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REVIEW

Microbiota homeostasis: Signaling mechanism of plants to differentiate friend and foe microbes

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Abstract

Plants have been associated with microflora for more than 400 million years, and this long-standing interconnection takes place in different regions of the plants. The complex community of microbes can be beneficial or pose a threat as pathogens. Previous studies have investigated plant immune responses and interactions with diverse microbes however, several aspects remain unclear and require further exploration. Plants utilize several small molecules through their associated biochemical pathways to aid this recognition process. This review examines recent progress on the distinct signaling pathways of various plant small molecules, including amino acids, lipids, and plant secondary metabolites, as well as the receptor-like kinases engaged in recruiting and scrutinizing the microbes involved in interactions. This review additionally explores how the rhizosphere and phyllosphere interact to shape the microbiome, facilitating plant homeostasis. Furthermore, it highlights the remarkable similarities between markets in human societies and those found in microbe-plant biological systems. Together, these ideas offer a framework for understanding how plants interact with advantageous microorganisms while simultaneously limiting harmful pathogens. The specific biochemical mechanisms and their interconnections are gradually being elucidated, providing a potential foundation for the development of novel plant protection strategies. With a holistic approach, these plant-microbe interactions can be exploited to engineer plants with multiomics approaches for improved performance, which can enhance crop resilience, promote sustainable agriculture, and address global food security in the long term.

Keywords: biological market, homeostasis, immunity, plant-microbe signaling, plant small molecules, symbiosis

Introduction

In a natural environment, plants are constantly exposed to diverse abiotic and biotic stresses, and they have developed a complex immune response to withstand biotic stress (Pieterse *et al.* 2016). Plants interact with various pathogenic and beneficial microbiota in the intricate microbial communities that make up the microbiome. The interactions may be mutualistic where the microbes manipulate plant metabolism and benefit the plant in other ways or as commensals, where they do not benefit the plant, or as pathogens, where they cause damage to the plants. Interestingly, the interactions between plants and microorganisms can also be categorized on the basis of their duration. In some instances, plants exhibit transient associations with some microbes, and these interactions can be influenced by environmental conditions (Orozco-Mosqueda and Santoyo 2021). On the other hand, some plant–microbe relationships are long-lasting, spanning the plant's life cycle and beyond. The entire microbiota associated with a plant can live, thrive, and interact with a variety of tissues, such as leaves, flowers, roots, and shoots, and is known as the core microbiome (Arif *et al.* 2020). These specific sets of microbial taxa play important roles in plant fitness, stability, and health. These microbial communities, shaped by evolutionary processes, benefit both the plant and the associated microbiota (Kumar *et al.* 2023). In the rhizosphere, specific fungal and bacterial phyla, such as Glomeromycota, Ascomycota, and Proteobacteria, are particularly prevalent and frequently observed (Backer *et al*. 2018). These insights shed light on the diverse and intricate relationships within the plant microbiome.

Microbes ultimately interact with plants for nutrients, and plants preferentially allocate their resources according to the benefits they receive from the microbes, which features the concept of a biological market framework. This theory was traditionally used to explain cooperative behaviors in animals and is now being applied to plant-microbe interactions, viewing these relationships as a form of "trade" (Hammerstein and Noe 2016). Biological market theory provides a valuable framework for understanding cooperation and resource exchange in plant-microbe interactions. Economic principles are applied to analyze how plants and microbes engage in cooperative behaviors, both with hosts and other microbes. In addition to the mechanism of plant interactions to differentiate friend and foe microbes, several factors play pivotal roles, including the environment, types of microbes that interact, immunity of the plants and so on. Thoms *et al.* (2021) reported that by integrating environmental signals with immunity, plants fine-tune their "immune thermostat" to foster a nonharmful microbiome and employ receptor-mediated decision making to respond dynamically to potential pathogens or mutualists. Other groups of researchers have shown that MAMP-triggered immunity (MTI) is a key plant defense response, but commensal microbes have evolved strategies to bypass it for symbiosis (Zhang and Kong 2022). Recent studies carried out by Fröschel *et al.* (2021), Teixeira *et al.* (2021), and Zhang *et al.* (2021) have advanced our understanding of how commensals regulate MTI.These studies have emphasized the interaction between individual plant-microbe relationships, disregarding the crucial role of small molecules, the complexity of metabolic pathways and the interplay of different groups of microorganisms. Deciphering these secrets and understanding the manipulation of microbiomes according to the events occurring in plant systems can support the development of next-generation microbial inoculants to control particular diseases and increase plant growth.

This manuscript explores the sequential integration of environmental cues by plants to differentiate beneficial and pathogenic interactions, initiating either immunity or symbiosis. It highlights the roles of plant parts in signaling, key interaction molecules, fine-tuning of recognition, inheritance of traits, and the concept of biological market theory. Emphasizing the broad influence of cues on plant-host interactions, this review underpins recent studies on plant molecular signatures,*viz.,* amino acids, lipids, receptor-like kinases, and secondary metabolites, in microbiome recruitment, providing insights into how plants distinguish between beneficial and harmful microbes. Harnessing these molecules through genetic engineering, breeding, or exogenous applications can improve plant–microbe symbiosis, leading to better growth and resistance to biotic and abiotic stresses.

Unveiling the master program of symbiotic and pathogenic interactions

Plants are crucial in providing carbon, an essential nutrient for microbes. They have evolved distinct mechanisms to recognize microbial molecules, leading to symbiotic relationships or defense responses. The interactions among plantsand microbes include antagonism, competition, predation, and cooperation (Fig. 1). In arbuscular mycorrhizal fungal interactions and legume-rhizobia interactions, plants discern discrete microbial chemical signals, instigating important priming events, such as mutualistic symbiosis. Conversely, the recognition of pathogens by plants results in robust defense responses and the inhibition of microbial development. The three stages of symbiotic engagement and the restriction of potential pathogens, as corroborated by Thoms *et al.* (2021), include metabolic gating, dual receptor recognition, where multiple receptor signals initiate either immunity or symbiosis, and the incorporation of environmental cues to optimize decision-making in symbiosis. Plants offer some distinct mechanisms to specifically hamper symbiotic microbes from secreting specialized metabolites, nutrients that only certain microbes can utilize (Cheng *et al.* 2017), antimicrobial substances that are harmful to some but not all microbes, and signals that attract mainly distinct microbes (Thoms *et al.* 2021). Several chemicals found in root exudates, such as malic acid, fumaric acid, and citric acid, play a functional role in promoting the symbiosis of beneficial bacteria with plants. In rhizobia–legume symbiosis, lipochitooligosaccharides (LCOs), exopolysaccharides (EPSs) and lipopolysaccharides (LPSs) collectively promote symbiotic signaling in plants. In the case of the symbiotic

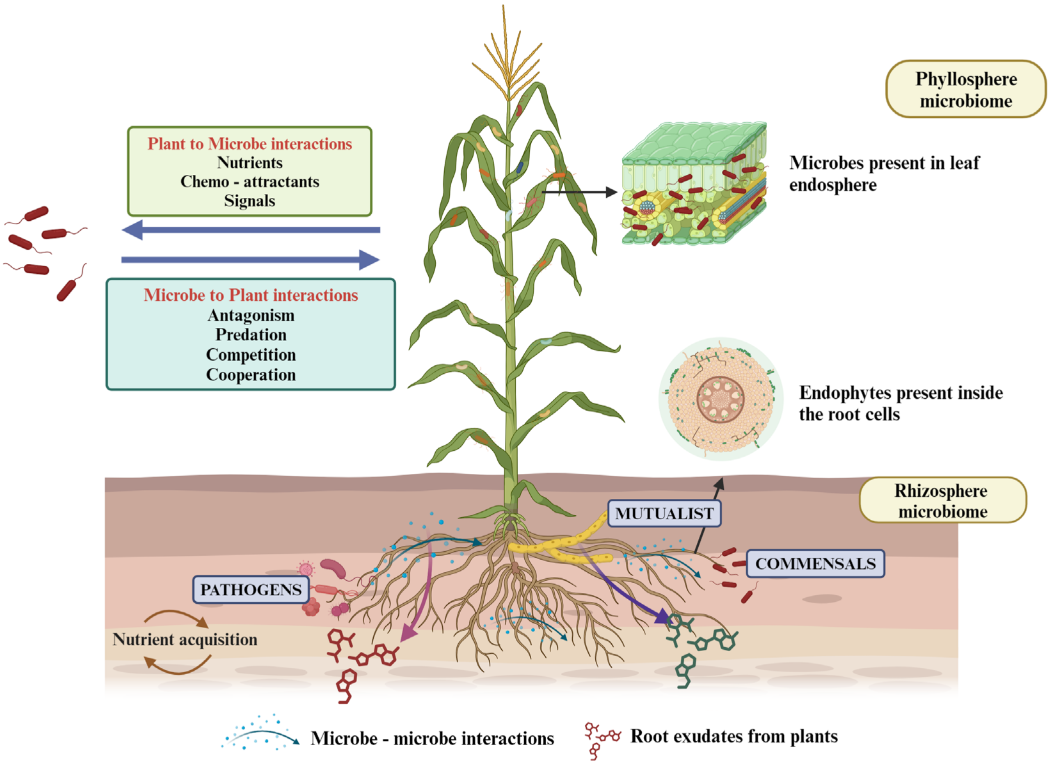

Fig. 1. Plant – microbe interaction in rhizosphere and phyllosphere regions
Plants interact with thousands of microbes and with intrinsic and extrinsic cues, the plant must decide whether the microbe is a mutualist or a pathogen. Generally, all the microorganisms interact with plants for nutrient acquisition where the root exudates containing a significant proportion of the photosynthetic products play a decisive role in recruiting the microbiome. This image was created with BioRender.com

interactions between arbuscular mycorrhiza and ectomycorrhizal fungi, lipochromes (LCOs) play a pivotal role (Cope *et al.* 2019). Delving deep into the molecular mechanism of interactions, chitin is the primary MAMP that causes plant immunity when recognized by pattern recognition receptors. Chitin elicitor receptor kinase (CERK1) is the PRR present in plants. When recognized, chitin releases enzymes known as chitinases, which breakdown chitin into chitooligosaccharides (COs) to defend themselves against fungal infection. Plant immunological responses are linked to long-chain carbohydrates such as chitooctaose (CO_8), whereas plant symbiotic responses are linked to short--chain carbohydrates such as chitotetraose (CO_4) and lipochitooligosaccharides (LCOs) (Zhang *et al.* 2021). As a result, plants can distinguish whether a fungus is a friend or foe on the basis of the different types of compounds produced during interaction.

During interactions with the microbiome, plants can experience positive, negative, or balanced outcomes depending on their immune responses. This variability is described with distinct terms. Maintaining microbiota homeostasis in plants is called eubiosis (Paasch and He 2021), where the balance between host plants and microorganisms is maintained. Disruption of this equilibrium results in dysbiosis, which has a negative impact on plant health (Petersen and Round 2014). Pathogen infections can cause immunological suppression and alter the composition of the microbiota. Deviation from eubiosis may also result in positive impacts on plants, termed meliorbiosis, which has been extensively studied in many host-pathogen relationships (Paasch and He 2021). Hence, with this background, it is clear that plants use specific mechanisms to discern beneficial and pathogenic microorganisms, but the typical framework of interaction and fine-tuning recognition is either distinct or overlapping, principles that remain elusive and must be untapped by exploring the small molecules involved in plant-microbe interactions.

Recruitment dynamics of friend and foe microbes

A primitive filamentous fungus colonizes land plants and facilitates nutrient acquisition and water absorption. In return, the fungus photosynthetically fixes carbon to the host plant. Approximately 5 to 21% of the total carbon fixed in photosynthesis is excreted at the root level, influencing the composition of the microbiota in the rhizosphere (Vandenkoornhuyse *et al.* 2015). In addition to containing nutrients, root exudates also encompass chemoattractant and signaling molecules. This paves the way for microorganisms to communicate with plants (Pantigoso *et al.* 2022). Intriguingly, during initial plant colonization, symbionts and pathogens produce effector proteins. Effector proteins are small molecules, mostly proteins, produced by microorganisms that play a central role in plant-pathogen interactions. Effectors act in multiple ways on different targets, suppressing plant immunity, manipulating plant physiology, and being recognized by host defense mechanisms. They thus promote pathogen infestation, expansion, and colonization (Yu *et al.* 2019). Effector proteins have both negative and positive impacts on symbiotic associations. The effector promotes phytopathogen virulence, leading to effector-triggered susceptibility (ETS). Plants have evolved sophisticated detection systems that recognize conserved molecules from microbes. When the Avr protein of a phytopathogen is recognized, an important phenomenon of effector-triggered immunity (ETI), called the hypersensitive response (HR), is triggered. HR results in localized cell death in the host at the site of infection, preventing further pathogen invasion and maintaining plant health (Zipfel 2014).The receptors and coreceptors of plants perceive MAMPs, such as fungal cell wall chitin, peptidoglycan in the bacterial cell envelope, flagellar components flagellin 22, elongation factor (Ef-Tu), and eicosapolyenoic acid (EP) of the oomycete, β-glucans of the oomycete cell wall, and secreted peptides that trigger specific retrograde signaling or balance MAMP recognition receptors (Saijo *et al.* 2018). The leucine-rich repeat domains of receptor-like kinases (LRR – RLK) found on membrane-associated receptor kinases and the cytoplasmic Nod-like receptors detect MAMPs. In response to MAMPs, a mitogen-activated protein kinase (MAPK) cascade is triggered, leading to transcriptional changes. Consequently, the immune response is mediated by the formation of reactive oxygen species and antimicrobial peptides (Roudaire *et al.* 2021).

The central component that plays a crucial role in plant-microbe interactions, specifically in recognizing and responding to various microbial signals, is LysM (Lysin Motif) receptor kinase (Bozsoki *et al.* 2020). It contains two motifs, the LysM domain and ligand-recognizing motifs. The specificity of these receptors is largely determined by distinct ligand-recognizing motifs present in their structure. They function in the perception of molecules from microorganisms, which can activate plant responses leading to either symbiosis or defense against pathogens (Buendia *et al.* 2018). LysM-RLKs are vital for the establishment of both arbuscular mycorrhizal (AM) and rhizobium-legume (RL) symbioses (Gough *et al.* 2018). LysM receptors also play a role in plant-pathogen interactions by activating the immune system upon the detection of pathogens. For example, the rice protein OsCEBiP, which contains LysM domains, is involved in resistance to fungal pathogens (Buendia *et al.* 2018). Modifying LysM receptors to increase their recognition of pathogen-associated molecular patterns (PAMPs) or to trigger a stronger immune response could improve plant resistance to diseases (Bozsoki *et al.* 2020). The functions of LysM-RLKs in *Brassica* for genome editing have been investigated with bioinformatics techniques (Abedi *et al.* 2021). Two motifs in the LysM domain determine the specific recognition of ligands and discriminate between their functions in plants. By understanding these specificities, researchers can potentially manipulate these receptors to fine-tune plant responses to different microbes (Boszoki *et al.* 2018).

Basal immunity pathways and common symbiotic pathways share overlapping components, including signaling cascades, posttranslational modifications, and gene induction mechanisms. These pathways are intricately designed to initiate appropriate responses according to the type of microbe detected. A study conducted in ricedid not explores the dual function of the plant genetic component *RAM2* (required for arbuscular mycorrhization 2). OsRAM2 and its homologue OsRAM2L, identified in rice, are essential for the colonization of arbuscular mycorrhizal (AM) fungi and the blast pathogen *Magnaporthe oryzae*. The plants lacking these genes are unable to be colonized by mycorrhizae or pathogens, which indicates that both organisms recruit RAM2-mediated fatty acid biosynthesis to facilitate invasion (Wang *et al.* 2012). These findings suggest that plants have evolved to utilize the same genetic pathways for mutualistic and antagonistic interactions with microbes to maintain plant–microbe homeostasis. Understanding these signaling pathways can shed light on their evolutionary adaptations and opens avenues for engineering plants with increased abilities to establish beneficial symbiotic relationships. This could improve agricultural practices and crop yields by optimizing plant responses to microbial partners.

Interplay of root architecture and the rhizosphere microbiome

Roots hidden below the ground are important for plant responses to myriads of biotic and abiotic stresses and play a significant role in plant life. The root system of mature plants is a complex network with a unique arrangement of root cell types known as the cellular architecture. Each root cell type produces a unique set of molecular signatures, and the response of roots to the environment depends on cell type specificity. Plants distinguish soil-borne pathogens from commensal microorganisms through spatially restricted immune responses and transcriptome reprograming specific to a specific cell type (Kawa and Brady 2022). Upon intruding into root cells, soilborne organisms penetrate radially from the epidermis first, then the exodermis (in some plants), the inner cortex, and the endodermis to reach the vascular system, from whichthey spread to other parts of the plant. The endoderm is likely to hinder the spread of several pathogens across kingdoms (Fig. 2).

Suberized cell walls and lignified Casparian strips are two forms of apo plastic diffusion barriers observed in endodermal cells in the maturation zone that act as barriers against biotic agents (Gao *et al.* 2024). The potential of biotic microorganisms to pass through the endodermis determines their successful niche inside plants and their potential success in thriving as symbionts or parasites (Kawa and Brady 2022). The stability of endodermal diffusion barriers is crucial for plant-soil microbe interactions and for maintaining plant nutrient homeostasis (Durr *et al.* 2021). The cells in the endoderm are responsible for microbe perception, signaling, and the assembly of microbial communities in specific ways (Zhou *et al.* 2020). The microbiome and root endodermal barriers have a bidirectional relationship. Thus, the stability of the endodermis acts as a clincher in perpetuating plant-microbiome homeostasis. The cellular structure of the root cortex affects the interaction of fungi with roots (González-Mas *et al.* 2021). For example, Arabidopsisis affected by two soilborne pathogens, *Verticillium longisporum* and *Phytophthora parasitica,* where the former downregulates Casparian strip and suberin formation in the endodermis, which collectively weakens the diffusion barrier and paves entry for the pathogen into the vasculature. The latter do not incite any changes in the cellular architecture and colonize only the cortex and epidermis but do not cross the endodermis (Fröschel *et al.* 2021). In contrast to *P. parasitica*, which represses the transcription of specific gene sets within vascular tissues, infection by *V. longisporum* leads to the upregulation of genes involved in the biosynthesis of antimicrobial aliphatic glucosinolates in cortical tissues (Fröschel *et al.* 2021). This represents the pivotal role of innate cell type-specific barriers in counteracting the intrusion of soil-borne pathogens. Suberin deposition and accumulation of phenolic compounds in the epidermis and endodermis, lignin and callose deposition in the vasculature and cortex, and tylose deposition in the vasculature are associated with various types of cell type-specific barriers present in the roots.

Root cell architecture differs from species to species and between individual plants of the same species. Population variations in bacterial and fungal communities have been noted in monocots between the tip and base regions of various root types, as well as between the crown and seminal roots of rice (*Oryza sativa*) and wheat (*Triticum aestivum*) (Kawasaki *et al.* 2021). The root-associated microbiota and their

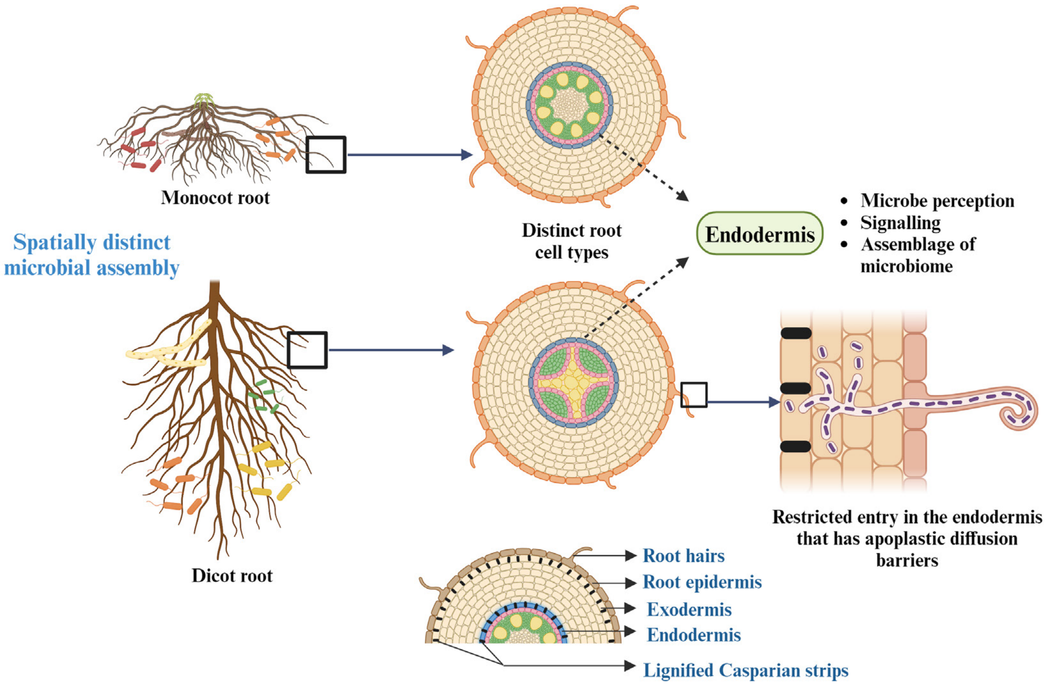

Fig. 2. Diverse cellular architecture recruit microbiome differently
Plants belonging to monocot and dicot families exhibit distinct mechanisms for attracting microbiomes, which are influenced by their root systems, exudation profiles, as well as phylogenetic traits. The monocot roots are characterized by a typical fibrous root system with distinct crown roots. Dicot roots are comprised of tap roots where the primary roots grow deeper into the soil. The difference in root cellular anatomy recruits spatially distinct microbial communities. Variations are also exhibited in the cellular architecture of monocot and dicot roots where each layer produces layer specific responses against mutualist and pathogens. The endodermis is a cellular barrier for the entry of microbiomes and is comprised of suberized cell walls and casparian strips

volatile organic compounds are potent enough to modulate the root exudates produced by plants. A pioneering work conducted by Kong *et al*. (2021) revealed that the inoculation of tomato plants with the PGPR *Bacillus amyloliquefaciens* GB-03 revived microbe-induced plant volatiles (MIPVs), namely, β-caryophyllene and specific volatile production. Once neighboring plants detect these VOCs, they alter the production of root exudates. Salicylic acid reshapes the recruitment of microbiota by producing salicylic acid as a critical root exudate. In this type of interaction, emitting and receiving plants reveal similarities in the rhizosphere-associated microbial communities of neighboring plants. Roots have been shown to play a significant role in plant fitness (Fig. 3). However, additional research is needed to focus on specific root phenotypes since the same type of interactions do not occur with all plant species. Modelling root architectural and molecular properties will reduce the impact of pathogens but significantly reduce the recruitment of beneficial microbes. Relying on the wisdom of the past, root–centric ideotypes will be a cut corner to specifically strengthen beneficial interactions, equivalently minimizing pathogen attack (Schmidt and Gaudin 2017). This ideology has already been explored for nutrients in maize, where minimal crown roots grow deeper into soil horizons and absorb nitrogen (Lynch 2019). Elaborative research is needed on these untapped avenues to reinforce plant microbiome homeostasis.

Lipids – facilitators or modifiers?

Lipids are highly evolved and perform versatile roles at different stages in critical underground processes of plant microbe interactions by serving as chemical signals, regulating stress responses (Fig. 4) (Ruelland and Valentova 2016). Lipids are classified into eight different classes according to LIPID MAPS, which cover both eukaryotic and prokaryotic origins. Included are: prenol lipids [PR], saccharolipids [SL], fatty acyls [FA], glycerolipids [GL], glycerophospholipids [GP], sphingolipids [SP], sterol lipids [ST], and polyketides [PKs] (Liebisch *et al.* 2020). Lipids, a major component of the plasma membrane, form physical barriers on cell surfaces and act as elicitors or second messengers for recognizing microbial colonization (Venturi and Keel 2016). Glycerophospholipids (GPs), sphingolipids (SPs), sterol lipids (STs), and glycerolipids (GLs) are the foremost lipid components present in the plasma membrane. Membrane phospholipids play a decisive role in the interaction between pathogens and signaling downstream cascades of plants in response to external stimuli (Okazaki and Saito 2014). Glycerophospholipids (GPs), sphingolipids (SPs), sterol lipids

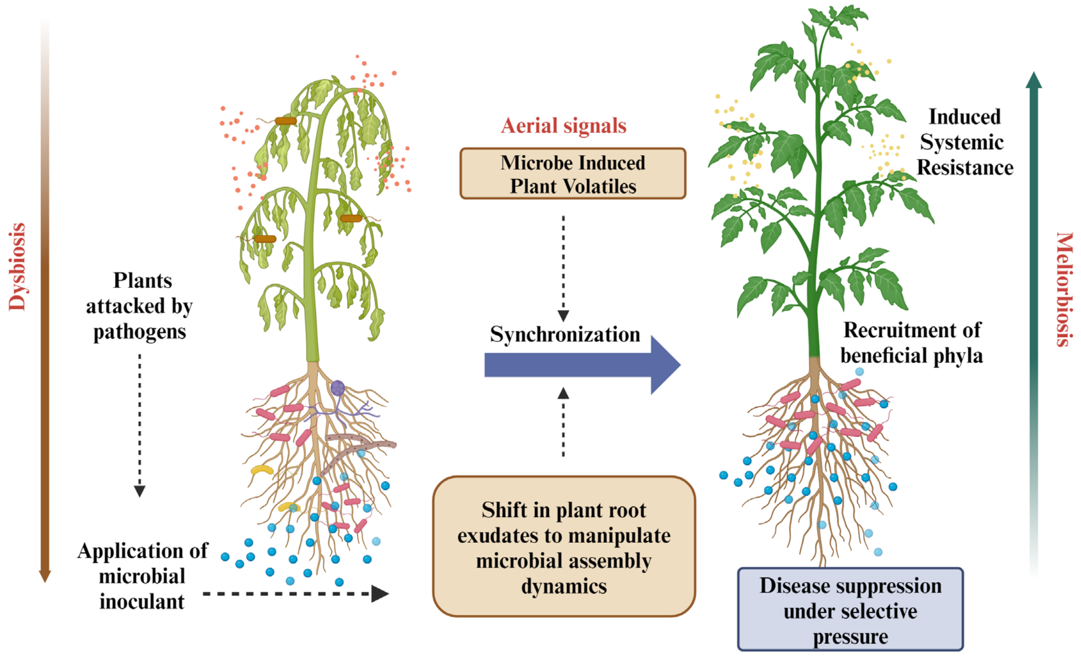

Fig. 3. Conceptual diagram of plant - microbe interaction and plant to plant signaling during pathogen attack
Plants maintain optimal balance with the microbiome and the surrounding environment i.e.,eubiosis,which is disrupted when the pathogen attacks the plant. Changes in the metabolic activity and functional composition of microbiome that negatively impacts plants is known as dysbiosis. Under this condition, inoculation of beneficial microbiome to the plant alters the root exudates production which in turn has a short-term shift in the root microbiome assembly of the neighboring plants. The manipulation of microbiome assembly is in accordance with the build-up of induced systemic resistance. The phyllosphere region of diseased plants also emits volatiles that warn the neighboring plant to change its microbiome recruitment similar to that transmitting plant which facilitates plant immunity

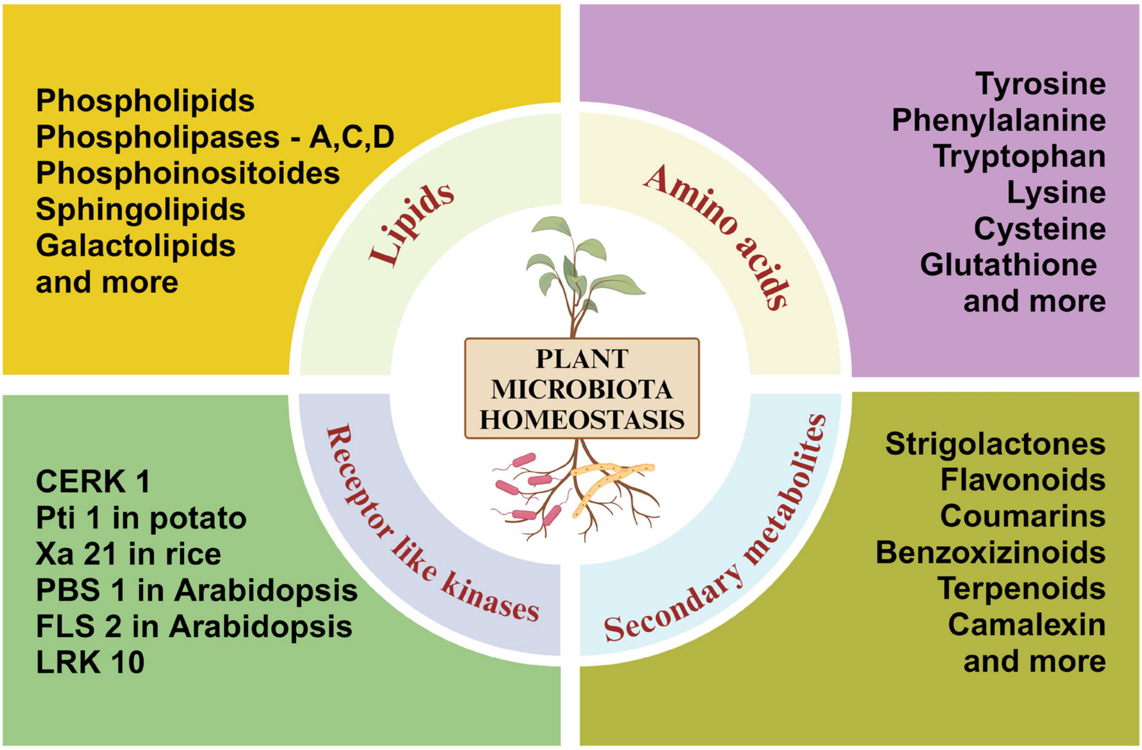

Fig. 4. Different plant molecules involved in the maintenance of plant microbe homeostasis
Amino acids, lipids, secondary metabolites secreted into the rhizosphere, receptor like kinases collectively contribute to the recruitment of beneficial microbiome and fend off the attack of pathogens

(STs), and glycerolipids (GLs) are the foremost lipid components present in the plasma membrane.

Rhizosphere interactions are classified into three categories: signaling from plant roots to microbes, inter- and intraspecific microbial signaling, and signaling from microbes to plants (Venturi and Keel 2016). In the first stage of these complex communication routes between the plant and rhizosphere microbiomes, the plant secretes rhizo deposits, which are composed of sugars, amino acids, enzymes, growth factors, flavanones, and lipid molecules such as fatty acids and sterols (Sasse *et al.* 2018). When perceived by microbe signals, these small biomolecules produce differential responses in microbes according to their needs. Plant communication with the rhizosphere can influence the gene expression of microbes. Recent progress in lipid omics research has shed light on the crucial role of phospholipases and phospholipid-derived molecules in plant signaling and immunity. Extensive studies on phospholipases have revealed that three types, A, C, and D, are primarily involved in plant defense mechanisms against pathogen invasion (Zhao 2015). Phosphatidic acid (PA), an enzymatic product of phospholipase D, acts as a potent second messenger in critical defense signaling. It involves activating parallel signaling pathways of kinases, phospholipases, Ca^{2+} signaling and the oxidative burst (Macabuhay *et al.* 2022). PA is perceived as a universal lipid signaling molecule. During plant-pathogen interactions, enzymes that hydrolyze phospholipids promote the synthesis of defense signaling molecules such as oxylipins and jasmonic acid (JA), which are formed from patatin-like proteins of phospholipase A, to form PAs. Phosphoinositides, another group of regulatory membrane lipids, are implicated in plant microbe interactions. Recent evidence has reappraised the role of phosphoinositides, where fungal, bacterial and viral pathogens use these membrane lipids to enter plant cells, colonize, and promote hyphal growth, intracellular movement, transmission and replication of virus particles (Shimada *et al.* 2019; Sasvari *et al.* 2020; Kovalev *et al.* 2020; Feng *et al.* 2021). Another crucial plant process carried out by lipids is lipid peroxidation, where lipids are degraded due to oxidative damage. Reactive oxygen species can cause oxidative attack on polyunsaturated lipids, initiating a distinct chain reaction that produces end products such as malondialdehyde (MDA). This occurs during plant stress conditions that cause programed cell death (PCD) (Ramírez *et al.* 2019).

Exploiting the role of key lipids in beneficial microbe–plant interactions, associated signaling, and biochemical pathways will strengthen plant immunity. Lipid nanoparticles (LNPs) offer several promising avenues for integration into crop management practices. LNPs can address various challenges in agriculture, including the delivery of pesticides, enhancing nutrient absorption, and improving the bioavailability of bioactive compounds (Pathak *et al*. 2024). Leveraging research concerning microbial lipids and manipulating them for biocontrol will also be important for escaping endemic pathogen attacks. To increase antimicrobial lipid production in plants and improve plant immunity, transgenic approaches involving crop development and the exogenous application of antimicrobial lipids constitute a sustainable strategy to improve plant yield.

Amino acids and orchestration of plant – microbe signaling

The building blocks of proteins are amino acids, which are closely linked to plant metabolism (Yang *et al.* 2020). Recent studies have shed light on the specific mechanisms by which plants proclaim amino acids that serve as precursors for several specialized metabolites that pave the way for the selective proliferation of beneficial microbes (Moormann *et al.* 2022). Insights into the role of amino acids, their biochemical pathways, signaling, transport, and metabolism during plant–microbe communication will reveal the role of different amino acids in stress signaling and defense responses. These specialized metabolites are used either as signaling molecules by the plants or to shape the microbiome composition in favor of the plant (Moormann *et al.* 2022). Amino acids are pivotal for immune signaling, and plants can sense changes in specific patterns of amino acid metabolism and act as a fingerprint for lurking pathogen attacks (Fig. 4). Plant-specific metabolites may be used as nutrient sources, signaling molecules, or toxins, thereby shaping the plant microbiome (Pascale *et al.* 2020).

The aromatic amino acids tyrosine (Tyr), phenylalanine (Phe), and tryptophan (Trp), which are synthesized through the shikimate pathway (Lynch and Dudareva 2020), serve as precursors for the production of assorted sets of specialized metabolites exploited for defense activities, such as the cell wall component lignin (Jacoby *et al.* 2020). To produce a variety of tailored active compounds, aromatic amino acids serve as tools. Intriguingly, genome-wide ribosomal profiling in Arabidopsis revealed that effector-triggered immunity (ETI) accentuated the biosynthetic pathways of aromatic amino acids and derived specialized metabolites as an additional layer of defense mechanism (Yoo *et al.* 2020). Chemoreceptors in microbes recognize amino acid areas rich in nutrients surrounding a plant's roots, and further utilization plays a crucial role in establishing the symbiotic relationship between plants and microbes (Yang *et al.* 2015). Amino acids are exuded across several membranes of the host plant through transporters, of which the 'usually multiple acids move in and out transporters' (UMAMIT) are currently the new center of interest. UMAMITs play important roles in nutrient transport, the response to stress, and the activation of immune mechanisms (Zhao *et al.* 2021). Recent studies indicate that UMAMITs, which are bidirectional facilitators of amino acid transport, can positively correlate with stress phenotypes and pathogen resistance (Tünnermann *et al.* 2022). The UMAMITs from *Oryza sativa, Arabisopsis thaliana, Physcomitrella patens*, *Selaginella moellendorffii,* and two conifers, *Picea abies* and *Pinus pinaster,* were compared (Zhao *et al.* 2021). The tissue-specific expression of UMMAITs in wheat was compared, and notably, TaUMAMIT17 exhibited strong amino acid export activity, suggesting its role in amino acid transfer during grain filling (Fang *et al.* 2022). For example, overexpression of *AtUMAMIT14* in *Arabidopsis* enhances the expression of salicylic acid (SA) marker genes and increases SA levels, leading to increased resistance to the biotrophic oomycete *Hyaloperonospora arabidopsidis* (Besnard *et al.* 2021). Despite this importance, little is known about the relationship between amino acid transporters and immunity or susceptibility to pathogens or pests.

Upon attack, plants generate systemic Ca^{2+} waves and electrical signals. These electrical signals are passed long distances in plants by glutamate receptor-like proteins (GLRs), which trigger a cascade of anticipatory defense mechanisms (Toyota *et al.* 2018). Interestingly, these plant GLRs are activated by amino acids, including glutamic acid, glycine, asparagine, alanine, cysteine, methionine, serine, and glutathione (Alfieri *et al.* 2020). In plant−microbe interactions, GLRs directly channel the transmembrane Ca^{2+} flux necessary for systemic wound signaling. The Glu receptor-like (GLR) proteins GLR 3.3 (27 kDa protein) and GLR 3.6 are responsible for the early expression of glutamate-inducible genes (Shao *et al.* 2020). Exogenous treatment of Arabidopsis roots with glutamate activates the expression and overlapping of salicylic acid and jasmonic acid-inducible genes (PAMPs) in leaves against attack by the fungal pathogen *Colletotrichum higginsianum* (Goto *et al.* 2020). In cucumber plants treated with the biocontrol agent *Bacillus* 1JN2, the disease severity of FW was reduced by altering the root exudates of the cucumber plants. An increase in the content of four amino acids, namely, glutamine, tryptophan, glycine, and glutamic acid, changes rhizomic microbiome recruitment in favor of plant immunity, thus supporting the 'cry for help' hypothesis (Yang *et al.* 2024). Compared with topsoil, plants distinguish their specific microbiome, and first-generation plants swap the native soil microbiome to the next generation and maintain the microbial legacy, which is known as a plant−soil feedback system (Mariotte *et al.* 2018). Research on amino acids is now considered a gold mine that provides information for fortifying crops against pathogen attack. Amino acids are also involved in intricate plant-microbe interactions, and further understanding of the signaling and biochemical pathways by which microbes manipulate amino acids for their wellness will provide a deeper understanding of maintaining plant homeostasis.

Game of plant secondary metabolites in root microbiome recruitment

Tapping further into plant-microbe interactions reveal the role of plant-specialized metabolites (PSMs), which serve as chemical dialogues in the complex and mysterious network of interactions in the rhizosphere, shaping microbial communities and combatting biotic and abiotic stress (Fig. 4). PSMs are divided into three main types depending on the chemical structure of their metabolites and their metabolic pathway: (i) terpenoids (terpenes, steroids, sterols, glycosides, saponins, carotenoids), (ii) polyphenols (flavonoids, coumarins, phenolic acids, tannins, stilbenes, lignans, etc.), and (iii) nitrogen-containing compounds (amines, alkaloids, cyanogenic glycosides, and glucosinolates) (Yadav *et al.* 2021). Relying on the wisdom of the past, these metabolites clearly act as a bridge in the assembly of plant microbes. Approximately 20% of the carbon plants produced through photosynthesis are used to create metabolites secreted for communication between organisms in the rhizosphere (Abedini *et al.* 2021). Metabolites play an intricate role in the selection and suppression of microbial communities for the benefit of plants. Additionally, plant age and developmental stage influence metabolite exudation and microbial proliferation around plant roots (Pascale *et al.* 2020). Strigolactones (SLs), a category of carotenoid-derived phytohormones that were initially discovered as plant physiological regulators, are also root-derived signaling molecules (Mashiguchi *et al.* 2021). The possible role of strigolactones in plant-microbe interactions was characterized in the context of arbuscular mycorrhiza–plant interactions. The molecular mechanism of strigolactone upregulation in the rhizosphere has been extensively studied in the Solanaceaefamily (Xie *et al.* 2015) and Fabaceae family (McAdam *et al.* 2017). Isoflavones are a group of metabolites that are significant signaling molecules in arbuscular mycorrhiza interactions (Pang *et al.* 2021). Flavonoids are a group of metabolites secreted by legume plant roots during nitrogen deficiency that serve as nodulation gene (Nod) inducers and chemo attractants for symbiotic *Rhizobia*, benefitting both plants and microbes (Zgadzaj *et al.* 2016). The concentration and diversity of flavonoids leverage symbiosis specificity and fine-tune the molecular signals in root exudates to recruit microbes (Mishra *et al.* 2022). In addition to facilitating nodulation, other plant families also produce flavonoids (Dent and Cocking 2017).

Many reports have explained the role of aromatic amino acids in pathogen defense, but the role of aromatic amino acids in the recruitment of beneficial microbes is unclear (Jacoby *et al.* 2020; 2021). Camalexin, a sulfur-containing indolic phytoalexin, is specific to *Brassicaceae*, and its precursor is tryptophan (Trp). Indeed, camalexin synthesis is essential for the recruitment of beneficial microbes from the rhizosphere and conditionally limits the growth of pathogenic fungi (Koprivova *et al.* 2019). Research has focused on the role of camalexin in pathogen defense and its crucial role in response to the necrotrophic pathogens *Botrytis cinerea*, *Alternaria brassicicola* and *Phytophthora brassicae* (Nguyen *et al.* 2022). Glucosinolates, another group of sulfur-containing metabolites originating from the precursor tryptophan, constitute a well-studied class of defense compounds and are a hallmark feature of the *Brassicaceae* family. These compounds profoundly contribute to the antifungal and antibacterial machinery and are prerequisites for the recruitment of the root microbiome (Monchgesang *et al.* 2016). Coumarins, a phenolic group of compounds, are ubiquitous in diverse plant species and in the rhizosphere and play intricate roles in the recruitment of microbiomes (Stringlis *et al.* 2018) and disease resistance (Stringlis *et al.* 2019). Coumarins are produced in iron-deficient soil around roots (Tsai and Schmidt 2017), and the coumarins produced are scopoletin, esculin, scopolin, esculetin, fraxetin, and sideretin from the precursor phenylalanine through the phenyl propanoid pathway (Tsai *et al.* 2018; Rajniak *et al.* 2018).

Benzoxazinoids, a class of defensive secondary metabolites and heteroaromatic compounds, are released by roots of the *Poaceae* family, such as wheat, maize, and rice. These compounds are highly produced during the early stages of plant growth and decline in later stages (Kudjordjie *et al.* 2019). These compounds, which are derived from a common precursor, tryptophan, are involved in biotic interactions that shape the root microbiota (Hu *et al.* 2018). These metabolites alter root-associated fungal and bacterial communities that suppress pathogen attack by acting as toxins and chemo attractants for beneficial microbiota (Cotton *et al.* 2019). Terpenoids constitute the major group of specialized metabolites, and triterpenes constitute a diverse structured subgroup of terpenoids orchestrated by the mevalonate pathway involved in plant defense, signaling and antimicrobial activities (Jacoby *et al.* 2020). Terpenoids are garnered in plant tissues as triterpene glucosides (Pascale *et al.* 2020). Huang *et al.* (2019) reported that a range of specialized triterpene-tailored compounds maintain *Arabidopsis*-specific root microbiota, particularly bacteria. These findings suggest that plants adjust their root exudation profiles to promote the proliferation of microorganisms that facilitate nutrient acquisition or participate in plant-microbe signaling (Table 1). The metabolic diversity within the plant kingdom facilitates the sculpting of microbiota tailored to the needs of the host. Digging more into metabolite–plant interactions will open the next frontier to engineer plants that colonize more beneficial microbes and subsequently suppress pathogen attack.

The nexus between plant receptor-like kinases and the microbiome

During growth, development and reproduction, plants are vulnerable to diverse environmental cues that subsequently trigger stress responses. Plants use a variety of signal transduction pathways to regulate growth and stress simultaneously in response to the changing environment, ensuring maximum fitness (Zhu *et al.* 2023). Cell-to-cell communication is pivotal for a eukaryotic organism to respond to and protect itself from a changing environment. In this context, the role of the eukaryotic protein kinase (EPK) superfamily, which consists of approximately 250 amino acids, has been extensively unearthed, expediting intracellular signal transduction and cell-to-cell communication (Liu *et al.* 2024). Receptor-like kinases (RLKs) are the predominant surface receptor group from plants in the eukaryotic protein kinase superfamily (Fig. 4). Another group of EPKs that act as cell surface receptors is receptor-like proteins (RLPs) (Couto and Zipfel 2016). RLKs have been reported in almost all plants to date (Zhu *et al.* 2023). The RLKs are divided into different subgroups: LRR receptor-like kinases (LRR RLKs), S-domain RLKs, pathogenesis-related protein-5-like receptor kinases (PR5Ks), lectin receptor-like kinases (Lec-RLKs), lysin motif-type receptor-like kinases (LysM-RLKs), wall-associated receptor-like kinases (WAK-RLKs), epidermal growth factor-like kinases (EGF-RLKs), tumor necrosis factor receptor-like protein kinases (TNRF-RLKs), proline-rich extension-like receptor kinases (PERK-RLKs), pathogenesis-related protein-5-like receptor kinases (PR5K-RLKs), cysteine-rich receptor-like kinases (CRKs), Catharanthus roseus receptor-like kinase 1-like kinases (CrRLK1Ls), leaf rust kinase-like kinases (LRKs), receptor-like kinases in flowers (RKFs), and kinases with unknown functions (Jose *et al.* 2020; Liu *et al.* 2024). Cellular signaling is critically dependent on the abundance and location of RLKs on the cell

Table 1. Plant secondary metabolites and microbiome interactions aids in plant growth promotion

S. No.	Secondary metabolites	Crop	Microbes associated	Mechanism of interaction	References
1	Strigolactones	paddy	rhizopshere microbiome	increased concentration strongly correlated with abundance of soil micro organisms	Kim *et al.* (2022)
2	Flavonoids	*Medicago trunculata*	arbuscular mycorrhiza	symbiotic signalling	Maillet *et al.* (2011)
		chinese tallow (*Triadica sebifera)*	arbuscular mycorrhiza	higher concentration of quercitin in soil increases arbuscular mycorrhiza association	Tian *et al.* (2021)
3	Flavones	maize	*Oxalobacteraceae*	improves plant performance under nitrogen deprivation	Yu *et al.* (2021)
3	Camalexin	arabidopsis	*Pseudomonas* sp. CH267	different associations with plant growth promoting microbiome	Koprivova *et al.* (2019)
4	Glucosinolates	*Brassica rapa*	root microbial communities	feed back cycle in plant microbe interactions	DeWolf *et al.* (2023)
5	Coumarins	arabidopsis	*Burkholderiaceae, Rhizobiaceae, Streptomycetaceae*	coumarin induced microbial activity and iron mobilization to plants	Harbort *et al.* (2020)
6	Benzoxazinoids	maize	*Flavobacteriaceae* and *Comamonadaceae*	secretion of Benzoxazinoids have selective impact on microbiome assembly	Cadot *et al.* (2021)
7	Terpenoids	arabidopsis	bacteria	thalianin, thalianyl fatty acid sters, arabidin biosynthesis mediates association with specific microbiota	Huang *et al.* (2019)

surface. These RLKs are membrane proteins with an extracellular receptor domain in the plasma membrane that acts as the deciding factor for the plant to encourage the accommodation of beneficial microbes or block the infection of intruding pathogens (Yan *et al.* 2023). These RLKs act as inducers of symbiosis or defense mechanisms in plants and interacting microbes. Chitin elicitor receptor kinase (CERK1), a pattern recognition receptor, is a key receptor for symbiosis and immunity (Yang *et al.* 2022). CERK 1 differentiates between chitin, b-glucans, peptidoglycans, and lipopolysaccharides fromfungi and bacteria to initiate signaling. Upon the perception of effectors from interacting partners, ligand binding commences receptor complex formation, which ultimately initiates signaling events that scrutinize beneficial microbes and lurking pathogens (Antolín-Llovera *et al.* 2014). Plant defense is triggered by the recognition of a variety of pathogen- or microbe-associated molecular patterns or PAMPs, such as bacterial flagellin or fungal chitin hepta- and octamers. Conversely, symbiotic signaling is activated by the perception of (lipo)-chitooligosaccharides with N-acetylglucosamine (GlcNAc) residues produced by symbiotic rhizobia and arbuscular mycorrhizal (AM) fungi. Lysin motif receptor-like kinases (LysM-RLKs) and LysM proteins recognize N-acetylglucosamine (GlcNAc)-containing ligands that trigger symbiosis or defense signaling (Desaki *et al.* 2018). Notably, leucine-rich repeats (LRRs), malectin-like domains (MLDs), and RLK symbiosis receptor-like kinases (SYMRKs) are also involved in symbiotic signaling. Malectin is a protein located in the endoplasmic reticulum (ER) that binds exclusively to carbohydrates (Yang *et al.* 2022).

RLKs act as sentinels in plant defense responses, mediating both broad-spectrum, elicitor-initiated defense and pathogen-specific resistance. The ubiquitin/proteasome system regulates RLKs, emerging as a central theme in their function. RLKs do not function in isolation; they engage in intricate cross-talk during both symbiotic and pathogenic interactions (Antolín-Llovera *et al.* 2014). This cross-talk allows plants to fine-tune their responses on the basis of the specific microbes they encounter (Sun *et al.* 2020). Lysin motif RLKs recognize GlcNAc-containing signaling molecules such as chitin, Nod factors, and likely Myc factors, enabling plants to distinguish between pathogens and symbionts despite their ligand similarity. The ectodomain differentiates between chitooligosaccharides and lipochitooligosaccharides, whereas the kinase domain determines downstream signaling outcomes (Wang *et al.* 2014). Chimeric receptor studies highlight the role of kinase domain motifs in nodulation competence, with OsCERK1 demonstrating bifunctionality in both defense and symbiosis signaling (Miyata *et al.* 2014). Notably, AM symbiosis in rice depends on OsCERK1 but not OsCEBiP, suggesting that coreceptors are key to differentiating between immune and symbiotic responses (Kouzai *et al.* 2014). However, the specific interaction partners directing these pathways remain to be identified. These pieces of evidence summarize the role of receptor-like kinases and how plants have potentially evolved mechanisms to use the same receptor in symbiotic and immune signaling. Although several plant receptors have been identified to date, further research is expected to reveal the different ways in which membrane receptor domains interact and how plants integrate these signals for downstream signaling cascades. More research into the biological role and molecular mechanism of RLK is needed to develop novel crop varieties with robust resilience and high yield.

Communication highways of the leaf microbiota

Plant leaves, *i.e.*, the phyllosphere region, are colonized by microbes, including pathogenic and beneficial microbiomes. These distinct microbiota interactions in leaves may involve interspecies, intraspecies or cross-kingdom assembly of microbes (Hardoim *et al.* 2015). The phyllosphere is considered to be the most abundant niche of microbes on Earth. In sharp contrast, increasing evidence has shed light on the mechanism of rhizosphere‑microbe interactions, but the characteristics and ecological functions of phyllosphere‑microbiome interactions remain elusive (Xu *et al.* 2022). Diverse microorganisms have coevolved with plants and inhabit the phyllosphere region, which are classified into epiphytes that inhabit the surface of the leaves and endophytes that are present in the interior of the leaves. These species are referred to as keystone microbial taxa that are predominant in a particular plant and are transferred through inheritance. The primary sources of phyllosphere microorganisms are seeds, soil, air, insects, and herbivores (Grady *et al.* 2019). Host genotypes, metabolites, environmental factors, and anthropogenic changes significantly affect the microorganisms harbored in the phyllosphere (De Mandal and Jeon 2023). The phenotype of a plant is characterized by genotypes that sequentially affect the assemblage of microbiota in the phyllosphere (Li *et al.* 2018). Plant primary and secondary metabolites and phytohormones also play vital roles in the recruitment of the phyllosphere microbiome (Gupta *et al.* 2022; Zhang *et al.* 2023). The environmental factors, including temperature fluctuations, water, light intensity, CO_2, moisture, relative humidity, and spatial variations, are associated with residing phyllosphere microorganisms (Xu *et al.* 2022).

Among phyllosphere microorganisms, bacteria are present profusely, representing approximately 10^6–10^8 cell cm^{-2} of leaf tissues, among which Proteobacteria are more dominant (Kembel *et al.* 2014). The population of microbes in the phyllosphere is also influenced by priority effects, where early leaf colonizers increase the likelihood of colonization and utilize nutrients that reduce the colonization of late species (Tucker and Fukami 2014). The timing of arrival during community assembly determines their supremacy (Carlström *et al.* 2019). Insect and pathogen attack reshape the abundance of microbial communities in the phyllosphere. The incursion of herbivorous insects modifies the microbial population and copiously increases the population of endophytic bacteria in *C. cordifolia* (Humphrey and Whiteman 2020). The secondary metabolites secreted by phyllosphere microorganisms act as deciding factors for promoting and inhibiting the growth of certain microorganisms. These microbes also modify plant volatile organic compound (VOC) emission and alter host gene expression to induce pathogen defense. In the phyllosphere, both beneficial and pathogenic microbes interact with plants, triggering distinct defense mechanisms. Beneficial microbes can prime plants for increased resistance to pathogens (Chaudhry *et al.* 2020). They achieve this through various mechanisms, including microbe–microbe interactions, modulation of host metabolism, and activation of plant immunity. For example, some phyllosphere bacteria can colonize the phloem of citrus leaves and reduce pathogen density, suppressing diseases such as Huanglongbing (Wang and Cernava 2023).

The apoplastic spaces inside leaves act as key determinants for the profitable colonization of beneficial and harmful microbes, as they contain water and play a crucial role in the gas exchange and photosynthesis of plants (Chen *et al.* 2020). The host microbial community constantly competes for nutrients present in the apoplast space and for survival. The order of arrival of microbes and initial colonization of the leaf surface by either beneficial or harmful microbes is imperative for host disease resistance and susceptibility (Chaudhry *et al.* 2021). Environmental factors and circadian rhythms control stomatal opening and closing (Wu and Liu 2022). The concept that stomatal defense is a part of the cascade of events occurring during plant resistance or susceptibility came to the limelight in the study conducted by Melotto *et al.* (2006) using the Arabidopsis–Pseudomonas pathosystem. Plants have significantly evolved a mechanism to close stomata upon recognizing microbe-associated molecular patterns (MAMPs) as a part of pattern-triggered immunity (PTI) to combat intruders and alert surrounding tissues. The PAMPs in guard cells trigger ion and anion channels that ultimately lead to stomatal closure, referred to as stomatal immunity or defense (Melotto *et al.* 2017). Ahead of the game, effective pathogens hijack and open the stomata by producing phytotoxins or bacterial type III secretion system effectors to enter the substomatal layer and apoplast by manipulating them in favor of their proliferation and disease incidence in plants. During later stages of infection, *i.e.,* days after initial infection, the T3SS effectors avirulence E1 (AvrE1) and HopM1 induce abscisic acid (ABA) responses that trigger stomatal closing mechanisms to maintain hydrated apoplasts for the benefit of pathogen multiplication where stomatal defense fails (Wang *et al.* 2022). Stomatal immunity is also suppressed by T3SS effectors generated by *P. syringae*, such as avirulence B (AvrB), Hrp outer protein F2 (HopF2), Hrp outer protein X1 (HopX1), Hrp outer protein M1 (HopM1), and Hrp outer protein Z1 (HopZ1) (Melotto *et al.* 2017). To encourage water loss and promote nutrient and water starvation in pathogens, resistant plants often open their stomata through defense signals, limiting the ability of the pathogen to multiply. This entire mechanism of opening and closing of stomata upon various cues from pathogens and downstream signaling is termed a close-open-close-open (COCO) pattern (Wu and Liu 2022). Harnessing the potential of phyllosphere microbiome interactions also paves the way for the management of foliar pathogens. Elucidating the proximal mechanisms underlying the interaction of beneficial microbes and intruding pathogens in the phyllosphere, the adaptation of microbes, and their interaction with plant hosts as well as highlighting the significant knowledge gap will profoundly increase our understanding of the role of phyllosphere microbes in plant host defense strategies.

From seed to seed: The impact of microbial inheritance

Research on the coevolutionary dynamics of the host and microbiome and its potential in host evolution is still scarce. As a link between one generation and the next, seeds play a unique role in facilitating the transmission of endophytes from one generation to the next. Seeds acquire diverse microbial communities through subsequent generations present on the surfaces of epiphytes or within their tissues as endophytes (Nelson 2018). Seeds are primarily populated with fungal and bacterial endophytes that are beneficial to plants and are involved in various physiological processes (Bergna *et al.* 2018). A distinct set of microbial communities inhabit various seed tissues, including the seed coat, embryo, endosperm, and perisperm (Shade *et al.* 2017). Although the microbiome profoundly influences its host, every host harbors a distinct set of microbiomes, which vary considerably across plant lineages. Despite its crucial role and presence, the seed microbiome has largely gone unnoticed for a decade (Kong *et al.* 2019). Information on the subsequent migration or inheritance of the seed microbiome from one generation to another remains unexplored.

Microbial inheritance is a process that encompasses vertical transmission from parent to seed and consecutive migration of the seed microbiome to the seedlings, and it excludes horizontal acquisition. Vertical transmission is the direct transfer of endophytes from parents to their offspring, specifically from plants to their seeds. This process allows the endophytes to migrate and establish themselves within the developing seedlings, ensuring their presence in the next generation of plants (Shahzad *et al.* 2018). Domestication and breeding are known to have specific impacts on the seed microbiome, which also depends on the plant lineage. The diversity of the microbial community has been reduced due to domestication in the case of wheat, but rice and other cereals are known to harbor more microbiomes than their wild relatives (Abdullaeva *et al.* 2021). The seeds of plants harbor significantly 100-fold fewer microbial communities than other plant parts do, which remains a significant obstacle in the transmission of the plant microbiome from one generation to the next (Abdelfattah *et al.* 2023).

Understanding the microbiome transmission mechanism from parents to offspring may provide more information on inheritance. This transmission can be differentiated into three ways: (a) plant to seed, (b) seed dormancy, and (c) seed to seedling (Abdelfattah *et al.* 2023). Inheritance and acquisition are the two ways in which the microbiome is transmitted from plant to seed, as depicted in Figure 5. From plant to seed, the microbiome may travel through sexual (male and female gametophytes that colonize the embryo and endosperm) or asexual (vascular system and intercellular cavities to the developing seed) routes. Seed dormancy may be either natural or induced. There is no definite evidence about the relationship between seed dormancy and the existence of a microbiome on the seed. Studies have reported that storage duration or seed dormancy reduces the microbiome composition and shifts specific microbial taxa. Bacteria are believed to have developed strategies to enter a dynamic, non-proliferative state during extended periods of starvation. Another strategy that the seed microbiome uses to survive during a dormant state is the 'feast and famine strategy' (Navarro Llorens *et al.* 2010). To

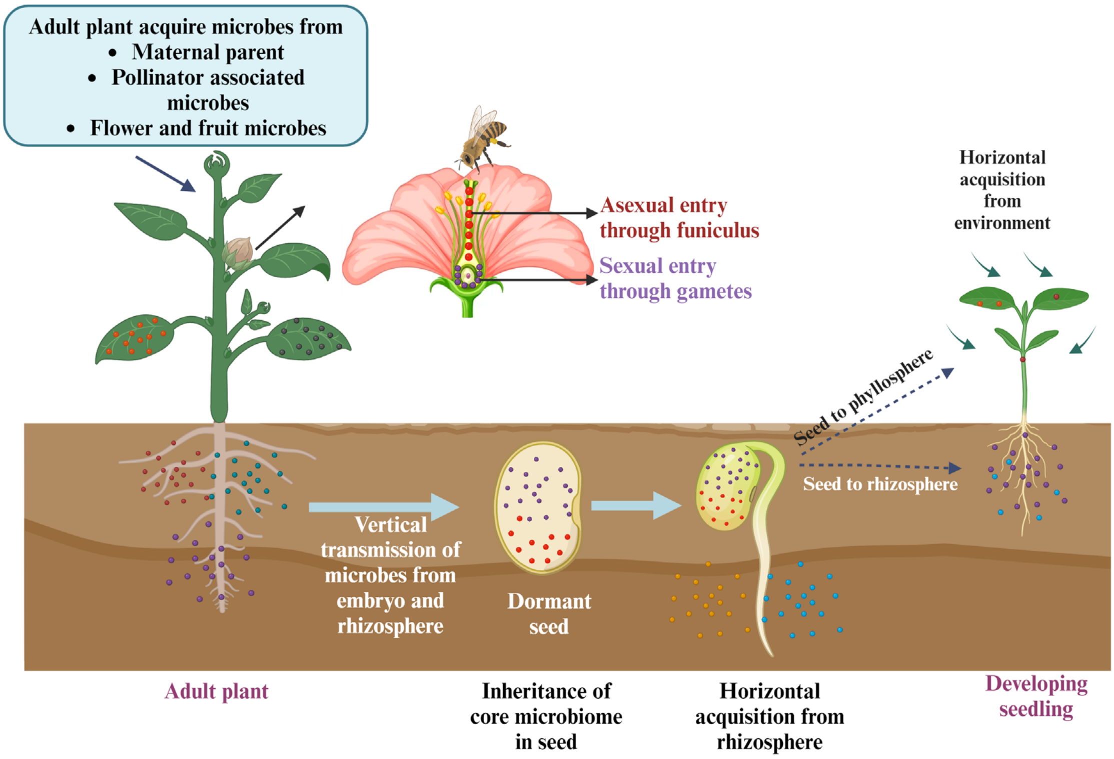

Fig. 5. Schematic representation of inheritance of microbiome in plants between generations
The microorganisms are vertically and horizontally transmitted during different stages of the plants.The core microbiome transfers from adult plant to seed via sexual or asexual pathways. Red dots on the leaves represents the core microbiome present in the phyllosphere and purple dots present on the roots represent the core microbiome of the rhizosphere. The microbiome is vertically transmitted to the seed where it survives until germination through famine and feast strategy. An abundance of exudates is released from the developing seedlings that act as a zone of intense microbial activity known as the spermosphere. During seedling germination, the respective microbiome is transferred to the rhizosphere and phyllosphere. The microbiome is also horizontally acquired from the surrounding environment

transfer specialized microbiomes from seeds to plants, they follow a distinct migration route to be transferred to their respective tissues. Seeds harbor greater microbial diversity than do seedlings because of the dynamic interaction of seeds with neighboring soil. Not all the microbes are inherited by the seedlings. Transient microorganisms are those inherited by parents and present in the seed but not passed to the seedlings. The growing seedlings contain persistent seed endophytes. In this phase, the horizontal acquisition of microbial entities also occurs when the seed comes into contact with the soil via a process termed synchronization (Shade *et al.* 2017). The persistence of at least a subset of the seed-borne community is crucial to ensure the persistence of the microbiota for future generations (Abdelfattah *et al.* 2023). External factors such as the host genotype and environment also affect microbe inheritance. The microbial communities recruited and accumulated by plants act as bio shields by triggering plant innate immunity against biotic and abiotic stress through plant–soil feedback and soil memory, termed microbiota-induced soil inheritance (MISI) (Kong *et al.* 2019). Microbial inheritance has potential roles in enhancing plant immunity by priming defense responses, selecting microbiome structure, defense modulation and stress response. Research on microbial inheritance is still in a contradictory phase. Delving further into the understanding of the core microbiome of each plant species will leverage plant immunity at its own cost without disturbing plant microbiota homeostasis.

Equal pay for equal work – Biological trade and market

Plants and microbes are indispensable partners. The interactions between plants and microbial communities are similar to those in the economic market; they are complex ecosystems where microorganisms trade resources similarly to those in human markets. Microbes generally interact with roots for essential metabolites, including sugars, fatty acids, essential amino acids, and cofactors. Microorganisms and plants exchange their resources with cooperation, or competition, resembling the human market, where the trade of goods and services seeks market share (Bragazzi *et al.* 2024). Microbial communities are considered biological markets, and microbes are economic agents. However, trade does not occur for mutual benefits alone; it may be competitive, which paves the way for the evolution of specialization (Hammerstein and Noe 2016). If a different partner provides a better deal, organisms have the ability to reject a certain trade, which is similar to the human market. The biological market is a new perspective that defines plant-microbe interactions from a different perspective related to economics. The study of market patterns among non-associated organisms started in the early 1990s. The term biological market theory (BTM) was formulated by Noë and Hammerstein (1994). The biological market paradigm has been studied extensively in the context of mutualistic interactions. The characteristics of the biological market include commodity swapping, distinct classes of traders, choosing and switching partners, price variations, and supply and demand variations (Werner *et al.* 2014). Despite mutually beneficial exchanges, there is still a need for each partner to negotiate to obtain more benefits at a lower cost. Insights into these biological markets imply that the individuals involved in the interactions will undergo outbidding competitions similar to price wars in human economies. There is less convincing information regarding how microbes discriminate between partners in interactions, and how the demand and supply between trading partners are met remains untapped. Werner *et al.* (2014), in their article ‘Evolution of biological markets’, have deliberated six salient strategies followed by microbes to thrive in biological markets, which include avoiding bad trading partners, building local business ties, diversifying or specializing, becoming indispensable, saving for a rainy day and eliminating competition. Microbes evolve in every trade and may use multiple strategic plans to gain monopolistic control when market choices become limited. A microbe must discriminate between various trading partners on the basis of the actual benefit of an interaction.

Table 2 is gleaned and modified from the information obtained from exploring the parallels of the human gut microbiome and economic markets from the paper “Economic microbiology: exploring microbes as agents in economic systems” written by Bragazzi *et al.* (2024). The concept of biological trade is explained by arbuscular mycorrhizal fungi and plant interactions (Ullah *et al.* 2024). Plants share nutrients through common mycorrhizal networks (CMNs) facilitated by arbuscular mycorrhizal fungi (AMF), which can benefit the entire network.AMF can differentiate between host plants and reassign nutrients according to the plant’s carbon gain. Interactions can be “socialist,” with resources distributed evenly, or “capitalist,” where resources are controlled for the benefit of certain plants, increasing competition. Insights into social microbiology and biological markets have increased our understanding of complex host-microbe interactions from a new perspective. By using biological market theory, researchers can make predictions about microbial interactions, including the evolution of partner discrimination and the roles of spatial structures. This approach can be applied to sustainable agriculture by harnessing plant-associated microbiomes.

Table 2. Exploring the similarities of economic microbiology and human market dynamics in plant-microbe interactions

Hypotheses in Economic Microbiology	Concepts in Economic Markets	Applications in plant-microbe interactions and human trade
Exchange of resources	systems of barter and trade	nutrient cycle in microbes, metabolic exchanges, market exchange of products
Resource competition	competition in market	competition for resources underground and survival of the fittest, commercial tactics in markets with intense competition
Reciprocal benefits between partners	partnerships in business	symbiotic relationships of microbes in legume – N_2 interactions, plants – arbuscular mycorrhizal interactions, beneficial microbes – plant interactions for defence activation, joint ventures in business
Flexibility in response to shifting environment	market evolution and adaptation	microbes adjusting to shifting environment based on natural selection, businesses evolving in response to market changes.
Communication between microbiota (Quorum Sensing)	market communication, signalling and response	bacteria communicating with one another to make collective decisions and response strategies, market cues affecting the choices made by investors.
Depletion of resources and Sustainability	economics of resource management	resource overuse resulting in the loss of microbial habitat, economic principles of sustainable resource use.

Conclusion and perspectives

The mechanisms by which plants recruit beneficial microbes while simultaneously restricting pathogens were among the top 10 unanswered questions at the 18th International Society for Molecular Plant–Microbe Interactions Congress in 2019. In the wild, a single plant faces countless decisions throughout its life regarding whether to engage with or defend against various environmental challenges. Despite the critical role played by plants in their ecosystems, the complex mechanisms by which plants integrate both external and internal signals to identify microbes remain unknown. This “master program” enables plants to restrict microbial growth or create a hospitable environment for beneficial microorganisms. This article describes the different molecules engaged in recruiting and scrutinizing microbes that interact with plants. In spite of this, we have only scratched the tip of the iceberg in perceiving how plants assimilate and activate signals for further responses. The formidable potential of plant small molecules must be investigated concurrently with that of microbe small molecules, which could enhance our understanding of the mechanism used by plants to discern friend and foe microbes.

Using multiomics approaches will provide a comprehensive understanding of different small plant molecules that interact specifically with different plant families. With this information, future research can harness the potential of small plant molecules and manipulate their signaling pathways to develop holistic and innovative strategies to maintain plant microbiota homeostasis, increase plant resilience, foster beneficial microbe interactions, and prevent pathogen attacks. Understanding these complex interactions is crucial for advancing agricultural practices, as it can provide insights into strategies to increase crop resilience and productivity by manipulating these signaling pathways.

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