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Review Article

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Bacterial Antagonists against Plant Pathogens: Mode of Actions

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Abstract: Plant pathogens pose a significant threat to global crop production, responsible for 20-40% of crop losses worldwide due to pre- and post-harvest diseases. Chemical control methods have long been used in agriculture to combat these losses. However, growing concerns over the environmental and health impacts of chemical pesticides have driven interest in biological control as a sustainable and effective alternative. Biological control, particularly through bacterial antagonists (BAs) offers a promising solution for integrated plant disease management and has the potential to enhance crop yields in an environmentally friendly manner. Bacterial antagonists inhibit the growth of plant pathogens through various mechanisms such as direct competition (for nutrients and space, antibiosis, production of antimicrobial compounds) and indirect competition (induction of plant defense responses and plant growth). Many of these beneficial bacteria are naturally occurring members of the microbial community, found ubiquitously in the environment. This review discusses the primary modes of action of bacterial antagonists, detailing the mechanisms and molecules involved in their biocontrol activity.

Keywords: Biological Control, Bacterial Antagonists, Sustainable Agriculture.

Introduction

Plant pathogens cause severe threats to crop production in every region of the world, about 20–40% of all the crops losses are due to pre- or post-harvest plant diseases globally. To avoid these significant losses chemical control strategies have been used to reduce diseases in crops, farms and greenhouses (Oerke, 2006). Use of chemicals to control pests and diseases leads to a number of issues, including pesticide resistance, negative health effects on humans, loss of beneficial soil microorganisms, entry of leftover harmful material into the food chain, and decreased biodiversity of macro-microorganisms (Sindhu et al., 2016).Biological control is regarded as a promising alternative and a wide array of microbial biocontrol agents (BCA) have been developed in the past decades for the management of fungal and bacterial diseases (Kohl et al., 2019).Biological control of plant diseases is the suppression of populations of plant pathogens by living organisms (Heimpel & Mills, 2017). Biological control against plant diseases has recently been seen as a helpful and effective alternative to chemical control, due to its potential for integrated plant disease management

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and its ability to increase output in a sustainable way (Guo et al., 2013). Pathogen's destructive impacts are generally reduced through biocontrol agents with antagonistic activities or those that affect plant physiology and morphology. Many antagonists of plant diseases are ubiquitous and prevalent members of the microbial community that naturally reside in the environment because they frequently do not depend on the presence of a pathogen. Viruses can also operate as antagonists by inducing plant defense responses although their manner of action is very different (Hajek & Eilenberg, 2018). The advantages of beneficial microbes for associated plants include the establishment of antagonistic microorganisms, prevention of phytopathogens, general improvement of plant health, promotion of plant growth, enhanced nutrient availability and uptake, and increased resistance to both biotic and abiotic stresses in the hosts (Vinale *et al.,* 2014). Most antagonists that only affect a small number of plant pathogen species are typically obligate parasites, whereas antagonists that use a variety of antagonism strategies, including parasitism occasionally have a wider host range. Compared to antagonists that only suppress one disease, those that suppress several diseases are more likely to be commercialized (Dukare *et al.,* 2019). Fungi and bacteria are principally used for biological control against fungal and bacterial pathogens. Large populations of helpful microorganisms live in a dynamic environment called the rhizosphere. It is generally known that rhizosphere microorganisms aid in the direct and indirect growth and development of plants. Rhizobacteria that promote plant growth and yield actively colonize plant roots are known as plant growth-promoting rhizobacteria (PGPR). To increase plant growth and biologically combat plant diseases, PGPRs are frequently utilized (Reyad et al., 2017). The use of plant growth-promoting rhizobacteria (PGPRs) for biological control as an alternative disease management method has the potential to be successful (Jetiyanon & Kloepper, 2002). Bacterial biocontrol agents use a great variety of mechanisms to protect plants from pathogen infections. They may use one or a combination of mechanisms to prevent or reduce plant disease, interacting directly or indirectly with the pathogen (Legein *et al.,* 2020) (Figure 1).

In this review, the primary modes of action of known BA will be discussed and provide information on their main modes of action, including details concerning the mechanisms and molecules involved in the biocontrol activity.

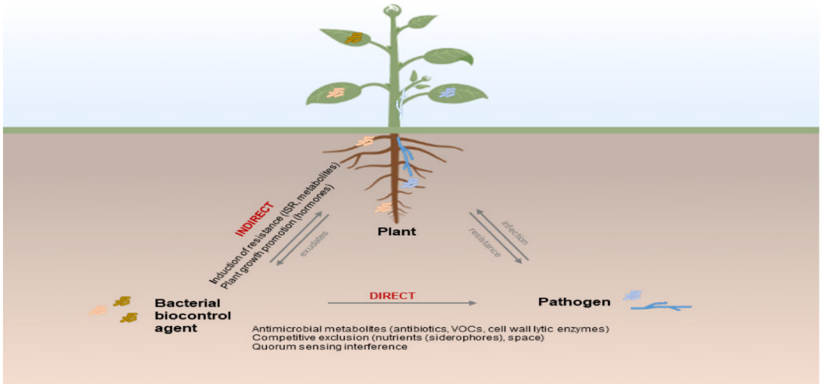

Figure 1: An overview of the interactions between the bacterial biocontrol agent, the pathogen, and the plant that make up the direct and indirect mechanisms of biocontrol.

Bacterial Antagonists

Bacterial antagonists (BA) are bacteria that negatively affect the growth of harmful microorganisms. In the world of bacteria, antagonism is the most popular phenomenon in which species of one bacterium inhibits the growth and suppresses the development of other microorganisms. They use a great variety of mechanisms to protect plants from pathogen infections. Through direct or indirect interactions with the pathogen, they may employ one or a combination of methods to prevent or minimize plant diseases. Many of the bacterial species used as antagonists have anti-soil-borne plant pathogen activity (Egorov, 2004). Some of the most intensively studied are bacteria belonging of the genus *Pseudomonas* spp., *Bacillus* spp., and *Streptomyces* spp., that have been already registered as commercial products and marketed. Some antagonistic bacteria used as biopesticides (Table 1).

Antagonists	**Plant Part**	**Pathogen and Disease**	**Mode of Action**
Agrobacterium radiobacter	Woody stems and roots	Agrobacterium tumefaciens (causes crown gall)	Competition and antibiosis
Bacillus subtilis	Seeds Foliage	Damping off, Botrytis, mildews and other fungi	Competition Prevents germination, disrupts growth
Pseudomonas fluoroscens	Seeds, roots Flowers Mushrooms	Damping off, Erwinia amylovora (causes fire blight) Pseudomonas tolassi	Competition and antibiosis
Pseudomonas syringae	Harvested vegetables and fruits	Fungal pathogens of stored products	Mechanism unknown
Streptomyces grisioviridis	Seeds, roots	Seed and soil-borne Fungi	Competition and antibiosis

***Pseudomonas* species**

The rhizosphere and phyllosphere of plants as well as the endosphere are both effective habitats for many *Pseudomonas* species. Due to their rapid growth rate and capacity to utilize a range of plant exudates as nutrients, they can successfully compete with other microorganisms in the plant environment for resources including nutrients and space (Lugtenberg *et al.,* 2001). The activity of *Pseudomonas* species in pathogen reduction is based on their strong ability to colonize plant tissues as they have a better growth potential and nutrient usage efficiency than the target pathogens (Cabrefiga *et al.,* 2007; Gómez-Lama Cabanás *et al.,* 2014).*Pseudomonas* are producers of bioactive metabolites viz antibiotics (phenazines, phloroglucinols and pyoluterorin), cyclic lipopeptides (CLPs) and enzymes (chitinase, glucanase and cellulase) which play a vital role in inhibiting fungal and bacterial pathogens. Induce and systemic resistance is also produced by *Pseudomonas* species by activating jasmonic acid and salicylic acid defensive pathways (Lakkis *et al.,* 2019; Nunes *et al.,* 2001; Raaijmakers *et al.,* 2006).

***Bacillus* species**

One of the most common antagonistic bacteria which is also used as biopesticides is the *Bacillus* genus. They are extensively distributed in a variety of habitats, including soil and plant surfaces. They have a wide range of physiological abilities and the capacity to produce endospores, which confers resilience to unfavorable climatic conditions (Bonaterra *et al.,* 2022). They can create antagonistic relationships with a variety of bacterial and fungi that cause plant diseases. The most notable characteristic ability of *Bacillus* spp. to create a wide range of bioactive chemicals useful for agricultural applications, including surface-active metabolites with antibacterial activity and nematicidal action, enzymes, exotoxins, and linked to the generation of plant defense responses (Mouloud *et al.,* 2013). The antibiotics produced by *Bacillus* are helpful in controlling post-harvest diseases.

Mode of Action of Bacterial Antagonists

Various bacterial biocontrol agents protect plants from diseases. Without coming into direct contact with the phytopathogen, these chemicals could cause resistance or initially improved resistance against infections. Additionally, competition for resources and space is another indirect way that phytopathogens interact (Köhl *et al.,* 2019). Antibiosis is the direct interaction of these agents with the pathogens (Raaijmakers & Mazzola, 2012). Bacterial antagonists frequently use the excretion of antifungal compounds to inhibit plant pathogens (AFMs). Antibiotics, poisons, and bio-surfactants are prominent AFMs (Raaijmakers *et al.,* 2002). Bacterial volatile organic compounds (VOCs) may also possess antifungal properties. The VOCs of soil bacteria affects the growth of fungi (Stotzky *et al.,* 1976). Enzyme-producing bacterial antagonists can hydrolyze chitin, proteins, cellulose, and hemicellulose and may also help to control plant diseases. Many fungal cell walls mostly consist of chitin and 1,3-glucans (Lam & Gaffney, 1993).

Direct Competition with pathogens

In the direct way of disease control, BCAs act through a direct antagonistic effect on the pathogen, encompassing (i) antibiosis, (ii) competition for nutrients and space and (iii) parasitism, and (iv) reducing pathogen virulence (Dukare *et al.,* 2019).

Antibiosis

Antibiosis by antimicrobial metabolites are secondary metabolites created by bacteria that are harmful to the growth or metabolic processes of other microbes. These secondary metabolites are members of heterogeneous categories of organic, low-molecular weight molecules (Thomashow, 2002). Many microbes make them and release little amounts of them into the environment. Actinomycetes (8700 distinct antibiotics), bacteria (2900), and fungus are responsible for producing a significant portion of the known antibiotics (4900) (Gavrish *et al.,* 2014). Production of antimicrobial metabolites, mostly with broad-spectrum activity, has been reported for biocontrol bacteria belonging to Agrobacterium, *Bacillus*, *Pantoea*, *Pseudomonas* and *Serratia*.*Pseudomonas fluorescens* and *Streptomyces griseoviridis* are two examples of *Actinomycetes* that frequently combine competition and antibiosis to thrive in the challenging soil environment. *Pseudomonas* species are also used for suppression of diseases of aerial plant parts as well as soil-borne diseases. Some of the bacterial antagonists of plant pathogens belong to the Family *Bacillaceae*. These are spore-forming bacteria, and several are known to produce antibiotics, just as *Bacillus thuringiensis*

(Bt) produces a secondary metabolite toxic to insects. These species that produce spores have the capacity to endure in harsh environments, and this quality prolongs their presence after application. Both foliar and soil-borne diseases are combated by members of the *Bacillaceae* family (Heydari & Pessarakli, 2010).

Competition

Food and space competition is an important antagonistic mechanism utilized by bacteria for managing various phytopathogens (Di Francesco *et al.,* 2016). Plant pathogens need nutrients for development and germination. Bacteria have the ability to colonize on scratched fruit to ingest the food (Carbon source) for their survival, restricting carbohydrate tendency for fungus, decreasing its germination rate, and accordingly reduced invasion capability on a host (Hernandez-Montiel et al., 2018).Obligate biotrophic pathogens are solely dependent on nutrients from living, infected host cells and are not dependent on any foreign nutrient sources in the environment outside the host plant (Agrios, 2005). Necrotrophic plant pathogenic bacteria attack host plant tissues, kill them, and then colonize them using the nutrients that are left over. Once the pathogen has caused necrosis, non-pathogenic bacteria with a saprophytic lifestyle may also colonize the necrotic tissues, resulting in a saprophytic competitive substrate colonization that is common and leads to competition for nutrients and space. Highly competitive antagonistic bacteria are possible biological control candidates that use competition for nutrients and space as a mode of action. The antagonistic interactions are primarily characterized by competition for carbohydrates in the carbohydrate-rich wound environment and competition for the limited nitrogen sources, such as amino acids (Vickers, 2017). This mechanism has been investigated for isolates of *Pseudomonas* species.

Parasitism

Parasitism is an essential biological control mechanism used by bacterial antagonists (BA) to target phytopathogens. This process occurs when the antagonist feeds on or within the pathogen, resulting in its destruction. Some BAs produce propagules around or inside the pathogen (Xu and Hu 2020). The effectiveness of BAs can be influenced by factors such as environmental conditions such as temperature and space. BAs are also influenced by their quality and quantity when introduced to a targeted ecosystem. Pathogen resistance can be determined by measuring the proportion of pathogen propagules that remain infective as a function of the number of BCAs introduced to the system (Harman *et el.,* 2021).

Indirect Competition with pathogen:

Indirect mechanisms include the induction of resistance by stimulating plant defense reactions and stimulating plant growth and soil fertilization. BCAs can initiate plant systemic resistance, which results in an accumulation of structural barriers and elicitation of many biochemical and molecular defense responses in the host. This action requires a signalization of the pathway of phytohormones, phytoalexins, and defense enzymes such as phenylalanine ammonia-lyase, chitinase, PR-proteins, and phenolic compounds (Yu *et al.,* 2022).

Induced Resistance

Induced resistance offers the possibility of long-term and broad-spectrum disease control using the natural resistance of plants. The resulting resistance is usually broad and long-lasting but rarely complete, with most inducing agents only lowering the disease prevalence by 20% to 85% (Walters *et al.,* 2013). Stimulation of resistance includes the BA capacity of inciting host defensive chemical and biochemical response, comprising the variation in the assembly of tissues and protein formation interlinked to pathogenesis; their expression occurs locally or either systemically. A wide range of physical and chemical defense mechanisms are used by plants to protect themselves from diseases. One of the most effective agronomic methods for preventing biotic losses in crops is to increase resistance. Beneficial microbes i.e. bacterial antagonists are helpful in enhancing defensive capacities of plants against many pathogens (Catoni *et al.,* 2022). The antagonistic bacteria help plants in attaining induced resistance (IR) and systemic acquired resistance (SAR) by enriching the stimuli produced by pathogens. Pathogen associated molecular patterns (PAMPs) and Microbe associated molecular patterns (MAMPs) recognize IR and SAR respectively (Mouloud, *et al.,* 2013).

Conclusion

Bacterial antagonists (BAs) represent a promising and sustainable alternative to chemical control for managing plant diseases. Through various mechanisms, including antibiosis, competition for resources, parasitism, and the induction of plant resistance, BAs effectively suppress harmful plant pathogens. Bacteria such as *Pseudomonas*, *Bacillus*, and *Streptomyces* are widely studied for their biocontrol potential and are used in commercial biopesticides. The ability of BAs to produce antimicrobial compounds, outcompete pathogens for nutrients, and stimulate plant defense mechanisms makes them effective agents for both pre- and post- disease control. Furthermore, BAs can enhance plant health by promoting growth, improving nutrient uptake, and boosting resistance to both biotic and abiotic stresses. Induced resistance mechanisms such as ISR, SAR, and phytohormonal signaling, offer long-term protection and can be integrated into sustainable agriculture practices. Despite the promising benefits, the success of bacterial biocontrol in the field depends on factors such as environmental conditions, pathogen resistance, and the quality and quantity of biocontrol agents applied. Continued research into optimizing the application and efficacy will help overcome these challenges and support the development of more effective and eco-friendlier pest and disease management strategies for agriculture.

Conflict of Interest: No potential conflict of interest is declared by any author.

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