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Review Article

Reshaping the Plant Microbiomes for Sustainable Disease Management

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ABSTRACT

Extensive farming usually depends on the use of chemicals to mitigate crop losses from diseases; however, sustainable alternatives have been getting popular as they are our only hope for the future. The plant microbiome, especially the microbial communities in the rhizosphere and endosphere, is a line of research that indicates how disease resistance can be improved through the microbiome of the root while, at the same time, environmental sustainability is being promoted. Plant root exudates are the leading impetus for diversity and favor the host plant between these microbial populations. They contribute to the plant growth development, as well as strengthening the plant's mechanisms to resist biotic and abiotic stresses. Microbes in the rhizosphere and endospores trigger the mechanism to increase plant resistance to diseases, such as the induction of systemic resistance and the production of siderophores, secondary metabolites, and antimicrobial compounds. This review highlights the possibility of converting the plant microbiome into a new program for sustainable disease management by going deeper into the complex relations between different plants and their related microbiomes. A lack of understanding of these microbiome dynamics remains the main bottleneck to precise microbiome-based interventions. Yet, there is a ray of hope for microbiome-engineering-based interventions to our environmental issues and economically unstable plant disease management in modern agriculture.

Keywords: Endosphere, endophytes, microbiomes, rhizosphere, siderophores

INTRODUCTION

The plant microbiome, which includes a variety of microorganisms such as bacteria, fungi, viruses, and archaea, is very important for plant health as well as disease resistance (Khan *et al.*, 2021; Arshad *et al.*, 2024). The microbiome is divided into phyllosphere, rhizosphere, and endosphere according to the location of those microorganisms (Saeed *et al.*, 2021). Influenced by root secretions, the rhizosphere is crucial for nutrient cycling and disease suppression. During evolution, plants interacted with the microbial world of unicellular and multicellular organisms. During this long period, plants have screened out subsets of microbes in their endospheres and the soil near their root systems ("rhizosphere"). These subsets of microbes



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associated with different plant parts are collectively known as plant-associated microbiota. Plants allocate priority to interactions with these species from the bulk of microbes that favor them in terms of their growth, suppression of disease, reproductive success, and other beneficial aspects (Brien *et al.*, 2021). Many microorganisms have colonized terrestrial plants in the endosphere and rhizosphere. The endosphere microbiome is composed of the microbes inhabiting the systemic tissues of the plants. The rhizosphere is a diminutive ecological zone near the roots of plants. It holds a large amount of microbial diversity, and this environmental zone is considered a zone that has maximum biotic diversification (Yadav *et al.*, 2021). The total number of microbes in the rhizospheric region is collectively termed as “rhizosphere microbiome.” Most microbial communities in the rhizosphere microbiome are favourable to plants. However, several bacteria and fungi inhabiting this zone are also pathogenic and cause severe plant diseases. Another category of harmful rhizospheric microbes is the plant-parasitic nematodes, which cause plant diseases, decrease crop yields and lead to substantial economic losses (Ali *et al.*, 2017a). We have recently reviewed and summarized these three categories of the rhizosphere microbiome as the good, the bad, and the ugly components (Ali *et al.*, 2017b). The beneficial microbe communities help plants tolerate and adapt to various abiotic or biotic stresses. Microbes employ multiple strategies, such as nutrient solubilization, root growth stimulation, abiotic stress management, disease suppression, and rhizoremediation. These mechanisms are well-defined in the rhizobacteria of the phyla Proteobacteria and Firmicutes, *Bacillus* spp., and *Pseudomonas* spp., and fungi including *Trichoderma* spp. and *Piriformospora indica* (Gezaf *et al.*, 2021). Many other bacterial and fungal species inhabiting endospheres and rhizospheres have shown good promise as antagonists of several plant pathogens.

Thus, plants have developed several specific and complex interactions with microbial communities that can regulate various physiological processes of plants and directly or indirectly affect plant health. The plant microbiome is a determinant of plant health and can also influence the productivity of different crop species (Poppelier *et al.*, 2023). The review assessed the main plant microbiomes, emphasizing enhancing plant disease resistance. Over the last century, various researchers have investigated the beneficial role of exudates in plant-microbe interactions (Upadhyay *et al.*, 2022; Lamichhane *et al.*, 2023). This review discusses the main rationale for root exudation and rhizosphere microbiome in shaping plant health by emphasizing their perspectives on effective disease management. Through the optimization of the relationships between plants and microorganisms, we can diminish reliance on traditional toxic-based methods and improve crop resiliency. Further, the article investigates creative techniques and complications related to microbiome modifications, supplying the reader with a new dimension to organic ways of agriculture. A thorough comprehension of these intricate associations is imperative when one wants to discover ecologically and economically sound solutions to the plant disease problems in modern agriculture.

ENDOSPHERE MICROBIOME

Endophytes, the unnamed tiny factory workers living in the plant tissues at various places, such as roots, stems and leaves, make up the endosphere microbiome that envelops the host plant. The figure indicates fungi, bacteria, and actinomycetes, among those microorganisms, which settle down in plant living tissues both intracellularly and intercellularly without interfering with the plant's health (Azeem *et al.*, 2020). Endophytes can be seen taking shelter in various parts of the plant such as the meristem, resin ducts, scale primordia, stem, bark, leaf blade, petiole, buds, leaf segments, and roots (Sangeetha *et al.*, 2020). At first, the tissue-inhabiting species of microorganisms were the agents of plant diseases. The identification of these microbes within these infected tissues by certain pathogens was the cause of that thought. But, in 1866, De Bary opposed this idea by the detection of the non-pathogenic cells inside the plant tissues. Additionally, Petrini (1991) used the term ‘endophytes’ to describe such organisms that live within the bodies of hosts without damaging the plants.

Endophytes are now divided into two groups, primarily obligate and facultative. Obligate endophytes, which rely entirely on the host plant's metabolism, are transmitted vertically or via vectors (Durand *et al.*, 2021). In contrast, facultative endophytes can exist outside host tissues and enter plants through the rhizosphere (Carroll, 1988; Samreen *et al.*, 2021). Endophytes' production of beneficial natural compounds has made them valuable in medicine, agriculture, and industry. Their interaction with plants enhances growth, development, sustainability, and protection against biotic and abiotic stresses. Some endophytic compounds benefit humans, serving as drugs or being used in food processing (Nadeem *et al.*, 2016; Tiwari *et al.*, 2023). Additionally, endophytes contribute to bioremediation, nutrient cycling, and protection against herbivores, pathogens, and environmental stressors (Chaudhary *et al.*, 2022; Devi *et al.*, 2023). They also produce growth-regulating elements that enhance host plants' nutrient uptake, grain yield, and biomass

(Vishwakarma *et al.*, 2021). This review focuses on reshaping these microbial communities to develop sustainable disease management strategies in agriculture.

THE DYNAMICS OF DISEASE RESISTANCE INDUCED BY THE ENDOSPHERE MICROBIOME

Besides pathogenic, the role of endophytes was also thought to be neutral, without any positive or negative effects on the host plants, until 1970 (Azevedo 1998). However, meticulous studies regarding endophytes have highlighted their significant role in pathogens and predators (Azeem *et al.*, 2020). For instance, endophytic rhizobacteria has been shown to enhance plant resistance against insect pests and environmental stresses (David *et al.*, 2018). Bacterial endophytes produce and release many chemical compounds, including antibiotics and chitinase enzymes, which can lead to safeguarding plants against pathogens (Latha *et al.*, 2022). These compounds can interfere in the development of pathogens and, hence, can be deployed as biological control agents for sustainable disease management. There are two main bacterial genera, *Bacillus* and *Pseudomonas*, highly abundant in agricultural plants (Khaskheli *et al.*, 2020). These endophytes can protect the host plant from several plant pathogenic fungi, surface-feeding insect pests, and plant-parasitic nematodes that establish natural epibiotic associations and can obtain nutrients from the host tissues by subsequently modifying their physical and biochemical nature (Ali *et al.*, 2015).

In another study, palm oil endophytes, *Pseudomonas aeruginosa* (P3) and *Burkholderia cepacia* (B3) were tested against the fungal pathogen *Ganoderma boninense* in four-month-old palm oil seedlings (Sharma *et al.*, 2022). Both P3 and B3 strains were shown to interact with each other to restrict the entry of pathogens. They maintained their population below the threshold level, limiting basal stem rot disease initiation. Different biochemical compounds such as 3-nitropropionic acid and 3-hydroxypropionic acid are synthesized by specific endophytes such as *Melanconium botulinum* and *Phomopsis phaseoli*, which possess nematicidal activity for controlling plant-parasitic nematodes in plants (Omomowo *et al.*, 2023). Several bacterial endophytes (*Bacillus* spp., *Arthrobacter* sp., *Curtobacterium* sp., *Micrococcus* sp., *Serratia*, and *Pseudomonads*) isolated from the host plant *Piper nigrum* L. showed significant results against the nematode *Meloidogyne incognita* during an in vitro bioassay (Aravind *et al.*, 2009). A study has been reported using endophytic bacteria such as *Pseudomonas putida* and *Pantoea agglomerans* for controlling *M. incognita* in different species of ornamental plants (Din *et al.*, 2018a). Besides the microbial pathogens, endophytes have also contributed to the resistance of insects. For example, two endophytes, *Festuca arundinacea* and *Acremonium coenophialum*, offer defence against froghoppers and leafhoppers attacking the tall fescue (Sharma *et al.*, 2018). The endophytes use several mechanisms to induce resistance in the host plants against diseases. The most significant phenomena are explained in more detail in the following sections.

Endophytes and induced systemic resistance (ISR)

Endophytes can guard the host plant against multiple pathogens by regulating its defense system via ISR (Pieterse *et al.*, 2014; Oukala *et al.*, 2021). The involvement of endophytes in provoking induced systemic resistance in plants was first reported in Douglas fir trees by Carroll (1991). Bacterial strains from the two genera *Bacillus* and *Pseudomonas* have primarily been reported as the most common inducers of ISR; however, ISR induction is not limited to these species (Dimkić, *et al.*, 2022). Bacterial elicitors involved in the induction of host plant ISR include flagellin, antibiotics, salicylic acid, N-acylhomoserine lactones, jasmonic acid, volatiles (e.g., acetoin), siderophores, and lipopolysaccharides (Prši and Ongena, 2020). The shoot is inhabiting the endophytic strain IMBG290 of *Methylobacterium* spp. Induces resistance in the potato against *Pectobacterium atrosepticum*, which causes potato blackleg disease (Chaubey *et al.*, 2023).

Antimicrobial compounds

Endophytic fungi are renowned for their capability to synthesize antimicrobial compounds that can ensure the growth inhibition of plant pathogenic microbes and insect pests. These antimicrobial compounds primarily include steroids, alkaloids, polyketones, peptides, terpenoids, phenols, quinols, flavonoids, and some chlorinated compounds (Abo Nouh *et al.*, 2021). Of these compounds, alkaloids produced by clavicipitaceous fungi are well-characterized antimicrobial compounds produced by fungal endophytes.

Several studies have revealed that fungal endophytes produce various antibacterial, antiviral, insecticidal, and antifungal compounds (Deshmukh *et al.*, 2018; Manganyi *et al.*, 2020). In addition to fungi, bacterial pathogens produce different antimicrobial compounds. For example, a strain of *Serratia marcescens* bacterium isolated from the *Rhynholacis penicillata* plant exhibited effective antifungal activity. Moreover, 638 strains of *Enterobacter* sp. synthesized antibiotic compounds such as 4-hydroxybenzoate and 2-phenylethanol (Taghavi *et al.*, 2010). Actinomycetes endophytes are the best-known producers of antimicrobial compounds and include mainly kakadumycins, munumbicins and coronamycins (Khan and Rasool., 2022). A previous study revealed that the invading

plant pathogens can trigger the biosynthesis of antimicrobial compounds by endophytic fungi. An antibacterial compound named multicyclic indolosesquiterpenes has been reported from *Streptomyces* sp. HKI0595 exhibits an endophytic relation with *Kandelia candel* (mangrove tree) (Aamir et al., 2020).

Biosynthesis of secondary metabolites

Secondary metabolites are biologically potent molecules recognized for their significant antioxidant, antifungal, antibacterial, antioomycete, nematocidal, antiviral, antidiabetic, immunosuppressive, anticancer, and insecticidal properties (Brader et al., 2014; Rana et al., 2019). Endophytes synthesize secondary metabolites, which are reportedly involved in defense signaling mechanisms and regulate genetic events in the host plants to establish symbiotic relationships (Kumar and Nautiyal, 2023). As an example, amines and amide alkaloids have been reported to be produced by the fungus *Neotyphodium* sp. (grass-endophyte) which offers insect and nematode resistance to its host (Bush et al., 1997; Anamika et al., 2018). To employ antifungal and antibacterial status to its host (*A. annua*), indole derivative, namely 6-isoprenylindole-3-carboxylic acid, is another secondary metabolite secreted by *Colletotrichum* sp. endophytes (Rani et al., 2021). Hydroheptelidic acid belonging to sesquiterpenes class of secondary metabolites has been identified from *Abies balsamea* endophyte (*Phyllosticta* sp.) that exerts toxic effects on the larvae of spruce budworm (Mousa and Raizada 2013). In the same way, various endophytes also produce aliphatic compounds to protect their host from plant pathogenic bacteria. For example, *fusarium oxysporum* produces specific secondary metabolites that can paralyze the motile phase of the *Radopholus similis* nematode (Kinalwa, 2023). These secondary metabolites can also interfere with the hatching of *R. similis* eggs and can be used as a biocontrol agent owing to their nematocidal activity. However, certain types of secondary metabolites identified from endophytes are not shown to be involved in plant defense. For example, lignan and Phenylpropanoid compounds produced by fungal endophyte, namely *Epichloë typhina*, are not involved in plant defense but play a significant role in fungus-plant interaction (Bagheri et al., 2021). In addition to the production of secondary metabolites, endophytes can also affect the secondary metabolism of the host plant (Naik et al., 2019). This was well exemplified in the strawberry, where the plants inoculated with *Methylobacterium* sp. influenced the biosynthesis of furanone (Verginer et al., 2010). In the same way, the production and accumulation of oligomeric proanthocyanidin as well as flavan-3-ols phenolic acid in the bilberry plant were increased after interaction with the fungal endophyte *Paraphaeosphaeria* sp. (Yu et al. 2020).

Iron homeostasis

Several endophytic bacterial and fungal species are well-known for their biosynthesis of siderophores (Chowdappa et al., 2020; Dudeja et al., 2021). Siderophores play a crucial role in iron acquisition by soil-inhabiting microorganisms and play a significant role during animal pathogen-host interaction (Srivastava, 2023). Siderophore biosynthesis has been shown to contribute significantly to the establishment of a symbiotic relationship between ryegrass and *Epichloë festucae*, where the expression of genes responsible for the biosynthesis of siderophore in *E. festucae* was interrupted (Johnson et al., 2013). In another study, the siderophores synthesized by *Methylobacterium* strains were directly involved in *Xylella fastidiosa* suppression in citrus trees, causing citrus variegated chlorosis (Azevedo et al., 2016). A schematic diagram is shown in Figure 1, which demonstrates the different direct and indirect strategies endophytes use to suppress plant diseases.

RHIZOSPHERE MICROBIOME

The rhizosphere is a biologically rich nutritional zone and reservoir for many microbial species that aid plant growth and establishment in the soil. The term rhizosphere microbiome represents the aggregate of all the microbes present in the immediate vicinity of plant roots. Rhizospheric soil comprises 10¹¹ microbial cells per gram (Egamberdieva et al., 2008; Chauhan et al., 2023) and contains more than 30,000 prokaryote species (Mendes et al., 2011). Plants have evolved complex interactions with the rhizospheric microbiota. The rhizospheric communities mainly promote plant growth, improve the uptake of nutrients that are vital for plants, enable plants to survive in harsh environmental conditions, and induce various defense mechanisms in plants to mitigate biotic stresses. We have recently called these beneficial microbial communities “the good” ones of the rhizosphere microbiome (Ali et al., 2017b). *Pseudomonas* spp., *Bacillus* spp., *Trichoderma* spp., and mycorrhizal fungi are some common examples of good microbes in the rhizosphere. However, several microbes in the rhizosphere are extremely devastating plant pathogens and result in huge losses of crops. These microbes are considered “the bad” ones, e.g., *Fusarium* spp., *Heterodera* spp., and *Meloidogyne* spp. The rhizosphere also contains a comparatively small number of microbes that are potential pathogens for human beings. These microbes are opportunistic parasites of humans and can cause various infectious diseases. They are hazardous, attack humans directly, and have been termed “the ugly” ones of the rhizosphere

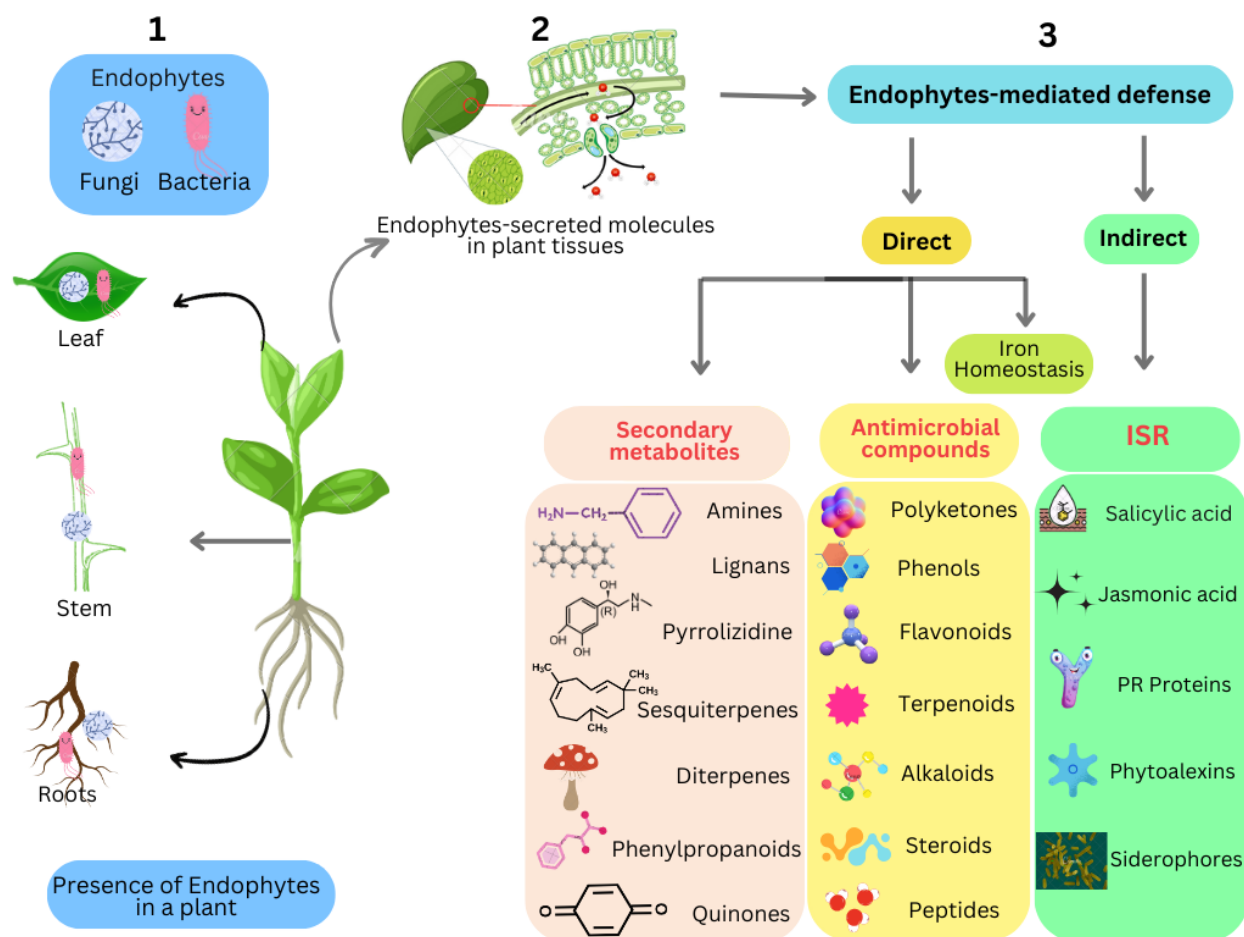


Figure 1: Direct and indirect strategies endophytes use to suppress plant diseases. Part 1 of the figure represents different endophytic species in various plant parts, such as roots, stems, and leaves. Part 2 shows the plant-endophytes interaction and describes different kinds of compounds secreted by endophytes inside plant tissues. Similarly, part 3 denotes direct and indirect defense strategies mediated by endophytes.

microbiome. *Aspergillus* spp., *Fusarium* spp., *Ochrobactrum* spp., and *Stenotrophomonas* spp. are several microbes that fall into this category. We have recently given a detailed account of the rhizosphere microbiome's good, bad, and ugly categories (Ali *et al.*, 2017b). A graphical representation of the bad, the good, and the ugly ones in the rhizosphere microbiome is shown in Figure 2, with examples. The plant's root system in the rhizosphere governs the microbes and their mediated mechanisms differently. Various substances, such as root exudates, the regulatory players in microbe interactions, can be neutral, beneficial, or harmful to plants (Vives-Peris *et al.*, 2020). Hence, the root exudates act as a stimulator of diversity in the microbial rhizosphere.

Root exudates are the prime modulators of rhizosphere microbiomes

Root exudates contain inorganic and organic substances that are secreted by the plant root to create a certain environment in the rhizosphere. These substances regulate the chemotaxis process and enable plants to interact with symbiotic as well as pathogenic microbes in the rhizosphere, which afterwards may invade the plants to perform various functions (Feng *et al.*, 2021; Benaissa, 2023). These root exudates aid in the development and establishment of beneficial plant-microbe interaction. However, several other compounds released by some plants, e.g., cucurbitacin A, bithienyl, inositols, and the metabolites derived from them repel the parasitic microbes (i.e., nematodes) away from the rhizospheric zone (Ali *et al.*, 2017b; Haldar *et al.*, 2022). There are several plants, environmental, edaphic, and microbial-related factors that affect the types and number of different compounds. Plant-related factors include age, species, and genotype of the plant that determine the concentration and composition of the exudates (Chen *et al.*, 2022). Similarly, plant species diversity in a specific locality affects the secretion of root exudates. Environmental aspects such as low or high temperatures, rainfall, availability of light, and cultural practices are some important aboveground characteristics affecting root exudates (Canarini *et al.*, 2019).

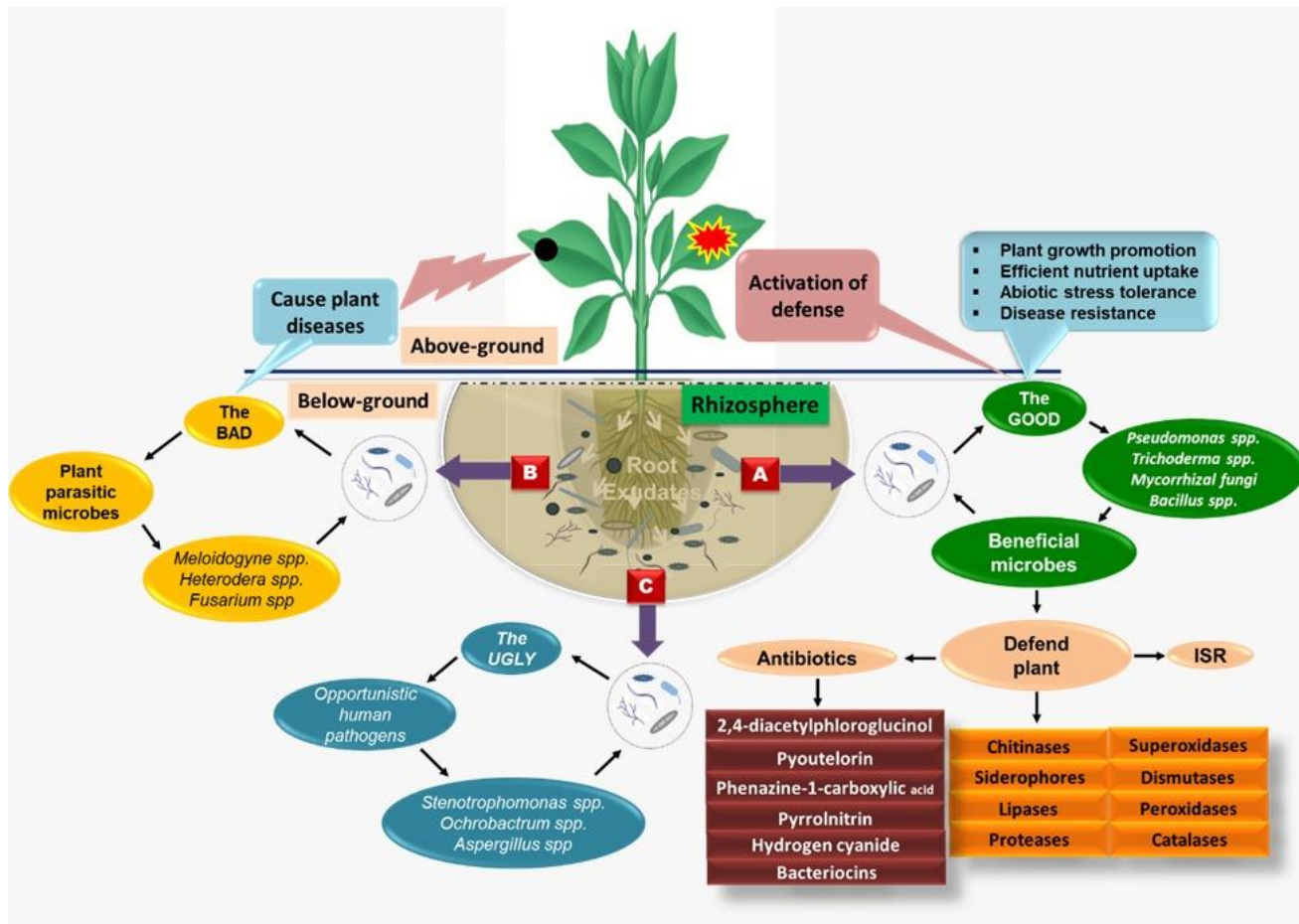


Figure 2: Systematic representation of 'Rhizosphere microbiome' presenting different groups of microbes inhabiting the proximity to plant roots and soil. Part A, The GOOD, shows beneficial microbes and microbes-mediated plant defense through several strategies. Part B, The BAD, displays the plant-pathogenic part of the 'Rhizosphere microbiome'. Part C, The UGLY, represents opportunistic human pathogens (Ali *et al.*, 2017b).

Additionally, belowground edaphic factors have a determining role as some of the major types of soil, the texture, moisture, pH, porosity, nutrients, and co-restriction related to the root exudates have a direct impact on the plants and rhizosphere microbiome (Ma *et al.*, 2022). The interactions between different species of microorganisms in the rhizosphere are responsible for the variation and type of microbial diversity at this location. Different aboveground and belowground factors responsible for the diversity of microbes in the rhizosphere are described briefly in Figure 2. In the past few years, the identification and manipulation of the rhizosphere microbe has been an important research area, and a lot of work has been done to engineer the rhizosphere that way i.e. to use beneficial microbes for the promotion of agricultural productivity (Kumar and Dubey, 2020; Kaul *et al.*, 2021). Certain fungi or bacteria in the rhizosphere function as potential antagonists through the action of several soil-dwelling fungi or plant pathogenic nematodes that may be prevented in various ways. Some of these mechanisms include antibiosis (warding off other plants and diseases) (Raaijmakers and Mazzola 2012), nutrient competition, parasitic microbes that are pathogenic to plants, plant immune response induction and quorum sensing coupled to virulence suppression (Ramesh *et al.*, 2019).

Dynamics of disease resistance mediated by the rhizosphere microbiome

Different plant species secrete different forms of root exudate, allowing plants to modify their microbiome according to their needs (Afridi *et al.*, 2023). The age and stage of the plant's development can also affect these exudates (Vives *et al.*, 2020). Conversely, microbial communities can influence the root exudation of plants, with axenically grown plants having significantly different types of exudates compared to those plants exposed to microbes. In addition to root exudates, sloughing of the root cells and mucilage deposits, including polymers of the plant cell wall such as pectin and cellulose, are considered prime constituents of the rhizodeposition of the rhizosphere (Nazari, 2022). All these exudations are of the utmost significance because they permit microbial species to grow in the rhizosphere, which can then actively participate in the betterment of plant health, growth, and defence system.

The major microbial group that inhabits the rhizosphere microbiome is the Proteobacteria, which is generally dominant among all other groups, e.g., Bacteroidetes, Planctomycetes, Actinobacteria, Firmicutes, Acidobacteria, and Verrucomicrobia (Turner *et al.*, 2013). Although all these microbial species play their role in plant health, the rhizobacteria residing in the rhizosphere are of major interest owing to their considerable contribution to plant growth via various mechanisms (Khan *et al.*, 2021). Nitrogen-fixing bacteria such as *Azotobacter* spp. and root-nodulating *Rhizobium* spp. offer fixed nitrogen to the plant for its development throughout its life cycle. Many other bacteria can also solubilize and mobilize mineral nutrients and increase the bioavailability of macro-nutrients such as phosphorus. Some microbial communities regulate the production of plant hormones such as auxins, ethylene, and gibberellins, and promote plant growth or contribute to stress tolerance. Many plant-growth-promoting rhizobacteria (PGPR) act antagonistically toward plant pathogens by producing antimicrobials or interfering with virulence factors via effectors delivered by type 3 secretion systems (Rezzonico *et al.*, 2005; Lucke *et al.*, 2020). Rhizobacteria improves plant growth via direct and indirect processes. Direct processes promote the growth of plants when rhizobacteria produce compounds to facilitate plants and increase the uptake of nutrients.

Growth promotion via indirect mechanisms involves averting some adverse effects produced by the pathogens (Glick 1995). The phenomena indicating their use as biocontrol agents include phytohormone production such as auxin and gibberellins; synthesis of antibiotic and antifungal activity via hydrogen cyanide (HCN) production; release of iron-binding siderophores; the synthesis of lipases, protease enzymes, and chitinases for fungal cell wall hydrolysis (Chet and Inbar 1994), and the biosynthesis of peroxidase, superoxide dismutase, catalase, and polyphenol oxidase to compete with reactive oxygen for controlling oxidative stress. For instance, potato seed inoculation with PGPR enhanced potato plant growth and tuber yield in the field (Tkachenko *et al.*, 2021). Further, Zaidi *et al.* (2015) described an increase in the fresh weight of shoots and roots of cucumber, tomato, potato, and lettuce because of *Pseudomonas* spp. inoculation. Similarly, the iron present in the rhizosphere facilitates the pathogens that are low in iron supply, which is essential for their pathogenicity and growth. The synthesis of iron-chelating substances such as siderophores is an important feature of some fluorescent pseudomonades. However, the bioavailability of iron and optimum pH is abiotic edaphic, which are regulatory factors of siderophore biosynthesis and their role in the biological control of diseases (Pattnaik *et al.*, 2021).

Various bacteria, particularly the pseudomonades, can synthesize some types of antibiotics. Howell and Stipanovic (1979) were the first to study the bacterial strains involved in antibiotic synthesis and their effect on phyto-pathogens. There are several types of antibiotics synthesized by *Pseudomonas* species that have antimicrobial effects, including 2,4-diacetyl phloroglucinol, pyoluteorin, phenazine-1-carboxylic acid, HCN, pyrrolnitrin, and protein-type substances (bacteriocins) (Ali *et al.*, 2017b) and scientists have confirmed their potential for the suppression of plant pathogens. HCN, a secondary metabolic compound produced by several rhizosphere pseudomonads, has a negative effect on the metabolism and growth of root-invading pathogens. Such rhizobacteria that produce HCN demonstrate various effects on plant growth, ranging from beneficial to harmful (Patwardhan *et al.*, 2022).

RESHAPING RHIZOSPHERE AND ENDOSPHERE MICROBIOMES FOR ENHANCED DISEASE RESISTANCE

Keeping in mind the importance of endosphere and rhizosphere microbiomes for the enhancement of disease resistance in plants, it is essential to engineer these microbiomes using those microbial communities that have specific antagonistic properties against pathogens. Rhizodeposition is one of the significant mechanisms by which plants can modify their rhizosphere. During this process, the plant releases inorganic and organic exudates from its roots (Hassan *et al.*, 2019). These exudates are essential elements that are involved in the interactions of plants and microbial communities at the rhizospheric interface. The exudates comprise carbohydrates, amino acids, fatty acids, and proteins that regulate plant growth and maintain the correct microbial component of the rhizosphere (Ma *et al.*, 2022). There are different examples of the modification of root exudates. For instance, the uptake of essential nutrients triggers the electrochemical gradient via the plasma membrane of the root cell owing to the H⁺ efflux in plants and contributes to rhizosphere acidification that is used to increase the bioavailability of phosphorous and iron from the soil (Hinsinger *et al.*, 2003). Phytosiderophore production facilitates plant growth and antagonism against the invading pathogens, and it can be applied by intercropping peanuts (*Arachis hypogaea*) with maize (*Zea mays*). In this combination, the peanut acts as a caliphate crop and maize as a Fe-efficient crop (Zuo *et al.*, 2000). Various genes have been identified that govern the secretion of exudates, and the modification of the rhizosphere via the alteration of the expression patterns of these genes by genetic engineering might be possible. A more achievable method of rhizosphere engineering is the direct exploitation of the rhizospheric microbiome via microbe inoculation. However, a couple of new methods that

might increase the persistence of the introduced microbe and its efficiency in the soil are also known (Kumawat *et al.*, 2022). The introduction of advantageous microorganisms that are local to the environment can lead to the enhanced uptake of nutrients, improved growth, and resistance against abiotic and biotic stresses in plants (Santoyo *et al.*, 2021). A creative modification technique for the microbiome is the combined application of bacteria and fungi. This type of microbial inoculation group assists in the eradication of pathogens from the environment and shortening the period of niche saturation (Ayaz *et al.* 2023).

Recently, we have performed the seed and drenching application of endophytic *Trichoderma* spp. with *Bacillus* spp. as a consortium that resulted in the enhancement of wheat growth and grain yield (Din *et al.*, 2018b). Conventional practices of applying external substances as amendments to the soil with effective microbes have been described in the literature. Colbert *et al.* (1993) reported the dynamics of different metabolically active strains (PpG7 and pNAH7) of *Pseudomonas putida* populations where PpG7 resulted in the breakdown of sodium salicylate in the amended or non-amended soil. After two weeks of the application of salicylate to the soils, the population concentration of salicylate downgrading strains was 100-fold higher than that of the non-amended soils. Various biological and chemical-originated amendments can be applied to engineer the rhizosphere microbiome. Likewise, biochar-amended soil showed a gradual increase in the reproduction rates of various soil microbes. Biochar-amended soil positively influenced mycorrhizal fungal growth (Warnock *et al.*, 2007).

In another study, biochar-amended soil enhanced arbuscular mycorrhizal colonization up to 20%–40% in wheat roots, whereas in the non-amended soil, it was only 5%–20% (Solaiman *et al.* 2010). These previous studies confirm that the techniques involved in the engineering of microbiomes are vital for agriculture. The microbes primarily enter the plant system through the rhizosphere, and any strategy to engineer the rhizosphere will be a way forward for engineering the endosphere. Agricultural practices like fertilizer application, soil tillage, and irrigation can alter the chemistry of the rhizosphere by affecting soil aeration, root function, and microbial communities. These changes can, in turn, modify the rhizosphere microbiome, influencing plant health and growth (Xiao *et al.*, 2023). The competitive potential of advantageous microbes that are genetically engineered could be increased using substances such as antibodies to enhance disease resistance in plants may adapt and change over time.

CHALLENGES AND PROSPECTS

An alternate approach to disease management is the current restructuring of the worldwide agricultural atmosphere toward sustainability and plant microbiome adaptation. Finding ways to make use of these interactions could minimize the need for traditional pesticides, mitigate the influences on the environment, and promote plant resilience in line with the microbial networks that are connected to them. In addition, the employment of microbial biocontrol agents showed the potential to control pathogenic organisms and subsequently lower disease rates (Piotti *et al.*, 2019). Changing the shape of plant microbiomes also enhances nutrient use in plants, improves crop performance, and increases productivity (Poppeliers *et al.*, 2023). The multi-dimensional nature of these approaches is expected to emphasize viability for future sustainable agriculture by manipulation of plant microbiomes. With the continuous advancement of omics technologies, a deeper knowledge of microbial communities, as well as their intricate functions in plant ecosystems, is becoming more attainable (Trivedi *et al.*, 2020).

Synthetic Biology Approaches to Engineer Plant Microbiomes Rodriguez and Redman (2021) describe how synthetic biology approaches offer the exciting possibility for improving engineered plant microbiome designs that could enable selective disease resistance or improved function overall. In addition, we also need collaborative efforts that combine knowledge from microbiologists, and this is what helps us move forward. Collaboration between the experts of different disciplines is essential to perform integrated analysis on plant microbiomes, facilitating the identification of their vast applications in sustainable agriculture (Thaku *et al.*, 2023). However, before these technologies can be adopted into a broad context, we must deal with the challenges of the experiment. Plant root exudation has shown quite a lot of variability among plant species, making it difficult to come up with universal methods for managing diseases that could work on different kinds of crops. One of the greatest issues to be solved is dissecting the interactions between plants and their respective microbiota. The microbiota is a complex ecosystem and alterations in one unit may affect the other one of them (Ramesh 2019). Another challenging task is the development of microbiome manipulation techniques. The plant microbiome is composed of a variety of microorganisms, and their presence and absence impact the plant in different ways. Scientists will have to conduct more research in the field of the relationships between different microorganisms and their plant hosts, as well as how these connections develop at different stages. Dealing with microbial complexity in terms of plant-microbe interaction is a strenuous mission because of the schematic and dynamic

essence of the relationships (Kabir, 2024). The transition from controlled environments to large-scale field applications introduces substantial logistical and ecological challenges when scaling up microbiome manipulation, warranting careful consideration (Knoester *et al.* 1999).

CONCLUDING REMARKS

With the emergence of various plant disease preventions, researchers have investigated the possibility of using the microbiomes present in plants as a natural way of combating growth as well as the spread of pathogens. It has been observed that some plant microbiota species act as poison to the pathogens, which means they neutralize the deleterious effect of a pathogen on the host plant. Furthermore, several plant microbiomes act as antagonists against infections, either by blocking their progression close to the rhizosphere or by preventing them from settling on the plant roots once they have invaded. Using high-throughput technologies like transcriptomics and metagenomics, microbiomes can be characterized according to their positive traits. Furthermore, “the good” ones of the rhizosphere microbiome would increase the environmental stability of crop plants in the current situation of global warming and environmental change. In the age of globalization, advantageous microbiomes might be engineered to cope with climate change and the increasing food demand by the increasing world population. This would result in the cheap, long-lasting, eco-friendly, and bio-friendly management of biotic and abiotic stresses in crop plants and ultimately result in the stability of agricultural yields, leading to the social and economic betterment of the population.

AUTHOR CONTRIBUTIONS

AZ Writing – original draft, UA. Visualization, ZN Helped with figures, MSS Resources, NS Helped with literature, FA review, and MJ reviewed and edited the manuscript. All authors have read and agreed to the published version of the manuscript.

COMPETING OF INTEREST

The authors declare no competing interests.

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REFERENCES

- Aamir, M., Rai, K. K., Zehra, A., Dubey, M. K., Samal, S., Yadav, M., & Upadhyay, R. S. (2020). Endophytic actinomycetes in bioactive compounds production and plant defense system. In *Microbial endophytes* (pp. 189-229). Woodhead Publishing.
- Abo Nouh, F. A., Gezaf, S. A., & Abdel-Azeem, A. M. (2021). Recent advances in fungal antimicrobial molecules. In *Industrially Important Fungi for Sustainable Development: Volume 2: Bioprospecting for Biomolecules*, pp. 177-203.
- Afridi, M. S., Kumar, A., Javed, M. A., Dubey, A., de Medeiros, F. H. V., & Santoyo, G. (2023). Harnessing root exudates for plant microbiome engineering and stress resistance in plants. *Microbiological Research*, 279, 127564.
- Ali, M. A., Abbas, A., Azeem, F., Javed, N., & Bohlmann, H. (2015). Plant-nematode interactions: From genomics to metabolomics. *International Journal of Agriculture and Biology*, 17, 1071-1082.
- Ali, M. A., Azeem, F., Abbas, A., Joyia, F. A., Li, H., & Dababat, A. A. (2017a). Transgenic strategies for enhancement of nematode resistance in plants. *Frontiers in Plant Science*, 8, 750.
- Ali, M. A., Naveed, M., Mustafa, A., & Abbas, A. (2017b). The good, the bad, and the ugly of rhizosphere microbiome. In *Probiotics and Plant Health*, pp. 253-290, Springer Nature.
- Arshad, U., Altaf, M. T., Liaqat, W., et al. (2024). Biochar: Black gold for sustainable agriculture and fortification against plant pathogens—A review. *Journal of Crop Health*, 76, 385–396.
- Anamika, J. S., Sahgal, M., Sahu, S., & Prakash, A. (2018). Fungal endophytes and their secondary metabolites: Role in sustainable agriculture. In *Fungi and Their Role in Sustainable Development: Current Perspectives* (pp. 121-146).
- Andrianopoulos, A., Johnson, L. J., Koulman, A., Christensen, M., Lane, G. A., Fraser, K., Forester, N., Johnson, R. D., Bryan, G. T., & Rasmussen, S. (2013). An extracellular siderophore is required to maintain the mutualistic interaction of *Epichloë festucae* with *Lolium perenne*. *PLoS Pathogens*, 9, e1003498.
- Aravind, R., Kumar, A., Eapen, S. J., & Ramana, K. V. (2009). Endophytic bacterial flora in root and stem tissues of black pepper (*Piper nigrum* L.) genotype: Isolation, identification and evaluation against *Phytophthora capsici*. *Letters in Applied Microbiology*, 48, 58–64.

- Athman, S. Y., Dubois, T., Coyne, D., Gold, C. S., Labuschagne, N., & Viljoen, A. (2006). Effect of endophytic *Fusarium oxysporum* on host preference of *Radopholus similis* to tissue culture banana plants. *Journal of Nematology*, 38, 455–460.
- Ayaz, M., Li, C. H., Ali, Q., Zhao, W., Chi, Y. K., Shafiq, M., ... & Huang, W. K. (2023). Bacterial and fungal biocontrol agents for plant disease protection: Journey from lab to field, current status, challenges, and global perspectives. *Molecules*, 28(18), 6735.
- Azeem, F., Rashid, F., Shahzadi, M., Abbas, A., Batool, R., Nadeem, H., Moosa, A., Siddique, M. H., Hussain, S., & Ali, M. A. (2020). Endophytes as guardians of plants against diseases. In Prasad, R., et al. (Eds.), *Recent developments in microbial technologies, environmental and microbial biotechnology* (pp. 221–242). Springer Nature.
- Azevedo, J. L. (1998). *Microrganismos endofíticos*. *Ecologia Microbiana*, EMBRAPA-CNPMA, 117–137.
- Azevedo, J. L., Araújo, W. L., & Lacava, P. T. (2016). The diversity of citrus endophytic bacteria and their interactions with *Xylella fastidiosa* and host plants. *Genetics and Molecular Biology*, 39, 476–491.
- Badri, D. V., Weir, T. L., van der Lelie, D., & Vivanco, J. M. (2009). Rhizosphere chemical dialogues: Plant–microbe interactions. *Current Opinion in Biotechnology*, 20, 642–650.
- Bagheri, A., Askari Seyahooei, M., & Fathipour, Y. (2021). The endophytes. In *Microbial approaches for insect pest management* (pp. 151–215).
- Bary, A. de. (1866). *Morphologie und Physiologie der Pilze, Flechten und Myxomyceten*. <https://doi.org/10.5962/bhl.title.120970>
- Benaissa, A. (2023). Rhizosphere: Role of bacteria to manage plant diseases and sustainable agriculture—A review. *Journal of Basic Microbiology*, 64, 1–14.
- Berg, G., Grube, M., Schlöter, M., & Smalla, K. (2019). The plant microbiome and its importance for plant and human health. *Frontiers in Microbiology*, 10, 1–7.
- Berg, G., & Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology*, 68, 1–13.
- Brader, G., Compant, S., Mitter, B., Trognitz, F., & Sessitsch, A. (2014). Metabolic potential of endophytic bacteria. *Current Opinion in Biotechnology*, 27, 30–37. <https://doi.org/10.1016/j.copbio.2013.09.012>
- Burkholder, W. F., et al. (2010). Genome sequence of the plant growth-promoting endophytic bacterium *Enterobacter* sp. 638. *PLoS Genetics*, 6, e1000943. <https://doi.org/10.1371/journal.pgen.1000943>
- Bush, L. P., Wilkinson, H. H., & Schardl, C. L. (1997). Bioprotective alkaloids of grass-fungal endophyte symbioses. *Plant Physiology*, 114, 1–7. <https://doi.org/10.1104/pp.114.1.1>
- Canarini, A., Kaiser, C., Merchant, A., Richter, A., & Wanek, W. (2019). Root exudation of primary metabolites: Mechanisms and their roles in plant responses to environmental stimuli. *Frontiers in Plant Science*, 10, 157.
- Carroll, G. (1988). Fungal endophytes in stems and leaves: From latent pathogen to mutualistic symbiont. *Ecology*, 69, 2–9. <https://doi.org/10.2307/1943155>
- Carroll, G. C. (1991). Fungal associates of woody plants as insect antagonists in leaves and stems. In *Microbial mediation of plant-herbivore interactions* (pp. 253–271).
- Cavaglieri, L., Orlando, J., & Etcheverry, M. (2009). Rhizosphere microbial community structure at different maize plant growth stages and root locations. *Microbiological Research*, 164, 391–399. <https://doi.org/10.1016/j.micres.2007.03.006>
- Chaubey, A. K., Sharma, V., Prajapati, P. K., Mishra, S., Pandey, R., Dwivedi, S. V., ... & Soni, R. (2023). Induction of stress tolerance in plants by metabolic secretions of endophytes for sustainable development. In *Microbial bioactive compounds: Industrial and agricultural applications* (pp. 225–248). Cham: Springer Nature.
- Chaudhary, P., Agri, U., Chaudhary, A., Kumar, A., & Kumar, G. (2022). Endophytes and their potential in biotic stress management and crop production. *Frontiers in Microbiology*, 13, 933017. <https://doi.org/10.3389/fmicb.2022.933017>
- Chauhan, P., Sharma, N., Tapwal, A., Kumar, A., Verma, G. S., Meena, M., Seth, C. S., & Swapnil, P. (2023). Soil microbiome: Diversity, benefits, and interactions with plants. *Sustainability*, 15(19), 14643. <https://doi.org/10.3390/su151914643>
- Chen, Y., Yao, Z., Sun, Y., Wang, E., Tian, C., Sun, Y., Liu, J., Sun, C., & Tian, L. (2022). Current studies of the effects of drought stress on root exudates and rhizosphere microbiomes of crop plant species. *International Journal of Molecular Sciences*, 23(5), 2374.
- Chet, I., & Inbar, J. (1994). Biological control of fungal pathogens. *Applied Biochemistry and Biotechnology*, 48, 37–43.
- Chowdappa, S., Jagannath, S., Konappa, N., Udayashankar, A.C., Jogaiah, S. (2020) Detection and characterization of antibacterial siderophores secreted by endophytic fungi from *Cymbidium aloifolium*. *Biomolecules* 10, 1412.
- Colbert, S.F., Henderson, M., Ferri, M., Schroth, M.N. (1993) Enhanced growth and activity of a biocontrol bacterium genetically engineered to utilize salicylate. *Applied and Environmental Microbiology*, 59, 2071-2076.
- Cummings, S. (2009). The application of plant growth promoting rhizobacteria (PGPR) in low input and organic cultivation of graminaceous crops: potential and problems. *Environmental Biotechnology*, 5, 43-50.

- David, B. V., Chandrasehar, G., & Selvam, P. N. (2018). *Pseudomonas fluorescens*: A plant-growth-promoting rhizobacterium (PGPR) with potential role in biocontrol of pests of crops. In J. Smith (Ed.), *Crop improvement through microbial biotechnology* (pp. 221-243). Elsevier.
- Deshmukh, S. K., Gupta, M. K., Prakash, V., & Saxena, S. (2018). Endophytic fungi: A source of potential antifungal compounds. *Journal of Fungi*, 4, 77.
- Devi, R., et al. (2023). A systematic review on endophytic fungi and its role in commercial applications. *Planta*, 257, 70.
- Dimkić, I., Janakiev, T., Petrović, M., Degrassi, G., & Fira, D. (2022). Plant-associated *Bacillus* and *Pseudomonas* antimicrobial activities in plant disease suppression via biological control mechanisms - A review. *Physiological and Molecular Plant Pathology*, 117, 101754.
- Din, G. M., Ali, M. A., Abbas, A., Naveed, M., Naveed, K., Anwar, J., & Tanveer, M. H. (2018). Consortium application of endophytic bacteria and fungi improves grain yield and physiological attributes in advanced lines of bread wheat. *Turkish Journal of Agriculture and Food Science Technology*, 6, 136-144.
- Din, G. M., Moosa, A., Ghummen, U. F., Jabran, M., Abbas, A., Naveed, M., Jabbar, A., & Ali, M. A. (2018). Host status of commonly planted ornamentals to *Meloidogyne incognita* and management through endophytic bacteria. *Pakistan Journal of Zoology*, 50(4), 1393-1402.
- Dudeja, S. S., Suneja-Madan, P., Paul, M., Maheswari, R., & Kothe, E. (2021). Bacterial endophytes: Molecular interactions with their hosts. *Journal of Basic Microbiology*, 61, 475-505. <https://doi.org/10.1002/jobm.202000657>
- Durand, A., Leglize, P., & Benizri, E. (2021). Are endophytes essential partners for plants and what are the prospects for metal phytoremediation? *Plant and Soil*, 460, 1-30.
- Egamberdieva, D., Kamilova, F., Validov, S., Gafurova, L., Kucharova, Z., & Lugtenberg, B. (2007). High incidence of plant growth-stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. *Environmental Microbiology*, 9, 1-16.
- Feng, H., Fu, R., Hou, X., Lv, Y., Zhang, N., Liu, Y., Xu, Z., Miao, Y., Krell, T., Shen, Q., & Zhang, R. (2021). Chemotaxis of beneficial rhizobacteria to root exudates: The first step towards root-microbe rhizosphere interactions. *International Journal of Molecular Sciences*, 22, 6655.
- Fließbach, A., Winkler, M., Lutz, M. P., Oberholzer, H.-R., & Mäder, P. (2009). Soil amendment with *Pseudomonas fluorescens* CHA0: Lasting effects on soil biological properties in soils low in microbial biomass and activity. *Microbial Ecology*, 57, 611-623.
- Flores, H. (1999). 'Radicle' biochemistry: The biology of root-specific metabolism. *Trends in Plant Science*, 4, 220-226.
- Geza, S. A., Abo Mahas, H. H., & Abdel-Azeem, A. M. (2021). Rhizosphere microbiomes and their potential role in increasing soil fertility and crop productivity. In *Current Trends in Microbial Biotechnology for Sustainable Agriculture* (pp. 183-201).
- Glick, B. R. (1995). The enhancement of plant growth by free-living bacteria. *Canadian Journal of Microbiology*, 41, 109-117.
- Haas, D., & Keel, C. (2003). Regulation of antibiotic production in root-colonizing *pseudomonas* spp. and relevance for biological control of plant disease. *Annual Review of Phytopathology*, 41, 117-153.
- Haldar, S., Mondal, S., Kumari, A., Ghosh, A., Chattopadhyay, D., & Ghosh, A. (2022). Rhizosphere microbiome engineering. In *Current Developments in Biotechnology and Bioengineering* (pp. 377-396). Elsevier.
- Hassan, M. K., McInroy, J. A., & Kloepper, J. W. (2019). The interactions of rhizodeposits with plant growth-promoting rhizobacteria in the rhizosphere: A review. *Agriculture*, 9(7), 142.
- Hata, K., Atari, R., & Sone, K. (2002). Isolation of endophytic fungi from leaves of *Pasania edulis* and their within-leaf distributions. *Mycoscience*, 43, 369-373.
- Anwar, H., Jabran, M., Moosa, A., Arshad, U., Haseeb, A., Jabbar, A., Burhan, M., Abbas, A., Naveed, M., & Ali, M. A. (2022). Effect of sole and consortium application of endophytic bacteria on plant growth promotion and inhibition of *Meloidogyne incognita* infection in okra. *Pakistan Journal of Nematology*, 40(2), 138-146.
- Hinsinger, P., Plassard, C., Tang, C., & Jaillard, B. (2003). Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. *Plant and Soil*, 248, 43-59.
- Howell, C. R., & Stipanovic, R. D. (1979). Control of *Rhizoctonia solani* on cotton seedlings with *Pseudomonas fluorescens* and with an antibiotic produced by the bacterium. *Phytopathology*, 69, 480-482.
- Kabir, A. H., Baki, M. Z. I., Ahmed, B., & Mostofa, M. G. (2024). Current, faltering, and future strategies for advancing microbiome-assisted sustainable agriculture and environmental resilience. *New Crops*, 1, 100013.
- Kaul, S., Choudhary, M., Gupta, S., & Dhar, M. K. (2021). Engineering host microbiome for crop improvement and sustainable agriculture. *Frontiers in Microbiology*, 12, 635917.
- Khan, N., Ali, S., Shahid, M. A., Mustafa, A., Sayyed, R. Z., & Curá, J. A. (2021). Insights into the interactions among roots, rhizosphere, and rhizobacteria for improving plant growth and tolerance to abiotic stresses: A review. *Cells*, 10, 1551.
- Khan, S. S., & Rasool, S. (2022). Endophytes: A hunt for important bioactive compounds. In *Endophyte Biology: Recent Findings from the Kashmir Himalayas*.

- Khaskheli, M. A., et al. (2020). Isolation and characterization of root-associated bacterial endophytes and their biocontrol potential against major fungal phytopathogens of rice (*Oryza sativa* L.). *Pathogens*, 9(3), 172.
- Kinalwa, N. (2023). Utilization of fungal and bacterial endophytes for the management of the banana nematode *Radopholus similis* in East African Highland Bananas (Doctoral dissertation, Makerere University).
- Knoester, M., Pieterse, C. M., Bol, J. F., & Van Loon, L. C. (1999). Systemic resistance in Arabidopsis induced by rhizobacteria requires ethylene-dependent signaling at the site of application. *Molecular Plant-Microbe Interactions*, 12(8), 720–727.
- Kumar, A., & Dubey, A. (2020). Rhizosphere microbiome: Engineering bacterial competitiveness for enhancing crop production. *Journal of Advanced Research*, 24, 337-352.
- Kumar, V., & Nautiyal, C. S. (2023). Endophytes modulate plant genes: Present status and future perspectives. *Current Microbiology*, 80(11), 353.
- Kumawat, K. C., Razdan, N., & Saharan, K. (2022). Rhizospheric microbiome: Bio-based emerging strategies for sustainable agriculture development and future perspectives. *Microbiological Research*, 254, 126901.
- Lambers, H. J. P. (1980). The physiological significance of cyanide-resistant respiration in higher plants. *Cell and Environment*, 3, 293-302.
- Lamichhane, J. R., Barbetti, M. J., Chilvers, M. I., Pandey, A. K., & Steinberg, C. (2023). Exploiting root exudates to manage soil-borne disease complexes in a changing climate. *Trends in Microbiology*. 32, 27-37.
- Latha, P., Karthikeyan, M., & Rajeswari, E. (2019). Endophytic bacteria: Prospects and applications for plant disease management. In *Plant Health Under Biotic Stress: Volume 2: Microbial Interactions* (pp. 1-50).
- Lu, H., Zou, W. X., Meng, J. C., Hu, J., & Tan, R. X. (2000). New bioactive metabolites produced by *Colletotrichum* sp., an endophytic fungus in *Artemisia annua*. *Plant Science*, 151, 67-73.
- Lucke, M., Correa, M. G., & Levy, A. (2020). The role of secretion systems, effectors, and secondary metabolites of beneficial rhizobacteria in interactions with plants and microbes. *Frontiers in Plant Science*, 11, 589416. <https://doi.org/10.3389/fpls.2020.589416>
- Ma, W., Tang, S., Dengzeng, Z., Zhang, D., Zhang, T., & Ma, X. (2022). Root exudates contribute to belowground ecosystem hotspots: a review. *Frontiers in Microbiology*, 13, 937940.
- Maloy, O. C. T. D. M. (2000). *Encyclopedia of Plant Pathology*. John Wiley & Sons, Inc, New York, NY.
- Manganyi, M. C., & Ateba, C. N. (2020). Untapped potentials of endophytic fungi: A review of novel bioactive compounds with biological applications. *Microorganisms*, 8(12), 1934.
- Mattoo, A. J., & Nonzom, S. (2021). Endophytic fungi: Understanding complex cross-talks. *Symbiosis*, 83(3), 237-264.
- Mousa, W. K., & Raizada, M. N. (2013). The diversity of anti-microbial secondary metabolites produced by fungal endophytes: an interdisciplinary perspective. *Frontiers in Microbiology*, 4, 65.
- Muhae-Ud-Din, G., Ali, M. A., Naveed, M., Naveed, K., Abbas, A., Anwar, J., Tanveer, M. H. (2018a). Consortium application of endophytic bacteria and fungi improves grain yield and physiological attributes in advanced lines of bread wheat. *Turkish Journal of Agriculture and Food Science Technology*, 6, 136-144.
- Muhae-ud-Din, G., Moosa, A., Ghummen, U. F., Jabran, M., Abbas, A., Naveed, M., Jabbar, A., Ali, M. A. (2018b). Host status of commonly planted ornamentals to *Meloidogyne incognita* and management through endophytic bacteria. *Pakistan Journal of Zoology*, 50, 2257-2263. <https://doi.org/10.17582/journal.pjz/2018.50.6.2257.2263>
- Nadeem, H., Rashid, M. H., Siddique, M. H., Azeem, F., Muzammil, S., Javed, M. R., Ali, M. A., Rasul, I., & Riaz, M. (2015). Microbial invertases: A review on kinetics, thermodynamics, and physicochemical properties. *Process Biochemistry*, 50, 1202-1210. <https://doi.org/10.1016/j.procbio.2015.05.023>
- Naik, S., Shaanker, R. U., Ravikanth, G., & Dayanandan, S. (2019). How and why do endophytes produce plant secondary metabolites? *Symbiosis*, 78, 193-201. <https://doi.org/10.1007/s13199-019-00636-1>
- Nazari, M. (2022). Functions of root mucilage for plant and soil: Quantifying its exudation, characterizing its composition, and assessing its influence on plant water and nitrogen uptake and rhizosphere microorganisms.
- O'Brien, A. M., Ginnan, N. A., Rebolledo-Gómez, M., & Wagner, M. R. (2021). Microbial effects on plant phenology and fitness. *American Journal of Botany*, 108(10), 1824-1837.
- Omomowo, I. O., Amao, J. A., Abubakar, A., Ogundola, A. F., Ezediuno, L. O., & Bamigboye, C. O. (2023). A review on the trends of endophytic fungi bioactivities. *Scientific African*, e01594.
- Pattnaik, S., Mohapatra, B., & Gupta, A. (2021). Plant growth-promoting microbe mediated uptake of essential nutrients (Fe, P, K) for crop stress management: Microbe–soil–plant continuum. *Frontiers in Agronomy*, 3, 689972.
- Patwardhan, R. B., Abhyankar, P. S., Gore, S. S., Kalekar, S. V., & Umrani, S. P. (2022). Biofungicidal properties of rhizobacteria for plant growth promotion and plant disease resistance. In *Antifungal Metabolites of Rhizobacteria for Sustainable Agriculture* (pp. 103-133). Cham: Springer International Publishing.
- Pavlo, A., Leonid, O., Iryna, Z., Natalia, K., & Maria, P. A. (2011). Endophytic bacteria enhancing growth and disease resistance of potato (*Solanum tuberosum* L.). *Biological Control*, 56, 43-49. <https://doi.org/10.1016/j.biocontrol.2010.10.005>
- Petrini, O. (1991). Fungal endophytes of tree leaves. In *Microbial Ecology of Leaves* (pp. 179-197). https://doi.org/10.1007/978-1-4684-7657-0_11

- Pieterse, C. M. J., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C. M., & Bakker, P. A. H. M. (2014). Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology*, 52, 347-375. <https://doi.org/10.1146/annurev-phyto-102313-045912>
- Piotti, G., Montecchio, L., Berti, A., et al. (2019). Biological control of chestnut ink disease by antagonistic endophytes. *Biological Control*, 134, 51-59. <https://doi.org/10.1016/j.biocontrol.2019.05.005>
- Poppeliers, S. W., Sánchez-Gil, J. J., & de Jonge, R. (2023). Microbes to support plant health: understanding bioinoculant success in complex conditions. *Current Opinion in Microbiology*, 73, 102286.
- Pršić, J., & Ongena, M. (2020). Elicitors of plant immunity triggered by beneficial bacteria. *Frontiers in Plant Science*, 11, 594530.
- Raaijmakers, J. M., & Mazzola, M. (2012). Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. *Annual Review of Phytopathology*, 50, 403-424. <https://doi.org/10.1146/annurev-phyto-081211-172908>
- Ramesh, R. (2019). Microbiome in plant health and disease: Challenges and opportunities. In *Microbiome in Plant Health and Disease: Challenges and Opportunities* (pp. 191-213). Springer. https://doi.org/10.1007/978-981-13-2089-7_10
- Rana, K. L., Kour, D., Sheikh, I., Yadav, N., Yadav, A. N., Kumar, V., & Saxena, A. K. (2019). Biodiversity of endophytic fungi from diverse niches and their biotechnological applications. In *Advances in Endophytic Fungal Research* (pp. 105-144). Springer. https://doi.org/10.1007/978-981-13-2092-4_6
- Rani, A., Saini, K. C., Bast, F., Varjani, S., Mehariya, S., Bhatia, S. K., ... & Funk, C. (2021). A review on microbial products and their perspective application as antimicrobial agents. *Biomolecules*, 11(12), 1860.
- Rezzonico, F., Binder, C., Défago, G., & Moëgne-Loccoz, Y. (2005). The type III secretion system of biocontrol *Pseudomonas fluorescens* KD targets the phytopathogenic chromista *Pythium ultimum* and promotes cucumber protection. *Molecular Plant-Microbe Interactions*, 18, 991-1001. <https://doi.org/10.1094/MPMI-18-0991>
- Rodriguez, R. J., & Redman, R. S. (2021). Fungal endophytes: Diversity and functional roles. *New Phytologist*, 201(9), 9-12. <https://doi.org/10.1111/nph.16529>
- Rosconi, F., et al. (2013). Identification and structural characterization of serobactins, a suite of lipopeptide siderophores produced by the grass endophyte *Herbaspirillum seropedicae*. *Environmental Microbiology*, 15, 916-927. <https://doi.org/10.1111/1462-2920.12049>
- Saeed, Q., Xiukang, W., Haider, F. U., Kučerik, J., Mumtaz, M. Z., Holatko, J., ... & Mustafa, A. (2021). Rhizosphere bacteria in plant growth promotion, biocontrol, and bioremediation of contaminated sites: A comprehensive review of effects and mechanisms. *International Journal of Molecular Sciences*, 22(19), 10529.
- Samreen, T., Naveed, M., Nazir, M. Z., Asghar, H. N., Khan, M. I., Zahir, Z. A., Choudhary, M. (2021). Seed associated bacterial and fungal endophytes: Diversity, life cycle, transmission, and application potential. *Applied Soil Ecology*, 168, 104191. <https://doi.org/10.1016/j.apsoil.2021.104191>
- Sangeetha, J., Unnikrishnan, R., Jasmin, H., & Maxim Steffi, S. (2020). Isolation and morphological identification of culturable endophytic fungal species from mangrove ecosystem. *Applied Ecology and Environmental Sciences*, 8, 128-134.
- Santoyo, G., Gamalero, E., & Glick, B. R. (2021). Mycorrhizal-bacterial amelioration of plant abiotic and biotic stress. *Frontiers in Sustainable Food Systems*, 5, 672881.
- Sharma, A., Kaushik, N., Sharma, A., Marzouk, T., & Djéballi, N. (2022). Exploring the potential of endophytes and their metabolites for bio-control activity. *3 Biotech*, 12(10), 277.
- Sharma, M., Kansal, R., & Singh, D. (2018). Endophytic microorganisms: Their role in plant growth and crop improvement. In *Crop Improvement through Microbial Biotechnology* (pp. 391-413). Elsevier.
- Solaiman, Z. M., Blackwell, P., Abbott, L. K., & Storer, P. (2010). Direct and residual effect of biochar application on mycorrhizal root colonisation, growth and nutrition of wheat. *Soil Research*, 48, 1-10. <https://doi.org/10.1071/SR10007>
- Srivastava, N. (2023). Siderophore production in iron uptake and plant biofortification. In *Plant Microbiome for Plant Productivity and Sustainable Agriculture* (pp. 313-329). Springer Nature Singapore.
- Tang, C.-S., Cai, W.-F., Kohl, K., & Nishimoto, R. K. (1995). *Plant stress and allelopathy*. ACS Publications.
- Thakur, N., Nigam, M., Mann, N. A., Gupta, S., Hussain, C. M., Shukla, S. K., ... & Khan, S. A. (2023). Host-mediated gene engineering and microbiome-based technology optimization for sustainable agriculture and the environment. *Functional & Integrative Genomics*, 23(1), 57.
- Tiwari, P., Kang, S., & Bae, H. (2023). Plant-endophyte associations: Rich yet under-explored sources of novel bioactive molecules and applications. *Microbiological Research*, 266, 127241. <https://doi.org/10.1016/j.micres.2022.127241>
- Tkachenko, O. V., Evseeva, N. V., Terentyeva, E. V., Burygin, G. L., Shirokov, A. A., Burov, A. M., ... & Shchyogolev, S. Y. (2021). Improved production of high-quality potato seeds in aeroponics with plant-growth-promoting rhizobacteria. *Potato Research*, 64, 55-66.
- Trivedi, P., et al. (2020). Plant-microbiome interactions: From community assembly to plant health. *Nature Reviews Microbiology*, 18, 607-621. <https://doi.org/10.1038/s41579-020-0377-1>

- Turner, T. R., Ramakrishnan, K., Walshaw, J., Heavens, D., Alston, M., Swarbreck, D., Osbourn, A., Grant, A., & Poole, P. S. (2013). Comparative metatranscriptomics reveals kingdom-level changes in the rhizosphere microbiome of plants. *ISME Journal*, 7, 2248-2258. <https://doi.org/10.1038/ismej.2013.119>
- Upadhyay, S. K., Srivastava, A. K., Rajput, V. D., Chauhan, P. K., Bhojiya, A. A., Jain, D., & Minkina, T. (2022). Root exudates: Mechanistic insight of plant growth-promoting rhizobacteria for sustainable crop production. *Frontiers in Microbiology*, 13, 916488. <https://doi.org/10.3389/fmicb.2022.916488>
- Validov, S. F., Mavrodi, O. V., La Fuente, L., Boronin, A. M., Weller, D. M., Thomashow, L. S., & Mavrodi, D. V. (2005). Antagonistic activity among 2,4-diacetylphloroglucinol-producing fluorescent *Pseudomonas* spp. *FEMS Microbiology Letters*, 242, 249-256. <https://doi.org/10.1016/j.femsle.2004.11.040>
- Verginer, M., Siegmund, B., Cardinale, M., Müller, H., Choi, Y., Míguez, C. B., Leitner, E., & Berg, G. (2010). Monitoring the plant epiphyte *Methylobacterium extorquens* DSM 21961 by real-time PCR and its influence on the strawberry flavor. *FEMS Microbiology Ecology*, 74, 136-145. <https://doi.org/10.1111/j.1574-6941.2010.00921.x>