

Plant microbiome in crop health, disease suppression, and sustainable agriculture

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ABSTRACT

Over the past few years, the intricate association between the plants and microorganisms has uncovered the crucial role of microbial communities in plant growth promotion and maintaining soil fertility, ultimately supporting sustainable agriculture. Plant microbiome comprises bacteria, fungi, viruses, protozoans, and archaea, colonizing multiple tissues in the rhizosphere, phyllosphere, and endosphere. These microbes help in plant growth directly by acquiring the nutrients. Furthermore, these beneficial microbes also prime the immune response of the plant, protecting it from biotic and abiotic stresses. The multi-omics techniques have paved the way in understanding the genotypic-specific nature of the phyto-microbiome and its regulation by abiotic factors. Plant-microbiome engineering in relation to synthetic microbial communities delivered predictable and consistent functional performance. Targeted deployment of these microbial communities promotes functional stability over single-strain inoculants. Despite major progress, insufficient field-level validation, host-microbiome compatibility constraints, and regulatory ambiguities restrict their broader application. This review examines plant-microbiome functionality, emphasizes their role in reducing chemical dependency, and presents an integrative framework bridging microbiome science with sustainable farming systems.

1. INTRODUCTION

Agriculture faces a persistent threat from frequent pest and disease outbreaks, accounting for up to 40% of annual crop losses, adversely affecting farmer livelihood [1]. Farmers extensively use the chemical pesticides which affect non-target organisms including beneficial insects, birds, fish, and soil microorganisms that are vital for healthy ecosystems [2,3]. Beyond environmental damage, pesticides pose considerable risk to human health through food residues, skin contact, and inhalation [4,5].

Growing concerns regarding environmental protection and food safety have spurred interest in regulating microbiomes using organic formulations harboring beneficial microbes [6]. During the course of evolution, microorganisms adapted to inhabit higher organism developing symbiotic associations ranging from beneficial to

harmful. The term plant microbiome refers to the native microbial community which dynamically interacts with the plant host, influencing plant health by improving nutrient uptake, boosting stress resilience, and strengthening defenses against pathogens [Figure 1]. The application of bioinoculants and biostimulants has emerged as an effective strategy to enhance crop productivity [7]. Sufficient literature is available on the effects of beneficial microorganisms on plant health, yet limited research is there on their effect on native microbial communities [8].

Mutual interactions between plants and microbes foster a harmonious micro-ecological environment [9]. Endophytic microbes bridge below and above-ground microbiomes, drawing specific microbes from the rhizosphere and phyllosphere into plant tissues [10].

Interest in agricultural microbiomes is rising because of their capacity to enable sustainable and eco-conscious crop management [11]. This review consolidates the current literature on microbial communities inhabiting plant tissues and surfaces. It explores microbiomes' role in plant health and disease control and the emerging potential and challenges of integrating them into contemporary farming.

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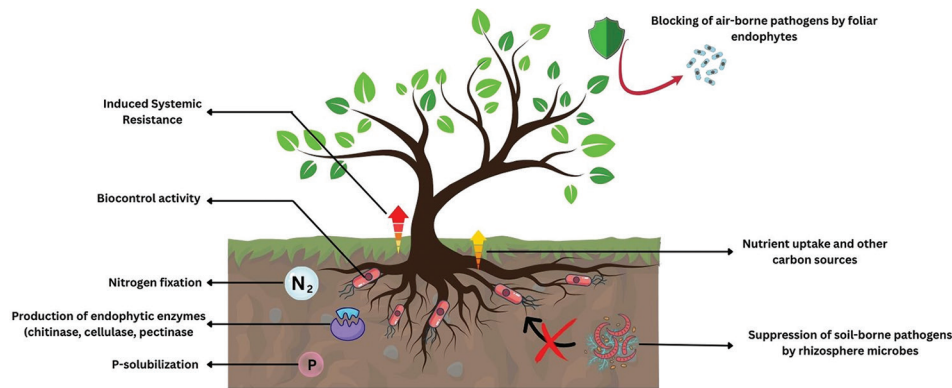


Figure 1: Function and impact of plant-microbiome on the host plant (Source: Made by authors).

2. MICROBIAL HABITATS ON AND IN PLANTS

A large number of microorganisms colonize the inner and outer surfaces of the plant. The organization of different microbial communities varies across plant tissues [12]. The microbes living in the rhizosphere, endosphere, and phyllosphere are key to maintaining plant health and suppressing pathogens [13]. Microbiomes act as an extended layer of defense in the plant system [14,15]. There are a number of factors affecting plant microbiomes including environmental and metabolic activities of the plant [16]. Metabolites secreted from the plant roots aid in attracting beneficial microbes or deterring harmful ones, influencing pathogen invasion [17-19].

2.1. Rhizosphere: The Root Microbiome

The soil region adjacent to plant roots is referred to as the rhizosphere. This confined zone hosts bacteria, fungi, archaea, and other microorganisms that participate in nutrient cycling, enhance mineral uptake, and provide protection against pathogens [20]. Root-zone microorganisms are majorly influenced by root exudates such as sugars, amino acids, organic acids, enzymes, and secondary metabolites [21]. Apart from the physiological functions, root exudates signal the microbes of its root zone. These signals affect the microbial community in the rhizosphere by either attracting beneficial microbes or deterring harmful ones [22]. This plant-microbe signaling is bidirectional and the rhizospheric communication is classified into three major types: microbe-to-microbe, plant-to-microbe, and microbe-to-plant signaling [23].

Certain rhizosphere microbes release compounds that inhibit weed growth and soil-borne pathogens without harming crops [24]. Studying the rhizosphere microbiome helps in understanding their nature and developing sustainable alternatives to chemical pesticides. Rhizosphere microbes enhance nutrient availability by converting organic and inorganic compounds into forms usable by plants, thereby improving growth, yield, and quality [25].

The rhizospheric biocontrol agents suppress the plant pathogens by various mechanisms, namely antibiosis, competition for nutrients and space, mycoparasitism, and siderophore-mediated competition for iron acquisition [26]. *Trichoderma* species are proved to act as biocontrol agents as well as bio stimulants [26].

The rhizosphere sustains a complex microbial consortium that contributes to the overall well-being of the plant. Rhizosphere-derived microbial metabolites are emerging as key regulators of plant growth, development, and resilience to environmental stresses. This diverse

group of metabolites, such as phytohormones, VOCs, antibiotics, siderophores, and exopolysaccharides, differentially influences the plant performance and the local rhizosphere environment. Phytohormones including auxins (IAA), gibberellic acid (GA), abscisic acid (ABA), and cytokinin (CK), directly influence root development, nutrient acquisition, and plant responses to stress [44]. *Bacillus velezensis* GB03, a plant growth-promoting rhizobacterium from wheat fields, enhances growth through auxin biosynthesis and volatile compounds like 2,3-butanediol, and its resilience as endospores has enabled its use in commercial biostimulants [45]. Many studies have demonstrated that diazotroph inoculation boosts plant growth, often as a result of nitrogen (N₂) supplied by the bacteria [46].

Likewise, antibiotics and VOCs help in defending the pathogenic organisms and environmental stressors [47]. Siderophores make the iron available by acting as iron-chelating compounds [48]. Exopolysaccharides contribute to improved soil aggregation and moisture retention, supporting plant growth under drought conditions [49].

Plant growth-promoting rhizobacteria group is also one such example which is involved in plant growth promotion and protection [26]. The rhizosphere stands out among plant-associated microbiomes as a dynamic hub of microbial activity which helps in overall development of the plant and provides protection against disease-causing pathogens [Table 1].

2.2. The Endosphere: Microbial Life Inside Plant Tissues

Some microorganisms penetrate into the plants and reside in the tissues forming the endospheric microbiome. These endophytic microbes employ different strategies to penetrate and colonize plant tissues [39]. The series of events involved in successful colonization are attachment, entry, motility, transmission, and multiplication within the host plant [43]. The microbes produce hydrolytic enzymes such as pectinase, xylanases, cellulase, and proteinase to help penetrate the plant tissues [50]. Colonization of the endosphere by beneficial microorganisms is highly rewarding to sustainable agricultural production but also brings to the fore unique challenges. Endophytes and pathogens also follow the same methodology of entry and therefore induce competition that motivates plants to develop mechanisms for selective microbial penetration [51].

Endophytes engage with plants in ways that extend from mutual benefit to minor pathogenic influence [52]. Plants supply carbohydrates, essential for endophyte growth, while endophytes provide metabolites

Table 1: Rhizospheric biocontrol agents.

S. No.	Host	Rhizospheric biocontrol agent	Pathogen controlled	Mechanism of action	References
1.	Tomato	<i>B. subtilis</i> SL44, <i>Enterobacter hormaechei</i> Wu15	<i>Colletotrichum gloeosporioides</i>	Production of VOCs and mycolytic enzyme activity (chitinase, β -1,3-glucanase, cellulase) causing fungal cell wall damage and disrupts ergosterol-dependent membrane integrity	[27]
2.	Tomato	<i>P. fluorescens</i> Pfl	<i>F. oxysporum</i> , <i>Sclerotium rolfsii</i>	Production of DAPG antibiotic, siderophore, HCN, and other metabolites collectively inhibit fungal mycelial growth	[28]
3.	Tomato	<i>Chitinophaga</i> , <i>Bacteroidetes</i> , <i>Sphingobacterium</i> , <i>Actinobacteria</i>	<i>R. solanacearum</i>	Production of hydrolytic enzymes, nutrient competition, ISR induction, and quorum-sensing disruption	[29]
4.	Tomato	<i>Leifsonia aquatica</i>	<i>R. solanacearum</i>	Production of antimicrobial metabolite, antibiotics, nutrient/space competition, with protective biofilms blocking pathogen colonization	[29]
5.	Cucumber	<i>B. subtilis</i> 1JN2	<i>F. oxysporum</i> f. spp. <i>cucumerinum</i>	Production of mycolytic enzymes (chitinase, glucanase), antibiotics that suppress the pathogen by degrading hyphae and competing for nutrients	[30]
6.	Cucumber	<i>Paenibacillus polymyxa</i> J2-4	<i>Meloidogyne incognita</i>	VOCs with contact and fumigant nematicidal effects, including “honeytrap” attraction, followed by killing and repellent action against invading nematodes	[31]
7.	Lettuce	<i>Pseudomonas jessenii</i> RU47	<i>Rhizoctonia solani</i>	Antibiosis through DAPG and phenazine production; siderophore-mediated iron competition; enzymatic lysis of fungal cell walls; PISR	[32]
8.	Potato	<i>Bacillus velezensis</i> Y6	<i>Streptomyces scabies</i>	Lipopeptide antibiotics (fengycin, bacillomycin), antimicrobial VOCs, rhizosphere niche competition, and induction of plant defense responses	[33]
9.	Kiwifruit	<i>Paenibacillus polymyxa</i> YLC1	<i>P. syringae</i> pv. <i>actinidiae</i>	Antibiotic biosynthesis, siderophore production limiting iron availability to pathogen; HCN production, quorum sensing disruption, and enzymatic degradation of virulence factors	[34]
10.	White clover	<i>Bacillus cereus</i> B1, <i>P. fluorescens</i> P2	<i>Heterodera trifolii</i>	Nutrient and niche competition, along with ISR through SA/JA/ET signaling and direct antibacterial antagonism	[35]
11.	Thale cress	<i>B. subtilis</i>	<i>P. syringae</i>	Antagonistic VOCs, biofilm-mediated exclusion, iron competition, and activation of plant defense genes	[36]
12.	Grape	<i>Bacillus velezensis</i>	<i>B. cinerea</i>	Antimicrobial lipopeptides (fengycin, bacillomycin) that compete with pathogens and can trigger SAR in the host plant	[37]
13.	Agarwood	<i>Glomus fasciculatum</i>	<i>Pythium aphanidermatum</i>	Mycoparasitism with hyphal coiling and CWDEs (chitinase, β -1,3-glucanase), antibiotic metabolites, and competition for carbon and nitrogen	[38]
14.	Wheat	<i>B. subtilis</i>	<i>F. oxysporum</i> , <i>B. cinerea</i>	Mycolytic enzymes (chitinase, cellulase, β -1,3-glucanase), siderophore-based iron chelation, VOCs, and nutrient competition suppress fungal growth	[39]
15.	Wheat	<i>P. fluorescens</i>	<i>F. oxysporum</i>	2,4DAPG, phenazines, pyrrolnitrin, siderophores, HCN, and lytic enzymes jointly damage fungal cells and block their growth	[39]
16.	Maize	<i>Trichoderma atroviride</i>	<i>Spodoptera frugiperda</i>	Produces insecticidal metabolites, digestive enzymes, parasitizes fungal pathogens, and releases toxins causing larval death	[40]
17.	Rice	<i>Bacillus atrophaeus</i> , <i>Bacillus cabrialesii</i>	<i>Xanthomonas oryzae</i>	Produces antibiotics, antimicrobial enzymes, and volatiles, suppresses pathogen genes, and outcompetes pathogens for iron	[41]
18.	Cannabis	<i>Paenibacillus mobilis</i> , <i>Paenibacillus polymyxa</i>	<i>Alternaria</i> , <i>Aspergillus</i> , <i>Fusarium</i> , <i>Penicillium</i> spp.	VOCs, bacteriocins/peptides, and lytic enzymes that attack fungi, compete for space, and stimulate plant defenses	[42]
19.	Cannabis	<i>Bacillus</i> spp., <i>Paenibacillus</i> spp.	<i>F. oxysporum</i> , <i>B. cinerea</i>	Lipopeptide antibiotics (fengycin, bacillomycin), enzyme-based mycoparasitism, nutrient and niche competition, and biofilm-mediated secondary metabolite antibiosis	[43]

HCN: Hydrogen cyanide, PISR: Pseudomonas-induced systemic resistance, VOCs: Volatile organic compounds, *B. cinerea*: *Botrytis cinerea*, *B. subtilis*: *Bacillus subtilis*, *F. oxysporum*: *Fusarium oxysporum*, *P. fluorescens*: *Pseudomonas fluorescens*, *P. syringae*: *Pseudomonas syringae*, *R. solanacearum*: *Ralstonia solanacearum*, SA: Salicylic acid, JA: Jasmonic acid, ET: Ethylene.

that help plants tolerate stresses like drought and salinity [53]. Recent metabolic profiling of endophytes has revealed a rich array of secondary metabolites such as flavonoids, alkaloids, carotenoids, terpenoids, phenolics, and peptides, with antimicrobial, anticancer, and pesticidal properties [54]. Endophytes are well known to produce VOCs themselves and stimulate VOC production in plants through the jasmonic acid (JA) pathway [55].

Endophytic fungi belonging to the phylum Ascomycota are recognized for synthesizing a wide range of bioactive compounds that enhance plant growth [56] and strengthen tolerance to environmental stresses [Figure 2]. The fungal genera *Fusarium* and *Trichoderma* synthesize secondary metabolites that help plants develop resistance to pathogenic infections [57,58]. These fungi expand their hyphal networks into the soil, enhancing the plant's absorption of key nutrients such as phosphorus and N₂ [50].

Most dominant endophytic bacteria belong to the proteobacteria, firmicutes, and Actinobacteria phyla, and dominant genera include *Bacillus*, *Pseudomonas*, and *Burkholderia* [59]. Endophytic bacteria have been proven to improve plant growth, suppress the growth of pathogens [Table 2] and enhance stress tolerance [60]. Two endophytic isolates, i.e., *Staphylococcus warneri* and *Bacillus velezensis* from *Gnetum gnemon* successfully controlled the bacterial wilt disease [61]. The growth of *Phytophthora parasitica* was inhibited by over 80% due to volatiles produced by *Pseudomonas taiwanensis* [62].

Endophytes enhance plant growth through nutrient solubilization, N₂ fixation, phytohormone production, and control through biocontrol mechanisms [39,50]. The bacterial endophytes, *Pseudomonas* spp., *Enterobacter* spp., and *Acinetobacter* spp., boost phosphate solubilization by synthesizing growth hormones such as IAA, GA, and CK in plants [74]. Endophytes promote plant growth primarily by producing or stimulating phytohormones, a key mechanism responsible for physiological and structural adaptations in plants [75]. Endophytes influence both the phyllosphere and rhizosphere microbiomes, fostering a more favorable microbial environment for the host plant. The bacterial endophytes, *Pseudomonas fluorescens* is known to fix atmospheric N₂, solubilize phosphate, and produce siderophores for tolerating stress in eggplant [76]. The filamentous

hyphae of arbuscular mycorrhizal fungi colonize both the internal and external root surfaces, facilitating improved absorption of water and nutrients [77].

2.3. Phyllosphere: The Above-Ground Surface Microbiome

The phyllosphere of the plant means the aerial or above-ground surfaces of plant. It hosts diverse microbial communities including bacteria, fungi, viruses, and other microorganisms [78], essential for plant growth [79] and protecting plants from harmful pathogens [Table 3]. Phyllospheric biocontrol agents protect plants through direct mechanisms, such as antibiosis, production of reactive oxygen species (ROS), and cell wall-degrading enzymes for mycoparasitism and indirect mechanisms, including induced resistance and growth promotion through effectors and elicitors [80]. Host genotype and phenotype shape the microbial communities of the phyllosphere [81]. In addition to the genotype, the developmental stage and age of the plant modulate phyllospheric microbial communities through the secretion of specific hormones and bioactive compounds [82]. Disruptions in the phyllosphere microbiota, from pathogen, stress, or agricultural practices, can cause dysbiosis, adversely affecting plant health and key ecological functions such as carbon and oxygen cycling [83].

Manipulating phyllosphere microbial communities by applying beneficial microbes or their metabolites onto plant leaves can suppress foliar pathogens, occupy ecological niches, and enhance plant resistance to disease and environmental stress [11]. Reduction in foliar diseases in tomatoes and cucumber has been reported due to strategic modulation of the phyllosphere through bacterial antagonists [84].

To explore the inherent microbial resilience, it is essential to design phyllosphere-modulating syncoms. The development which follows a top-down approach, involving simplification of natural microbial communities to understand interactions, or a bottom-up framework that integrates selected beneficial microbiota for predefined objectives. These techniques produce more precise outcomes if combined with artificial intelligence (AI) [103]. As compared to the other two microbiomes, very limited studies are conducted on the phyllosphere microbiome, underscoring the imperative for additional research for better crop productivity [104].

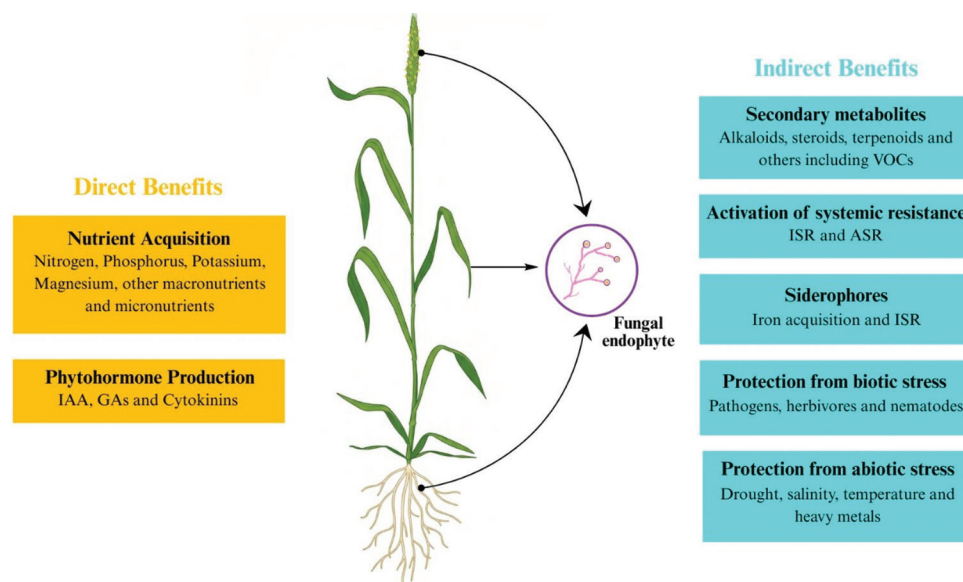


Figure 2: Benefits of endophytic colonization by fungi (Source: Made by authors).

Table 2: Endospheric biocontrol agents.

S. No.	Host	Endospheric biocontrol agent	Pathogen controlled	Mechanism of action	References
1.	Tomato	<i>Bacillus pseudomycoloides</i> HP3d, <i>Bacillus velezensis</i> A6, <i>Paenibacillus polymyxa</i> PGSS1	<i>A. solani</i>	Production of siderophore, HCN, and VOCs.	[63]
2.	Tomato	<i>B. subtilis</i>	<i>Botrytis cinerea</i> , <i>Colletotrichum gloeosporioides</i>	Hydrolytic enzyme secretion (chitinase, β -1,3-glucanase, proteases)	[64]
3.	Tomato	<i>B. subtilis</i> A9	<i>P. infestans</i>	ISR, enhanced plant defense-related enzyme activity	[65]
4.	Tomato	<i>F. oxysporum</i> EF119	<i>P. infestans</i>	Mycoparasitism, Induction of systemic plant resistance	[66]
5.	Tomato	<i>Enterobacter cloacae</i>	<i>A. solani</i>	ISR, Enhanced plant defense-related enzyme activity	[67]
6.	Cucumber	<i>Pseudomonas</i> spp. IALR1619	<i>P. ultimum</i>	Plant growth promotion, ISR	[68]
7.	Lettuce	<i>Pseudomonas</i> spp. IALR1619	<i>P. ultimum</i> , <i>Pythium dissotocum</i>	Stress mitigation under pathogen pressure, Plant growth-promoting activity	[68]
8.	Potato	<i>Pseudomonas putida</i> P9	<i>Pythium</i> spp., <i>R. solani</i>	ISR, Mycoparasitism	[69]
9.	Rice	<i>Streptomyces</i> spp.	<i>Sclerospora graminicola</i>	Competition for nutrients and root niches, ISR	[64]
10.	Rice	<i>Trichoderma harzianum</i>	<i>Magnaporthe grisea</i>	Mycoparasitism, Antibiosis through secondary metabolites	[70]
11.	Passion fruit	<i>B. subtilis</i>	<i>Nigrospora sphaerica</i>	Hydrolytic enzyme secretion (chitinase, β -1,3-glucanase), Plant growth promotion	[64]
12.	Kiwi	<i>Fusarium tricinctum</i>	<i>Pseudomonas syringae</i> pv. <i>actinidiae</i>	Antibiosis through metabolite production, cell membrane, and wall disruption	[64]
13.	Banana	<i>P. indica</i>	<i>F. oxysporum</i> f. spp. <i>cubense</i> tropical race 4	ISR, Enhanced plant defense enzyme activity	[66]
14.	Cacao	<i>Gliocladium catenulatum</i>	<i>Moniliophthora perniciosa</i>	Mycoparasitism, antibiotic production	[66]
15.	Barley	<i>P. indica</i>	<i>Blumeria graminis</i> , <i>Fusarium</i> spp.	ISR, mycoparasitism	[66]
16.	Wheat	<i>P. indica</i>	<i>Fusarium</i> spp.	Enhanced nutrient assimilation	[66]
17.	Wheat	<i>Streptomyces</i> spp.	<i>R. solani</i>	Production of VOCs	[71]
18.	Wheat	<i>Rhodotorula glutinis</i>	Mycotoxigenic fungi	Yeast-mediated mycotoxin control, microbiome level protection	[72]
19.	Soybean	<i>Trichoderma</i> spp.	<i>Macrophomina phaseolina</i>	Competition for nutrients and space, plant growth promotion	[73]

HCN: Hydrogen cyanide, ISR: Induced systemic resistance, VOCs: Volatile organic compounds, *A. solani*: *Alternaria solani*, *B. subtilis*: *Bacillus subtilis*, *F. oxysporum*: *Fusarium oxysporum*, *R. solani*: *Rhizoctonia solani*, *P. indica*: *Piriformospora indica*, *P. ultimum*: *Pythium ultimum*, *P. infestans*: *Phytophthora infestans*.

3. ROOT-TO-SHOOT CONNECTIONS: MICROBIAL NETWORKS IN CROP PROTECTION

The co-evolution of plants and microorganisms led to the intricate networks, coordinating recognition, signaling, and physiological responses within the plant system [105]. Such plant-microbe interactions function in multiple hormone-based regulatory processes, especially JA-based signaling, where crosstalk confers both specificity and robustness of plant immunity to multiple pathogens [106]. Microbial bioagents utilize multiple processes such as production of volatile compounds having antimicrobial properties and engage in signaling interactions even without direct pathogen contact [107].

The plant holobiont refers to an integrated set of physically disconnected plant compartments that communicate with each other through communication networks of molecules and metabolic processes that modulate both plant-microbe and microbe-microbe associations during plant development [108]. Elucidation of such communication systems yields promising biotechnologies suitable for sustainable agriculture. Systemic resistance processes allow plants to acquire broad-spectrum protection against pathogens through communication with plant defense-inducing microorganisms.

Activation of plant defenses in a systemic manner results in long-term, broad-spectrum protection and constitutes a safe substitute to the application of fungicides, especially against economically important

Table 3: Phyllospheric biocontrol agents.

S. No.	Host	Phyllospheric biocontrol agent	Pathogen controlled	Mode of action	Reference
1.	Tomato	<i>Rhizobium</i> spp. b1, <i>B. subtilis</i> b2	<i>P. syringae</i> pv. tomato, <i>Alternaria solani</i>	Production of protease and cellulase, Induction of SA, JA, ET pathways	[85]
2.	Tomato	<i>Enterobacter cloacae</i> TR1, <i>Bacillus</i> spp.	<i>B. cinerea</i>	Production of volatile compounds and antibiotics	[86]
3.	Tomato	<i>Bacillus amyloliquefaciens</i>	<i>B. cinerea</i>	Biofilm formation and competition	[87]
4.	Rice	<i>Panicum microbes</i>	<i>Ustilaginoidea virens</i>	Modulation of BCAA metabolism, competition	[88]
5.	Rice	<i>Aspergillus cvjetkovicii</i>	<i>Magnaporthe oryzae</i>	Production of antimicrobial compounds and competition	[89]
6.	Rice	<i>Actinomycetes</i>	<i>Pyricularia oryzae</i>	Production of antibiotics and secondary metabolite synthesis	[90]
7.	Tobacco	<i>Stenotrophomonas</i> , <i>Achromobacter</i> , <i>Enterobacter</i>	<i>P. syringae</i> pv. <i>tabaci</i>	Barrier formation and competition	[91]
8.	Tobacco	<i>Bacillus velezensis</i> SYL-3	<i>Alternaria alternata</i> , tobacco mosaic virus	Production of lipopeptides, ISR	[92]
9.	Chinese cabbage	<i>Brevibacillus brevis</i>	<i>B. cinerea</i>	Lipopeptide antibiotics, Antibiosis	[93]
10.	Chinese cabbage	<i>B. subtilis</i> PMB102	<i>Alternaria brassicicola</i> ABA-31	Production of antifungal metabolites	[94]
11.	Maize	<i>B. subtilis</i> DZSY21	<i>Bipolaris maydis</i>	Production of lipopeptides, ISR	[95]
12.	Wheat	<i>Pseudomonas piscium</i>	<i>Fusarium graminearum</i>	Secretion of phenazine-1-carboxamide	[96]
13.	Lemon	<i>Pseudomonas protegens</i> CS1	<i>Xanthomonas citri</i> subsp. <i>citri</i>	Siderophore production, iron sequestration, and oxidative stress induction	[97]
14.	Potato	<i>Microbacterium testaceum</i>	<i>Pectobacterium carotovorum</i>	Disruption of quorum sensing	[98]
15.	Thale cress	<i>Albugo laibachii</i>	<i>Moesziomyces bullatus</i> ex <i>Albugo</i>	Secretion of enzymes that inhibit the growth of oomycetes	[99]
16.	Thale cress	<i>Paenibacillus polymyxa</i>	<i>P. syringae</i>	SA and JA-mediated defense pathways	[100]
17.	Thale cress	<i>Sphingomonas</i> spp.	<i>P. syringae</i>	Competition for nutrition	[101]
18.	Apple	<i>Pseudomonas orientalis</i>	<i>Erwinia amylovora</i>	Antibiosis	[102]

BCAA: Branched chain amino acid, ISR: Induced systemic resistance, *B. cinerea*: *Botrytis cinerea*, *B. subtilis*: *Bacillus subtilis*, *P. syringae*: *Pseudomonas syringae*, SA: Salicylic acid, JA: Jasmonic acid, ET: Ethylene.

pathogens such as *B. cinerea* [109]. There exist two main routes: Systemic acquired resistance, which targets salicylic acid (SA)-based signaling, and induced systemic resistance (ISR), which was originally linked to JA and ethylene (ET) signaling processes [110]. However, it is assumed that SA and JA/ET signaling processes may both participate in ISR, and in such processes, small RNAs have important regulatory functions [111].

Biocontrol organisms including *Trichoderma* and *Pseudomonas* species induce plant growth and boost nutrient uptake [110]. Biocontrol agents of the phyllosphere, including *Sphingomonas* and *Methylobacterium*, redesign microbial communities and induce plant defense systems through multiple hormone signaling networks including ABA, ET, JA, and SA [112]. In addition, rhizobia contain the potential to induce ISR-like reactions other than the capability to fix N₂ and thus boost the health of plants through the mechanism of

systemic resistance [113]. Such beneficial microorganisms are elicitors that trigger plant defensive strategies through different mechanisms, including the secretion of enzymes, the biosynthesis of antimicrobial molecules, and the induction of resistance [114].

The signaling mechanism comprises intricate interactions among molecules, wherein microorganisms produce a set of chemical cues, i.e., N-acyl homoserine lactones, phytohormones, and bioactive molecules but plants respond by synthesizing carbon substrates, carbon-derived signals, and secondary metabolites [115]. Recent innovations depict combined strategies including entomopathogenic fungi and mycoparasitic fungi that attack both insect vectors and fungal symbionts in a single shot, such as in ambrosia beetle control [116]. Such eco-intelligent strategies minimize diseases such as bacterial wilt, fire blight, and crown gall while boosting native microbiomes [117].

4. MICROBIOME-MEDIATED MECHANISMS OF PATHOGEN SUPPRESSION

The plant microbiome confers protection against pathogens through both direct and indirect strategies [Figure 3]. Direct suppression occurs through the production of antimicrobial compounds and competition for nutrients and ecological niches, whereas indirect suppression is achieved by stimulating and modulating the plant immune system [16].

4.1. Direct Pathogen Suppression by Microbiome

Disease-suppressive soils host diverse microbial communities that act as sources of novel antibiotic compounds. Numerous antimicrobial metabolites produced by antagonistic microorganisms isolated from such soils have been identified and characterized. Sulfur-containing VOCs released by *Paraburkholderia graminis* PHS1 [118], along with VOCs such as methyl 2-methyl pentanoate and 1,3,5-trichloro-2-methoxybenzene produced by *Streptomyces* spp. [119], have been shown to inhibit *Rhizoctonia solani*. Similarly, the thiopeptide conprimycin synthesized by strain S4-7 effectively suppressed *Fusarium oxysporum* [120]. Antimicrobial compounds have also been discovered in microbial isolates obtained from healthy plants. For instance, *Bacillus amyloliquefaciens* OR2-30 produces iturins that inhibit the growth of *Fusarium graminearum* [121]. *Pseudomonas putida* IsoF confers protection to tomato plants against *R. solanacearum* by employing a type IVB secretion system (T4BSS) to deliver toxic effectors that inhibit the pathogen [122].

Coralloccoccus spp. EGB produces thiaminase, which reduces the virulence of *Phytophthora sojae* by degrading thiamine, a compound required for its growth and pathogenicity [123]. *Aspergillus cvjetkovicii* secretes 2,4-di-tert-butylphenol that scavenges intracellular ROS, leading to the suppression of bZIP-activated AMT1 transcription in *R. solani* [124]. *Pantoea agglomerans* ZJU23 produces herbicolin A, which has antifungal activity against both plant and human pathogens, by directly binding to and disrupting ergosterol-containing lipid rafts [125].

Microbiomes suppress pathogens by limiting nutrient availability, with higher microbial diversity strengthening this competitive effect [126]. Iron plays a central role in microbe-pathogen competition, with its uptake being crucial for commensal *Pseudomonas* to protect against

pathogenic strains [127]. *Pseudomonas brassicacearum* R401 secretes pyoverdine, a siderophore, which inhibits *R. solanacearum* by restricting the pathogen's access to iron [128].

4.2. Indirect Pathogen Suppression by Microbiome

Plant-associated microbiomes can stimulate the plant's immune system, leading to the suppression of pathogens. In particular, native soil microbial communities' prime plants into a heightened state of defense. To protect itself from the pathogens, plants recruit microbes rather than directly attacking the pathogens [129,130].

The microbiome members are also capable of activating pattern-triggered immunity (PTI) in plants [131]. Activation of PTI through EFR, which recognizes bacterial elongation factor Tu, is essential for *B. velezensis* FZB42 to confer resistance against *R. solani*. By priming lateral root development and ROS signaling, FZB42 indirectly promotes bacterial auxin production, resulting in increased plant resistance to *R. solani*. Auxin mitigated protection against ROS stress in FZB42, enhances root colonization, facilitating the suppression of fungal infection [132].

Colonization of roots by the ISR-inducing bacteria *P. fluorescens* PTA-CT2 and *Bacillus subtilis* PTA-271 stimulated camalexin accumulation in leaves, enhancing plant defense against *B. cinerea* and *Pto* DC3000 [133]. Stomata act as a passive entry point for pathogens during infection [134], and microbes that induce ISR can block pathogen invasion by triggering stomatal closure. *Bacillus* species have been shown to prevent pathogen-induced reopening of stomata by regulating the ABA and SA signaling pathways [135]. Microbe-induced ferroptosis can activate plant immune responses. Recent research demonstrated that moderate ferroptosis triggered by the rice endophyte *S. hygroscopicus* OsiSh-2 is essential for its colonization, and it also primes plant defenses against rice blast disease [136].

5. ROLE OF SYNTHETIC MICROBIAL COMMUNITIES IN CROP HEALTH

Synthetic microbial communities (SynComs) assemble compatible microbial taxa with complementary functional traits that can generate modular consortia with emergent properties to deliver desired outcomes.

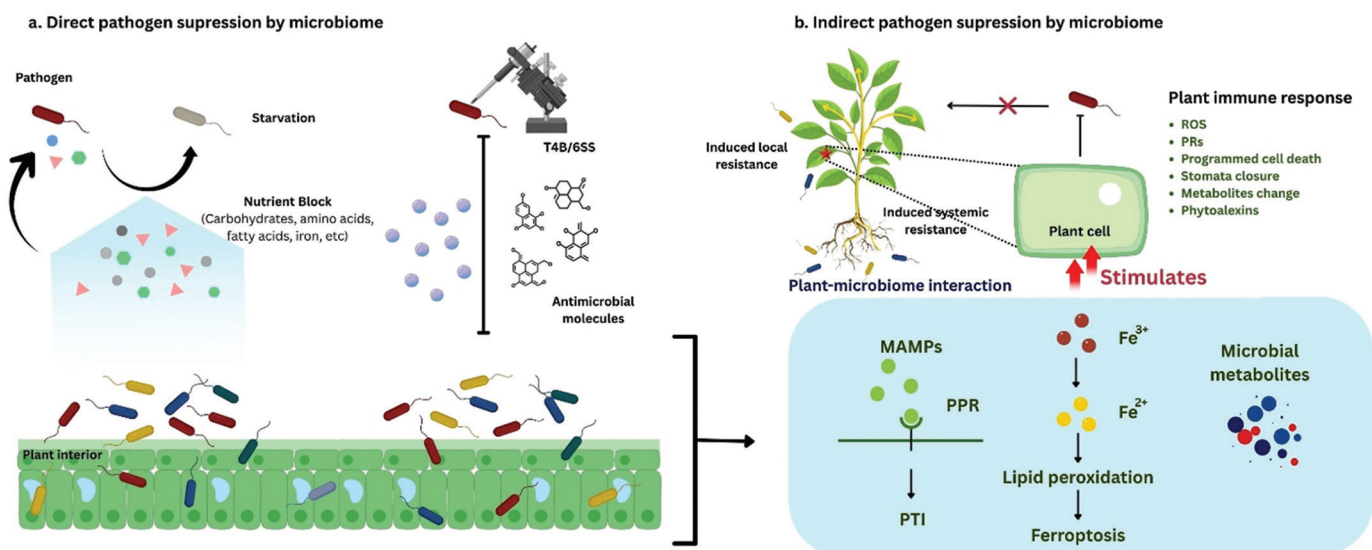


Figure 3: Mechanism for pathogen suppression by microbiomes (Source: Made by authors).

Engineering synComs helps reveal microbial community structure, function, and environmental factors shaping their development [137]. The steps involved in designing SynComs include finding the origin of microorganisms, selecting the required microbes, and refining the microbial interactions by engineering synergistic microbial networks. SynComs can directly boost plant growth or through reinforcing rhizosphere community functions. For instance, the manipulation of bacterial strain *Enterobacter cloacae* resulted in a reduction of blight-inducing pathogen (*Fusarium verticillioides*) in maize [138]. SynComs derived from indigenous endophytes have shown better performance than others [139]. With the tools like NGS, it has become very convenient to identify beneficial crop microbiome [140]. Incorporation of SynComs derived from sugarcane microbiome gave reduced yield loss and improved drought tolerance in maize [141]. Seed application of SynCom resulted in improved germination, plant height, and yield in cotton [142]. Inoculation with SynCom resulted in 36% increase in soybean yield [143]. SynComs provide functional backup, leading to greater stability unlike single strains [144].

6. CHALLENGES AND FUTURE PROSPECTS

Understanding of the intricate associations within diverse microbiomes is difficult because of their complex nature [145]. As these microbiomes are highly influenced by abiotic factors and the host species, they are associated with affecting their efficacy [146]. The incorporation of microbiome research in practical life demands proper strategies [147]. The functional scope of microbial communities often outpaces current sequencing methods, hindering accurate prediction of their behavior in natural settings [148]. Several ethical and regulatory challenges still persist regarding the emerging genetically modified microorganisms. There is a great need to understand the concept of microbial synergy within the plant microbiome. This could help in the production of tailored microbial consortia optimized for particular crops. The combination of microbiome advancements along with genomics and AI may improve predictive model accuracy [43]. Future studies must focus on the interaction between the beneficial microbiomes and the plant immune system and how to make use of these interactions to enhance crop health.

7. CONCLUSION

There are a number of biotic and abiotic stresses substantially affecting the crop yields and threatening the food security. Therefore, it is required to look up for strategies that are efficient as well as sustainable. Exploitation of the potential plant microbiomes is one such strategy. Mindful use of microorganisms associated with plants has the potential of replacing chemicals as these can suppress pathogens, boost nutrient uptake, and improve tolerance to environmental stresses, thus promoting agricultural sustainability. This review talks about the role of microbial communities in regulating plant health through multiple direct and indirect mechanisms. Insights into plant microbiome can be leveraged to understand climate change impacts, addressing agro-economic challenges, and food security. SynComs support the agricultural production by improving plant health and elucidating the functional complexity of phytomicrobiome communities. However, there are certain challenges in transferring in-vitro findings to in-vivo conditions due to variation in climate and host-microbiome compatibility. Therefore, it is essential to evaluate microbiome-based approaches under diverse environmental settings and supported by robust experimental validation and interdisciplinary research efforts.

8. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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10. CONFLICTS OF INTEREST

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11. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

12. DATA AVAILABILITY

Data is available with the authors and shall be provided upon request.

13. PUBLISHER'S NOTE

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14. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declare that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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