reduce the disease incidence by 55% and 74%, while under field conditions, these were by 86% and 96% in year-1 and	Ankati et al. (2021)

							by 54% and 69% in year-2	
<i>Nocardiopsis</i> sp. KWC01 and <i>Streptomyces</i> sp. KBR01 and fungicide	Seed bacterization and low dose of bavistin	<i>Fusarium oxysporum</i>		Field	Fusarium wilt	India	Increase in wilt protection by 2.66% and grain yield by 8.69%	Singh et al. (2022)
<i>Streptomyces</i> sp. 385 with <i>Paenibacillus</i> Pb300 at different ratio	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>		Pot	Fusarium wilt	India	The addition of combinations of <i>Paenibacillus</i> sp. 300 and <i>Streptomyces</i> sp. 385 to potting medium reduced disease incidence, but to different levels depending on the ratio of each strain	Singh et al. (1999)
<i>Streptomyces olivaceus</i> strain 115	Dry crude extract	<i>Fusarium oxysporum</i> f. sp. <i>melonis</i>	Cucumber	Pot	Fusarium wilt	Iran	<i>S. olivaceus</i> strain 115 acts as a biofungistatic natural product applied as an amendment in greenhouse soil mix will lead to inhibition or reduction of the pathogen effects	Shahidi Bonjar et al. (2006)
<i>Streptomyces bikiniensis</i> HD-087	Seed soaking in fermentation broth	<i>Fusarium oxysporum</i>		Pot	Fusarium wilt	China	Under broth root irrigation after pathogen infection treatment, the disease ratio and disease index dropped, and the	Zhao et al. (2012)

							biocontrol effect reached 53.7%	
<i>Streptomyces bikiniensis</i> HD-087-18	Seed bacterization or culture filtrate	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>		Pot	Fusarium wilt	China	Soaking cucumber seeds in broth of the genome-shuffled strain resulted in an improved bio-control effect (67.5%) that was statistically significant compared to 61.2% for broth of the wild-type strain	Zhao et al. (2014)
<i>Streptomyces</i> sp. strain CNS-42	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>		Pot	Fusarium wilt	China	9 plantlets (45 %) showed wilt symptoms and the disease index was reduced to 25	Li et al. (2014)
<i>Streptomyces albospinus</i> CT205	Spore suspension or organic fertilizer enriched with <i>T. harzianum</i> SQR-T037	<i>Fusarium oxysporum</i>		Pot and field	Fusarium wilt	China	BOF-CT205 treatment yielded significantly lower disease incidences than the control a with reduction of 55%	Wang et al. (2016)
<i>Streptomyces rimosus</i> M527	Fermentation broth	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>		Pot	Fusarium wilt	China	Strain M527 could promote the shoot growth and prevent the development of the disease. The control efficacy against was up to 72.1% as compared to control	Lu et al. (2016)
<i>Streptomyces</i> strain	Spore	<i>Fusarium</i>		Pot	Fusarium	China	The disease	Cao et al. (2020)

HAAG3-15	suspension	<i>oxysporum</i> f. sp. <i>cucumerinum</i>			wilt		incidence and disease severity indices greatly decreased while the height and shoot fresh weight of cucumber significantly increased after inoculating strain HAAG3-15	
<i>Streptomyces</i> spp. DAUFPE 11470 and DAUFPE 14632	Spore suspension	<i>Fusarium moniliforme</i>	Maize	Pot	Seedling blight and rot	Brazil	The lowest value for disease incidence occurred for both isolates. The highest disease reductions were 55% and 62.2% for DAUFPE 14632 and DAUFPE 11470	Bressan and Figueiredo (2008)
<i>Amycolatopsis</i> sp. BX17	Spore suspension	<i>Fusarium graminearum</i>		Pot	/	Mexico	<i>F. graminearum</i> RH1 caused root necrosis and effects on the biometric properties of maize plants, which were prevented by <i>Amycolatopsis</i> BX17	Cabrera et al. (2020)
<i>Streptomyces</i> sp. ST03	Spore suspension	<i>Fusarium verticillioides</i>		Pot	Fusarium ear rot	Belgium	Strain ST03 not only inhibited the proliferation of <i>F. verticillioides</i> but also significantly repressed fungal fumonisin	Tran et al. (2021)

							production 7 days after inoculation	
<i>Streptomyces griseus</i> and <i>Micromonospora globosa</i>	Spore suspension	<i>Fusarium udum</i>	Pigeon pea	Pot	Fusarium wilt	India	The strains exhibited a high fungistatic activity against <i>F. udum</i>	Upadhyay and Rai (1987)
<i>Streptomyces</i> sp. A6 and chemical fungicides	Spore suspension	<i>Fusarium udum</i>		Field	Fusarium wilt	India	Combining the EC ₅₀ dose of the culture of <i>Streptomyces</i> sp. A6 and culture filtrate with test fungicides was found to be more effective for controlling the disease	Singh and Chhatpar (2011)
<i>Streptomyces</i> sp. S-9	Spore suspension	<i>Fusarium udum</i>		Pot	Fusarium wilt	India	<i>Streptomyces</i> sp. strain S-9 treated plants under challenged inoculation condition resulted in better plant growth and vigor vis-à-vis plants challenge with pathogens in the absence of seed bacterization	Dave and Ingle (2021)
<i>Streptomyces corchorusii</i> UCR3-16	Powder formulation	<i>Fusarium oxysporum</i>	Rice	Pot and field	/	India	Talc powder treated rice plants challenged with pathogen showed significant increase in root and shoot	Tamreihao et al. (2016)

							length and, fresh root weight over plants challenged with pathogen alone	
<i>Streptomyces chilikensis</i> RC1830	Spore suspension	<i>Fusarium oxysporum</i>		Pot	Fusarium wilt	India	<i>Streptomyces</i> -treated rice seedlings showed significantly reduced disease severity index by 80.51%	Behera et al. (2022)
<i>Streptomyces griseoviridis</i>	Seed bacterization	<i>Fusarium culmorum</i>		Pot	Seedling blight	Finland	The <i>S. griseoviridis</i> prepare gave some protection and was able to increase yield	Tahvonen et al. (1994)
<i>Streptomyces</i> spp.	Seed bacterization	<i>Fusarium culmorum</i>	Barley	Field	Seedling blight	Algeria	Surface bacterized seeds with TW3, RI3 and TW2 strains expressed the highest performances and permit to reduce significantly both the disease occurrence on seedlings (62–76%) and the extent of seedling blight symptoms (over than 95%)	Yekkour et al. (2012)
<i>Streptomyces goshikiensis</i> YCXU	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>niveum</i>	Watermelon	Pot	Fusarium wilt	China	The incidence of disease was decreased by 67% when the strain enriched by a bioorganic fertilizer was applied to both	Faheem et al. (2015)

							nursery soil and pot soil	
<i>Streptomyces spectabilis</i> SC11, <i>Actinomyces</i> QLP12 and <i>F. oxysporum</i> strain Fo47	Solid integration agents	<i>Fusarium oxysporum</i> f. sp. <i>niveum</i> and <i>F. oxysporum</i> f. sp. <i>vasinfectum</i>		Pot	Fusarium wilt	China	The suppressive effects of Fo47 combined with strain QLP12 reached 58.47%	Zhang et al. (2018)
<i>Streptomyces aureofaciens</i>	Seed coating	<i>Fusarium solani</i>	Sugar beet	Pot	/	Egypt	<i>S. aureofaciens</i> nullified or even reversed the inhibitory effects of <i>Fusarium solani</i>	Moussa and Rizk (2002)
<i>Trichoderma hamatum</i> , <i>Bacillus subtilis</i> and an <i>Actinomyces</i> isolate	Suspension, powder or granules	<i>Fusarium oxysporum</i>		Pot and Field	/	Egypt	Powder formulae of the tested bioagents had the efficacy to control <i>Fusarium oxysporum</i>	El-Kazzaz et al. (2002)
<i>Streptomyces viridosporus</i> HH1 and <i>Rhizophagus irregularis</i>	Formylated spore suspension	<i>Fusarium solani</i> f. sp. <i>pisi</i>	Pea	Pot	Fusarium wilt	Egypt	77% reduction in disease severity in pea plants treated with <i>S. viridosporus</i> HH1 and colonized with <i>R. irregularis</i>	El-Sharkawy et al. (2022)
<i>Streptomyces panaciradicis</i> ARK 13, <i>S. tritolerans</i> ARK 17 (F17), <i>S. recifensis</i> ARK 63, <i>S. tendae</i> ARK 91 and <i>S. manipurensis</i> ARK 94 (F94)	Seed coating method	<i>Fusarium oxysporum</i>	Soybean	Pot	Fusarium rot	Indonesia	Two formulas, F17 and F94, were the best formulas to control disease with disease suppression of 74% in sterile soil and 80-85% in non-sterile soil	Sari et al. (2021)
<i>Kitasatospora putterlickiae</i>	Spore	<i>Fusarium solani</i>	Tea	Field	Fusarium	India	20 % concentration	Babu et al. (2022)

MBK05 and <i>Streptomyces bungoensis</i> MBK21	suspension				dieback disease		of both isolates gave maximum percent disease reduction over control, 72.25 % with MBK05 and 70.3 % with MBK21	
<i>Streptomyces</i> sp. isolate NSP4	Spore suspension	<i>Fusarium oxysporum</i> f. sp. <i>capsici</i>	Chilli (<i>Capsicum annuum</i> L.)	Pot	Fusarium wilt	Thailand	Preventive reduction of disease severity (DS 2.8) higher than applied after inoculated pathogen, as eradication method (DS 3.3)	Saengnak et al. (2013)
<i>Saccharothrix algeriensis</i> NRRL B-24137	Solution of antibiotics	<i>Fusarium oxysporum</i> f. sp. <i>lini</i> (FOLi) and <i>F. oxysporum</i> f. sp. <i>lentis</i> (FOLe)	Flax (<i>Linum usitatissimum</i> L.) and lentil (<i>Lens culinaris</i>)	Pot	Fusarium wilt	Algeria	Reduction of the disease incidence of FOLi and FOLe, by 71.0% and 73.3%, respectively	Merrouche et al. (2017)

1736 /: Not mentinned.

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Mycotoxin	Strain/agent	Isolation source	Fungi/Fungal growth inhibition (%)	Reduction rate (%)	Toxin Level	degradation condition	Possible mechanism of detoxification	Reference
Zearalenone	<i>Streptomyces</i> spp.	Soil, decaying plant parts, peat moss and compost samples	/	100.00	1 µg/mL	5 days, 28 °C, 170 rpm, liquid LB medium	Production of toxin degrading enzymes	Harkai et al. (2016)
	Dye-decolorizing peroxidase from <i>Streptomyces thermocarboxydus</i> 41291	Culture collection	/	/	/	/	The catalytic properties of manganese peroxidase and laccase	Qin et al. (2021)
Deoxynivalenol	<i>Streptomyces</i> strains DEF09, DEF20, DEF39 and DEF48	Inner root tissues of graminaceous plants; DEF09 from wheat, DEF20 from <i>Carex</i> sp., DEF39 from rye and DEF48 from corn	<i>Fusarium graminearum</i> / up to 60	Up to 99.00	/	14 days at 24 °C, Czapek yeast extract medium	/	Colombo et al. (2020)
	<i>Streptomyces albidoflavus</i> RC 87B	Wheat anthers	<i>Fusarium graminearum</i> / 30	17	4.43 µg/g	48 h at 28 °C, 150 rpm, liquid basic medium	/	Palazzini et al. (2018)
Fumonisin B1, B2 and B3	<i>Streptomyces</i> ST03	Soil	<i>Fusarium verticillioides</i>	50.00	/	7 days, 28 °C in TSA medium	/	Tran et al. (2021)
Fumonisin B1	<i>Streptomyces</i> sp. AS1	Malaysian maize	<i>Fusarium verticillioides</i>	/	/	14 days, at 25 °C	/	Samsudin and Magan (2016)
Fumonisin B1 and B2	<i>Streptomyces</i> sp. strain AV05	Organic amendment	<i>Fusarium verticillioides</i>	56.6 (3-day-old) 69.3% (5-day-old)	72.5 (3-day-old), 97.4% (5-day-old)	3, 5 and 7 days at 25 °C, PDA medium	/	Nguyen et al. (2020)

				and 76.9% (7-day-old fungal cultures)	and 43.4% (7-day-old fungal cultures)			
Fumonisin, zearalenone and T-2 toxin	<i>Streptomyces</i> <i>plicatus</i> , <i>S. rimosu</i> , <i>S.</i> <i>rutgersensus</i> and <i>S.</i> <i>griseus</i>	Date palm rhizosphere soil	/	/	/	7 days at 27°C, Sucrose, magnesium sulfate, potassium nitrate and yeast extract liquid medium	/	El-Naggar et al. (2012)

1739 /: Not mentinned.

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1741 **Supplementary Table** Patent list of actinobacteria used in biocontrol of plant diseases with a particular focus on *Fusarium* disease

Publication number	Publication date	Actinobacterial strains	Role against*	Origin	Title of patent	Reference
CN1246890A	2000-03-08	<i>Streptomyces</i> sp. WYE20 or WYE324	<i>Fusarium oxysporum</i> , <i>F. sambucinctum</i> and <i>F. solani</i>	Korea	Antifungal biocontrol agents, process for preparing and treating the same	https://worldwide.espacenet.com/patent/search/family/019496479/publication/CN1246890A?q=pn%3DCN1246890A
WO0234884A1	2002-05-02	<i>Streptomyces kasugaensis</i> GBA-0927	<i>Fusarium oxysporum</i>	Korea	<i>Streptomyces kasugaensis</i> inhibiting the fungal pathogens of plant	https://worldwide.espacenet.com/patent/search/family/019695260/publication/WO0234884A1?q=TREPTOMYCES%20KASUGAENSIS%20GBA-0927
BRPI0412386A	2006-09-19	<i>Microbispora</i> , <i>Streptomyces</i> , <i>Micromonospora</i> , <i>Streptosporangiaceae</i> , <i>Nocardiodetes</i> , <i>Tsukamurella</i> or <i>Streptosporangium</i>	<i>Fusarium</i> sp.	Australia	Method for improving plant productivity, endophytic actinomycete, agricultural composition, metabolites, antibody, methods for improving plant productivity, for facilitating biodegradation of biodegradable material, and for therapeutic and/or prophylactic treatment of a patient, and use of actinomycete or metabolites	https://worldwide.espacenet.com/patent/search/family/033567761/publication/BRPI0412386A?q=pn%3DBRPI0412386A
KR100726864B1	2007-06-11	<i>Streptomyces griseofuscus</i> VSG-16	<i>Fusarium</i> sp.	Korea	A novel <i>Streptomyces griseofuscus</i> VSG-16 KCTC 10930BP active against plant fungal pathogens and preparation of microbial pesticide	https://worldwide.espacenet.com/patent/search/family/038358954/publication/KR100726864B1?q=pn%3DKR100726864B1
CN100467588C	2009-03-11	<i>Streptomyces lydicus</i> A02	<i>Fusarium graminearum</i>	China	One strain of <i>Streptomyces lydicus</i> and its application in treatment and prevention of plant's disease	https://worldwide.espacenet.com/patent/search/family/037002127/publication/CN100467588C?q=pn%3DCN100467588C
KR100914225B1	2009-08-26	<i>Streptomyces</i> sp. strain	<i>Fusarium oxysporum</i>	Korea	<i>Streptomyces</i> sp. SM008S strain	https://worldwide.espacenet.com/patent/search/family/037002127/publication/KR100914225B1?q=pn%3DKR100914225B1

		SM008S	and <i>F. graminearum</i>		and method of controlling plant pathogens using the same	ent/search/family/041210300/publication/KR100914225B1?q=KR100914225%20B1
CN101518264A	2009-09-02	<i>Streptomyces noursei</i> Da07210	<i>Fusarium</i>	China	Microbial preparation for preventing and controlling plant silborne fungal diseases, and application thereof	https://worldwide.espacenet.com/patent/search/family/041079228/publication/CN101518264A?q=pn%3DCN101518264A
CN101525587A	2009-09-09	<i>Streptomyces</i> sp. YL04	<i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i> and <i>F. graminearum</i>	China	<i>Streptomyces</i> strain and application thereof	https://worldwide.espacenet.com/patent/search/family/041093658/publication/CN101525587A?q=pn%3DCN101525587A
CN101698827A	2010-04-28	<i>Streptomyces erythrochromogenes</i>	<i>Fusarium</i>	China	Erythrochromogenes and use thereof in biological control of diseases	https://worldwide.espacenet.com/patent/search/family/042147292/publication/CN101698827A?q=CN101698827%20A
CN101822272A	2010-09-08	<i>Streptomyces griseoflavus</i> NMG6-3-9CGMCC No.3441	<i>Fusarium solani</i> , <i>F. oxysporum</i> , <i>F. avenae</i> , <i>F. avenaceu</i> , <i>F. graminearum</i> , <i>F. semitectum</i> , <i>F. oxysporum</i> f. sp. <i>cubense</i> and <i>F. meliloti</i>	China	<i>Streptomyces griseoflavus</i> and application thereof in biological prevention and control of plant diseases	https://worldwide.espacenet.com/patent/search/family/042686614/publication/CN101822272A?q=pn%3DCN101822272A
CN101851597A	2010-10-06	<i>Streptomyces griseoflavus</i> NMG6-3-9	<i>Fusarium</i> spp.	China	<i>Streptomyces griseoflavus</i> for resisting alfalfa diseases and screening method thereof	https://worldwide.espacenet.com/patent/search/family/042803278/publication/CN101851597A?q=pn%3DCN101851597A
WO2010115802A1	2010-10-14	<i>Streptomyces</i> sp. S37	<i>Fusarium oxyysporum</i> f. sp. <i>albedinis</i>	Morocco	New actinomycetes strain compositions and their use for the prevention and/or the control of microorganism inducing plant diseases	https://worldwide.espacenet.com/patent/search/family/040909048/publication/WO2010115802A1?q=pn%3DWO2010115802A1
AU2011203357A1	2011-07-28	<i>Streptomyces</i> sp.	<i>Fusarium</i> sp.	Australia	A method and agents for	https://worldwide.espacenet.com/pat

					improving plant productivity involving endophytic actinomycetes and metabolites thereof	ent/search/family/045420096/publication/AU2011203357A1?q=pn%3DAU2011203357A1
CN102433281A	2012-05-02	<i>Streptomyces catarrhalis</i> NB20	<i>Fusarium graminearum</i> and <i>F. oxysporum</i>	China	<i>Streptomyces katrae</i> NB20, as well as culture method and application thereof	https://worldwide.espacenet.com/patent/search/family/045981628/publication/CN102433281A?q=CN102433281%20A
CN102876622A	2013-01-16	<i>Streptomyces rochei</i> 42561	<i>Fusarium oxysporum</i>	China	Biocontrol bacterium and application of biocontrol bacterium to preventing and controlling cotton blight and cotton greensickness	https://worldwide.espacenet.com/patent/search/family/047478143/publication/CN102876622A?q=pn%3DCN102876622A
EP2548973A1	2013-01-23	<i>Streptomyces</i> sp. BG76	<i>Fusarium oxysporum</i> f. sp. <i>albedinis</i>	Morocco	New actinomycete strain composition and its use	https://worldwide.espacenet.com/patent/search/family/046551558/publication/EP2548973A1?q=pn%3DEP2548973A1
CN103114064A	2013-05-22	<i>Streptomyces</i> sp. A3202	<i>Fusarium moniliforme</i> , <i>F. graminearum</i> and <i>F. oxysporum</i>	China	Marine actinomycete with antibacterial activity to multiple plant pathogens	https://worldwide.espacenet.com/patent/search/family/048412481/publication/CN103114064A?q=CN103114064
CN103275892A	2013-09-04	<i>Streptomyces albospinus</i> CT205	<i>Fusarium oxysporum</i>	China	Antagonism actinomycetes for preventing and killing continuous cropping cucumber <i>Fusarium</i> wilt and microorganism organic fertilizer with antagonism actinomycetes	https://worldwide.espacenet.com/patent/search/family/049058518/publication/CN103275892A?q=pn%3DCN103275892A
CN103642725A	2014-03-19	<i>Streptomyces griseus</i> Y1B	<i>Fusarium oxysporum</i>	China	Biocontrol strain for antagonistic phytopathogen and use thereof	https://worldwide.espacenet.com/patent/search/family/050248012/publication/CN103642725A?q=pn%3DCN103642725A
CN102835423B	2014-04-16	<i>Streptomyces mediolani</i> ZW-1	<i>Fusarium oxysporum</i> and <i>F. graminearum</i>	China	<i>Streptomyces mediolani</i> ZW-1 bacterial strain, and bacteriostatic	https://worldwide.espacenet.com/patent/search/family/047363358/public

					application of fermentation broth thereof	ation/CN102835423B?q=CN102835423%20B
CN103820351A	2014-05-28	<i>Streptomyces cavourensis</i>	<i>Fusarium solani</i> and <i>F. oxysporum</i>	China	<i>Streptomyces cavourensis</i> and application thereof	https://worldwide.espacenet.com/patent/search/family/050755645/publication/CN103820351A?q=CN103820351%20A
CN104130965A	2014-11-05	<i>Streptomyces</i> sp. Syjd3	<i>Fusarium moniliforme</i> and <i>F. solani</i>	China	<i>Streptomyces</i> with inhibiting effect on poplar gray leaf spot pathogen	https://worldwide.espacenet.com/patent/search/family/051803822/publication/CN104130965A?q=CN104130965%20A
CN104140982A	2014-11-12	<i>Streptomyces</i> sp. Syjd3	<i>Fusarium solani</i>	China	Method for preparing <i>Streptomyces</i> fermentation liquor for preventing and treating alamo grey speck disease germs	https://worldwide.espacenet.com/patent/search/family/051850323/publication/CN104140982A?q=CN104140982%20A
CN104342389A	2015-02-11	<i>Streptomyces</i> sp. 2013 and <i>Streptomyces</i> sp. M929	<i>Fusarium oxysporum</i> f. sp. <i>cucumebrium</i>	China	<i>Streptomyces</i> strains and joint application thereof in prevention and treatment of cucumber Fusarium wilt	https://worldwide.espacenet.com/patent/search/family/052498853/publication/CN104342389A?q=pn%3DCN104342389A
WO2015053482A1	2015-04-16	<i>Streptomyces</i> sp. DUCC501	<i>Fusarium oxysporum</i>	Korea	Novel strain of <i>Streptomyces</i> sp., ducc501, having antifungal activity and plant disease controlling composition comprising said novel strain	https://worldwide.espacenet.com/patent/search/family/052593687/publication/WO2015053482A1?q=WO201553482
CN104403976A	2015-03-11	<i>Streptomyces hygroscopicus</i> B04	<i>Fusarium oxysporum</i>	China	Antagonistic actinomycete for preventing and controlling continuously cropped strawberry root rot and preparation method of biocontrol agent of antagonistic actinomycete	https://worldwide.espacenet.com/patent/search/family/052641646/publication/CN104403976A?q=pn%3DCN104403976A
KR101524651B1	2015-06-03	<i>Streptomyces griseus</i> S4-7'	<i>Fusarium oxysporum</i> f. sp. <i>fragariae</i>	Korea	Composition for plant disease control containing <i>Streptomyces griseus</i> S4-7' or its culture fluid as an active ingredient	https://worldwide.espacenet.com/patent/search/family/052571837/publication/KR101524651B1?q=pn%3DKR101524651B1

CN105349455A	2016-02-24	<i>Streptomyces malaysiensis</i> A8	<i>Fusarium oxysporum</i>	China	<i>Streptomyces malaysiensis</i> and application thereof	https://worldwide.espacenet.com/patent/search/family/055325520/publication/CN105349455A?q=pn%3DCN105349455A
CN105886428A	2016-08-24	<i>Streptomyces albidoflavus</i> strain W68	<i>Fusarium verticillioides</i> and <i>F. oxysporum</i>	China	<i>Streptomyces albidoflavus</i> and applications thereof in microbial fertilizers	https://worldwide.espacenet.com/patent/search/family/057012624/publication/CN105886428A?q=CN105886428%20A
CN105754891A	2016-07-13	<i>Streptomyces sinensis</i> RS15	<i>Fusarium oxysporum</i>	China	Crop pathogenic antagonistic actinomycetes and screening and application thereof	https://worldwide.espacenet.com/patent/search/family/056342554/publication/CN105754891A?q=pn%3DCN105754891A
EP3048890A1	2016-08-03	<i>Streptomyces</i> sp.	<i>Fusarium culmorum</i>	France	Isolated bacterium of the genus <i>Streptomyces</i>	https://worldwide.espacenet.com/patent/search/family/050137744/publication/EP3048890A1?q=EP3048890%20A1
KR101700597B1	2017-02-01	<i>Streptomyces</i> sp. BK185	<i>Fusarium oxysporum</i> and <i>F. solani</i>	Korea	Microbial agent possessing antifungal activity against ginseng root rot pathogens containing soil actinomycete strain	https://worldwide.espacenet.com/patent/search/family/056114256/publication/KR101700597B1?q=pn%3DKR101700597B1
CN106399167A	2017-02-15	<i>Streptomyces</i> sp.	<i>Fusarium</i>	China	Biocontrol agent for lily continuous cropping obstacles and preparation method	https://worldwide.espacenet.com/patent/search/family/057999429/publication/CN106399167A?q=pn%3DCN106399167A
CN106399152A	2017-02-15	<i>Streptomyces</i> sp. M1H	<i>Fusarium oxysporum</i> , <i>F. avenaceum</i> and <i>F. graminearum</i>	China	<i>Streptomyces</i> having inhibitory effect on <i>Phytophthora sojae</i> root rot fungi, biocontrol preparation and preparation method of biocontrol	https://worldwide.espacenet.com/patent/search/family/058004278/publication/CN106399152A?q=pn%3DCN106399152A
CN106434493A	2017-02-22	<i>Streptomyces blastmyceticus</i> JZB130180	<i>Fusarium oxysporum</i>	China	Strain of biocontrol <i>Streptomyces</i> and application thereof	https://worldwide.espacenet.com/patent/search/family/058223491/publication/CN106434493A?q=pn%3DCN106434493A

CN106635878A	2017-05-10	<i>Streptomyces</i> sp. 5X4	<i>Fusarium oxysporum</i>	China	<i>Streptomyces</i> sp. 5X4 and applications thereof as biocontrol bacterium in preventing and treating plant diseases	https://worldwide.espacenet.com/patent/search/family/058820993/publication/CN106635878A?q=pn%3DCN106635878A
CN106676040A	2017-05-17	<i>Streptomyces griseus</i>	<i>Fusarium graminearum</i> and <i>F. oxysporum</i>	China	<i>Streptomyces griseoplanus</i> , application thereof and microbial agent	https://worldwide.espacenet.com/patent/search/family/058869673/publication/CN106676040A?q=CN106676040
CN107058131A	2017-08-18	<i>Streptomyces netropsis</i> AFKCK-10	<i>Fusarium graminearum</i>	China	Strain of <i>Streptomyces netropsis</i> and application thereof	https://worldwide.espacenet.com/patent/search/family/059605303/publication/CN107058131A?q=CN107058131
CN107164259A	2017-09-15	<i>Streptomyces spectabilis</i> FX-H-51	<i>Fusarium falciparum</i>	China	Antagonistic actinomycete and application thereof	https://worldwide.espacenet.com/patent/search/family/059816639/publication/CN107164259A?q=pn%3DCN107164259A
CN107287130·	2017-10-24	<i>Streptomyces</i> sp. W68	<i>Fusarium verticillioides</i> and <i>F. oxysporum</i>	China	<i>Streptomyces albidoflavus</i> strain as well as application thereof in pesticide	https://worldwide.espacenet.com/patent/search/family/060092865/publication/CN107287130A?q=CN107287130%20A
CN107699526A	2018-02-16	<i>Streptomyces chungwhensis</i> LA-5	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i> and <i>F. oxysporum</i> f. sp. <i>vasinfectum</i>	China	Actinomycete for preventing and treating gray mold and application thereof	https://worldwide.espacenet.com/patent/search/family/061180498/publication/CN107699526A?q=pn%3DCN107699526A
CN108048380A	2018-05-18	<i>Streptomyces deccanensis</i> QY-3	<i>Fusarium oxysporum</i>	China	<i>Streptomyces deccanensis</i> QY-3 and application thereof	https://worldwide.espacenet.com/patent/search/family/062125961/publication/CN108048380A?q=pn%3DCN108048380A
CN108102961A	2018-06-01	<i>Streptomyces</i>	<i>Fusarium oxysporum</i>	China	<i>Streptomyces samsunensis</i> and	https://worldwide.espacenet.com/pat

		<i>samsunensis</i> strain XJC-2-6			application thereof	ent/search/family/062211745/publication/CN108102961A?q=CN108102961%20A
CN108165506A	2018-06-15	<i>Streptomyces sanglieri</i> XJC-SDSIM1	<i>Fusarium oxysporum</i>	China	<i>Streptomyces sanglieri</i> and application thereof	https://worldwide.espacenet.com/patent/search/family/062521979/publication/CN108165506A?q=CN108165506
CN108220194A	2018-06-29	<i>Streptomyces parvus</i> HS57	<i>Fusarium oxysporum</i> and <i>F. solani</i>	China	<i>Streptomyces parvus</i> having disease preventing and growth promoting functions, and application thereof	https://worldwide.espacenet.com/patent/search/family/062640320/publication/CN108220194A?q=pn%3DCN108220194A
CN108208016A	2018-06-29	<i>Streptomyces faecalis</i> BWL-H1	<i>Fusarium graminearum</i> and <i>F. oxysporum</i>	China	Application of volatile substance produced by <i>Streptomyces fimicarius</i> in control of plant diseases	https://worldwide.espacenet.com/patent/search/family/062642251/publication/CN108208016A?q=CN108208016
CN108576059A	2018-09-28	<i>Streptomyces faecalis</i>	<i>Fusarium oxysporum</i> and <i>F. solani</i>	China	<i>Angelica sinensis</i> ditylenchus decructorthorne biocontrol agent and preparation method thereof	https://worldwide.espacenet.com/patent/search/family/063627070/publication/CN108576059A?q=pn%3DCN108576059A
CN108587981A	2018-09-28	<i>Streptomyces amritsarensis</i> 2A	<i>Fusarium graminearum</i>	China	Multi-functional <i>Streptomyces amritsarensis</i> and application thereof	https://worldwide.espacenet.com/patent/search/family/063630280/publication/CN108587981A?q=CN108587981
CN108676750A	2018-10-19	<i>Streptomyces hygroscopicus</i>	<i>Fusarium oxysporum</i>	China	<i>Streptomyces hygroscopicus</i> capable of producing salicylic acid and rapamycin and application of <i>Streptomyces hygroscopicus</i> to prevention and control of plant oomycetes and fungal diseases	https://worldwide.espacenet.com/patent/search/family/063808794/publication/CN108676750A?q=pn%3DCN108676750A
CN109082389A	2018-12-25	<i>Streptomyces costaricanus</i> CP99	<i>Fusarium oxysporum</i>	China	Soil <i>Streptomyces costaricanus</i> with biofertilizer and biopesticide potential	https://worldwide.espacenet.com/patent/search/family/064838576/publication/CN109082389A?q=Soil%20St

						reptomycetes%20costaricanus%20with%20biofertilizer%20AND%20biopesticide%20potential
CN109182216A	2019-01-11	<i>Streptomyces</i> sp. SCFJ-05	<i>Fusarium oxysporum</i>	China	A marine <i>Streptomyces</i> sp. SCFJ-05 capable of inhibiting stem rot of succulent plants	https://worldwide.espacenet.com/patent/search/family/064945224/publication/CN109182216A?q=pn%3DCN109182216A
TW201923067A	2019-06-16	<i>Streptomyces melanosporofaciens</i> AGL225	<i>Fusarium oxysporum</i>	Spain	Use of compositions containing <i>Streptomyces melanosporofaciens</i> AGL225 in controlling plant diseases	https://worldwide.espacenet.com/patent/search/family/060162164/publication/TW201923067A?q=pn%3DTW201923067A
CN110029078A	2019-07-19	Endophytic <i>Streptomyces</i> MS001	<i>Fusarium graminearum</i> and <i>F. oxysporum</i>	Australia	<i>Streptomyces</i> with double functions of preventing diseases and killing pests, application and culture method thereof, and biocontrol agent	https://worldwide.espacenet.com/patent/search/family/067243817/publication/CN110029078A?q=pn%3DCN110029078A
CN110218685A	2019-09-10	<i>Streptomyces</i> sp. CGMCC 17115	<i>Fusarium oxysporum</i> and <i>F. graminearum</i>	China	Biocontrol actinomycete and application	https://worldwide.espacenet.com/patent/search/family/067815493/publication/CN110218685A?q=pn%3DCN110218685A
CN110591937A	2019-12-20	<i>Streptomyces microflavus</i> G33	<i>Fusarium</i>	China	Antagonistic actinomycetes and biological organic fertilizer for preventing and controlling tomato bacterial wilt, and method and purpose	https://worldwide.espacenet.com/patent/search/family/068853105/publication/CN110591937A?q=pn%3DCN110591937A
CN110791458A	2020-02-14	<i>Streptomyces</i> CYS92	<i>Fusarium oxysporum</i> f. sp. <i>momordica</i>	China	Biocontrol strain for prevention and control of wilt of <i>Momordica charantia</i> , biological agent and preparation method and application of biological agent	https://worldwide.espacenet.com/patent/search/family/069447548/publication/CN110791458A?q=pn%3DCN110791458A
CN110885769A	2020-03-17	<i>Streptomyces</i> sp. CGMCC No. 15109	<i>Fusarium oxysporum</i> f. sp. <i>cucumebrium</i> , <i>F. graminearum</i> and	China	<i>Streptomyces</i> , antibacterial drug and application thereof	https://worldwide.espacenet.com/patent/search/family/069746227/publication/CN110885769A?q=pn%3DCN110885769A

			<i>F. oxysporum</i> f. sp. <i>vasinfectum</i>			110885769A
CN111334458A	2020-06-26	<i>Streptomyces scabies</i>	<i>Fusarium graminearum</i> and <i>F. oxysporum</i>	China	Biocontrol actinomycetes and application thereof in aspect of preventing and treating ginger stem rot or soybean epidemic disease	https://worldwide.espacenet.com/patent/search/family/071179045/publication/CN111334458A?q=pn%3DCN111334458A
CN111500501A	2020-08-07	<i>Streptomyces misionensis</i> Q1C-5CGMCC NO. 18008	<i>Fusarium graminearum</i> and <i>F. pseudograminearum</i>	China	<i>Streptomyces millitosus</i> and application thereof in prevention and treatment on wheat root rot and stem rot	https://worldwide.espacenet.com/patent/search/family/071868106/publication/CN111500501A?q=pn%3DCN111500501A
CN112931534A	2021-06-11	<i>Streptomyces spiroverticillatus</i> HS1	<i>Fusarium oxysporum</i> , <i>F. moniliforme</i> and <i>F. tricinctum</i>	China	Application of <i>Streptomyces</i> in biological control	https://worldwide.espacenet.com/patent/search/family/070943383/publication/CN112931534A?q=pn%3DCN112931534A
WO2021110981A1	2021-06-10	<i>Streptomyces</i> spp.	<i>Fusarium oxysporum</i>	Switzerland	Formulation comprising <i>Streptomyces</i> spp. for use in seed treatment	https://worldwide.espacenet.com/patent/search/family/069232733/publication/WO2021110981A1?q=pn%3DWO2021110981A1
CN113832074A	2021-12-24	<i>Streptomyces crystalline</i> XG4	<i>Fusarium oxysporum</i>	China	Actinomycetes as well as biocontrol inoculant and application thereof	https://worldwide.espacenet.com/patent/search/family/078965805/publication/CN113832074A?q=pn%3DCN113832074A
CN112899181A	2021-06-04	<i>Streptomyces luteovorticillatus</i> YY-38	<i>Fusarium solani</i>	China	<i>Streptomyces luteovorticillatus</i> with inhibiting effect on peanut soil-borne pathogenic fungi and screening method of <i>Streptomyces</i>	https://worldwide.espacenet.com/patent/search/family/076111329/publication/CN112899181A?q=pn%3DCN112899181A
CN113151104A	2021-07-23	<i>Streptomyces shannanensis</i> A148	<i>Fusarium graminearum</i> , <i>F. avenae</i> and <i>F. oxysporum</i>	China	<i>Streptomyces shannanensis</i> A148 with bacteriostatic effect and application thereof	https://worldwide.espacenet.com/patent/search/family/076875054/publication/CN113151104A?q=pn%3DCN113151104A
CN113957003A	2022-01-21	<i>Streptomyces hygroscopicus</i> PA-4	<i>Fusarium oxysporum</i>	China	Antifungal <i>Streptomyces hygroscopicus</i> and application	https://worldwide.espacenet.com/patent/search/family/079460524/publication/CN113957003A?q=pn%3DCN113957003A

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CN113999794A	2022-02-01	<i>Streptomyces</i> sp. HNBCa1	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i> and <i>F. lychee</i>	China	<i>Streptomyces</i> and application thereof	https://worldwide.espacenet.com/publication/search/family/079928888/publication/CN113999794A?q=pn%3DCN113999794A
CN114164137A	2022-03-11	<i>Streptomyces diastatochromogenes</i> 1-9	Fusarium wilt	China	<i>Streptomyces diastatochromogenes</i> capable of resisting banana wilt and application of <i>Streptomyces diastatochromogenes</i>	https://worldwide.espacenet.com/publication/search/family/080476977/publication/CN114164137A?q=pn%3DCN114164137A
CN114164136A	2022-03-11	<i>Streptomyces</i> sp. 2-11	<i>Fusarium oxysporum</i>	China	<i>Streptomyces</i> new strain for resisting banana wilt and application of <i>Streptomyces</i> new strain	https://worldwide.espacenet.com/publication/search/family/080476938/publication/CN114164136A?q=pn%3DCN114164136A
CN114181873A	2022-03-15	<i>Streptomyces rochei</i> G6	Fusarium wilt	Korea	<i>Streptomyces rochei</i> for preventing and treating greenhouse cucumber soil-borne Fusarium wilt and biocontrol agent	https://worldwide.espacenet.com/publication/search/family/080545697/publication/CN114181873A?q=pn%3DCN114181873A
CN114214224A	2022-03-22	<i>Streptomyces kronopolitis</i> 6G-OA-10	<i>Fusarium</i> spp.	China	Biocontrol bacterium for preventing and treating <i>Colletotrichum</i> pathogenic bacteria and application of biocontrol bacterium	https://worldwide.espacenet.com/publication/search/family/080698057/publication/CN114214224A?q=pn%3DCN114214224A
US11286458B2	2022-03-29	<i>Streptomyces</i> spp. MH71 and MH243	<i>Fusarium</i> spp.	Australia	Methods and compositions for the biological control of plant pathogens	https://worldwide.espacenet.com/publication/search/family/065633325/publication/US11286458B2?q=pn%3DUS11286458B2
CN114540213A	2022-05-27	<i>Streptomyces</i> sp. 5-6	<i>Fusarium oxysporum</i>	China	Actinomycetes with bacteriostatic activity and application thereof	https://worldwide.espacenet.com/publication/search/family/081668552/publication/CN114540213A?q=pn%3DCN114540213A

CN114854631A	2022-08-05	<i>Streptomyces</i> sp. ITBB-ZK-a5	Fusarium wilt	China	Sponge-sourced biocontrol <i>Streptomyces</i> ITBB-ZK-a5 and application thereof	https://worldwide.espacenet.com/patent/search/family/082637551/publication/CN114854631A?q=pn%3DCN114854631A
CN115851553A	2023-03-28	<i>Streptomyces virginiae</i> XDS3-6	Fusarium wilt	China	<i>Streptomyces virginiae</i> capable of preventing and treating clubroot and application of <i>Streptomyces virginiae</i>	https://worldwide.espacenet.com/patent/search/family/085656455/publication/CN115851553A?q=pn%3DCN115851553A
KR20230065690A	2023-05-12	<i>Streptomyces</i> sp. JCK-6116	<i>Fusarium graminearum</i> and <i>Fusarium oxysporum</i>	Korea	Composition for controlling plant disease comprising culture solution of <i>Streptomyces</i> sp. JCK-6116 strain or extract thereof manufacturing methods thereof and controlling method for phytopathogenic fungi	https://worldwide.espacenet.com/patent/search/family/086385701/publication/KR20230065690A?q=pn%3DKR20230065690A

1742 * Not excluding other pathogens

1743 Data were obtained combining the results of Espacenet and PatentscopWipo with the following search words, “Actinobacteria” and “biocontrol” and “*Fusarium*”.



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