**Role of Actinomycetes in Agriculture**

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The technological development of agriculture comes with several problems and challenges. Some estimates suggest that the need to produce agricultural sources will grow up to 70% by 2050 (Bindraban *et al.,* 2018). To increase plant nutrition and protection, chemical fertilizers and pesticides are commonly applied. However, when misused, these products tend to accumulate in nature and promote eutrophication of water bodies, besides the presence of compounds that may be toxic to human health at overexposure (Bonner *et al.,* 2017; Khan *et al.,* 2014).

 In this sense, microorganism-based products work as an efficient alternative for reducing the use of agrochemicals, combining high productivity with a responsible view of the planet and human health (Umesha *et al.,* 2018). Biopesticides based on microbial biological control agents (MBCAs) show excellent results against phytopathogens of agricultural importance (Thakur *et al.,* 2020), especially due to the high specificity of targets provided by their natural molecular mechanisms, able to decrease pest population and reestablish the ecological balance of the environment (O’Brien *et al.,* 2017; Abbey *et al.,* 2019).

 Among the many varieties of microorganisms that can be part of a product for agricultural application, actinomycetes stand out for their bioactive particularities (Matsumoto *et al.,* 2017). These are bacteria primarily found in soil with biologically important properties, capable of producing numerous metabolites of commercial interest, such as enzymes, hormones, and antibiotics. These compounds are generally products of secondary metabolism, which are not used in the vital stages of their development and reproduction (Jakubiec-Krzesniak *et al.,* 2018).

Therefore, this article aims to elucidate some of the main aspects involving the study of actinomycetes and their applications as inoculants and defensives in agriculture.

**Actinomycetes as successful biocontrol agents**

Pests, plant-parasitic nematodes and phytopathogenic microorganisms, such as fungi, bacteria, and viruses, are considered to cause significant impacts in production, capable of causing diseases that compromise plant performance (Mashela *et al.,* 2017, Penha *et al.,* 2020). Thereby, among many microbial biological control agents (MBCAs), actinomycetes are considered the potential ones because of their mechanism of mode of action.

 Actinomycetes can act by indirect and direct mechanisms. The direct mechanism is characterized by controlling unwanted species without having direct contact with them such as antibiotics, lytic enzymes, and insecticidal and nematicidal metabolites, while the indirect mechanism happens when the unwanted species are directly affected by actinomycetes like systemic acquired resistance (SAR) and the induced systemic resistance (ISR) (O’Brien *et al.,* 2017, Beneduzi *et al.,* 2012), Competition for nutrients and space (Köhl *et al.,* 2019).

Antibiosis is direct biocontrol among actinomycetes, where the growth of a pathogen is compromised by toxic metabolites produced by an antagonistic presence (Maramorosch *et al.,* 2009, Arseneault *et al.,* 2017). *Streptomyce*s is the actinomycete genus most known for antibiotics production, being responsible for synthesizing about 60% of all the antibiotics applied in agriculture and horticulture. Lytic enzymes are an important part of antibiosis biocontrol mechanisms, through which MBCAs can lyse vital structures of pathogen cells and inhibit their development (de Oliveira *et al.,* 2020). Other biocontrol direct mechanisms, like hyperparasitism (when an organism gains nutrients by colonizing a pathogen), are also potential interactions to be explored in formulations of biopesticides. However, they are more common among fungal species, with rare occurrences in bacteria (Köhl *et al.,* 2019).

**Commercialized actinomycete products**

|  |  |  |  |
| --- | --- | --- | --- |
| **Product name** | **Organism** | **Target pathogen** | **Biocontrol mechanism** |
| **Fungicide** |  |  |  |
| Mycostop | *Streptomyces griseoviridis* strain K61 | *Ceratocystis radicicola, Alternaria* spp., *Rhizoctonia solan*i, *Fusarium* spp., *Phytophthora* spp., *Pythium* spp. | Competition, hyperparasitism, and antibiosis |
| Actinovate, Micro108 Actino-Iron | *Streptomyces lydicus* strain WYEC108 | *Fusarium* spp., *Rhizoctonia* spp., *Pythium* spp., *Phytophthora* spp., *Erisiphe* spp., *Sphaeroteca* spp., *Laveillula* spp., *Sclerotinia* spp. | Antibiosis and hyperparasitism |
| **Insecticide** |  |  |  |
| Vertimec, Agri-Mek SC | Abamectin from *Streptomyces avermitilis* | Mite, leafminers, leafhoppers | Antibiosis |
| Entrust SC, Tracer | Spinosad and spinosyn D from *Saccharopolyspora spinosa* | Lepidopterous larvae (worms or caterpillars), leafminers, thrips, and red imported fire ants | Antibiosis |
| **Nematicide** |  |  |  |
| Actinovate | *Streptomyces lydicus* strain WYEC108 | *Heterodera* spp., *Meloidogyne* spp., *Pratylenchus* spp | Antibiosis |
| Avicta | Abamectin from *Streptomyces avermitilis* | *M. incognita*, *M. arenaria*, *M. javenica*, *Heterodera* spp. and *Pratylenchus* spp. | Antibiosis |

**Plant growth-promoting effect of actinomycetes**

Many MBCAs can either exhibit biocontrol abilities (direct or indirect) by protecting the plant against pathogen attacks and enabling better growth. Plant-growth-promoting actinomycetes (PGPA) benefit the host plant through two main strategies: phytohormones modulation (synthesis of auxins, gibberellins, cytokines, and production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase) and increase in nutrients bioavailability (biological nitrogen fixation, phosphate solubilization and production of siderophores). PGPA that produces IAA tends to promote more significant root growth of the plants associated with it, increasing their access to soil nutrients and improving their development behaviour (Alori *et al.,* 2018).

Actinobacteria, such as *Streptomyces* spp., influence soil fertility through the involvement of many components and serve as nutrient enhancers. Besides producing siderophores and solubilizing phosphate, they are known to produce various enzymes—including amylase, chitinase, cellulase, invertase, lipase, keratinase, peroxidase, pectinase, protease, phytase, xylanase which make the complex nutrients into simple mineral forms. This nutrient-cycling capacity makes them ideal candidates for natural fertilizers (Jog *et al.,* 2016).

Most streptomycetes are free-living in the soil as saprophytes and can colonize the rhizosphere and rhizoplane of the host plant. For instance, some soil-dwelling microorganisms were found to efficiently colonize the inner tissues of selected host plants as endophytes, therefore proving their ability to fully or partly conduct their life cycle inside plant tissues (Meschke *et al.,* 2010). Additionally, a wide variety of *Streptomyces* species may establish beneficial plant–microbe interactions (Palaniyandi *et al*., 2013). Thus *Streptomyces* species acquire an endophytic status without causing any visible harm or symptoms in the host plant. Such streptomycetes, are reported to have marked plant growth-promoting activity in their host plants and are most likely present in the apoplast of different parts of the plant (that is, roots, stems, leaves, flowers, fruits, and seeds) (Qin *et al.,* 2011).

**List of streptomycetes isolated from plants or the rhizosphere showing plant growth-promoting (PGP) activity.**

|  |  |  |  |
| --- | --- | --- | --- |
| **Species** | **Host plant** | **PGP traits observed on the plants** | **References** |
| *Streptomyces spiralis* | Cucumber | Plant growth promotion | El-Tarabily *et al.,* 2009 |
| *Streptomyces* sp | Soil | Siderophore production, phosphate solubilization, and N2 fixation | Franco-Correa *et al.,* 2010 |
| *Streptomyces rochei, S. carpinensis, S. thermolilacinus* | Wheat rhizosphere | Production of siderophore, IAA synthesis, and phosphate solubilization | Jog*et al.*, 2012 |
| *Streptomyces* sp | Mung bean | Enhanced plant growth | Rungin *et al.*, 2012 |
| *Streptomyces* spp. | Sorghum | Enhanced agronomic traits of sorghum | Gopalakrishnan *et al.*, 2013 |
| *Streptomyces aurantiogriseus* | Rice | IAA production | Harikrishnan *et al.,* 2014 |
| *Streptomyces* sp. RP1A-12 | Groundnut | Increase in seed germination, root and shoot length, nodule number and plant biomass | Jacob *et al.,* 2018 |
| *S. violaceusniger* AC12AB | Potato | Indole-3-acetic acid production, siderophores production, nitrogen fixation and phosphates solubilization | Sarwar *et al.,* 2019 |
| *Streptomyces* A20 | Rice | Siderophores, Indoleacetic acid (IAA), extracellular enzymes and solubilizing phosphate | Rocio *et al.,* 2020 |

**Actinobacteria to Induce Systemic Resistance in Plants**

Induced systemic resistance (ISR) exerts a broad-spectrum response against pathogens, and it can be effective in different plant species. The elicitors of ISR produced by or derived from bacteria include lipopolysaccharides (LPS), flagella, siderophores, biosurfactants, volatile organic compounds (VOCs), quorum-sensing molecules and antibiotics. The perception of some of the beneficial microorganisms involves early responses such as ion fluxes, MAP kinase cascade activation, extracellular medium alkalization, and the production of reactive oxygen species (ROS) followed by the activation of various molecular and cellular host defence responses (Verhagen *et al.,* 2010). Jasmonic acid (JA) and ethylene (ET) are central players in the priming of plant resistance by bacteria. Beneficial microorganisms trigger ISR through the JA/ET pathway, several plant growth-promoting rhizobacteria have been shown to trigger ISR through salicylic acid (SA)-dependent mechanisms.

Martinez-Hidalgo *et al.* (2015) demonstrated that *Micromonospora* strains ALFpr18c and ALFb5 stimulated defence responses of different tomato cultivars against *Botrytis cinerea* attack due to jasmonates which played a key role in the defence mechanism. Singh and Gaur (2017) reported that *Streptomyces griseus* triggered systemic resistance against *Sclerotium rolfsii* in chickpeas by increases in the amount of defense-related enzymes such as PAL and PPO along with the accumulation of total phenolics and flavonoids. Helped also in mitigating the oxidative stress generated by the production of superoxide dismutase (SOD), PAL, peroxidase (PO), ascorbate peroxidase (APX), catalase (CAT), chitinase (CHI), and β-glucanase (GLU) after priming with *S. griseus*.

*Streptomyces* sp. strain NSP3 triggered tomato defence responses against *F. oxysporum* f.sp. *lycopersici* (Vilasinee *et al.,* 2019). The effects of seed treatment and soil application with the *Streptomyces* sp. strain NSP3 against the pathogen was more effective for the induction of PR genes including PR-1a, Chi3, Chi9, and CEVI-1. Lee *et al*. (2021) showed plant protection by *Streptomyces* sp. JCK-6131 takes place via two mechanisms: antibiosis with antimicrobial compounds, streptothricins, and priming. JCK-6131 treatment induced the expression of pathogenesis-related protein genes, suggesting the simultaneous activation of the salicylate and jasmonate signalling pathways. Thus, priming by Actinobacteria activates plant defence responses in the absence of a pathogen by eliciting both JA/ET- and SA-related signalling, associated with enhanced PR protein and plant secondary metabolism levels.

**Conclusion**

Actinomycetes, both rhizospheric and endophytic, possess a strong ability to produce metabolites of interest directly related to their interactions with the microbiome in the environment and the plant host. Production of phytohormones modulators, nutrient-uptake, lytic enzymes, antibiotics, and other active metabolites makes actinomycetes an undeniable promising tool for developing microbial biofertilizers and biopesticides. Defence priming by Actinobacteria has great potential as a successful strategy for modern plant protection, as it involves JA/ET- and SA-mediated signalling which, helps in the production of defence compounds in the absence of a pathogen. Thus, the entire biological treasure of actinomycetes can be used to develop products that make agriculture more sustainable and productive, with better plant nutrition and protection.

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