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Plant-microbe Interactions and their Potential Application in Improving Disease Resistance in Vegetable Crops

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Microorganisms have a substantial impact on the environment and have been observed to either immunize or infect organisms from all kingdoms. Plants and microorganisms have undergone co-evolution and engage in interactions within their natural environment. Plant microbiota, often known as plant-associated microorganisms, are essential components of plant existence. Similar to other living systems, the plant body interacts with a range of living and non-living factors as it develops in an intricate environment. The plant microbiome can sustain disease suppression by providing essential tasks to their host, such as stress tolerance, vitality, and development. Plants and microorganisms have evolved molecular systems to mutually interact and derive advantages from

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their interaction. This symbiotic relationship is advantageous for both the microorganisms and the plants. Various pathways have been explored and are currently being utilized to achieve agricultural, environmental, and health benefits, based on this molecular interaction. Plant-associated microorganisms serve a vital role in the growth and development of plants. Microorganisms stimulate plant growth by directly increasing nutrient uptake and stimulating hormone production. The potential benefits of these mutually beneficial interactions between plants and microbes could be connected to develop microbial inoculants for application in agricultural biotechnology. In general, the utilization of microorganisms and the establishment of beneficial plant-microbe interactions offer promising and environmentally favourable approaches for sustainable and organic agriculture worldwide.

Keywords: Application; disease; interaction; microbes; plants; resistance.

1. INTRODUCTION

Communication between plants and microorganisms can take place on a number of different levels and in a variety of ways. Nearly every organ of a plant engages in interactions with microbes at some stages of its life cycle, and the plants that achieve this interaction reap benefits, either directly or indirectly, from the microbes [1]. Microbes that are associated with plants secrete substances that have the potential to either protect the plants from harmful microbes or make the plants more resistant to biotic and abiotic stress, hence increasing the plants' growth. Plants live along with various microorganisms, such as archaea, protists, bacteria, and fungi, together known as microbiota [2]. The emergence of microbial life can be traced back to nearly 3.5 billion years ago, indicating that the interactions between microorganisms have evolved and become more varied throughout time. This occurred long before plants adapted to live on land, specifically before 450 million years ago [3]. During the course of evolution, higher plants and photosynthetic algae incorporated cyanobacterial endosymbionts, which are now referred to as chloroplasts or plastids. Hence, the plant and microbial evolutionary histories have a shared origin, and their existence is mutually dependent. As a result, there has been increased focus on the "plant microbiota," which refers to the microorganisms that are present on or near the surfaces of plant parts [4,5,6,7,8].

Plants gather a wide range of natural substances, which are believed to play a role in their interactions with their environmental factors. These compounds have multiple roles, including interacting with bacteria, animals, and other plants. They also serve to protect the plant against UV radiation and oxidants. Certain substances possess the ability to allure advantageous insects or microorganisms, while others have the capacity to exterminate or deter predators [9,3]. Several of these molecules have been labeled as "secondary metabolites" in order to differentiate them from the "primary metabolites" that are essential for the growth of all plants. However, these secondary metabolites are probably necessary for the effective competition or reproduction of a certain plant species in its native habitat [10]. During the course of several years, researchers have been fascinated by the manner in which plants make use of the beneficial activities that are provided by microbial communities while simultaneously combating microbial diseases. Several studies have shed light on the extraordinarily intricate microbial communities that are associated with different plant species, stages of plant development, and specific organs of plants [11]. It is widely acknowledged that the plant microbiome is one of the most important variables that determines the health and production of plants.

Microorganisms play an essential part in the prevention of diseases and the management of unfavourable agroecological conditions [12]. For this reason, gaining an understanding of the functionality of plant-microbe interactions is helpful in gaining an appreciation for the ways in which plants might benefit from the microbial communities with which they associate. When it comes to the natural world, plants and animals are constantly interacting with a wide variety of microbial species throughout the entirety of their life cycles. Humans have been exposed to a diverse microbial environment since the beginning of their evolutionary history, which has had the effect of extending their capacity to adapt to a healthy lifestyle [13,10]. This review will discuss briefly the plant microbes interactions and their potential application in improving disease resistance (Fig. 1).

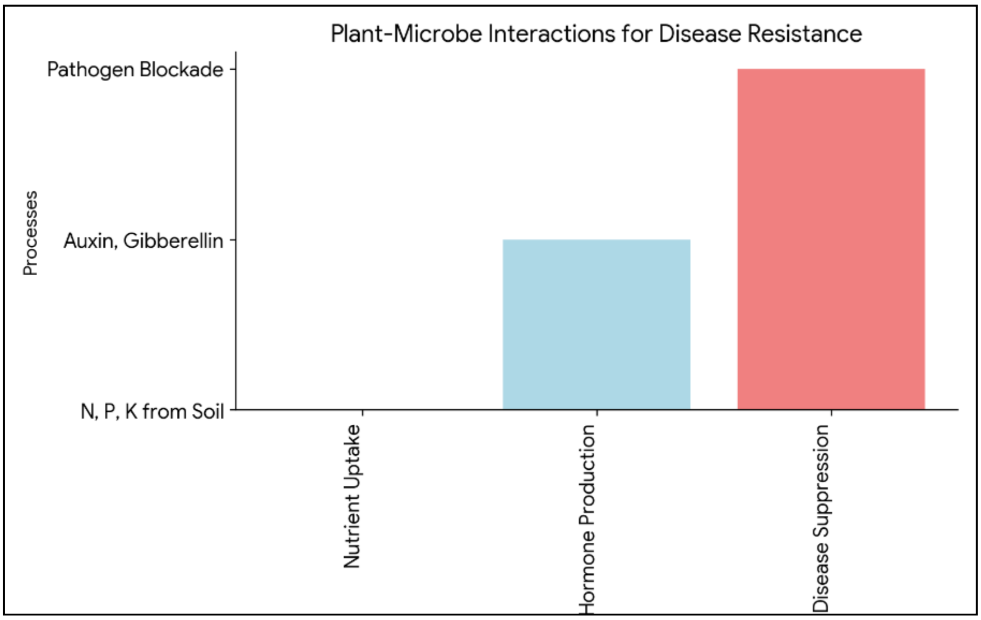

Fig. 1. Plant-microbe interaction for disease resistance

2. BENEFICIAL MICROBES AND DISEASE MANAGEMENT

Various plant pathogens, including fungi, bacteria, viruses, and nematodes, are responsible for different plant diseases. These pathogens can be managed by the use of biocontrol agents. Bioagents used in diverse mechanisms to suppress plant diseases and their pathogens [14]. These mechanisms encompass direct parasitism of pathogens, inhibition of pathogens through the use of antibiotics and extracellular cell wall-degrading enzymes, competition for essential nutrients (such as iron, nitrogen, or carbon) in colonization sites, and stimulation of plant defense mechanisms [15]. Beneficial bacteria involved in the biocontrol of plant diseases can employ multiple methods, which can be simultaneously engaged. Genetically modified biocontrol agents can enhance biocontrol by increasing the expression of one or more of these qualities, allowing diverse strains with multiple anti-pathogen properties to work together. Utilizing a variety of biocontrol chemicals can enhance plant development and effectively inhibit plant fungal infections [16]. Different ways by which microorganisms supress the diseases are discussed below:

2.1 Parasitism

Trichoderma, a type of free-living fungi, has been found to be an opportunistic and a virulent symbiont of plants, as well as a parasite of fungi. It has been shown in multiple studies that *Trichoderma* can be utilized as a biocontrol agent to combat plant-parasitic nematodes. The soil has shown the biocontrol actions of *T. asperellum*-203 and *T. atroviride* 16 beneficial microbes for disease suppression and plant growth promotion against *Meloidogyne javanica* [17]. Additional *Trichoderma* species have demonstrated significant biocontrol efficacy against *M. javanica* in diverse tests. *T. asperellum*-203 and *T. atroviride* have also parasitized nematode eggs. The significance of the gelatinous matrix in fungal parasitism is demonstrated by the parasitism of *Trichoderma* on *M. javanica*. *Trichoderma spp.* utilize biocontrol strategies that entail coiling around the pathogenic hyphae, generating appressorium-like structures [18]. This process inhibits the growth and spread of many fungal infections through mycoparasitism. *Trichoderma* has been extensively used for its ability to inhibit many plant pathogenic fungus, including *Rhizoctonia solani*, *Botrytis cinerea*, *Sclerotium rolfsii*, *Sclerotinia sclerotiorum*, *Macrophomina phaseolina*, *Pythium spp.*, and *Fusarium spp.* According to reports, *Trichoderma's* biocontrol activity is achieved by many methods, including as nutrition competition and the release of antifungal metabolites [19]. In addition, certain fungi, such as *arbuscular mycorrhizal fungi* (AMF), establish themselves in the internal tissues of plants and provide protection against various forms of biotic stress, including fungal and bacterial pathogens, as well as infections caused by plant-parasitic nematodes [17,19].

2.2 Competition

Soil-dwelling species of microbe often engage in competition for resources such as nutrients and oxygen. Various antagonists engage in direct competition with infections for these resources to exert biocontrol activity. Microorganisms residing in the roots engage in competition for appropriate locations on the root surfaces [20]. Research has shown that the primary factor leading to lower spore germination in soil is the competition for mineral resources, namely carbon, which causes fungistasis. Various *Pseudomonas* species possess a high level of efficiency in utilizing glucose by converting it into gluconic acid and 2-ketogluconic acid. This capacity gives them a competitive edge against microbes that cannot utilize glucose [21]. In soils, there is also competition for trace elements, such as iron, copper, zinc, manganese, and others. The exhaustion of soluble and bioavailable iron in soil leads to intense competition. However, certain microorganisms, such as biocontrol microbes, restore the necessary level of iron by synthesizing siderophores (small molecules with a strong affinity for iron) when iron levels are low. This process restricts the growth of other microbes [20,22] Some cases have reported the inhibition of soil borne plant pathogens by Pseudomonads that produce siderophores. *Trichoderma* is renowned for its strong capacity to compete as a saprophyte. Various chemical mutagens have been identified that enhance the competitive saprophytic capacities of *Trichoderma* species. *Arbuscular mycorrhizal* (AM) fungi and soil borne plant diseases both reside in the same root tissues, and they may directly compete for space during colonization [23,24,25].

2.3 Production of Lytic Enzymes

Cell wall-degrading enzymes are produced by biocontrol agents, which is one of the major strategies that they employ to control soil-borne diseases using biocontrol agents. Enzymes that degrade cell walls, such as β-1,3-glucanase, chitinase, cellulase, and protease, are released by biocontrol strains of plant growth promoting microorganisms [4]. These enzymes have the ability to directly restrict the growth of fungal pathogens by dissolving their cell wall tissue. The enzyme known as chitinase is responsible for the degradation of chitin, which is an insoluble linear polymer composed of β-1,4-N-acetyl-glucoseamine [13,10]. Chitin is the primary constituent of most fungal cell walls. *Paenibacillus* and *Streptomyces spp.* strains have the ability to produce β-1,3-glucanase, which has the ability to efficiently destroy the fungal cell walls of pathogenic *F. oxysporum*. In addition to having the ability to produce natamycin and chitinase, the strain A01 of *Streptomyces lydicus* that was isolated from the soil of a suburban vegetable field in Beijing, China, also has a substantial inhibitory effect on *Botrytis cinerea* [9,3]. Several species of *Bacillus*, including *Bacillus licheniformis*, *Bacillus cereus*, *Bacillus circulans*, *Bacillus subtilis*, and *Bacillus thuringiensis*, have the ability to operate as potential biocontrol agents that possess chitinolytic capabilities. There are a variety of Gram-negative bacteria that have been discovered to contain chitinolytic capabilities [19]. These bacteria include *Serratia marcescens*, *Enterobacter agglomerans*, *Pseudomonas aeruginosa*, and *P. fluorescens*. Through the production of chitinases and glucanases, numerous species of *Trichoderma* and *Streptomyces* mycoparasitize the many different types of phytopathogenic fungus [17].

2.4 Antibiotic Production

The interactions that plants have with their associated diseases are influenced by antibiotics, which are bioactive molecules that are produced by a variety of helpful bacteria. The genus *Bacillus* is responsible for the production of a multitude of antibiotics that are both antibacterial and antifungal [20]. Non-ribosomal peptide synthetases (NRPSs) and/or polyketide synthases (PKSs) produce bacilysin, chlorotetain, mycobacillin, rhizocticins, bacillaene, difficidin, and lipopeptides from the surfactin, iturin, and fengycin families. Some of these chemicals, such as subtilin, subtilosin A, TasA, and sublancin, are well-known and are formed from ribosomes [26]. However, they are also derived from ribosomes. There are many different antifungal metabolites that are produced by Bacillus subtilis strains. Some examples of these metabolites are zwittermicin A, kanosamine, and lipopeptides. In addition, many species of *Pseudomonas*, such as *Pseudomonas fluorescens* and *Pseudomonas aeruginosa*, are capable of producing antibiotics [27]. Different antibiotics such as phenazine-1-carboxylic acid (PCA), phenazine-1- carboxamide (PCN), pyoluteorin (Plt), pyrrolnitrin (Prn), 2,4-diacetylphloroglucinol (DAPG), oomycin A, viscosinamide, butyrolactones, kanosamine, zwittermicin A, aerugine, rhamnolipids, cepaciamide A, ecomycins, pseudomonic acid, azomycin, antibiotics FR901463, cepafungins, and karalicin are produced by these strains of *Pseudomonas*. The fungus that is used for biocontrol also produces a number of drugs [28]. *Trichoderma spp.* are capable of producing chemicals such as gliovirin, gliotoxin, viridin, pyrones, and peptaibols, which are effective against a variety of fungal infections. In addition, several mycorrhizal fungi species are capable of producing antibiotics [29]. The bacterium *Leucopaxillus cerealis* var. piceina was responsible for the production of an antibiotic called diatretyne nitrile, which may prevent the germination of *Phytophthora cinnamomi* zoospores. *Streptomycetes* that are connected with mycorrhiza have been shown to restrict the growth of both fungi and bacteria [30].

2.5 Induction of Plant Defences

The use of biocontrol strains of plant growth boosting microorganisms offers an alternative method of protecting the plant from diseases through the process of induced systematic resistance (ISR) [18]. The term "induced systemic resistance" (ISR) refers to the reduced spread of pathogenic propagules or the severity of disease that occurs as a result of the presence of PGPM-induced resistance mechanisms that are located in a geographically distant location from the pathogens [14]. Plants possess not just built-in chemical and physical barriers, but also highly evolved immune systems that can identify the structural patterns or conserved motifs that are unique to microorganisms and not found in plants. Pathogen- or microbe-associated molecular patterns (PAMPs or MAMPs, respectively) are the names given to these patterns [23]. Microbes that live in the rhizosphere have the ability to stimulate the production of secondary metabolites in plants. Furthermore, it has been discovered that a different siderophore known as pseudomanine, which is produced and secreted by some species of Pseudomonad, can stimulate the production of salicylic acid (SA) in radish [15]. As a result, pseudomanine plays an essential part in the defense response of plants. The reaction of enhanced specialized defense mechanisms that takes place as a result of the colonization of these fungi is the cause of the plant growth-promoting effect and defense response that is exhibited by some Arbuscular mycorrhizal fungi. The endophytic connection of plants with AM fungus activates the defensive mechanism in such a way that it exacerbates the inclination of the plant to respond quickly to an attack by a root pathogen [17].

Table 1. Importance of beneficial organisms and their role in disease management

Organisms	Used as	Benefits	References
Pseudomonas	Nitrogen fixation, Biocontrol agent, Stimulator, Suppressor	• Production of lytic enzymes • Promotes plant growth • Nutrients uptake • Antioxidant activities • Role in biodegradation • Combating plant diseases	[31,32]
Bacillus	Growth promotor, Biofertilizer, Biocontrol agent	• Survive harsh environmental conditions • Produce important enzymes • Antioxidant activities • Enhance crop yield • Protection from diseases and weeds	[30,33,34]
Streptomyces	Immunostimulatory, Biocontrol agent, Immunosuppressive, Antifungal agent, Antioxidative agents	• Produces antibiotics • Produce bioactive secondary metabolites • Crop growth and development • Supress diseases • Antioxidant activities	[34,35]
Trichoderma	Growth promotor, Biocontrol agent, Biofungicide,	• Control soil borne diseases • Improves nutrient efficiency	[30,36]

Organisms	Used as	Benefits	References
	Suppressor, Systemic resistance inducer	• Enhances plant resistance • Improves agrichemical environmental pollution • Promotes plant growth • Avoids plant pathogens	
Fusarium	Growth promotor, Biocontrol agent, Biofungicide, Antioxidative agents	• Resistance to biotic and abiotic stress • Promotes plant growth • Improves nutrients uptake • Supress diseases • Antioxidant activities	[17,37]
Pythium	Immunostimulatory, Biocontrol agent, Immunosuppressive, Antifungal agent	• Promotes plant growth • Improves plant immunity • Combat plant diseases • Antioxidant activities	[29,14]

3. STRESS TOLERANCE & DISEASE RESILIENCE

The application of stress-tolerant plant growth promoting microorganisms and *arbuscular mycorrhiza* fungi can enhance plant growth and survival in harsh conditions. Biotic and abiotic stress significantly limit crop output, food quality, and global food security. Various characteristics, including physiological, biochemical, and molecular aspects of plants, are influenced when they are subjected to stressful conditions [38]. Plants secrete root exudates and other chemicals that attract diverse microbial populations. Plant diseases, such as bacteria, fungi, viruses, and pests, have caused significant devastation to crop production. The typical effects of these biotic variables encompass disrupted hormone regulation, nutritional imbalance, and physiological dysfunction [39]. The abiotic stress of drought is widely acknowledged as a significant environmental stress that has captured the interest of environmentalists and agricultural experts [40,41]. Agricultural limitations caused by this issue are widespread and have a significant impact on plant growth and output globally [42]. The majority of significant agricultural land worldwide is impacted by drought-induced stress. It has a diverse range of implications in human society, including the economy. Drought stress impacts multiple growth metrics and stress-responsive genes under stressful conditions. Salinity stress is a prevalent abiotic stress in current agriculture. The majority of the world's agricultural areas are significantly impacted by salinity as a result of different factors [43,39]. The presence of high salinity levels negatively impacts microbial activity by causing toxicity from ions and osmotic stress, resulting in decreased plant growth and development. Soil pollution with heavy metals is caused by ongoing industrialization, intensive agricultural techniques, and human activities [44]. The presence of these toxic heavy metals has a significant detrimental effect on both plants and human health [45]. Heavy metals are metallic elements with a greater density that cannot be broken down and are toxic even at low concentrations. In order to protect and preserve the environment from the harmful impact of heavy metals, it is imperative to eliminate them using a sustainable and efficient method. The occurrence and severity of temperature stress have been heightened as a result of climate change [46]. Heat stress and cold conditions are increasingly becoming key abiotic stressors for crop growth and global food security. The primary consequence of temperature stress is the alteration of the plasma membrane, water content (transpiration), hindered photosynthetic activity, enzyme functionality, cell division, and plant growth [47].

Microbes utilized both indirect and direct strategies to enhance plant growth and development under stressful situations. Microbes used many biochemical and molecular pathways to facilitate growth and development [48]. For instance, the introduction of plant growth promoting microorganisms through inoculation stimulates plant development by controlling hormonal and nutritional equilibrium, generating plant growth regulators, and triggering resistance against phytopathogens. Plant growth boosting microorganisms secrete specific compounds that decrease the population of pathogens in the vicinity of the plant [49]. For instance, the bacteria in the rhizosphere create siderophores, which decrease the availability of iron to specific pathogens, leading to a reduction in their growth. Additionally, they enhance plant growth by converting atmospheric nitrogen into a usable form, making phosphate soluble, and generating plant hormones [50]. The mechanisms encompass nutrient mobilization, exopolysaccharide formation, rhizobitoxine synthesis, and other processes that aid the plant in adapting to unfavourable environmental conditions. Rhizobitoxine enhances plant growth and development in stressful conditions by suppressing the production of ethylene. In addition to these, microorganisms have the capacity to augment plant growth and development through the use of crucial enzymes such as ACC-deaminase, chitinase, and glucanase in stressful conditions [48,51]. Furthermore, certain bacteria possess sigma factors that facilitate alterations in gene expression in response to unfavourable conditions, enabling them to counteract detrimental effects. Aside from the presence of microorganisms that promote plant growth, the contact between fungi and the roots of higher plants is also a crucial factor in their growth and development. The predominant type of mycorrhizae found in agricultural fields is *arbuscular mycorrhiza* [52]. These fungi have a crucial function in the process of nutrient cycling, since they are responsible for the absorption and transfer of nutrients. The microbial systems aid in the plant's ability to sustain its growth in stressful environments by alleviating the adverse effects of stress on plant growth and development. The plant growth stimulating microorganisms were discovered to have the potential to replace inorganic fertilizers and pesticides [53]. Hence, the interaction between plants and microbes holds significance in the context of sustainable agriculture and the concern for future food security. The plant growth promoting bacteria *Bacillus* and *Paenibacillus* enhance plant growth and health through three distinct mechanisms: facilitating host plant nutrition and growth, antagonizing pathogens, and stimulating defense mechanisms to enable sustainable agriculture [54]. By utilizing stress-tolerant plant growth boosting bacteria in sustainable agriculture, can potentially increase crop yields and improve the nutritional quality of food grains, even in the face of climate change. Additionally, this method has the potential to reduce the cost of chemical fertilizers and pesticides by 20-25%. The implementation of these measures by farmers can significantly increase their financial earning through the production of organic goods and vegetables [55].

4. BIOCONTROL STRATEGIES

The "plant-microbiome language" could be useful for coming up with new biocontrol methods. By sending different chemicals through their leaves and roots, plants may have their own language that they use to talk to the microbiomes that live with them. This language might help the plant find and choose the microbes in the rhizosphere and phyllosphere that can give it the benefits it needs [56]. These bacteria will then have different effects on the health and growth of plants. As with individual plant-beneficial microbes, rhizosphere soil microbiomes are made up of many different microbes that help plants grow in a number of ways. These include directly increasing the availability of nutrients to plants, producing phytostimulators (which change the levels of plant hormones), or indirectly acting as biocontrol agents [12]. Learning how plants talk to each other will give us ideas and might even help us fight diseases without using drugs. In the rhizosphere, certain germs are drawn to certain signaling molecules, hormones, and root substances that plants make to meet their own needs. The large and well-studied symbiosis relationship between legumes and rhizobia is a good example of chemical language [17]. Plants release certain chemicals that draw certain rhizobacteria. A full study of the different bioactive exudates in the rhizosphere is needed to figure out how bacteria are drawn to different microbiomes. This will allow for more accurate control of soil microorganisms before they can be used in farming [21].

4.1 Use of Exudates as a way to Attract Beneficial Biocontrol Microbes

Root exudates significantly impact the composition and function of microbial communities in the rhizosphere. Particular root exudates selectively attract beneficial bacteria that are specifically suited to their requirements [57]. Extensive research has demonstrated that plants offer advantages to microorganisms by recruiting and sustaining certain microbiomes through the release of chemical exudates. Legumes emit flavonoids that attract certain nitrogen fixing rhizobacteria. Additionally, certain beneficial rhizobacteria have been discovered to stimulate plant defense responses, hence preventing foliar infections. Soil microbiomes have been widely utilized in agriculture to enhance plant nutrition and/or bolster disease resistance [58]. In addition, the plant hormone strigolactone not only attracts mycorrhiza but also other microorganisms that assist in phosphate solubilization, water provision, and defense. The manipulation of the rhizosphere microbial population can be achieved by either applying signaling chemicals to plants or modifying the genotype through plant breeding to attract advantageous bacteria [59].

4.2 Use of Substrates to Maintain Beneficial Biocontrol Microbes Near Crops

Beneficial biocontrol microorganisms can be maintained by cultivating them using substrates as a growth media. Substrates refer to the specific combination of nutrients that microbial cells need in order to develop, carry out metabolic processes, and engage in activity [60]. Most of the related microorganisms can be cultivated using systematic methods of bacterial isolation. This can be viewed as a benefit for recruiting advantageous microbiomes from the current soil microbiota, as well as introducing and sustaining beneficial bacteria for the purpose of controlling plant diseases [61]. This is achieved by supplying suitable growth substrates as a medium. Beneficial microorganisms, particularly bacteria, have a high degree of dietary adaptability, enabling them to thrive in various habitats and situations [62].

4.3 Phyllosphere Biocontrol

Foliar diseases provide a significant challenge for several crop varieties. Out of the eight most significant fungal plant pathogens globally, six of them are responsible for severe foliar diseases. Gaining a comprehensive and precise understanding of the role of foliar microbiomes is essential for obtaining valuable insights into crop protection [15]. The utilization of microbial biocontrol agents presents a sustainable and ecologically sound alternative approach to synthetic chemical control. Biological control agents have been evaluated for their efficacy in controlling foliar diseases such as powdery mildew, downy mildew, blights, and leaf spots through spray treatment [9,3]. Additionally, they have been utilized as a liquid commercial formulation to manage the stem-end rot pathogen on avocado trees. A further investigation discovered that certain bacterial antagonists effectively impede the proliferation of bacterial stem rot, induced by *Erwinia chrysanthemi*, in tomato plants inside a controlled greenhouse environment. The bacterial strain *B. substilis* QRD137, found in the biological product Serenade, effectively inhibits the infection of blueberry blossoms and decreases the growth of fungi in treated flowers [11]. Plants protect themselves on their leaves by generating antimicrobial substances or by stimulating the growth of helpful microorganisms through the secretion of nutrients and/or signals. Researchers have suggested that microorganisms that inhabit leaves are crucial for the development and control of diseases in plant foliage [16]. Analyzing the microbial and chemical environment of the phyllosphere, and studying the interactions between plants and microbes, as well as between different microbes on the leaf surface, can provide valuable information about the formation of foliar microbiomes by plants. This research may ultimately result in the development of new approaches to improve food security [63].

4.4 Breeding Microbe-optimized Plants

Arabidopsis ecotypes exhibit variations of up to four times in plant yield when exposed to *Pseudomonas simiae* WCS417r. This illustrates that the plant's genetic composition significantly influences the result of the advantageous interaction. Therefore, the objective of this novel strategy would be to cultivate plants that are specifically designed to attract and sustain advantageous biocontrol microorganisms [64]. Prior to making significant efforts, it is crucial for breeding programs to have a deeper understanding of the mechanisms by which beneficial bacteria are drawn and sustained, as this aspect has not been considered thus far. Through genetic engineering and plant breeding, we can create plants that are optimized for microorganisms, producing specific exudates to attract and sustain beneficial microbes, whether on the root or leaf surfaces, at the appropriate time [65]. Plants create their own rhizosphere ecosystem by releasing particular exudates to enhance nutrient availability and interact with beneficial microorganisms. In order for this to occur, it is necessary for the specific microorganisms to be present. Therefore, this approach may need to be coordinated with the introduction of the corresponding biocontrol microorganisms [66].

4.5 Microbiome Engineering, Plant-optimized Microbes and Plant-optimized Microbiomes

The objective of this novel strategy is to manipulate or selectively cultivate specific microorganisms or groups of microorganisms that possess advantageous characteristics, and to sustain their presence for the cultivation of crops in diverse soil environments [67]. Consequently, we would generate microorganisms and microbiomes that are specifically tailored for plants and soil, which can serve as inoculum for various crops in diverse soil conditions. However, there is evidence indicating that soil microbiomes naturally adjust to the crops they are associated with, resulting in enhanced plant-microbe interactions [53]. There is a significant amount of research that strongly supports the significant influence of the naturally occurring plant microbiome in the genesis and progression of diseases in plants. It is important to know the mechanisms by which beneficial bacteria are drawn and sustained [21].

4.6 Matching Microbe-optimized Plant Seed with the Optimal Microbiome and Soil Amendment Practices for Each Soil Type

Scientists strive to uncover bacteria that improve crop growth. Seeds coated with promising bacteria for the correct soil are one of the finest ways to optimize plant-microbe interactions. Due of the ephemeral nature of microbiomes, seeds with the correct microbiomes are best than sprays or root soaks [12]. Microbiomes may operate as inoculants to assist plants absorb nutrients or biocontrol products to protect them from pests and illnesses. Microbiomes from soil samples are cultivated, cryopreserved, and kept before applying to seeds. They should join the rhizosphere when the seeds germinate and the plant roots. Soil additives may be needed to retain beneficial bacteria. Perhaps “probiotics” could sustain healthy plant microbiomes [68]. Many potent legume seed inoculants made from helpful bacteria like Rhizobium are available. They may suppress disease-causing bacteria, speed nutrient availability and assimilation, and stimulate nitrogen-fixing nodules on leguminous plant roots for healthier, higher-yielding plants. Integrating microbial biofertilizers, biocontrol microorganisms, optimized microbiomes, soil amendments, and microbe-optimized crops for varied soil types is the penultimate goal to maximize plant-microbe interactions [69].

5. POTENTIAL FOR SUSTAINABLE DISEASE MANAGEMENT

The management of the pathogenic illnesses that affect crops of agronomic significance can help to preserve both the number and quality of the foods, fibers, and foods that are obtained from these crops. There are a variety of organisms that are responsible for the majority of plant pathogeneses [60]. These include bacterial species, fungal species, oomycetes, viruses, nematodes, and higher parasitic plants. Different microbial variety can be found among all plants, as well as bacteria that act as antagonists for plant pathogens, according to recent discoveries. In order to reduce the amount of agricultural chemicals that are used and the residues that they leave behind in the environment, the most effective and environmentally friendly technique is the utilization of biological control agents [70]. Extracellular products have a significant function in the rhizospheric zone, and bacteria that are connected with plant roots play a significant role in the fight against phytopathogens. It has been demonstrated beyond a reasonable doubt that biocontrol agents based on microbes have the capacity to manage a wide range of stresses, improve plant growth, and control diseases that affect plants [63]. Biological control agents often use two types of approaches and processes to inhibit plant pathogenesis: indirect and direct antagonism. Some examples of these strategies and processes include the synthesis of antifungal metabolites, proteolytic enzymes that biodegrade plant cell walls, induced host resistance, and competition for niches and nutrients [71]. Through the process of colonization and active entry into the plant host, bacteria or fungi can also induce systemic resistance against pathogens in plants. This resistance can be achieved through the induction of modifications in plant morphology and physiology, or through the stimulation of the production of bioactive components [72]. Different mechanisms for disease management are discussed below:

5.1 Direct Antagonism

The direct mechanisms responsible for promoting plant growth are attributed to the inhibition of detrimental microorganisms through the introduction of beneficial bacteria that are compatible with plants. The direct antagonism occurs when an antagonistic agent is highly selective or when there is physical contact with the pathogens [62]. The antagonistic effect on phytopathogens is attributed to the secretion of extracellular enzymes (such as β-1,3-glucanase, proteases, and chitinase), antibiotics, siderophores, and hydrogen cyanide by microorganisms. These microorganisms can also function as competitors of plant diseases in acquiring nutrients and colonizing roots [73]. Microorganisms can exhibit biological control activities through clearly defined processes such as antibiosis, competition, and hyperparasitism. Fungal strains and diverse bacteria obtained from many ecological habitats, including soils, sediments, plants, and animals, have been extracted to get multiple metabolites. It has been demonstrated that these metabolites possess strong bioactivity [42]. Different mechanisms are described below:

5.1.1 Hyperparasitism

Hyperparasitism is a microbial ecological strategy used to protect the host plant and is considered a direct form of hostility. Hyper parasitism occurs when microorganisms directly attack and kill the disease-causing pathogens or their disease-producing propagules [26].

5.1.2 Competition

Microbes tend to stay away from soils and surfaces of live plants because they don't have many nutrients. In order to cover the surface of a plant, a microorganism must be able to compete effectively for nutrients that are available [23]. There is competition between microbes and pathogens for niches and nutrients, which can slow or stop the pathogen from colonizing roots and make it harder for them to get minerals. For example, siderophores are good at gathering iron [47].

5.1.3 Antibiosis

Microbes make a secondary toxic metabolite that is harmful to another microorganism (the disease-causing agent). This is called antibiosis, and it is an important part of stopping illness [68]. It is known that antibiotics have direct effects on plants and can cause widespread resistance. This is a normal thing that happens with many biocontrol agents, like *Streptomyces*, *Bacillus spp.*, *Pseudomonas spp.*, and *Trichoderma spp.* [48].

5.2 Indirect Antagonism

Indirect antagonism arises from activities unrelated to the biocontrol agent's ability to identify a disease. An instance of indirect antagonism occurs when a non-pathogenic biocontrol agent stimulates the defensive pathways of the host plant through mechanisms such as induction and competition, hence encouraging host resistance [1]. The translation of host plant processes of chemical activation or physical defense through the use of inducers and monitoring of pathogenic activity are the mechanisms of antagonism, specifically induced systematic resistance (ISR) and systematic acquired resistance (SAR). The induction of acquired resistance is typically triggered by pathogenic invasion, which leads to the accumulation of pathogen-related proteins (PRPs) and is facilitated by salicylic acid [22] PRPs consist of a variety of enzymes, some of which may directly contribute to the destruction of disease-causing agents (microbial pathogens) such beta-1,3-glucanase and chitinase. They also enhance the cell wall's ability to resist infection or induce programmed cell death. The ISR is induced by a specific non-pathogenic stimulus and is triggered by either ethylene or jasmonic acid, independent of the buildup of PRP. The molecules implicated in the ISR partially overlap with those involved in antagonistic action by bacteria, including the formation of volatile organic compounds (VOCs), antibiotics, siderophores, and N-acyl-homoserine lactones. The induction of systemic resistance is triggered by specific bacterial genera, including *Pseudomonas, Bacillus*, and *Serratia,* in different plant pathogens [69]. This process involves complex signaling systems that are intricately connected to defense priming. While it has been acknowledged that certain bacteria might trigger an induced systemic resistance (ISR) through salicylic acid, it is important to note that phytohormones, particularly ethylene and jasmonic acid, actively contribute to the onset of ISR [73].

5.3 Consortium of Microbes in Plant Disease Management

Plant development and growth boosters coexist with various microbial strains in the rhizosphere or soil in varied combinations. Utilizing a combination of diverse microbial species that engage in activities that enhance plant growth is a more effective approach than relying on a single microbe for plant disease management and desired agricultural outcomes [74]. In addition, the utilization of microorganisms in a consortium can augment the efficiency, reliability, and consistency of microbes in various soil conditions and habitats. *Bacillus*, *Rhizobium*, *Glomus*, *Pseudomonas*, and *Trichoderma* have been employed in the formation of microbial consortia [75].

6. PLANT-MICROBE INTERACTIONS: FIELD APPLICATIONS AND CHALLENGES

Different field applications of plant microbe interaction are:

Plant growth promotion: Microbes that live on plants have been used to help plants grow better so that more food, fiber, energy, and key metabolites can be made. The two species working together can help each other by giving nutrients to the plant directly (biofertilizer) or making substances like iron and phosphate more available [75]. Free-living bacteria that help plants grow also make chemicals that have direct effects on plant metabolism or change the production or breakdown of phytohormones. Auxins, cytokinins, gibberellic acid (GA3), abscisic acid, and ethylene are phytohormones. They are signaling chemicals that plants need to grow and develop in many ways [61]. Because chemical fertilizers are bad for both farmers and the earth, making biofertilizers is an important and exciting field of study. Soil bacteria like rhizobium and some actinomycetes (like Frankia) work together to help plants get nitrogen (N). This nitrogen is then used by legumes and actinorhizal plant species. Scientists have found that bacteria in the rhizosphere and epiphytes that live in the phyllosphere make a number of phytohormones that help plants grow [76].

Plant disease control: The efficacy of biocontrol agents in combating plant diseases has been proven, and several agents are currently accessible for commercial use. Plant pathogen control involves several techniques, such as competing for nutrients and space at the infection site, inhibiting the growth of pathogens, parasitizing them, producing enzymes that break down their cell walls, inducing resistance in the plant, and manipulating bacterial signaling molecules [68]. An instance of plant disease prevention involves utilizing Pseudomonas strains with biocontrol capabilities to stimulate resistance in apple (*Malus domestica*) against the pathogenic fungus *Venturia inaequalis*, which is responsible for causing apple scab [77].

Production of bioactive compounds and biomaterials: Plants produce secondary metabolites that serve as a significant reservoir of bioactive chemicals, which can be utilized as medicinal agents or for the development of biomaterials. Recent research has demonstrated that the interaction between plants and microorganisms can be utilized to increase the synthesis of significant secondary metabolites [74]. *Agrobacterium rhizogenes* infection induced the formation of hairy roots in plants, characterized by rapid growth and extensive branching, which were subsequently utilized for the synthesis of valuable chemicals. The utilization of plant-bacteria interactions can enhance the synthesis of secondary metabolites in hairy roots, hence improving productivity [78,76]. The utilization of hairy root culture shows the stimulating symbiotic relationship between plants and microorganisms, and is currently progressing towards widespread implementation in industrial utilization. Expanding the hairy roots culture for the purpose of producing secondary metabolites may provide challenges due to the difficult characteristics of hairy roots [75].

Remediation: Scientists have investigated the application of plant-microbe symbiosis for the purpose of pollutant clean-up since the 1990s. In recent years, research in this topic has advanced from small-scale laboratory tests to focus on improving the efficiency of remediation methods in actual plant environments [74]. The phyto- or rhizo-remediation methods are designed to address persistent chlorinated chemicals, volatile organic carbons, and heavy metals. Phytoremediation has been used as a remedial technique for the extraction of pollutants from groundwater [79]. However, specific volatile organic chemicals including trichloroethylene (TCE) and BTEX (benzene, toluene, ethylbenzene, xylene) are emitted into the environment via the plant's vascular system [67]. The endophyte-plant interaction was employed to decompose the volatile organic pollutants and reduce evapotranspiration. The issue of heavy metal contamination persists due to the non-biodegradable nature of these metals, in contrast to organic substances. Recent studies have shown the efficacy of utilizing rhizosphere bacteria and plants for the extraction of metals from soil or groundwater [61].

Carbon sequestration: Carbon sequestration, an increasingly notable use of plant-microbe interaction, involves the deposition of atmospheric carbon as plant root material, which is then integrated into soil microbes and soil organic matter [80]. An increase in CO_2 results in an increase in rhizodeposition, which in turn

leads to a wider C/N ratio, ultimately slowing down decomposition [81]. The focus on describing techniques for quantifying CO_2 fluxes in various soil compartments, clarifying the process of root carbon stabilization, examining the impacts of increased CO_2 levels on belowground carbon storage, and investigating the capacity of roots to sequester carbon [55]. This emerging field is currently in the initial phase of exploration, with the majority of research dedicated to comprehending the impacts of increased CO_2 levels on microbial communities, below-ground plant material production, and biomass decomposition. Additionally, studies are investigating the long-term potential of carbon rhizodeposition in relation to land management practices and plant species [54].
Challenges related to plant microbe interactions are discussed below:

Urbanization: Urban canters development and the human activities occurring within them are significant contributors to a wide range of airborne contaminants. Urban tree leaves contain higher levels of chemicals, as well as more macro and micronutrients, compared to nonurban trees. This difference in nutrient enrichment has the potential to affect the dynamics and functions of plant-microbe interactions [82]. The composition of airborne microbial communities is influenced by the type of land use (such as urban or rural areas) and the local vegetation. Significantly, human activities have considerable effects on the microbiota of plants, which in turn can mitigate air pollutants (specifically, breaking down compounds that accumulate on leaves) and impact the health of human populations [83]. The leaf microbial populations have the potential to significantly contribute to urban phylloremediation by breaking down pollutants including as ultrafine particulate matter, black carbon, and atmospheric hydrocarbons [84].

Range shifts: Global change leads to the alteration of climatic conditions. Shifting ranges are primarily caused by two factors: (1) the introduction of species to new habitats through human activities, and (2) environmental changes, such as warming, which prompt species to either expand their range and colonize new environments where they previously could not survive, or contract their range due to heightened biotic and abiotic stresses [52]. Considering the relationships between plants and microorganisms, including the host plant and its interacting microbiota, invasive plant species may have unexpected effects on ecosystems due to their associated microorganisms [74].

Changing climate: The majority of creatures on Earth are currently undergoing an increase in temperatures. The temperature can impact distinct molecular pathways in bacteria that inhabit the surfaces of plant leaves. Microbes have the ability to detect and react to significant shifts in surrounding temperatures [49]. However, the impact of prolonged increases in ambient temperature remains largely uncertain. Drought causes a significant danger to global food security due to their destructive impact on vital crops. Furthermore, it was noted that dryness had varying effects on the functionality of the microbiota in the roots and leaves. There is a correlation between drier climate conditions and an increase in both the evenness and overall abundance of soil fungi [53].

7. CONCLUSION

The interactions of the plant microbiota, which are extremely diverse, are one of the primary variables that determine the health of plants and the amount of productivity they produce. The understanding of the fundamental mechanisms that are responsible for the activity of the microbiome is still in the process of developing, despite the fact that the awareness of the diverse functional capacities of the plant microbiome has significantly improved in recent times. Having this knowledge is essential in order to make use of the genomic potential of plants, which will ultimately lead to an improvement in the stress resistance of next crop production in the face of a changing climate. The community assembly and function of the plant microbiome are both influenced by a variety of circumstances, and it is vital to have a critical understanding of these interactions. Interactions between plant microorganisms are advantageous because they help to prevent diseases that are detrimental to plants and give plants with a role that is beneficial. It is the most appropriate way to meet the demand for food and to suppress diseases in the future to have a fundamental understanding of the interactions between plant microorganisms and their engineering for acceptable application in sustainable agriculture.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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