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Role of microbiome in the generation of disease-suppressive soil for sustainable agriculture

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ABSTRACT: The use of beneficial microorganisms to design disease-suppressive soil enhances sustainable agriculture by reducing pesticide dependence, increasing crop productivity, and maintaining long-term ecosystem health. Beneficial microbes naturally protect crops by fostering a balanced soil environment that discourages harmful diseases. These organisms produce antimicrobial chemicals that out-compete pathogens and strengthen the plant's defenses. This strategy not only protects biodiversity but also reduces the negative effects of agrochemicals on the environment. Although the results have been promising, further research is needed to fully understand the mechanisms of disease suppression to effectively translate this strategy into resilient agricultural practices.

KEYWORDS: disease suppressiveness, beneficial organisms, microbiome, disease management

INTRODUCTION

Soil-borne micro and macro-organisms can lead to crop diseases and yield losses, including damping-off, rots, and wilting, caused by oomycetes, fungi, bacteria, viruses, and nematodes [1]. Traditional control methods with chemical pesticides have limitations in combating soil-borne infections. Chemical fumigation, though effective, is now regulated due to environmental concerns. Sustainable approaches such as breeding resistant varieties, crop rotation, and organic amendments offer alternative strategies with a positive impact on environment and yield [2].

Soil microbiota which have been identified as crucial for soil health and disease control, are being studied extensively. The interaction between soil microbiota and plants play a vital role in maintaining soil stability and functionality [3]. Biological control agents (BCAs), are recognized as essential for sustainable agriculture. However, their success in commercial settings is hindered by challenges such as insufficient colonization and virulence of the soil-borne pathogens [4].

Understanding the plant-soil microbe interaction is crucial for exploiting beneficial microorganisms in disease-suppressive soils. This interaction, forming forms a complex network of relationships, that not only influences disease suppression but also contributes to nutrient cycling, soil structure, and overall ecosystem resilience. Harnessing this knowledge can lead to the development of tailored management strategies that optimizes the natural abilities of soil microbiota to promote healthy soils and sustainable crop production. Thus, ongoing research is imperative to unraveling the intricacies of these interactions and translate them into practical applications for agricultural systems worldwide [5].

WHAT IS DISEASE SUPPRESSIVE SOIL?

Soil-borne diseases are intricately linked to the degradation of the soil's micro-ecological environment, which disrupts the delicate balance of its microbial community. Pathogens typically thrive in the rhizosphere, the region of soil influenced by plant roots, before infecting their host plants. Maintaining a dynamic microbial balance, characterized by high microbial biomass and diversity, emerges as a critical factor in the suppression of soil-borne diseases [1]. A rich microbial diversity in the soil ecosystem serves as a natural barrier against pathogens, limiting their ability to establish and propagate. Moreover, the soil microbiome is multifaceted, playing diverse roles in nutrient cycling, stress tolerance, and disease suppression [6]. Extensive research endeavors have been dedicated to unraveling the microbial community structures in disease-conducive and suppressive soils. The concept of disease-suppressive soil (DSS) embodies a critical defense mechanism against root infections by soil-borne pathogens. DSS significantly reduces the presence of soil-borne pathogens, even in the presence of susceptible host plants [7]. Conversely, conducive soils foster disease spread by creating favorable abiotic and biotic conditions for pathogen propagation.

Disease suppression within soils operates through two fundamental mechanisms: general and specific suppression. In general suppression, the overall microbial community competes with pathogens for nutrients and space, often producing antimicrobial compounds. For example, bacteria like *Bacillus* and *Streptomyces* produce antibiotics that inhibit pathogens like *Rhizoc-*

tonia and *Fusarium* [8]. Specific suppression on the other hand is carried out by certain microorganisms that target specific pathogens. For instance, *Pseudomonas fluorescens* produces compounds that inhibit *Pythium*, while *Trichoderma* can directly attack fungal pathogens like *Sclerotinia*. Together, these mechanisms help create healthy soils that naturally protect plants from diseases [7]. Organic matter, enriched with various beneficial microorganisms, further enhances soil suppressiveness, offering a sustainable approach to disease management. Understanding the soil's immune responses and the intricate interactions between microbes and pathogens opens avenues for engineering microbiomes to bolster disease control. Harnessing the innate potential of soil microbiomes, plant species can selectively stimulate and support antagonistic microorganisms, offering a promising strategy for disease control [1].

Moreover, the buildup of disease suppressiveness in soils presents intriguing insights into long-term disease management strategies. Certain soils exhibit enduring suppressiveness, even after repeated monocultures, highlighting the pivotal role of antagonistic microorganisms in disease control [8]. The accumulation of antagonistic microorganisms, such as *Pseudomonas* spp., over time contributes to the decline of soil-borne diseases through the production of inhibitory compounds. Furthermore, diverse microbial taxa from Proteobacteria, Firmicutes, and Ascomycota have been reported to actively contribute to disease suppression by secreting various toxic compounds detrimental to pathogens [6, 9] (Fig. 1).

KEY BIOTIC CONTRIBUTORS TO DISEASE SUPPRESSIVENESS

Bacteria and archaea are key players in soil disease suppression, operating through interactions with plants, pathogens, and the soil environment [1]. In suppressive soils, a diverse array of bacterial species, including non-pathogenic *Bradyrhizobium*, *Burkholderia*, *Nitrospira*, and *Streptomyces*, thrive, while *Acidobacteria*, *Agrobacterium*, and *Pseudomonas* dominate in disease-conducive soils [7]. Building microbial networks has been advocated by Poudel et al [10] to understand microbial community structure for disease management, aided by network analysis to identify specific microbial consortia for disease suppression. Actinobacteria, like *Streptomyces*, produce beneficial secondary metabolites such as 2,4-diacetylphloroglucinol (DAPG) that hinders soil-borne pathogens [11]. Beneficial bacteria such as *P. fluorescens*, *Bacillus subtilis*, and *Streptomyces* spp. produce siderophores, which chelate iron from the soil, making it more available to plants. By sequestering iron, these bacteria outcompete pathogens, limiting their growth. For instance, *P. fluorescens* produces pyoverdine, a siderophore that enhances plant growth and suppresses pathogens like *Fusarium oxysporum*. Insoluble rock phosphate is solubilized by bacteria through the production of organic acids. Species such as *Bacillus megaterium* and *Rhizobium leguminosarum* produce acids like gluconic and citric acids, which solubilize phosphate, increasing its bioavailability to plants. This improves plant health and resilience against pathogens [12]. Other microorganisms produce substances like lipopeptides and antimicrobial volatiles, including sesquiterpenes that are secreted by beneficial microorganisms facilitating disease suppression [13].

Competition for resources and colonization sites in soil results in pathogen proliferation restriction by bacteria and archaea. These microorganisms induce systemic resistance in plants, triggering defense mechanisms like systemic acquired resistance (SAR) to combat pathogens [5]. While the archaeal community's contribution to disease suppression is often overlooked, studies by Kopecky et al [21] and Jayaraman et al [7] highlight its significance, alongside disease-suppressing traits of Proteobacteria, Firmicutes, Actinobacteria, and other microbial families (Table 1). However, Durán et al [22] suggest that bacterial endophytes, rather than rhizospheric microorganisms, primarily suppress certain diseases like take-all disease in wheat. Both groups of researcher are right in their observation as the disease suppressive organisms will have to be located at the site of infestation; i.e. soil for soil-borne diseases and plant tissue for above ground infections.

Fungi and microeukaryotes are also crucial for disease suppression, yet remain under-explored. Higher fungal diversity correlates with disease-suppressive soils, with species like *Fusarium*, *Malasezzia*, *Mortierella*, and *Trichoderma* implicated in suppression [7, 8]. Arbuscular mycorrhizal fungi (AMF) enhances disease suppression through various mechanisms, including improved plant nutrition and stress tolerance. AMF colonization leads to enhanced plant defense mechanisms, increased antioxidant activity, and the release of antibiotics and toxins against pathogens [23, 24]. Interactions between trophic levels and nutrient cycling dynamics influence soil suppressiveness. Hence this only goes to show that the entire process of disease suppression in complicated and requires the understanding of the intricate interplay between microbial communities and their environments for effective disease management in agriculture [25].

ABIOTIC FACTORS SHAPING DISEASE SUPPRESSION

Soil temperature exerts a profound influence on disease suppression, with microbial activity and community dynamics being highly temperature-sensitive. Nadarajah and Abdul Rahman et al [26] highlight the role of abiotic variables, including temperature, in

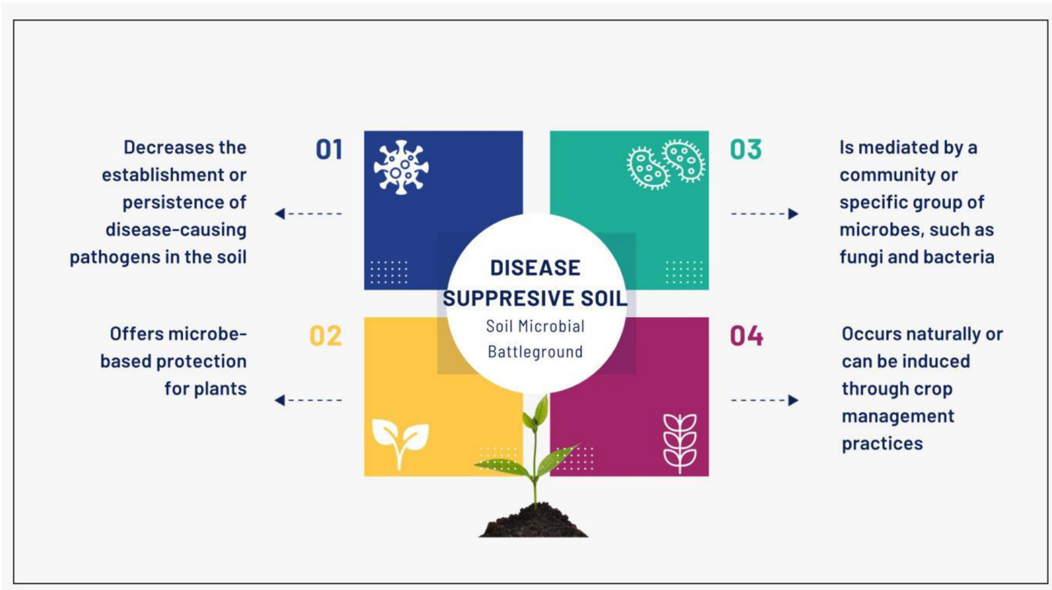

Fig. 1 Disease suppressiveness: Definition, contribution, general and specific method of generating disease suppressive soil.

Table 1 List of secondary metabolites produced by bacteria.

Bacterial species	Plant	Secondary metabolite	Function	Ref.
Actinomycetes sp.	Chili	Lipase, protease, β-1, 3 and β-1, 4 glucanase, and chitinase	Provided broad spectrum antifungal activity against multiple strains of *Alternaria* spp	[14]
Streptomyces sp. PM5 and *Streptomyces* sp. PM9	Eucalyptus	Indole acetic acid (IAA)	A rise in overall weight as well as root and shoot length	[15]
Achromobacter xylosoxydans (MM1)	Tomato	siderophores	Antifungal activity against *Fusarium* wilt disease	[16]
Alcaligenes faecalis subsp. faecalis str. S8	Tomato	HCN, volatile antibiotic	Antifungal and biocontrol activity against *Fusarium*	[17]
Bacillus subtilis GB03	*Arabidopsis thaliana*	acetoin (VOCs) and 2,3-Butanediol	Induces ISR against *Erwinia*	[18]
Bacillus licheniformis RS656	Canola	Exopolysaccharides (EPS)	Increased growth hormones, fresh weight, and vigor index; generation of enzymes that reduce stress	[19]
B. subtilis AK31	Wheat	IAA	Good IAA production and increased growth observed	[20]
Pseudomonas fluorescens WCS 374	Wild radish	Siderophore	Antifungal to *Fusarium* sp	[21]

shaping disease outcomes through their effects on soil microbial communities. The temperature sensitivity of various bacteria underscores their contributions to disease prevention mechanisms, with some exhibiting resistance to higher temperatures. Moreover, heat treatments have been shown to induce shifts in microbial community composition, impacting the resilience of soil ecosystems to disease stressors. Stress events such as heatwaves and drought can disrupt soil microbial communities, compromising their ability to suppress diseases [27].

The pH of soil plays a pivotal role in shaping microbial communities and disease dynamics. By influencing nutrient availability and microbial activity, soil pH can directly impact disease suppression mechanisms [28]. The manipulation of soil pH within specific ranges can alter microbial community composition and function, offering potential avenues for enhancing disease suppression in agricultural soils. Furthermore, understanding the intricate relationships between soil pH and disease outcomes can provide targeted soil management practices aimed at promoting soil health and resilience.

The physical properties of soil, including texture, exerts significant effects on disease suppression mechanisms [29]. Coarse-textured soils, characterized by improved drainage properties, can limit the availability of moisture, an essential factor for pathogen proliferation. Exploring the complex interactions between soil texture and disease dynamics can provide valuable insights into designing sustainable soil management strategies, particularly in regions prone to waterlogging and soil-borne diseases.

Soil nutrient availability profoundly influences microbial activity and disease suppression mechanisms [1]. The abundance of essential nutrients, such as carbon, nitrogen, and phosphorus, directly impacts microbial community dynamics and their ability to suppress pathogens. Interactions between different nutrients further modulates disease suppression pathways, highlighting the intricate nature of soil-plant-microbe interactions [5]. Investigating the specific roles of nutrients in disease suppression mechanisms can uncover novel approaches for enhancing soil health and resilience in agricultural systems.

The mineral composition of soil, particularly clay content and cation exchange capacity (CEC), influences disease suppression mechanisms [7]. Understanding the nuanced relationships between soil minerals and disease dynamics can provide insights into the design of tailored soil management strategies. Investigating the mechanisms underlying the impact of clay minerals on disease suppression pathways can unlock new avenues for enhancing soil health and resilience in agricultural systems [30].

PLANT DISEASE MANAGEMENT AND THE SOIL MICROBES

The soil microbiome harbors beneficial microorganisms, including mutualistic bacteria, which play vital roles in enhancing plant growth and development [6]. Among these, beneficial rhizosphere bacteria employ various mechanisms such as niche competition, antagonism, and microbial diversity to directly protect plants against diseases [31]. This defense mechanism often involves the activation of induced systemic resistance (ISR) in plants, which entails a rapid and systemic response to pathogen attack [32]. The transcription factor MYB72, localized in plant roots, plays a pivotal role in initiating ISR by mediating the production or translocation of systemic signals in *Arabidopsis* [33].

ISR typically involves the upregulation of defense-related genes and enhanced callose deposition at pathogen entry sites rather than direct pathogen killing. Hormones such as ethylene (ET) and jasmonic acid (JA), along with transcriptional activators like NPR1 and MYC2, are essential for establishing systemic ISR in plant leaves [34]. Beneficial fungi, including mycorrhizal fungi and *Trichoderma* spp., can also induce ISR in addition to rhizobacteria, thus contributing to plant defense against pathogens [32]. Specific strains of *Pseudomonas* spp., such as WCS417, have been identified as plant growth-promoting rhizobacteria (PGPR) capable of triggering ISR in plants by modulating gene expression associated with defense processes [35]. Another *Pseudomonas* strain, KT2440, inhibits disease incidence by releasing volatiles that disrupt pathogen transmission [36]. Moreover, mycorrhizal fungi, such as *Glomus mosseae*, can transmit resistance signals to neighboring plants through underground networks, thereby inducing systemic resistance [37].

While the regulation of systemic resistance induced by beneficial rhizobacteria in plants is often through phytohormones like JA and ET, some bacterial strains (*Bacillus* spp and *Pseudomonas* spp) activate systemic resistance through the salicylic acid (SA) pathway [38]. Others, like *Bacillus cereus* AR156, induce systemic resistance by stimulating both signaling pathways. Recent studies have elucidated the transcriptional and metabolic changes induced by rhizobacteria in plants, revealing the diverse effects on plant physiology and metabolism. Understanding the identities and functions of these phytochemicals induced by rhizobacteria is crucial for deciphering their roles in induced systemic resistance and other physiological processes [39].

MICROBIOME COMPLEXITY IN DISEASE SUPPRESSIVE SOIL

Culturing techniques have traditionally identified bacteria responsible for disease suppressiveness [26]. Since the age of culturing we have moved into the omics era with tools to speed up and improve identification and classification. Such culture-independent techniques have identified Firmicutes, Beta proteobacteria, and Gamma proteobacteria as key bacterial groups involved in disease suppression [7, 26]. Berendsen et al [40] through a PhyloChip characterized bacterial populations in the rhizosphere of sugar beet grown in *Rhizoctonia solani*-suppressive soils. They reported that both suppressive and conducive soils contained over 33,000 operational taxonomic units of bacteria and archaea. However, the total number of microbial taxa or their exclusivity was not linked to disease suppressiveness [40]. Instead, suppressiveness was related to the relative abundance of various taxa. Their study concluded that a consortium of microorganisms, rather than a single taxon, was responsible for suppressiveness in *R. solani*-suppressive soil. Conversely, soils conducive to *R. solanacearum* infections had a significant concentration of *Fusarium*, suggesting it may promote *Fusarium* growth within the fungal community. Suppressive soils had numerous keystone taxa and higher network complexity than conducive soils. A negative correlation was found between the abundance of *Ralstonia* and the cumulative abundance of keystone taxa, with *Pseudomonas* being the most prevalent keystone taxon. Greenhouse tests showed that several *Pseudomonas* spp could reduce the disease index in plants [11, 41].

Amplicon sequencing was employed in a different study on Panama disease of bananas to examine the soil microbiome at six distinct locations and determine the reasons behind disease suppression. A core community of suppressive soils had high abundance of Myxococcales, Pseudomonadales, and Xanthomonadales and low abundance of *F. oxysporum*. Significant enrichment was seen in five genera: *Anaeromyxobacter*, *Kofleria*, *Plesiocystis*, *Pseudomonas*, and *Rhodanobacter*. *Pseudomonas* spp was identified as a key taxon for Panama disease suppressiveness [42]. These findings indicate that certain microorganisms such as *Pseudomonas* can defend plants against infections directly or indirectly, with the broader microbial community significantly influencing their effectiveness. Pathogen-suppressing bacteria (e.g. certain species of *Bacillus* and *Pseudomonas*) must be present in sufficiently large quantities to be effective. Additionally, commensal microorganisms can compete with pathogen-suppressing biocontrol bacteria, and biocontrol bacteria can interact synergistically with other specific strains [26, 31].

In conclusion, soil disease suppressiveness can be artificially induced by manipulating the soil microbiome through adding microorganisms with disease-suppressive traits, such as those involved in biological control or inhibition of pathogenic microorganisms (soil amendments). Greenhouse and field experiments have achieved these manipulations by incorporating organic amendments, like compost, which enhance microbial diversity. Similarly, introducing suppressive soil as inoculum into conducive soils has also inhibited soil-borne pathogens. Additionally, introducing new plant species or genotypes with beneficial soil root microbiomes has been explored as a method to inhibit pathogenic organisms in the environment [7] (Fig. 2).

MECHANISMS OF SOIL-RELATED DISEASE SUPPRESSION

Disease-suppressive soils are produced through mechanisms like enhanced soil nutrient levels, parasitism, competition, activation of ISR, and disease-suppressive genes. However, the natural development of disease suppressiveness is a slow process reliant on the soil's physical and chemical characteristics, which may not benefit farmers seeking quick solutions. Hence, researchers have studied artificial acceleration of soil disease suppressiveness to facilitate field application [1, 7]. The following are some mechanisms of soil related disease suppression.

Disease suppression through metabolites and volatile organic compounds

Root exudates are responsible for recruitment of beneficial microorganisms to the plant root system. These microorganisms contribute towards increased growth, enhanced stress tolerance, and reduced disease occurrence. They use antibiotics, DAPG, endotoxins, enzymes, hydrogen cyanide (HCN), and siderophores to control pests and diseases [12]. The exudates or chemical produced by microorganism has been used in plant defense and protection. For instance, *Bacillus thuringiensis* (Bt) that produces delta endotoxin, has been used in biopesticides and transgenic plants for insect resistance [44]. *B. subtilis*, *B. megaterium*, and *B. velenzensis* were used as biopesticides and to enhance plant resistance. *Pseudomonas* spp. produce antifungal compounds like bacteriocin, HCN, DAPG, and siderophore, impacting several soil-borne pathogens [12]. *Trichoderma*, a common fungus, has been extensively used as a biocontrol agent through mycoparasitism and mitigation of unfavorable growth conditions. *Trichoderma* competes with and parasitizes phytopathogens, reducing disease incidence and acting as a biopesticide and biofertilizer [37, 45]. Another group of organism with a strong influence on disease is the *Streptomyces* which are known to produce volatile organic compounds (VOCs) that induce morphological defects in pathogens, reduce disease severity, and promote plant growth and resistance [46].

Inhibition of pathogen propagation

Suppressive soils have higher populations of bacteria, fungi, and protozoa colonizing pathogen propagules, making germination of these pathogens difficult, often leading to lysis by enzymes secreted by disease suppressive organisms. For example, bacterial colonization of *Cochliobolus* spp. can reduce pathogen virulence. Antagonistic organisms found in the *Cochliobolus* spp infested soil stimulate the lysis of this pathogens, degrading their spores and making propagation virtually impossible [7, 47].

Competing for nutrients and infection sites

Manipulating soil nutrients stresses microbial populations, suppressing pathogen spore germination and proliferation. Intense competition for organic substrates in the soil environment, particularly in the rhizosphere, suppresses diseases by out-competing pathogens for root colonization sites. For instance, non-pathogenic *Fusarium equiseti* suppresses *Verticillium* wilt by competing for root colonization [7].

Induced systemic resistance in disease suppression

Strengthening plant resistance to soil-borne diseases is an indirect strategy for reducing disease incidences. For example, non-pathogenic soil isolates of *F. oxysporum* induces systemic resistance to *Fusarium* wilt in tomato. Physical barriers in plant roots, such as callus-rich, multi-layered wall appositions, have also been associated with increased disease suppression [48].

METHODS OF STUDYING DISEASE SUPPRESSIVENESS

Researchers have isolated microbes from bulk soil, rhizospheres, and plant endospheres, testing their effectiveness against pathogens in laboratories and fields.

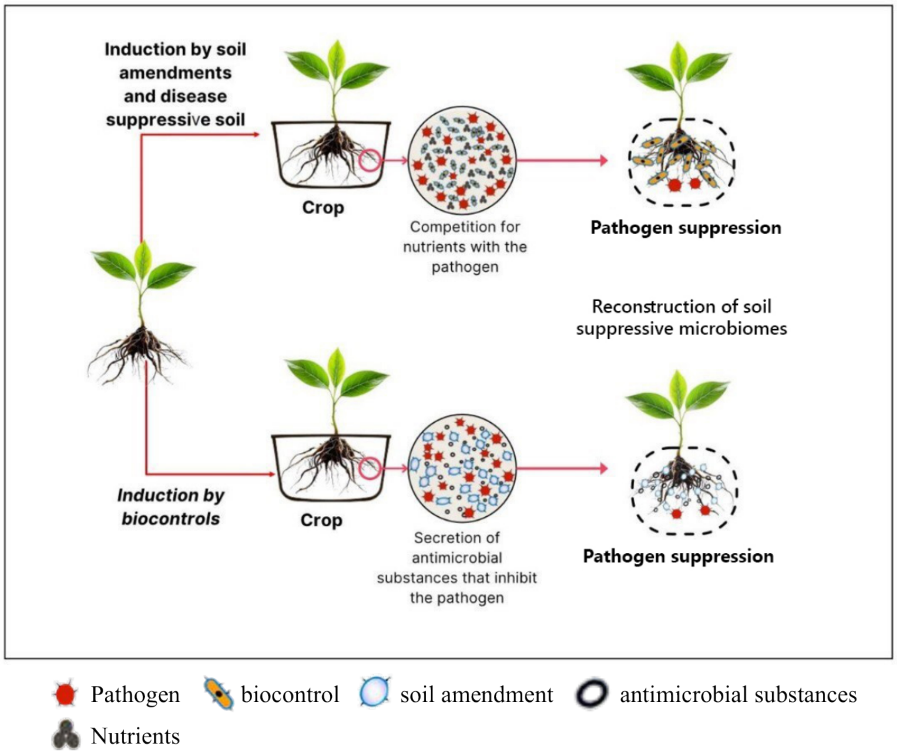

Fig. 2 The effect of soil amendments, biocontrol and beneficial microbes in reconstructing disease suppressive soils.

However, while many microorganisms show promise in controlled environments, their field effectiveness often varies [5, 49]. This inconsistency is due to difficulties in surviving, colonizing the rhizosphere, and expressing protective traits in the field. Disease suppressiveness is seen as a collective effort of microbial communities rather than individual species. For example, certain *Pseudomonas* strains can suppress *Fusarium* wilt only when combined with specific non-pathogenic *Fusarium* strains. Thus, using synthetic microbial communities with diverse actions has been proposed for more consistent pathogen control [50].

In the recent decades, we have moved from culture dependent, to culture independent techniques in isolation, identification and classification of microorganisms. The culture independent method also broke the barrier of identifying non-culturable microorganisms which brought forth hundreds and thousands of organisms that were unknown or non-identified through the traditional culture-based technique. Modern, cultivation-independent technologies have been employed to better understand these microbial communities, including RFLP, DGGE, qPCR, DNA-SIP, PhyloChip analysis, amplicon sequencing, metagenomics, metatranscriptomics, metaproteomics, and metabolomics [26]. Despite these advancements, challenges remain in understanding the complex mechanisms of soil disease suppressiveness. Soil management practices, crop diversity, and environmental conditions significantly influence microbial communities and disease outcomes [51]. Additionally, the inability to accurately identify causal agents hinders understanding of pathogen and beneficial microbe interactions [7]. These barriers continue to be a point of contention for researchers who are trying to piece the puzzle on the factors that collectively contribute towards disease suppressiveness.

CONCLUDING REMARKS AND FUTURE PROSPECTS

In conclusion, soil-borne diseases pose significant threats to agricultural productivity. By harnessing the natural capabilities of soil microbiota these threats may be alleviated to produce a solution for sustainable crop management. Disease-suppressive soils, rich in microbial diversity, provide a robust defense against pathogens by employing mechanisms such as competition for resources, production of antimicrobial compounds, and induction of plant systemic resistance. Key microbial players, including various bacteria, fungi, and archaea, contribute to this suppressiveness through complex interactions with plants and their environment.

Research advancements have identified specific microbial taxa and communities that are instrumental in disease suppression. Moreover, studies utilizing modern, cultivation-independent technologies have deepened our understanding of the microbial dynamics within suppressive soils, revealing the importance of microbial consortia over individual species in maintaining soil health. Manipulating soil microbiomes through the addition of organic amendments, inoculation with beneficial microorganisms, and the introduction of disease-resistant plant varieties are practical strategies that enhance soil suppressiveness. These approaches not only mitigate pathogen pressures but also promote overall soil fertility and ecosystem resilience.

However, challenges remain in translating laboratory successes to field applications, necessitating ongoing interdisciplinary research. To fully exploit the benefits of disease-suppressive soils, further exploration of the interactions between soil microbes, plants, and environmental factors is essential. By integrating insights from microbiology, soil science, and agronomy, sustainable agricultural practices can be developed to ensure long-term soil health and crop productivity. Ultimately, a deeper understanding of soil microbial communities and their roles in disease suppression will pave the way for innovative and eco-friendly disease management strategies in agriculture.

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