JETIR.ORG ISSN: 2349-5162 | ESTD Year : 2014 | Monthly Issue

JOURNAL OF EMERGING TECHNOLOGIES AND INNOVATIVE RESEARCH (JETIR)

An International Scholarly Open Access, Peer-reviewed, Refereed Journal

Plant-Growth-Promoting-Rhizobacteria (PGPR)-Mechanism, Applications and Scope

Potulwar Sandeep Vyankatrao.[1], Dr. Rakh Ravindra Raosaheb[2*], Jadhav Mahesh Panditrao[3] and Dr. Baisthakur Pankaj Onkarsingh[4]

[1] Department of Microbiology, N. S. B. College, Nanded (Maharashtra)

[2] Department of Microbiology, S. G. B. College, Purna (Maharashtra)

[3] School of Life Sciences, Swami Ramanand Teerth Marathwada University, Nanded

[4] Department of Microbiology, L. B. P. College, Hingoli (Maharashtra)

Abstract:

Plenty of microbes have magical tendency to establish development of plant, and a wide range of microbial products are commercially available that have these properties as well. The concentration of this review is on the bacteria said to be plant growth-promoting rhizobacteria, which are derived from plant roots and affect plant roots. These rhizobacteria may enhance plant development directly or indirectly. The introduction of the review discusses the environmental elements that affect the bacterial flora in the rhizospheric area. Since efficient root surface colonization is typically necessary for bacteria to manifest their beneficial effects, the following sections explain the bacterial properties necessary for effective root colonization. Then, numerous mechanisms by which microbes promote plant growth are discussed. Direct plant growth promotion includes, among other things, biofertilization, root growth stimulation, rhizoremediation, and a reduction in plant stress. The study also discusses a number of biological controls, such as antibiosis, the development of systemic resistance, and resource competition, and ecological niches, that rhizobacteria use to avoid the spread of disease and thereby stimulate the plant growth.

Keywords: Biological control, Competition for Food & Shelter, Resistance Development, Antifungal Bio-molecules.

Introduction:

This analysis grabs attention on beneficial bacteria that can either directly promote development of plants without diseases or indirectly protect plants from soil-borne diseases, which are mostly fungi-related.

Maarastawi et al., 2018 observed that the rhizospheric area: the area of the earth where the root has caused impacts - holds a larger bacterial concentration in contrast to the concerning bulk soil. Such rhizosphere bacteria are fed by the metabolites produced by these plant roots. This process results from the significant release of root exudate, which contributes between 5% and 21% of plants' ability to fix carbon (Marschner, 1995). The bacterial concentration within the rhizosphere exhibits a magnitude that is ten to thousands times more than that observed in the surrounding bulk soil. However, it remains notably lower, approximately 100 times, compared to the bacterial concentrations commonly encountered in laboratory settings. Rhizobacteria may therefore be thought of as having a nutrient-restricted lifestyle. In order to manifest their beneficial impacts inside the root environment, bacteria must be skilled at colonizing the rhizosphere and capable of out-competing other rhizosphere microbes for available root locations and supplies released by the roots.

The understanding of the various food sources within the rhizosphere and the mechanisms by which bacteria consume them remains limited (Uren, 2007). However, the tomato root exudate composition is an exception, with organic acids and sugars making up the majority of the mixture (Rohrbacher & St-arnaud, 2016). The significance of organic acids in root colonization has been verified by studies indicating that mutants unable to utilise organic acids exhibit lower competitive root colonization as considered with to the wild-type strains, while mutants deficient in sugar utilisation show no change in root colonization (M. Sharma et al., 2020).

The most opportune locations for bacterial colonization on the surface of plant root -which is confined to a limited part: the bonding between epidermal cells are the sites where side roots originate (Knights et al., 2021). Insufficient rhizoplane colonization has long been recognized as a barrier to the efficiency of biocontrol (Niu et al., 2020). Earlier investigations already reported necessity of root colonization in plenty of biocontrol strategies, viz antibiosis (Chin-a-woeng et al., 2000) and competitiveness for resources and habitats (Kamilova et al., 2005; Validov, 2007).

Available nutrients, colonization procedure, and the living conditions of the root is enveloped by bacteria in the first portion of this review. Beneficial bacterial processes rely on the competitive colonization of the rhizospheric area. The bacterial traits required for root colonization successfully in the face of competition from fungi, nematodes, and protozoa are also included (Saeed et al., 2021). The investigation of the diverse ways via which specialized helpful rhizobacteria stimulates the plant growth concludes in the review. It first discusses bacteria that directly enhances growth of plants in the absence of harmful microbes, after which it examines biocontrol bacteria that minimize infection-related damage and serve as biopesticides (Glick, 2012).

MICROBES' NUTRIENTS IN THE RHIZOSPHERE

Numerous organic molecules viz. fatty acids, nucleotides, amino acids, carbohydrates, organic acids, vitamins, fatty acids, sterols, putrescine and vitamins are secreted by plant roots (Uren, 2007 and Upadhyay et al., 2022). When analyzing data on exudate composition, there are a number of considerations that call for caution. First of all, scientists can only identify the components they actively search for, unless they are fortunate enough to come across unexpected molecules. For example, putrescine was not studied until a mutant for competitive colonization was discovered to suggest its existence (Liu et al., 2022). Second, it is frequently required to obtain aseptic plant specimens cultivated in controlled environments, viz. either inside a sterile plant feeding fluid or on sterile filter paper, it is necessary to employ certain collection methods, in order to obtain exudates with the right concentration for testing (Kamilova et al., 2008; Kamilova, Kravchenko, Shaposhnikov, Makarova, et al., 2006; Williams et al., 1992). Plant's physiological condition, existance of microorganisms, the impact of rhizobacteria-derived compounds like phenazines, 2,4-diacetylphloroglucinol, and zearalenone, along with the growth substrate, can all affect the composition of exudates (Phillips et al., 2004). Finally, it's crucial to keep in mind that in addition to secreting substances, plants also absorb exudates.

One of the most well-known exudate components is the exudate from tomato plants including the primary soluble carbon sources in tomato root exudate are organic acids (Kamilova et al., 2005, 2008; Kamilova, Kravchenko, Shaposhnikov, Azarova, et al., 2006; Kamilova, Kravchenko, Shaposhnikov, Makarova, et al., 2006; Upadhyay et al., 2022), followed by sugars (Kamilova, Kravchenko, Shaposhnikov, Azarova, et al., 2006; B. J. J. Lugtenberg et al., 1999; B. J. J. Lugtenberg & Dekkers, 1999) and amino acids (Simons et al., 1997). The amino acids and putrescine in the exudate are significant sources of nitrogen. Because of root exudates (P O Baisthakur et al., 2022), pathogenic fungus may behave differently. For instance, Spores of a disease of the root of tomato plant *(Forl) Fusarium oxysporum* f., sp. Radicis-lycopersici can more readily germinate when exposed to tomato root exudate, especially its main ingredients citrate and glucose. *Pseudomonas fluorescens* WCS365, a biocontrol strain, slows down this germination process (Kamilova et al., 2008).

COLONIZATION OF RHIZOPLANES

Introduction

The root epidermis's mucigel layer frequently masks the presence of germs. Thanks to the development of a modified technique of scanning electron microscopy method that has partially transparented this layer, scientists can now detect microorganisms on the rhizoplane (Chin-a-woeng et al., 2000). The visualization of specific microbial strains through fluorescence labeling has been made possible by the colour variations utilization of the green fluorescent protein (GFP) (Barbier & Damron, 2016). The simultaneous visualization of two bacterial strains or a fungus and a bacteria can be achieved by employing a combination of distinct fluorescent hues on the red auto-fluorescent surface of tomato roots (Bloemberg et al., 2000; Bolwerk et al., 2003; Rochat et al., 2010).

To investigate mechanisms of root colonization beginning with bacterized seeds, a monoaxenic system was constructed (Simons et al., 1996). A controlled setting for research was provided by this system. In this method, seeds or seedlings are planted without the need of an additional carbon source in sterile sand and a sterile plant feeding solution. One or two bacteria are coated on the seeds or seedlings. Throughout a developing phase of up to 7 days, during which root exudates are the only carbon source, the presence of bacteria is examined in various root sections. After 7 days, it was discovered that the dissemination of *Pseudomonas fluorescens* WCS365 bacteria differed along the root, ranging from 106 colony-forming units (CFUs) and 102 to 103 Colony Forming Units cm^{-1} near the root base and root tip respectively. During the investigation it was revealed that seed coat is the part of plant where *Pseudomonas fluorescens* WCS365 primarily multiplied. The root, as opposed to the stem, was gradually colonized, starting with one cells that later gave rise to bacterial colony. These bacterial colonies, often referred to as biofilms, frequently include many bacterial layers on top of a slimy layer (B. J. J. Lugtenberg et al., 2001; B. J. J. Lugtenberg & Dekkers, 1999).

Colonization Traits and Genes

The genes and features connected to competitive root tip colonization have been identified by monoaxenic protocol (Simons et al., 1996) that has been previously published. In a paired competition for colonization of the root tip, the parental strain *Pseudomonas fluorescens* WCS365 and mutants that displayed aberrant growth patterns in the lab were permitted to compete. When planted in potting soil, the mutants that had problems colonizing the sand system exhibited similar behaviors. Genetic and physiological research was done on these mutants. The lipopolysaccharide's O-antigenic side chain, the two-component ColR/ColS sensory system, the putrescine uptake system specific to a given site, the putrescine uptake system's fine-tuning (with a compromised pot operon), adhesion to the root, the rapid growth of root exudate, the synthesis of amino acids, uracil, and vitamin B1, and the O-antigenic side chain.

Chemotaxis related to root exudate has been found to be a crucial component of motility, which is necessary for colonization. Dicarboxylic acids and amino acids, with L-leucine being the most powerful, were shown that the existence of chemoattractants in the tomato plant’s root exudate has been observed to attract *Pseudomonas fluorescens* WCS365. The chemoattractiveness of sugars was nonexistent. It was assumed that malic acid and, to a lesser extent, citric acid were the primary chemoattractants for this strain in the tomato rhizosphere based on the amounts of these acids in root secretions (Weert et al., 2002). In the case of the Arabidopsis thaliana root exudate, L-malate was discovered as a primary chemoattractant to biological control rhizobacterium *Bacillus subtilis* FB17(Rudrappa et al., 2008).

Competitive tomato root colonization mutants in the ColR/ColS two-component system showed reduced growth rates in root exudate when cultivated with the wild-type *Pseudomonas fluorescens* WCS365. Additionally, these mutants were extremely toxic to the antibiotic polymyxin B, which binds to lipopolysaccharide (LPS). They showed greater resistance to the tested antibiotics than the wild type. The colR/colS genes regulate the downstream methyltransferase/wapQ operon. Individual gene alterations in the phosphatase and methyltransferase proteins reduced competitive colonization. The wapQ gene encodes a

potential heptose phosphatise. The products of both genes may change Lipopolysaccharide (LPS), which reacts with outer membrane porins, according to one theory (B. E. N. Lugtenberg & Alphen, 1983; Weert et al., 2006). When these chemical groups are not present, the LPS has a reduced pore diameter. *Pseudomonas fluorescens* SBW25 TTSS (type three secretion system) mutants showed decreased competitive colonization of tomato root tips, but when evaluated separately, their colonization capacity was unaltered. The mutants' altered LPS accounts for the mutants' increased interaction with polymyxin B, reduced exudate growth rate and reduced ability for competitive colonization (Weert et al., 2006). Due to binding to seeds and roots in interaction with the parent strain wasn't hindered, it was hypothesized that *Pseudomonas fluorescens* SBW25's TTSS enabled the insertion of a hollow needle into the plant epithelial cell's cytoplasm in order to access plant fluids. This system for injecting proteins may have originated as a means of protein delivery, then following the inclusion of a functional motor, it may have changed into rotating flagella (Zhuang & Lo, 2020). The finding that the hrcC gene mutation reduces the ability of Pseudomonas putida KD to biocontrol Pythium in cucumbers and Fusarium in tomatoes further validates the role of the TTSS in rhizosphere competence (Rezzonico et al., 2005).

Given that multiple genes are concerned in competitive root colonization, identifying genes and phenotypes linked to colonization is a difficult task that requires a genomic approach to properly understand this process.

PROMOTING DIRECT PLANT GROWTH

Plant growth is directly supported by rhizobacteria when pathogens are absent. An good review has been written with this subject in mind (Loon, 2007). Different bacteria promote plant development based on the method employed.

Biofertilizers

Some rhizobacteria can aid plant growth even when pathogen pressure is not present (Backer et al., 2018). Bacterial fertilizers provide food for plants. Leguminous plants, including soybean, pea, peanut, and alfalfa, grow N2-fixing bacteria like Bradyrhizobium and Rhizobium in nodules on their roots(Q. Wang et al., 2018). They transforms Nitrogen$_2$ into ammonia in this location, which the plant can utilise as a source of N (Spanic et al., 1998 and Rhijn & Vanderleyden, 1995). Azospirillum, an independent living N_2-fixing bacterial species, acts as fertilizer for plants like wheat, sorghum, and maize. Although Azospirillum can fix N2, the elevated rates of uptake of water and minerals that result from its inoculation are what are mostly to blame for the higher yield (Fukami et al., 2018).

Low quantities of soluble phosphate can prevent plants from growing. Certain microbes are capable to dissolve phosphate from both organic and inorganic phosphate molecules, which encourages plant growth (Kalayu, 2019; Oteino et al., 2015; Vassilev et al., 2006). Few of the enzymes that assist the soil in liberating soluble phosphorus from organic molecules include unspecific phosphatases, phytases,

phosphonatases, and C-P lyases. C-P lyases specifically cleave C-P bonds in organophosphonates. Certain bacteria have the capacity to soluble phosphate from both organic and inorganic phosphate molecules, which encourages plant growth (Dhuldhaj & Malik, 2022; Rodriguez et al., 2014).

Rhizoremediators

Since it decreases their efficacy after application, bacteria's limited capacity in order to acclimate to the environmental factors present in a large quantity of soil is an issue for the breakdown of soil pollutants. This reduction occurs as a result of the bacteria starving immediately after application since their primary metabolic depends on the breakdown of the pollutant (Alori et al., 2022; Bottiglieri & Keel, 2006). This issue can be resolved by separating the energy requirements for main metabolism from those for pollutant degradation. Kuiper et al. (2001) created the rhizoremediation (Kuiper et al., 2004) system to do this. They adopted a strategy in which they selected rhizobacteria that can degrade contaminants and are present on or near plant roots, enabling them to use root exudates as their primary source of nutrients. The researchers devised a viable approach to enhance the abundance of said bacteria by initiating the process with a basic amalgamation of bacteria derived from grass roots, employing supplementary criteria for promoting growth on the pollutant naphthalene, and proficiently establishing a presence within roots of grass (Kuiper et al., 2001). The promissing strains, *Pseudomonas putida* PCL1444, demonstrates effective usage of root exudates, naphthalene breakdown close to the roots, seed protection from naphthalene toxicity, and support for conventional plant growth. Plant protection is less effective in mutants that are unable to break down naphthalene (Kuiper et al., 2001).

Phytostimulators

Some bacteria carry ability to elevate the development of plant, even in absence of any pathogenic effects. In addition to other hormones, specifically volatiles, and the coenzyme pyrrolquinoline quinone (PQQ), are also implicated, a suitable example of example of a hormone that stimulates plant development is auxin (Choi et al., 2008).

Auxin, which is present in plant root exudates, is often created by tryptophan amino acid, which is present in the root secretions. Tryptophan contents in exudates vary greatly amongst plant species. After being inoculated with the auxin-producing bacterium *Pseudomonas fluorescens* WCS365, cucumber, sweet pepper, and tomato plants did not enhances in weight of shoot or root. However, radish had a significant enhances in root weight because it produces far more tryptophan per seedling than the other plants. Figure 1 shows an illustration of how bacteria can positively influence the growth of radish. As per Berger et al. (2015), radish plants grown in glasshouses were either inoculated with a 0.05 M NaCl control solution or 107 cfu ml−1 K. radicincitans cells prior to germination. It was observed that K. radicincitans was capable of colonizing and persisting in a member of the Brassicaceae and of promoting radish growth under both glasshouse and natural conditions. Following bacterial application, there was no change in the composition and content of glucosinolate, with the exception of aromatic 2-phenylethyl glucosinolate levels in the leaves.

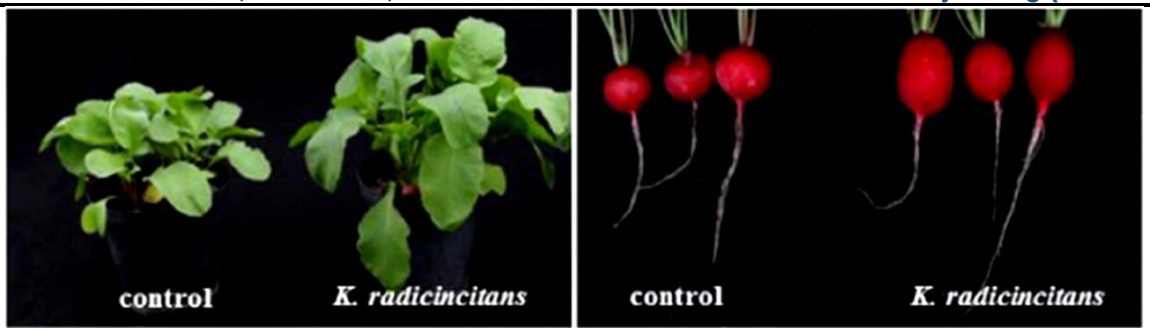

Figure1. Bacteria promotes plant growth: *K. radicincitans* inoculated radish plants.

(Photograph: Berger et al., 2015)

A subtropical grass species contains bacterium *Azotobacter paspali* having the N_2 fixing ability, which encourages the growth of numerous monocotyledonous as well as dicotyledonous plants. Inorganic nitrogen addition investigations show that the impact on growth improvement is because of the plant growth factors production such indole-3-acetic acid (IAA), gibberellins, and cytokinins rather than nitrogen fixation (Samuel et al., 2017).

Some rhizobacteria, including strains of *Bacillus subtilis*, *Bacillus amyloliquefaciens*, and *Enterobacter cloacae*, help plants develop by creating volatiles. The compounds 2,3-butanediol and acetoin have been observed to stimulate growth to the greatest extent. The mutant variants of *Bacillus amyloliquefaciens* IN937 lack the ability to promote plant development. *Bacillus amyloliquefaciens* IN937 who are unable to synthesize these compounds involved in the promotion of plant growth. Earlier this year, Zhang et al. (2008) discovered that B. *subtilis* GB03 increases the efficiency and the amount of chlorophyll in the plant, Arabidopsis thaliana's photosynthetic process by altering the body's normal signals for sensing glucose and abscisic acid. They summarized that the bacterium regulates the plant's ability to produce energy.

The cofactor PQQ has been found to encourage plant development. Synthetic PQQ is well received by tomato and cucumber plants, which shows that it serves a role as an antioxidant in plants. It is probable that the effect will be indirect because PQQ functions as a cofactor for several enzymes involved in systemic resistance development and antifungal activity (Naveed et al., 2017).

Stress Reducers

Bacteria that stimulate plant growth contain the biocatalyst 1-aminocyclopropane-1-carboxylate (ACC deaminase), that helps reduce ethylene levels of plants. The ACC ethylene precursor can be broken down by these microbes into 2-oxobutanoate and NH3. A variety of benefits are associated with the presence of ACC deaminase-producing bacteria in terms of stress reduction, including protection against phytopathogenic bacteria, resistance to polyaromatic hydrocarbon stress, heavy metal stress from Ca2+ and Ni2+, and resistance to salt and drought stress (Glick et al., 2007).

CONTROL OF SOIL-BORNE PLANT DISEASES THROUGH BIOLOGY

Introduction

Plant diseases cause massive agricultural losses each year that reach $200 billion (Agrios, 2005). Traditional disease control methods employ agrochemicals and resistant plant varieties. It takes time to develop resistant plants, and not all diseases have plant options that are resistant. In addition, the use of agrochemicals is being restricted due to unfavorable regulatory requirements and public perceptions, and genetically engineered resistance continues to be a contentious topic in the European Union.

An environmentally friendly way to prevent disease is by using microorganisms, a sort of biological control. These beneficial bacteria produce secondary metabolites on a local level, specifically surrounding to plant surface where their activity is needed. They act as the natural enemies of the diseases. Contrarily, a lot of agrochemicals do not effectively reach the plant. Biologically generated substances are also biodegradable, in contrast to many agrochemicals that are designed to stop microbial oxidation. The term "biocontrol" refers to both the management of diseases in living plants as well as the control of postharvest illnesses that emerge during fruit storage. The fact that some rhizobacteria also exhibit activity against weeds and insects should be noted, even though the majority of studies on the control of diseases by rhizobacteria focus on pathogenic microorganisms (Flores-Vargas & Hara, 2006; Péchy-tarr et al., 2008; Siddiqui et al., 2005).

Pathogens only manifest disease signs in conducive soils. It's interesting to note that spontaneous bacterial sickness control has been observed globally in many different domains. Although pathogens that cause illness are present in some soils, so-called suppressive soils also contain bacteria that protect plants from fungal infections. Combining small amounts of suppressive soil with a larger amount of favourable soil can have suppressive effects. References of Haas & Défago (2005) and Schroth & Hancock (1982) should be read carefully by readers if they want more in-depth information.

The complex process of microbial management of plant diseases involves many different players, including the pathogen, the plant, the biocontrol microbe, the native microflora, macrobiota like worms and protozoa, and the substrate for plant growth, such as soil, stonewool, or vermiculite (Bonaterra et al., 2022). Numerous reviews of biocontrol have been published (Compant et al., 2005, 2019; Ek-Saadony et al., 2022; Etesami & Maheshwari, 2018; Haas & Défago, 2005). The ability to function in a variety of settings, including those with shifting pH, temperature, and ion concentrations, is essential for biocontrol bacteria. To achieve these requirements is difficult. That some first-generation commercial biocontrol products (17 may not be sufficient is not shocking. However, as our understanding of biocontrol procedures and strategies for choosing active strains expands, it is projected that biocontrol products will get better, pointing to a bright future for the technology.

Principles of Biocontrol

We employ the fungal pathogen Forl-caused tomato disease tomato foot and root rot (TFRR) as a model system in our lab to examine the processes used by different bio-control strains. Different model

systems are used by other organizations (Folman et al., 2004; Haas & Défago, 2005; Rosier et al., 2018; H. Wang et al., 2021). You can tell the following mechanisms apart.

Antagonism

Antibiotic-producing bacteria use antagonism to carry out their biocontrol tasks since they can destroy infections. It is obvious how crucial antibiotic synthesis is when mutants lacking the structural genes in charge of antibiotic production exhibit a loss of biocontrol activity. In order for biocontrol to be effective, a bacteria must not only generate and release the antibiotic but also outcompete other organisms for resources and niches on the root, dispersing the antibiotic throughout the entire root system (Chin-a-woeng et al., 2000) (Figure 2). Additionally, the bacterium needs to be guarded against protozoan grazers, which consume rhizosphere bacteria (Jousset et al., 2006). Additionally, for the best biocontrol to happen, the bacterium needs to produce the antibiotic at the appropriate microniche on the root surface (Pliego et al., 2008).

Gram-negative biocontrol microorganisms have been connected to the genesis of many antibiotics. These include phenazines (Chin-a-woeng et al., 1998, Chin-a-woeng et al., 2003, Péchy-tarr et al., 2008), such as phenazine-1-carboxylic acid and phenazine-1-carboxamide, as well as the well-known compounds hydrogen cyanide (HCN) (Haas & Keel, 2003), 2,4-diacetyl phloroglucinol (Phl) (Thomashow & Weller, 1996 and Dunne C. et al., 1998), pyoluteorin (Nowak-thompson et al., 1999), and pyrrolnitrin (Kirner et al., 1998).

Wittermycin A (Emmert et al., 2004) and kanosamine (Milner et al., 2023) are two products that *Bacillus cereus* can make. Biocontrol strains have been found to harbor two newly identified antibiotics: 2-hexyl-5-propyl resorcinol (Cazorla et al., 2006) and D-gluconic acid (Kaur et al., 2006). Plants can also defend themselves by producing combinations of volatile molecules produced by fungi (Strobel, 2006) or Bacillus spp. (Ryu et al., 2003), as well as by 2,3-butanediol and other volatile compounds. Furthermore, *B. subtilis* has been linked to lipopeptide biosurfactants and pseudomonads produced by *Bacillus*. biocontrol (Bruijn et al., 2007). (Ongena et al., 2007). Rhamnolipid and phenazine work synergistically to treat soilborne illnesses caused by Pythium (Perneel et al., 2008).

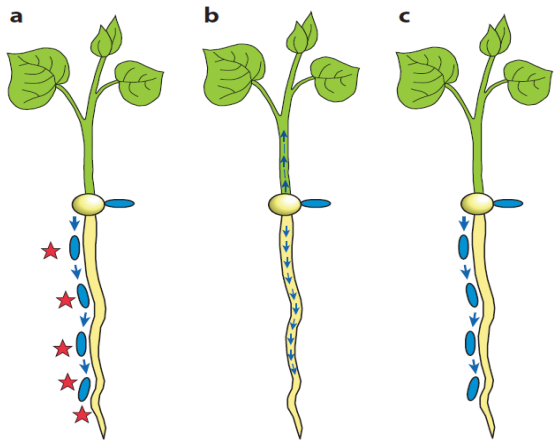

Figure 2. The graphically illustration of primary basic mechanisms by which microorganisms control plant diseases. In each of the aforementioned instances, the biocontrol process is initiated by spreading the biocontrol bacterium over the seeds. (a) Antibiosis: A bacterium colonizes a root system that is expanding and produces antibiotic compounds nearby that kill invading pathogens (shown by stars). (b) Induced systemic resistance (ISR): Local root colonization may result in ISR. Systemic signaling is stimulated by diverse bacterial chemicals, which shields the entire plant from diseases caused by various species. Similar to innate immunity, which occurs in both humans and animals, this ISR trait is present. Competition for nutrients and niches: When utilizing this method, biocontrol bacteria show adept chemotactic movement along the growing root, fervently pursuing root exudate elements. By out-competing pathogens for resources and occupying root niches, they excel at reducing pathogen colonization.

Interfering with Signals

As a component of a biocontrol system employed by bacteria, molecules that sense quorum, including homoserine lactones (AHLs), which concentrate at high bacterial cell densities, regulate the expression of pathogenicity or virulence proteins (Kumar et al., 2022). AHLs are essential for the synthesis of enzymes that dissolve cell walls in infections like Erwinia carotovora. AHLs can be broken down to interfere with signals, for instance, by AHL lactonases that break down the lactone ring or AHL acylases that break down the amide link. Recent research suggests that AHL acylases contribute to the formation of biofilms (Sikdar & Elias, 2021). The absence of biofilm formation undoubtedly makes the biocontrol process simpler.

Parasitism and Predation

The enzymatic breakdown of fungal cell walls is caused by parasitism and predation in several Trichoderma fungal species, which are significant biocontrol methods (S. Sharma et al., 2020). Although this method has not been fully characterized in bacteria, it is believed that the fungus eater Collimonas fungivorans uses CNN rather than predation and parasitism to suppress fungal root infections (B. Lugtenberg et al., 2017).

Induced Systemic Resistance

Induced systemic resistance (ISR), a different biocontrol technique, involves specific bacteria interacting with plant roots to build resistance to bacterial, fungal, and viral illnesses. In humans, ISR and innate immunity are similar (Choudhary & Johri, 2009). Inducers of ISR in bacteria include LPS, flagella, salicylic acid, siderophores, cyclic lipopeptides, the antifungal factor Phl, AHLs, and volatile mixtures (Iavicoli et al., 2003; Ongena et al., 2007; Ryu et al., 2003; Schuhegger et al., 2006). Contrary to other biocontrol mechanisms, ISR does not require extensive root colonization, as demonstrated by *Pseudomonas fluorescens* WCS365 mutants with impaired root colonization that still produce ISR (Dekkers et al., 2000; Kamilova et al., 2005).

The discovery that some strains of the Bacillus cereus, which are notoriously poor colonizers, may serve as effective biocontrol agents, however, shows that ISR rather than antibiosis is the cause of these strains' presence (Islam & Hossain, 2016). It is believed that many Bacillus strains utilise ISR to carry out their biocontrol activities.

According to studies, Pseudomonas syringae pv. Increased L-malic acid secretion by the roots as a result of tomato Pst DC3000 infection of Arabidopsis thaliana seedling leaves attracts the beneficial rhizobacterium Bacillus subtilis FB17, which performs as a biocontrol bacteria through ISR. Because it is unlikely that only good bacteria show chemotaxis to L-malic acid, the claim that enhanced L-malic acid secretion pulls only good bacteria is baseless (Rudrappa et al., 2008 and Weert et al., 2002).

Ferric iron ions are in competition

If a bacterial strain inhibits fungal growth on a test plate with low ferric iron content but not when additional Fe3+ ions are introduced, it is likely that the bacterial strain will produce a siderophore, a molecule that chelates Fe3+ ions. After the siderophore attaches to the Fe3+ ion to form a siderophore-Fe3+ complex, iron-limitation-dependent receptors on the surface of bacterial cells recognize and bind the complex. In the bacterial cytoplasm, the Fe3+ ion is then liberated and activates as Fe2+. Bacteria that produce a lot of high-affinity siderophores in the rhizosphere can inhibit the growth of fungal pathogens when Fe3+ concentrations are low, as they are in acidic soils (Schippers et al., 1987).

Competition for Resources and Niches

Competition for nutrients and niches (CNN), long regarded as a workable biocontrol strategy, lacked scientific backing. Kamilova et al. chose biocontrol strains to demonstrate this method after a number of enrichment cycles. After a variety of rhizosphere strains were added to sterilised seeds and allowed to sprout under carefully monitored conditions, the best competitive root colonisers were then isolated from the root tips. These solitary bacteria, which also grew on root exudate, successfully colonized the roots. The majority of the isolates, including Pseudomonas strains PCL1751 and PCL1760, were successful in avoiding the target fungal root rot (TFRR), which is notable. Mutant studies (Kamilova et al., 2005 and Validov, 2007 chapter 4) validated the proposed CNN mechanism. Although one of the extremely competitive root-tip colonizers lacked TFRR control, Kamilova et al. 2005 pointed this out.

Only one strain was capable of successfully preventing white root rot in avocados, despite the fact that Pliego et al., 2008 discovered and further tested two similar enhanced root colonisers. These strains' ability to colonize multiple locations on the root highlights the importance of precisely filling certain root niches for effective plant defense. After 3 weeks in the biocontrol of TFRR in stonewool substrate, the CNN strain Pseudomonas putida PCL1760 displayed noticeably increased root cell presence compared to all other culturable bacteria put together (Validov, 2007 chapter 4). This result highlights the CNN strain's incredible capacity for defense in this circumstance.

Interference with the survival, germination, sporulation, and activity of the pathogen

Pseudomonas fluorescens WCS365 cells are chemically drawn to fusaric acid, which is released by Forl hyphae. By extensively colonizing the pathogen Forl's hyphae and developing microcolonies on them, *P. fluorescens* WCS365 efficiently targets fungal root rot (TFRR). The virulence of the fungus will presumably decrease as a result of this colonization. Scanning electron microscopy studies show that *P. fluorescens* WCS365 also colonizes Forl hyphae when cultivated in root exudate. Studies employing different growth media have shown that the degree of hyphal colonization is greater in nutrient-poor environments, supporting the idea that bacteria utilise hyphae as a food source.

P. fluorescens WCS365 inhibits the germination of Forl's microconidia, which are spores, most likely due to a lack of nutrients. Additionally, the pathogen can be dispersed in the environment via Forl hyphae that develop into microconidia in root exudate. *P. fluorescens* WCS365 slows down the spore formation process, which limits the pathogen's capacity to spread. The pathogen's overall activity, survival, and germination are all inhibited by *P. fluorescens* WCS365, which also colonizes its hyphae and stops the development of fresh spores. These processes, which may not be specific to biocontrol strains, considerably aid in lowering TFRR when plants are grown in fresh stonewool, which is essentially sterile, and *P. fluorescens* WCS365 is given to the plant nutrition solution.

Other Biocontrol Aspects

To improve the effectiveness of disease control, seeds were inoculated with two distinct biocontrol strains. However, our research demonstrates that these mixtures did not lead to better illness management. This finding can be attributed, in part, to the fact that the population levels of each bacterium on the root were decreased below the level required for effective disease control.

Native soil bacteria have the ability to produce a variety of compounds that inhibit the beneficial effects of biocontrol strains and outcompete them for root colonization. New stonewool has advantages and disadvantages as a growing medium. However, biocontrol bacteria can be added to make up for this since it is essentially devoid of active microorganisms, which might result in considerable plant losses when exposed to invading pathogens in a greenhouse setting. Pseudomonas putida PCL1760, for instance, demonstrated enduring dominance over the root and a significant preference for stonewool. Similar results were observed in the salinated desert soil of Uzbekistan, which is devoid of native microbes and has a low concentration of organic matter. Both potential human diseases and plant pathogens are a component of the natural microflora. In these conditions, seed inoculation with biocontrol bacteria that are stress-adapted significantly reduces the occurrence of plant diseases and may also protect field workers from pathogen exposure.

Using the Past to Create a Glorious Future

Many bacterial strains are effective in lab culture, but only a small percentage are effective in lab greenhouses, and even fewer are effective in natural environments like commercial greenhouses or fields (Compant et al., 2019). Understanding the reasons behind these failures can lead to the isolation of improved strains. Antibiosis-based strains have been used extensively and are typically effective, but they can fail for a number of reasons (Pankaj O Baisthakur et al., 2022; Davies & Davies, 2010).

One reason for failures is phase variation, which happens when biocontrol properties like root colonization, motility, and the production of beneficial chemicals undergo reversible and frequent phenotypic switching caused by DNA mutation, reorganisation, or change (Woude & Baumler, 2004). The complex, poorly understood regulation of secondary metabolite production is another challenge. The creation of a particular molecule can be significantly influenced by a number of factors, including the growth temperature, salinity, and ion concentrations. Furthermore, biocontrol bacteria can degrade their own antibiotics to produce less effective derivatives. AHLs, essential signal molecules for the synthesis of several beneficial chemicals and enzymes, can also be destroyed by competing bacteria. Several useful compounds can't be synthesized by biocontrol bacteria because of the pathogen-produced metabolite fusaric acid, especially at the level of AHL production required for compound biosynthesis (Sanchez-contreras et al., 2007).

Not all fungi are merely susceptible to antagonistic biocontrol bacteria, as certain diseases can defend themselves and evolve resistance through a number of mechanisms, including enzymatic inactivation, gene suppression, target change, or toxin release (El-baky & Amara, 2021).

Taking into account these aspects and the disincentive to registering antibiotic-producing products due to concerns about antibiotic cross-resistance with human and animal antibiotics, it seems that biocontrol strains using mechanisms other than antibiosis may have a better chance of navigating the registration process and becoming viable products. In some environmental circumstances, it is currently possible to select for strains that depend on competition for nutrients and niches (CNN), as opposed to those that use mechanisms like induced systemic resistance (ISR), which are not currently conceivable (Paquette et al., 2018).

Acknowledgement:

The first author of this work is thankful to Mr. Kiran Jagtap, Divisional Forest Officer, Wildlife Pandharkawada (Maharashtra) and Mr. Bharat Khelbade, Assistant Conservator of Forest, Painganga Wildlife Sanctuary, Umerkhed (Maharashtra).

Grant information

The author(s) stated that this work was not supported by any grants.

References

Agrios, G. N. (2005). *Plant pathology* (5th ed.). Elsevier Academic Press.

Alori, E. T., Gabasawa, A. I., Elenwo, C. E., & Agbeyegbe, O. O. (2022). Bioremediation techniques as affected by limiting factors in soil environment. *Frontiers in Soil Sciences*, *2*(937186), 1–13. https://doi.org/10.3389/fsoil.2022.937186

Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., & Smith, D. L. (2018). Plant Growth-Promoting Rhizobacteria : Context , Mechanisms of Action , and Roadmap to Commercialization of Biostimulants for Sustainable Agriculture. *Frontiers in Plant Science*, *9*, 1–17. https://doi.org/10.3389/fpls.2018.01473

Baisthakur, P O, Kadam, T. A., & Bhosale, H. J. (2022). Studies On Rhizospheric Actinomycetes Of Legumes. *Bioinfolet*, *19*(2), 91–93.

Baisthakur, Pankaj O, Kadam, T. A., Bhosale, H. J., & Ramangire, M. A. (2022). Antibiotic-resistant bacterial pathogens associated with raw vegetables from Nanded city. *Journal of Emerging Technologies and Innovative Research*, *9*(1), 561–566.

Barbier, M., & Damron, F. H. (2016). Rainbow Vectors for Broad-Range Bacterial Fluorescence Labeling. *PLoS ONE*, *11*(3), e0146827. https://doi.org/10.1371/journal.pone.0146827

Berger, B., Wiesner, M., Brock, A. K., & Schreiner, M. (2015). K . radicincitans , a beneficial bacteria that promotes radish growth under field conditions. *Agronomy for Sustainable Development*, *35*, 1521–1528. https://doi.org/10.1007/s13593-015-0324-z

Bloemberg, G. V, Wijfjes, A. H. M., Lamers, G. E. M., & Stuurman, N. (2000). Simultaneous Imaging of Pseudomonas fluorescens WCS365 Populations Expressing Three Different Autofluorescent Proteins in the Rhizosphere : New Perspectives for Studying Microbial Communities. *Molecular Plant-Microbe Interactions*, *13*(11), 1170–1176. https://doi.org/10.1094/MPMI.2000.13.11.1170

Bolwerk, A., Lagopodi, A. L., Wijfjes, A. H. M., Lamers, G. E. M., Thomas, F. C., Lugtenberg, B. J. J., Bloemberg, G. V, & Wcs, P. (2003). Interactions in the Tomato Rhizosphere of Two Pseudomonas Biocontrol Strains with the Phytopathogenic Fungus Fusarium oxysporum f . sp . radicis-lycopersici. *Molecular Plant-Microbe Interactions*, *16*(11), 983–993.

Bonaterra, A., Badosa, E., & Daranas, N. (2022). Bacteria as Biological Control Agents of Plant Diseases. *Microorganisms*, *10*(1759), 1–17.

Bottiglieri, M., & Keel, C. (2006). Characterization of PhlG , a Hydrolase That Specifically Degrades the Antifungal Compound 2 , 4-Diacetylphloroglucinol in the Biocontrol Agent Pseudomonas fluorescens CHA0 Me. *Applied and Environmental Microbiology*, *72*(1), 418–427. https://doi.org/10.1128/AEM.72.1.418

Bruijn, I. De, Kock, M. J. D. De, Yang, M., Waard, P. De, Beek, T. A. Van, & Raaijmakers, J. M. (2007). Genome-based discovery , structure prediction and functional analysis of cyclic lipopeptide antibiotics in Pseudomonas species. *Molecular Microbiology*, *63*(2), 417–428. https://doi.org/10.1111/j.1365-

2958.2006.05525.x

Cazorla, F. M., Duckett, S. B., Bergström, E. T., Noreen, S., Odijk, R., Lugtenberg, B. J. J., Thomas-oates, J. E., & Bloemberg, G. V. (2006). Biocontrol of Avocado Dematophora Root Rot by Antagonistic Pseudomonas fluorescens PCL1606 Correlates With the Production of 2-Hexyl 5-Propyl Resorcinol. *Molecular Plant-Microbe Interactions*, *19*(4), 418–428.

Chin-a-woeng, T. F. C., Bloemberg, G. V, Mulders, I. H. M., Dekkers, L. C., & Lugtenberg, B. J. J. (2000). Root Colonization by Phenazine-1-Carboxamide- Producing Bacterium Pseudomonas chlororaphis PCL1391 Is Essential for Biocontrol of Tomato Foot and Root Rot. *Molecular Plant-Microbe Interactions*, *13*(12), 1340–1345.

Choi, O., Kim, J., Kim, J., Jeong, Y., Moon, J. S., Park, C. S., & Hwang, I. (2008). Pyrroloquinoline Quinone Is a Plant Growth Promotion Factor Produced by Pseudomonas fluorescens B16 1. *Plant Physiology*, *146*, 657–668. https://doi.org/10.1104/pp.107.112748

Choudhary, D. K., & Johri, B. N. (2009). Interactions of Bacillus spp . and plants – With special reference to induced systemic resistance (ISR). *Microbiological Research*, *164*, 493–513. https://doi.org/10.1016/j.micres.2008.08.007

Compant, S., Duffy, B., Nowak, J., Duffy, B., Nowak, J., & Cle, C. (2005). Use of Plant Growth-Promoting Bacteria for Biocontrol of Plant Diseases : Principles , Mechanisms of Action , and Future Prospects. *Applied and Environmental Microbiology*, *71*(9), 4851–4959. https://doi.org/10.1128/AEM.71.9.4951

Compant, S., Samad, A., Faist, H., & Sessitsch, A. (2019). A review on the plant microbiome : Ecology , functions , and emerging trends in microbial application. *Journal of Advanced Research*, *19*, 29–37. https://doi.org/10.1016/j.jare.2019.03.004

Davies, J., & Davies, D. (2010). Origins and Evolution of Antibiotic Resistance. *Microbial and Molecular Biology Reviews*, *74*(3), 417–433. https://doi.org/10.1128/MMBR.00016-10

Dekkers, L. C., Mulders, I. H. M., Phoelich, C. C., Chin-a-woeng, T. F. C., Wijfjes, A. H. M., & Lugtenberg, B. J. J. (2000). The sss Colonization Gene of the Tomato-Fusarium oxysporum f . sp . radicis- lycopersici Biocontrol Strain Pseudomonas fluorescens WCS365 Can Improve Root Colonization of Other Wild-type Pseudomonas spp . Bacteria. *Molecular Plant-Microbe Interactions*, *13*(11), 1177–1183.

Dhuldhaj, U. P., & Malik, N. (2022). Global perspective of phosphate solubilizing microbes and phosphatase for improvement of soil , food and human health. *Cellular, Molecular and Biomedical Reports*, *2*(3), 173–186.

Ek-Saadony, M. T., Saad, A. M., Soliman, S. M., Salem, H. M., Ahmed, A. I., Ek-Mageed, T. A., Negm, S. H., Selim, S., Babalghith, A. O., Elrys, A. S., El-Tarabily, K. A., & AbuQamar, S. F. (2022). Plant growth-promoting microorganisms as biocontrol agents of plant diseases : Mechanisms , challenges

and future perspectives. *Frontiers in Plant Science*, *13*(923880), 1–19. https://doi.org/10.3389/fpls.2022.923880

El-baky, N. A., & Amara, A. A. A. F. (2021). Recent Approaches towards Control of Fungal Diseases in Plants : An Updated Review. *Journal of Fungi*, *7*(900), 1–17.

Emmert, E. A. B., Klimowicz, A. K., Michael, G., & Handelsman, J. (2004). Genetics of Zwittermicin A Production by Bacillus cereus. *Applied and Environmental Microbiology*, *70*(1), 104–113. https://doi.org/10.1128/AEM.70.1.104

Etesami, H., & Maheshwari, D. K. (2018). Ecotoxicology and Environmental Safety Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture : Action mechanisms and future prospects. *Ecotoxicology and Environmental Safety*, *156*(January), 225–246. https://doi.org/10.1016/j.ecoenv.2018.03.013

Flores-Vargas, R. D., & Hara, G. W. O. (2006). Isolation and characterization of rhizosphere bacteria with potential for biological control of weeds in vineyards. *Journal of Applied Microbiology*, *100*, 946–954. https://doi.org/10.1111/j.1365-2672.2006.02851.x

Folman, L. B., Klein, M. J. E. M. De, Postma, J., & Veen, J. A. Van. (2004). Production of antifungal compounds by Lysobacter enzymogenes isolate 3 . 1T8 under different conditions in relation to its efficacy as a biocontrol agent of Pythium aphanidermatum in cucumber. *Biological Control*, *31*, 145–154. https://doi.org/10.1016/j.biocontrol.2004.03.008

Fukami, J., Cerezini, P., & Hungria, M. (2018). Azospirillum : benefits that go far beyond biological nitrogen fixation. *AMB Express*, *8*(73), 1–12. https://doi.org/10.1186/s13568-018-0608-1

Glick, B. R. (2012). Plant Growth-Promoting Bacteria : Mechanisms and Applications. *Scientifica*, *2012*(963401), 1–15.

Glick, B. R., Cheng, Z., Czarny, J., & Duan, J. (2007). Promotion of plant growth by ACC deaminase-producing soil bacteria. *European Journal of Plant Pathology*, *119*, 329–339.

Haas, D., & Défago, G. (2005). Biological Control of Soil-Borne Pathogens by Fluorescent Pseudomonads. *Nature Reviews Microbiology*, *3*, 307–319. https://doi.org/10.1038/nrmicro1129

Haas, D., & Keel, C. (2003). REGULATION OF ANTIBIOTIC PRODUCTION IN ROOT-COLONIZING PSEUDOMONAS SPP. AND RELEVANCE FOR BIOLOGICAL CONTROL OF PLANT DISEASE. *Annual Reviews in Phytopathology*, *41*(63), 117–153. https://doi.org/10.1146/annurev.phyto.41.052002.095656

Iavicoli, A., Boutet, E., Buchala, A., & Métraux, J. (2003). Induced Systemic Resistaance in Arabidopsis thaliana in Response to Root Inoculation with Pseudomonas fluorescens CHA0. *Molecular Plant-Microbe Interactions*, *16*(10), 851–858.

Islam, M. T., & Hossain, M. M. (2016). Chapter 7 Biological Control of Peronosporomycete Phytopathogen

by Bacterial Antagonist. In *Biological Control of peronosporomycete phytopathogens* (Issue November, pp. 167–218). https://doi.org/10.1007/978-3-642-33639-3

Jousset, A., Lara, E., Wall, L. G., Valverde, C., & Sa, R. (2006). Secondary Metabolites Help Biocontrol Strain Pseudomonas fluorescens CHA0 To Escape Protozoan Grazing. *Applied and Environmental Microbiology*, *72*(11), 7083–7090. https://doi.org/10.1128/AEM.00557-06

Kalayu, G. (2019). Phosphate Solubilizing Microorganisms : Promising Approach as Biofertilizers. *International Journal of Agronomy*, *2019*(491756).

Kamilova, F., Kravchenko, L. V, Shaposhnikov, A. I., Azarova, T., Makarova, N., & Lugtenberg, B. (2006). Organic Acids , Sugars , and L -Tryptophane in Exudates of Vegetables Growing on Stonewool and Their Effects on Activities of Rhizosphere Bacteria. *Molecular Plant-Microbe Interactions*, *19*(3), 250–256.

Kamilova, F., Kravchenko, L. V, Shaposhnikov, A. I., Makarova, N., & Lugtenberg, B. (2006). Effects of the Tomato Pathogen Fusarium oxysporum f . sp . radicis-lycopersici and of the Biocontrol Bacterium Pseudomonas fluorescens WCS365 on the Composition of Organic Acids and Sugars in Tomato Root Exudate. *Molecular Plant-Microbe Interactions*, *19*(10), 1121–1126.

Kamilova, F., Lamers, G., & Lugtenberg, B. (2008). Brief report Biocontrol strain Pseudomonas fluorescens WCS365 inhibits germination of Fusarium oxysporum spores in tomato root exudate as well as subsequent formation of new spores. *Environmental Microbiology*, *10*(6), 2455–2461. https://doi.org/10.1111/j.1462-2920.2008.01638.x

Kamilova, F., Validov, S., Azarova, T., Mulders, I., & Lugtenberg, B. (2005). Enrichment for enhanced competitive plant root tip colonizers selects for a new class of biocontrol bacteria. *Environmental Microbiology*, *7*(11), 1809–1817. https://doi.org/10.1111/j.1462-2920.2005.00889.x

Kaur, R., Macleod, J., Foley, W., & Nayudu, M. (2006). Gluconic acid : An antifungal agent produced by Pseudomonas species in biological control of take-all. *Phytochemistry*, *67*, 595–604. https://doi.org/10.1016/j.phytochem.2005.12.011

Kirner, S., Hammer, P. E., Hill, D. S., Altmann, A., Fischer, I., Weislo, L. J., Lanahan, M., & Ligon, J. M. (1998). Functions Encoded by Pyrrolnitrin Biosynthetic Genes from Pseudomonas fluorescens. *Journal of Bacteriology*, *180*(7), 1939–1943.

Knights, H. E., Jorrin, B., Haskett, T. L., & Poole, P. S. (2021). Deciphering bacterial mechanisms of root colonization. *Environmental Microbiology Reports*, *13*(4), 428–444. https://doi.org/10.1111/1758-2229.12934

Kuiper, I., Bloemberg, G. V, & Lugtenberg, B. J. J. (2001). Selection of a Plant-Bacterium Pair as a Novel Tool for Rhizostimulation of Polycyclic Aromatic Hydrocarbon-Degrading Bacteria. *Molecular Plant-Microbe Interactions*, *14*(10), 1197–1205.

Kuiper, I., Lagendijk, E. L., Bloemberg, G. V, & Lugtenberg, B. J. J. (2004). Rhizoremediation : A Beneficial Plant-Microbe Interaction. *Molecular Plant-Microbe Interactions*, *17*(1), 6–15.

Kumar, L., Kumar, S., Patel, S., Kharga, K., Kumar, R., Kumar, P., Pandohee, J., Kulshresha, S., Harjai, K., & Chhibber, S. (2022). Molecular Mechanisms and Applications of N-Acyl Homoserine Lactone-Mediated Quorum Sensing in Bacteria. *Molecules*, *27*(7584), 1–28.

Liu, Z., Hossaian, S. S., Moreira, Z. M., & Haney, C. H. (2022). Putrescine and Its Metabolic Precursor Arginine Promote. *Journal of Bacteriology*, *204*(1), 1–12.

Loon, L. C. Van. (2007). Plant responses to plant growth-promoting rhizobacteria. *European Journal of Plant Pathology*, *119*, 243–254. https://doi.org/10.1007/s10658-007-9165-1

Lugtenberg, B. E. N., & Alphen, L. V. A. N. (1983). MOLECULAR ARCHITECTURE AND FUNCTIONING OF THE OUTER MEMBRANE OF E S C H E R I C H I A C O L I AND OTHER GRAM-NEGATIVE BACTERIA. *Biochemical et Biophysica Acta*, *737*, 51–115.

Lugtenberg, B. J. J., Dekkers, L., & Bloemberg, G. V. (2001). Molecular Determinants of Rhizosphere Colonization by Pseudomonas. *Annual Reviews in Phytopathology*, *39*(1), 461–490.

Lugtenberg, B. J. J., & Dekkers, L. C. (1999). Minireview What makes Pseudomonas bacteria rhizosphere competent ? *Environmental Microbiology*, *1*(1), 9–13.

Lugtenberg, B. J. J., Kravchenko, L. V, & Simons, M. (1999). Tomato seed and root exudate sugars : composition , utilization by Pseudomonas biocontrol strains and role in rhizosphere colonization. *Environmental Microbiology*, *1*(5), 439–446.

Lugtenberg, B., Rozen, D. E., & Kamilova, F. (2017). Wars between microbes on roots and fruits. *F1000 Research*, *6*(343), 1–13. https://doi.org/10.12688/f1000research.10696.1

Maarastawi, S. A., Frindte, K., Linnartz, M., & Knief, C. (2018). Crop Rotation and Straw Application Impact Microbial Communities in Italian and Philippine Soils and the Rhizosphere of Zea mays. *Frontiers in Microbiology*, *9*(1295), 1–17. https://doi.org/10.3389/fmicb.2018.01295

Marschner, H. (1995). *Mineral Nutrition of Higher Plants: Vol. Second Edi*.

Milner, J. L., Silo-suh, L., Lee, J. C., He, H., Clardy, J. O. N., & Handelsman, J. O. (2023). Production of Kanosamine by Bacillus cereus UW85. *Appl Ied and Environmental Microbiology*, *62*(8), 3061–3065.

Naveed, M., Tariq, K., Sadia, H., Ahmad, H., & Mumtaz, A. S. (2017). The Life History of Pyrroloquinoline Quinone (PQQ): A Versatile Molecule with Novel Impacts on Living Systems. *International Journal of Molecular Biology*, *1*(1), 1–20. https://doi.org/10.15406/ijmboa.2016.01.00005

Niu, B., Wang, W., Yuan, Z., Sederoff, R. R., Sederoff, H., Chiang, V. L., & Borriss, R. (2020). Microbial Interactions Within Multiple-Strain Biological Control Agents Impact Soil-Borne Plant Disease.

Frontiers in Microbiology, *11*(585404), 1–16. https://doi.org/10.3389/fmicb.2020.585404

Nowak-thompson, B., Chaney, N., Wing, J. S., & Gould, S. J. (1999). Characterization of the Pyoluteorin Biosynthetic Gene Cluster of Pseudomonas fluorescens Pf-5. *Journal of Bacteriology*, *181*(7), 2166–2174.

Ongena, M., Jourdan, E., Adam, A., Paquot, M., Brans, A., Joris, B., Arpigny, J., & Thonart, P. (2007). Brief report Surfactin and fengycin lipopeptides of Bacillus subtilis as elicitors of induced systemic resistance in plants. *Environmental Microbiology*, *9*(4), 1084–1090. https://doi.org/10.1111/j.1462-2920.2006.01202.x

Oteino, N., Lally, R. D., Kiwanuka, S., Lloyd, A., Ryan, D., Germaine, K. J., & Dowling, D. N. (2015). Plant growth promotion induced by phosphate solubilizing endophytic Pseudomonas isolates. *Frontiers in Microbiology*, *6*(745), 1–9. https://doi.org/10.3389/fmicb.2015.00745

Paquette, S., Zaheer, R., Stanford, K., Thomas, J., & Reuter, T. (2018). veterinary sciences Competition among Escherichia coli Strains for Space and Resources. *Veterinary Sciences*, *5*(93), 1–15. https://doi.org/10.3390/vetsci5040093

Péchy-tarr, M., Bruck, D. J., Maurhofer, M., Fischer, E., Vogne, C., Henkels, M. D., Donahue, K. M., Grunder, J., Loper, J. E., & Keel, C. (2008). Molecular analysis of a novel gene cluster encoding an insect toxin in plant-associated strains of Pseudomonas fluorescens. *Environmental Microbiology*, *10*(9), 2368–2386. https://doi.org/10.1111/j.1462-2920.2008.01662.x

Perneel, M., Liesbet, D., Maeyer, K. De, Adiobo, A., Rabaey, K., & Höfte, M. (2008). Phenazines and biosurfactants interact in the biological control of soil-borne diseases caused by Pythium spp . *Environmental Microbiology*, *10*(3), 778–788. https://doi.org/10.1111/j.1462-2920.2007.01501.x

Phillips, D. A., Fox, T. C., King, M. D., Bhuvaneswari, T. V, & Teuber, L. R. (2004). Microbial Products Trigger Amino Acid Exudation from Plant Roots 1. *Plant Physiology*, *136*, 2887–2894. https://doi.org/10.1104/pp.104.044222.a

Pliego, C., Weert, S. De, Lamers, G., Vicente, A. De, Bloemberg, G., Cazorla, F. M., Ramos, C., & Avo, P. (2008). Two similar enhanced root-colonizing Pseudomonas strains differ largely in their colonization strategies of avocado roots and Rosellinia necatrix hyphae. *Environmental Microbiology*, *10*(12), 3295–3304. https://doi.org/10.1111/j.1462-2920.2008.01721.x

Rezzonico, F., Binder, C., Défago, G., & Moënne-loccoz, Y. (2005). The Type III Secretion System of Biocontrol Pseudomonas fluorescens KD Targets the Phytopathogenic Chromista Pythium ultimum and Promotes Cucumber Protection. *Molecular Plant-Microbe Interactions*, *18*(9), 991–1001.

Rhijn, P. Van, & Vanderleyden, J. (1995). The Rhizobium -Plant Symbiosis. *Miicrobiological Reviews*, *59*(1), 124–142.

Rochat, L., Péchy-tarr, M., Baehler, E., Maurhofer, M., & Keel, C. (2010). Combination of Fluorescent

Reporters for Simultaneous Monitoring of Root Colonization and Antifungal Gene Expression by a Biocontrol Pseudomonad on Cereals with Flow Cytometry. *Molecular Plant-Microbe Interactions*, *23*(7), 949–961.

Rodriguez, H., Vidal, R. F., & Bashan, Y. (2014). Genetics of phosphate solubilization and its potential applications for improving plant growth-promoting bacteria. *Plant and Soil*, *278*, 15–21. https://doi.org/10.1007/978-1-4020-5765-6

Rohrbacher, F., & St-arnaud, M. (2016). Root Exudation : The Ecological Driver of Hydrocarbon Rhizoremediation. *Agronomy*, *6*(19), 1–27. https://doi.org/10.3390/agronomy6010019

Rosier, A., Medeiros, F. H. V, & Bais, H. P. (2018). Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. *Plant Soil*, *1*, 1–21. https://doi.org/Rosier, Amanda; Medeiros, Flávio H. V.; Bais, Harsh P. (2018). Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. Plant and Soil, (), –. doi:10.1007/s11104-018-3679-5

Rudrappa, T., Czymmek, K. J., Pare, P. W., & Bais, H. P. (2008). Root-Secreted Malic Acid Recruits Beneficial Soil Bacteria. *Plant Physiology*, *148*(1), 1547–1556. https://doi.org/10.1104/pp.108.127613

Ryu, C., Farag, M. A., Hu, C., Reddy, M. S., Wei, H., Pare, P. W., & Kloepper, J. W. (2003). Bacterial volatiles promote growth in Arabidopsis. *Proceedings of the National Academy of Sciences*, *100*(8), 4927–4932.

Saeed, Q., Xiukang, W., Haider, F. U., Mumtaz, M. Z., Holatko, J., Naseem, M., Kintl, A., Ejaz, M., Naveed, M., Brtnicky, M., & Mustafa, A. (2021). Rhizosphere Bacteria in Plant Growth Promotion , Biocontrol , and Bioremediation of Contaminated Sites : A Comprehensive Review of Effects and Mechanisms. *International Journal of Molecular Sciences*, *22*(10529).

Samuel, O., Bernard, O., Olubukola, R. G., & Babalola, O. (2017). Mechanisms of action of plant growth promoting bacteria. *World Journal of Microbiology and Biotechnology*, *33*(11), 1–16. https://doi.org/10.1007/s11274-017-2364-9

Sanchez-contreras, M., Bauer, W. D., Gao, M., Robinson, J. B., Downie, J. A., Lane, C., & Nr, N. (2007). Quorum-sensing regulation in rhizobia and its role in symbiotic interactions with legumes. *Philosophical Transactions of The Royal Society B*, *362*, 1149–1163. https://doi.org/10.1098/rstb.2007.2041

Schippers, B., Bakker, A. W., & Bakker, P. A. H. M. (1987). INTERACTIONS OF DELETERIOUS AND BENEFICIAL RHIZOSPHERE MICROORGANISMS AND THE EFFECT OF CROPPING PRACTICES. *Annual Reviews in Phytopathology*, *25*, 339–358.

Schroth, M. N., & Hancock, J. G. (1982). Disease-Suppressive Soil and Root-Colonizing Bacteria. *Science*, *216*, 1376–1381.

Schuhegger, R., Ihring, A., Gantner, S., Bahnweg, G., Knappe, C., Vogg, G., Hutzler, P., Schmid, M., Breusegem, F. Van, Eberl, L., Hartmann, A., & Langebartels, C. (2006). Induction of systemic resistance in tomato by N -acyl-L- homoserine lactone-producing rhizosphere bacteria. *Plant, Cell and Environment*, *29*, 909–918. https://doi.org/10.1111/j.1365-3040.2005.01471.x

Sharma, M., Saleh, D., Charron, J., & Jabaji, S. (2020). A Crosstalk Between Brachypodium Root Exudates , Organic Acids , and Bacillus velezensis B26 , a Growth Promoting Bacterium. *Frontiers in Microbiology*, *11*(575578), 1–18. https://doi.org/10.3389/fmicb.2020.575578

Sharma, S., Kour, D., Rana, K. L., Dhiman, A., Thakur, S., Thakur, P., Thakur, S., Thakur, N., Sudheer, S., Yadav, N., Yadav, A. N., Rasegari, A. A., & Karan, S. (2020). Chapter 3 Trichoderma: Biodiversity, Ecological Significances, and Industrial Applications. In *Recent Advancement in White Biotechnology Through Fungi Volume 1 : Diversity and Enzymes Perspectives* (Issue October 2019, pp. 85–120).

Siddiqui, I. A., Haas, D., & Heeb, S. (2005). Extracellular Protease of Pseudomonas fluorescens CHA0, a Biocontrol Factor with Activity against the Root-Knot Nematode Meloidogyne incognita. *Applied and Environmental Microbiology*, *71*(9), 5646–5649. https://doi.org/10.1128/AEM.71.9.5646

Sikdar, R., & Elias, M. (2021). Quorum quenching enzymes and their effects on virulence, biofilm and microbiomes: a review of recent advances. *Expert Review of Anti-Infective Therapy*, *18*(12), 1221–1233. https://doi.org/10.1080/14787210.2020.1794815.Quorum

Simons, M., Permentier, H. P., Weger, L. A. De, Wijffelman, C. A., & Ben, J. J. L. (1997). Amino Acid SyntAmino Acid Synthesis Is Necessary for Tomato Root Colonization by Pseudomonas fluorescens Strain WCS365. *Molecular Plant-Microbe Interactions*, *10*(1), 102–106. https://doi.org/10.1094/MPMI.1997.10.1.102

Strobel, G. (2006). Harnessing endophytes for industrial microbiology. *Current Opinion in Microbiology*, *9*, 240–244. https://doi.org/10.1016/j.mib.2006.04.001

Upadhyay, S. K., Srivastava, A. K., Rajput, V. D., Chauhan, P. K., Bhojiya, A. A., Jain, D., Chaubey, G., Dwivedi, P., Sharma, B., & Minkina, T. (2022). Root Exudates : Mechanistic Insight of Plant Growth Promoting Rhizobacteria for Sustainable Crop Production. *Frontiers in Microbiology*, *13*(916488), 1–19. https://doi.org/10.3389/fmicb.2022.916488

Validov, S. (2007). *Biocontrol of tomato foot and root rot by Pseudomonas bacteria in stonewool* [Leiden University]. https://hdl.handle.net/1887/12480

Vassilev, M. N., Vassileva, M., & Nikolaeva, I. (2006). Simultaneous P-solubilizing and biocontrol activity of microorganisms : potentials and future trends. *Applied Microbiology and Biotechnology*, *71*, 137–144. https://doi.org/10.1007/s00253-006-0380-z

Wang, H., Liu, R., You, M. P., Barbetti, M. J., & Chen, Y. (2021). Pathogen Biocontrol Using Plant Growth-Promoting Bacteria (PGPR): Role of Bacterial Diversity. *Microorganisms*, *9*(1988), 1–18.

Wang, Q., Liu, J., & Zhu, H. (2018). Genetic and Molecular Mechanisms Underlying Symbiotic Specificity in Legume-Rhizobium Interactions. *Frontiers in Plant Science*, *9*, 1–8. https://doi.org/10.3389/fpls.2018.00313

Weert, S. de, Dekkers, L. C., Bitter, W., Tuinman, S., Wijfjes, A. H. M., Boxtel, R. Van, & Lugtenberg, B. J. J. (2006). The two-component colR / S system of Pseudomonas £ uorescens WCS365 plays a role in rhizosphere competence through maintaining the structure and function of the outer membrane. *Microbiology Ecology*, *58*(2), 205–213. https://doi.org/10.1111/j.1574-6941.2006.00158.x

Weert, S. De, Vermeiren, H., Mulders, I. H. M., Kuiper, I., Hendrickx, N., Guido, V., Vanderleyden, J., Mot, R. De, & Lugtenberg, B. J. J. (2002). Flagella-Driven Chemotaxis Towards Exudate Components Is an Important Trait for Tomato Root Colonization by Pseudomonas fluorescens. *Molecular Plant-Microbe Interactions*, *15*(11), 1173–1180.

Williams, R., Dodd, W. A., & Taji, A. M. (1992). *Plant Tissue Culture*.

Woude, M. W. Van Der, & Baumler, A. J. (2004). Phase and Antigenic Variation in Bacteria. *Clinical Microbiology Reviews*, *17*(3), 581–611. https://doi.org/10.1128/CMR.17.3.581

Zhang, H., Xie, X., Kim, M., Kornyeyev, D. A., Holaday, S., & Pare, P. W. (2008). Soil bacteria augment Arabidopsis photosynthesis by decreasing glucose sensing and abscisic acid levels in planta. *The Plant Journal*, *56*, 264–273. https://doi.org/10.1111/j.1365-313X.2008.03593.x

Zhuang, X., & Lo, C. (2020). Construction and Loss of Bacterial Flagellar Filaments. *Biomolecules*, *10*(1528), 1–14.