

MICROBIOME MEDIATED SIGNAL TRANSDUCTION IN PLANTS: A SYSTEMATIC REVIEW

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ABSTRACT:

The intricate relationships between plants and their associated microorganisms, collectively known as the Phyto microbiome, have garnered significant attention in recent years due to their profound impact on plant health, growth, and productivity. Plants, as holobionts, engage in intricate interactions with a diverse array of microorganisms, collectively known as the Phyto microbiome, which significantly influences plant health and productivity. The exchange of molecular signals between plants and microbes is crucial for establishing and maintaining these relationships. This systematic review delves into the multifaceted mechanisms of microbiome-mediated signal transduction in plants, exploring the diverse signaling molecules involved, the signal perception and transduction pathways activated, and the resulting physiological and ecological consequences for the host plant.

KEYWORDS: Microbiome, Signalling pathways, Plants, Physiology, Development

INTRODUCTION

The plant microbiome, a complex community of bacteria, fungi, archaea, viruses, and protists inhabiting the plant's surfaces and internal tissues, plays a pivotal role in plant growth, development, and stress resilience (Basu et al., 2018). Plants, as holobionts, have evolved intricate communication networks with their associated microorganisms, employing a diverse array of molecular signals to mediate these interactions (Smith et al., 2015). These interactions transcend superficial associations, exerting profound effects on plant physiology, development, and overall health (Meena et al., 2017). The plant microbiome plays a pivotal role in mediating signal transduction pathways, enabling plants to perceive and respond to a myriad of environmental cues, including nutrient availability, abiotic stresses, and pathogen attacks (Meena et al., 2017). Understanding the intricacies of these signaling networks is crucial for harnessing the potential of the microbiome to enhance plant productivity and resilience. The exchange of molecular signals between plants and their associated microbes orchestrates a complex interplay, finely tuning plant responses to environmental fluctuations and threats (Basu et al., 2018). Plants communicate with microorganisms through root-exuded metabolites, influencing microbial community structure and function (Jacoby et al., 2017). Microorganisms, in turn, directly affect plants by manipulating hormone signaling and providing protection against pathogens (Jacoby et al., 2017). The rhizosphere, the soil region directly influenced by plant roots, represents a dynamic interface where intricate signaling exchanges occur between plants and a myriad of microorganisms. This signaling is mediated by a diverse array of microbial molecules, including lipopolysaccharides, peptidoglycans, exopolysaccharides, and volatile organic compounds, which are perceived by specialized plant receptors, initiating downstream signaling cascades (Jacoby et al., 2017). Plants, as sessile organisms, have evolved sophisticated mechanisms to perceive and respond to a wide range of environmental signals. Microbial signals can activate plant defense responses, promote systemic resistance, and modulate plant growth and development (Meena et al., 2017). Studies have shown that microbial interactions are integral to the living ecosystem and modulate local and systemic mechanisms in plants, offering defense under adverse external conditions (Meena et al., 2017). The vast majority of plant-associated microorganisms remain poorly understood, highlighting the need for further research to decipher the plant microbiome and identify microbes that can improve plant growth and health (Khan et al., 2019). The composition of the root microbiome is influenced by root exudates, demonstrating the plant's capacity to actively recruit beneficial microbes (Pascale et al., 2020).

Microbiome-mediated signal transduction pathways in plants encompass a wide range of molecular mechanisms, including hormone signaling, nutrient signaling, and defense signaling. Humic substances present in the rhizosphere, can behave as signaling molecules, potentially releasing phytohormones or stimulating their production at the plant and/or soil biota level (Canellas et al., 2015). Phytohormones, such as auxins, cytokinins, gibberellins, abscisic acid, and ethylene, play crucial roles in regulating plant growth, development, and stress responses. Microbes can modulate plant hormone levels by synthesizing, degrading, or modifying plant hormones, influencing plant physiology. Silicon, for instance, has been shown to affect endogenous

phytohormone levels, particularly under stress conditions, influencing plant defense responses (Snehal & Lohani, 2018). This intricate interplay between plants and microbes underscores the importance of considering the microbiome as an integral component of plant signaling networks. In response to biotic stresses, plants have evolved sophisticated immune responses to protect themselves from pathogens and pests (Pascale et al., 2020). Systemic acquired resistance is a defense mechanism activated upon pathogen attack, providing long-lasting protection against a broad spectrum of pathogens (Subramanian et al., 2023). Beneficial microbes can trigger induced systemic resistance, enhancing plant immunity. Silicon, for example, can increase the transcript levels of various defense-related genes, contributing to plant resistance against pathogens (Snehal & Lohani, 2018). Understanding the molecular mechanisms underlying microbiome-mediated defense signaling is essential for developing sustainable strategies to enhance plant disease resistance.

The Rhizosphere: A Signaling Hub

The rhizosphere, the soil region directly influenced by plant roots, represents a dynamic interface where intricate signaling exchanges occur between plants and a myriad of microorganisms. This signaling is mediated by a diverse array of microbial molecules, including lipopolysaccharides, peptidoglycans, exopolysaccharides, and volatile organic compounds, which are perceived by specialized plant receptors, initiating downstream signaling cascades. Plants, as sessile organisms, have evolved sophisticated mechanisms to perceive and respond to a wide range of environmental signals. Microbial signals can activate plant defense responses, promote systemic resistance, and modulate plant growth and development. Studies have shown that microbial interactions are integral to the living ecosystem and modulate local and systemic mechanisms in plants, offering defense under adverse external conditions (Meena et al., 2017). The vast majority of plant-associated microorganisms remain poorly understood, highlighting the need for further research to decipher the plant microbiome and identify microbes that can improve plant growth and health. The composition of the root microbiome is influenced by root exudates, demonstrating the plant's capacity to actively recruit beneficial microbes.

Rhizosphere engineering is an emerging strategy to enhance plant productivity and resilience through the targeted manipulation of the root microbiome. Root exudates orchestrate the complex interactions taking place in the rhizosphere and are regarded as the driving force for rhizoremediation (Eze & Amuji, 2024).

Table 1. Enhancement of Rhizosphere Health Through Phyto-Microbiome Engineering

Plant microbiome	Host	Signalling genes	Effect	References
Oryza sativa, zea mays	Bacillus amyloliquefaciens	SN13, SQR9	Tolerance to salt	Nautiyal et al., 2013
Citrus sweet orange	Tobacco	FLS2 receptors	Cancer resistance	Hao et al., 2016
Tobacco	Bacillus subtilis	Volatile organic compounds related gene	Growth induction and promotion	Kim et al., 2015
Carica papaya	Carica papaya	Papaya ring spot coat protein gene	Anti-virus	Azad et al., 2014
transgenic lines	Golden kiwi tree	Pectin methyl esterase	Enhanced tolerance from fungal pathogens	Volpi et al., 2011

Mechanisms of Microbiome-Mediated Signal Transduction

Microbiome-mediated signal transduction pathways in plants encompass a wide range of molecular mechanisms, including hormone signaling, nutrient signaling, and defense signaling. Humic substances present in the rhizosphere can behave as signaling molecules, potentially releasing phytohormones or stimulating their production at the plant and/or soil biota level (Canellas et al., 2015). Phytohormones, such as auxins, cytokinins, gibberellins, abscisic acid, and ethylene, play crucial roles in regulating plant growth, development, and stress responses (Subramanian et al., 2023). Microbes can modulate plant hormone levels by synthesizing, degrading, or modifying plant hormones, influencing plant physiology. Silicon, for instance, has been shown to affect endogenous phytohormone levels, particularly under stress conditions, influencing plant defense responses (Snehal & Lohani, 2018). This intricate interplay between plants and microbes underscores the importance of considering the microbiome as an integral component of plant signaling networks.

Microbiome-Mediated Defense Signaling

In response to biotic stresses, plants have evolved sophisticated immune responses to protect themselves from pathogens and pests. Systemic acquired resistance is a defense mechanism activated upon pathogen attack, providing long-lasting protection against a broad spectrum of pathogens. Beneficial microbes can trigger induced systemic resistance, enhancing plant immunity. Silicon, for example, can increase the transcript levels of various defense-related genes, contributing to plant resistance against pathogens (Snehal & Lohani, 2018). Understanding the molecular mechanisms underlying microbiome-mediated defense signaling is essential for developing sustainable strategies to enhance plant disease resistance (Ali et al., 2023).

Microbiome-Mediated Nutrient Acquisition

In addition to their role in defense signaling, the soil microbiome also contributes to plant nutrition by facilitating nutrient uptake and assimilation (Jacoby et al., 2017). Microorganisms directly influence soil solution chemistry, promoting mineral weathering through pH changes, release of metal complexation agents, and alteration of redox potential. Plants and microorganisms obtain their nutrients from the soil and alter soil properties through organic litter deposition and metabolic activities, respectively (Jacoby et al., 2017). Mycorrhizal fungi, for example, form symbiotic associations with plant roots, enhancing phosphorus and nitrogen uptake (Enagbonma et al., 2023). Nano-sized formulations, such as those containing silicon, can substantially enhance the availability of otherwise sparingly soluble mineral micronutrients, due to their increased solubility and improved dispersion within the soil matrix, thereby minimizing soil fixation and adsorption phenomena (Snehal & Lohani, 2018).

Genes Signaling in microbiome plant interactions

Understanding the genes involved in microbiome-plant interactions is crucial for deciphering the molecular mechanisms underlying these complex relationships. Further research in this area will pave the way for developing targeted strategies to manipulate the microbiome for improved plant health and productivity. By unravelling the complexities of these signaling pathways, we can harness the potential of the microbiome to enhance plant resilience, productivity, and sustainability in agriculture.

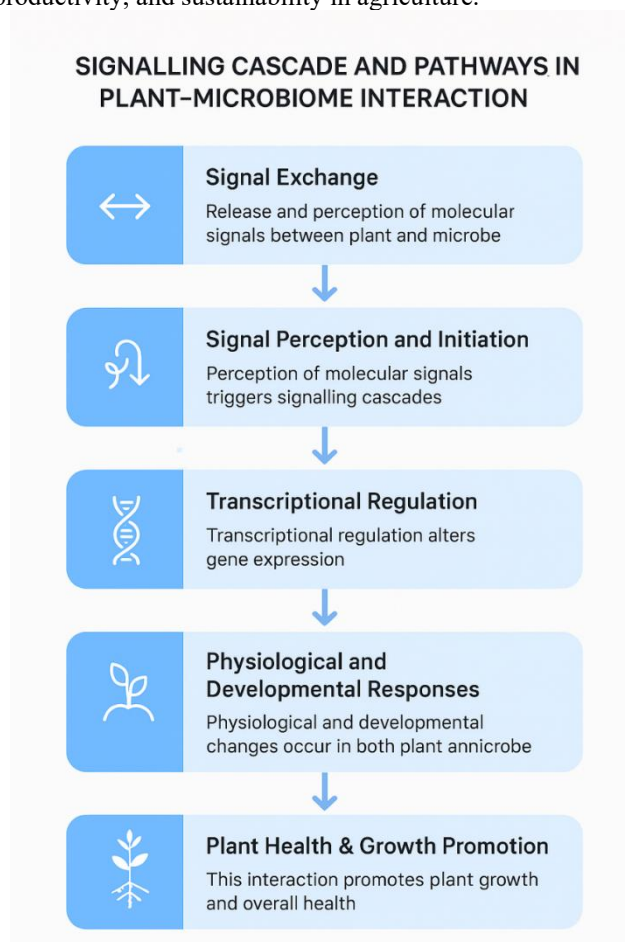


Figure 1 Signalling pathways in plant microbiome interactions

The interactions of plants with their environment are often modulated by soil microorganisms (Jacoby et al., 2017). The plant microbiome can influence plant growth and health by enhancing nutrient acquisition, producing plant hormones, or protecting against diseases (Pascale et al., 2020) (Jacoby et al., 2017) (Meena et

al., 2017). By understanding the molecular mechanisms underlying these interactions, we can develop strategies to harness the power of the microbiome to improve crop production and reduce our reliance on synthetic fertilizers and pesticides. Plants recognize pathogens via pattern recognition receptors that detect pathogen-associated molecular patterns. This recognition triggers downstream signaling cascades involving phytohormones like salicylic acid and jasmonic acid (Koley et al., 2022). For instance, the leucine-rich repeat receptor-like protein kinase FLS2 recognizes flagellin (2023; Gómez-Gómez & Boller, 2000). The plant-microbe partnership is projected to be understood at an ecological level by the year 2020 (Mitter et al., 2016). This can be achieved by manipulating the microbiome of crops in order to realize sustainable agriculture (Jacoby et al., 2017).

Biofertilizers have the potential to improve plant growth through various mechanisms, including nitrogen fixation, siderophore production, mineral solubilization, and phytohormone synthesis (Janmohammadi et al., 2016). Chemical fertilizers can have negative impacts such as leaching, water pollution, harm to microorganisms and insects, increased disease susceptibility, and reduced soil fertility; biofertilizer application can help mitigate these issues (Janmohammadi et al., 2016). By harnessing the power of beneficial microbes, biofertilizers can promote sustainable agriculture and reduce our reliance on synthetic inputs (Janmohammadi et al., 2016). Understanding plant-microbe interactions and community assembly is crucial for understanding the plant as a meta-organism and how plants benefit from their microbial partners (Compant et al., 2019).

The signaling networks in plant-pathogen interactions are regulated by WRKY proteins (Aamir et al., 2019). For example, in barley, HvWRKY1 and HvWRKY2 are activated by FLG22 and act as negative regulators of PTI against powdery mildew (Aamir et al., 2019). Humic substances in the rhizosphere may act as signaling molecules, potentially releasing phytohormones or eliciting their production (Canellas et al., 2015). They can influence nitric oxide regulation and root hair growth, with protein kinases acting as targets of NO signaling and Ca^{2+} fluxes (Canellas et al., 2015). HS can also modulate plasma membrane H^{+} -ATPase activity, controlling H^{+} efflux and triggering modifications in anion fluxes (Canellas et al., 2015). Humic acids can promote shoot growth by increasing abscisic acid root concentration and root hydraulic conductivity. This involves increased gene expression of plasma membrane aquaporins (Olaetxea et al., 2021). DREB and EAR motif protein 1 is a plant gene involved in immunity against infection and arthropods.

Key Signaling Components in Plant-Microbiome Interactions

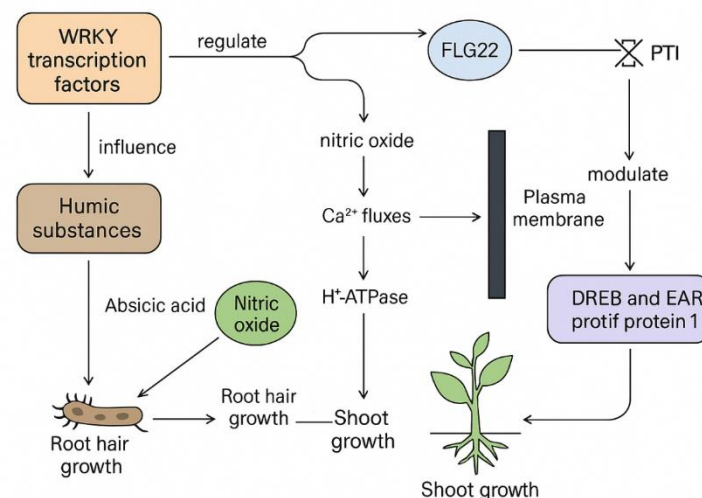


Figure 2 Important signalling genes in plant microbiome interactions. Plant pattern recognition receptors (PRRs) identify microbial signals such as FLG22, which initiate intricate signalling pathways that regulate interactions between microbiomes and plants. In barley, this activation induces WRKY proteins and other transcription factors that govern immune responses and often function as negative regulators of pattern-triggered immunity (PTI). Humic substances (HS) in the rhizosphere influence root development and immunological responses by acting as signalling modulators in the release or synthesis of phytohormones, nitric oxide (NO) signalling, calcium ion fluxes, and protein kinase activity. Besides affecting nutritional signals, HS enhance plasma membrane H^{+} -ATPase activity, hence promoting proton export and altering anion transport. Moreover, HS enhances shoot growth by elevating root concentrations of abscisic acid (ABA) and upregulating the expression of the aquaporin gene, thereby improving water transport and hydraulic conductivity in the roots.

A synergistic interplay of microbial, hormonal, and genetic signals enhances plant health and growth by activating defence genes, such as DREB and EAR motif protein 1, hence conferring resistance to diseases and arthropods.

The major knowledge gaps for understanding the mechanisms of plant-microbe interactions in the rhizosphere were explored (Jacoby et al., 2017). It is expected that by the application of nanotechnology in various fields of agriculture the second green revolution can be accelerated (Jacoby et al., 2017; Janmohammadi et al., 2016). For example, nanoparticles of TiO_2 were found to be effective in the photocatalytic degradation of agrochemicals in

contaminated waters, thus helping to remove pesticides from the water (Singh et al., 2019). This is a promising way to use nano- pesticide delivery systems to increase agriculture production and to help reduce destructive environmental impacts (Safaei et al., 2014; Singh et al., 2019).

The application of silica nanoparticles has shown to increase plant growth and development by enhancing gas exchange via stomata and chlorophyll fluorescence parameters, which are as follows: net photosynthetic rate, stomatal conductance for gas exchange, transpiration rate, potential activity of PSII.

Table 2. Signalling in Plant Microbiome

ORIGIN	SIGNAL	RECEPTOR	PLANT RESPONSE	MICROBIAL RESPONSE
Microbes	Lipopolysaccharides	Pattern Recognition Receptors like FLS2	Activation of defense responses, induced systemic resistance	Changes in gene expression, biofilm formation, altered metabolism
Microbes	Peptidoglycans	PRRs	Defense responses, ISR	Similar to LPS
Microbes	Volatile Organic Compound	Various receptors (often unknown)	Growth promotion, stress tolerance, defense priming	Altered gene expression, motility, production of other VOCs
Microbes	Phytohormones (e.g., auxins, gibberellins, cytokinins)	Hormone receptor	Altered growth and development, root architecture changes	Regulation of own hormone production, changes in metabolism
Plants	Root Exudates (sugars, amino acids, organic acids)	Microbial receptors	Recruitment of specific microbes, shaping of the rhizosphere microbiome	Chemotaxis, altered gene expression, increased nutrient uptake, biofilm formation
Plants	Strigolactones	Receptor D14	Regulation of arbuscular mycorrhizal symbiosis, shoot branching	Germination of AM fungal spores, hyphal branching
Humic	Complex mixtures; may release phytohormones	Various; Protein Kinases, PM H ⁺ -ATPase	Influences nitric oxide regulation, root hair growth, modulates plasma membrane H ⁺ -ATPase activity (Canellas et al., 2015)	Altered metabolism, nutrient uptake

Multiomics and Computer Framework Approach

Multiomics methodologies have revolutionised biological research by providing unparalleled understanding of the intricate mechanisms that regulate living systems. These approaches include genomics, transcriptomics, proteomics, and metabolomics. Subramanian et al. (2020) contend that these integrated methodologies, termed pan-omics or trans-omics, consolidate various omics datasets to enhance data processing, visualisation, and interpretation.

The integration of multiomics data offers a systematic and comprehensive understanding of complicated biology by providing insights about biomolecules across multiple layers. Although researchers, especially beginners, have access to numerous resources, understanding the data can be difficult without a theoretical framework

(Krassowski et al., 2020; Pazhamala et al., 2021). A thorough and accurate depiction of molecular system dynamics requires the amalgamation of multi-omics data; however, analysing these datasets is difficult due to technological constraints, the intricacy of biological systems, numerous biological variables, and a relatively small number of biological samples (Bersanelli et al., 2016; Krassowski et al., 2020). Despite its potential, utilising multiomics to study plants poses difficulties, such as the complexity of their metabolic networks, inadequate annotation of their extensive genomes, and the abundance of symbionts (Jamil et al., 2020).

The integration of diverse biological data has become essential due to improvements in systems biology facilitated by multiomics technology (Haas et al., 2017). Summarising the additional insights from each omics layer necessitates ways for integrating multiomics data (Picard et al., 2021). To progress crop genetics and breeding studies, robust methodology must be established. Conceptual frameworks are crucial in guiding multiomics studies as they establish the foundation for hypothesis creation, experimental design, and data analysis (Yang et al., 2021). These frameworks, grounded in established biological principles and specialised expertise, facilitate the navigation of complicated multiomics data to derive pertinent insights. To construct a specific framework, detailed assumptions must be made on the interactions among multiple molecular levels, including how changes in gene expression (transcriptomics) may affect protein quantities (proteomics) and subsequently influence metabolic patterns (metabolomics). Machine learning offers effective techniques for data integration in plant systems biology to address challenges presented by large datasets (Hesami et al., 2022).

Our knowledge of bacterial colonisation was enhanced when researchers used transcriptomic and proteomic approaches to identify the genes that actively control key metabolic pathways [183]. Using a combination of transcriptome and proteome techniques, Yang et al. [184] investigated metabolic alterations in the lignin production pathway following plant infection with the fungus *Alternaria panax*. To further pinpoint the exterior surfaces or colonising tissues of an injection-induced strain, further techniques like as confocal microscopy, structural and computational biology, and Rhizospheric or phyllo spheric habitats can be employed. Berlanga-Clavero et al. [185] used confocal and fluorescence imaging with in situ metabolomics to study the effects of inoculating melon seeds with *B. subtilis*. We found developmental, metabolic, physiological, and genetic problems.

Results showed that TasA and fengycin, extracellular matrix components, are crucial for seed growth due to their effects

on lipid metabolism and glutathione-related compounds [185].

The findings point to the possibility that growth-promoting mechanisms can be activated when bacterial cells invade and colonise tissues that store seeds. Applying state-of-the-art technical methods with theoretical models and hypothesis-driven studies is the most pressing concern in plant microbiome research. The foundation of microbiome research going forward will be multi-omics methods, which may greatly enhance the use of microbiology in agricultural studies [8]. However, this feat will not be possible without ecological and evolutionary theory. Phenomics frameworks should account for the plant microbiome in both space and time because of its impact on plant phenotypes. It is essential to take into account the consequences of interactions between different types of plants and the plant microbiome, as well as the holobiome as a whole. Hence, many branches of plant science will be crucial, including breeding, genetics, biochemistry, physiology, illness, communication, and interactions with the environment.

Future Prospects

The dynamic communication between plants and their associated microbiomes is an emerging field with immense potential to revolutionize agricultural practices and enhance plant resilience (Mitter et al., 2016). Understanding how microbes influence plant signaling pathways is essential for developing strategies to improve crop yield, disease resistance, and stress tolerance (Meena et al., 2017). Microbiome-mediated signal transduction involves a complex interplay of chemical signals, including plant hormones, volatile organic compounds, and other metabolites, that are exchanged between plants and microbes, triggering a cascade of molecular events within the plant (Wang et al., 2023). These signals can modulate plant growth, development, and defense responses, ultimately shaping the plant's overall phenotype (Jacoby et al., 2017).

One promising direction for future research is elucidating the specific microbial signals that elicit beneficial responses in plants. Identifying these keys signaling molecules will enable the development of targeted microbial inoculants and biostimulants that can enhance plant performance under various environmental conditions. The application of omics technologies, such as genomics, transcriptomics, proteomics, and metabolomics, is crucial for unravelling the complex interactions between plants and their microbiomes (Basu et al., 2018). These tools can provide a comprehensive understanding of the molecular mechanisms underlying microbiome-mediated signal transduction, leading to the identification of novel signaling pathways and regulatory networks (Jacoby et al., 2017). Researchers need to devote more attention to investigating the roles and impacts of the plant microbiome on plant health, productivity, and biogeochemical cycles, rather than solely focusing on the plant itself (Turner et al., 2013). Plant-associated microbial communities hold promise as biofertilizers and biopesticides, with growing interest in incorporating them into agricultural practices as alternatives to chemical products (Compant et al., 2019). The plant microbiome has the potential to improve agriculture, similar to the advancements made during the Green Revolution of the 1960s (Michl et al., 2023). Moreover, manipulating plant microbiomes through targeted interventions, such as introducing beneficial

microbes or modifying root exudate composition, offers great potential for enhancing plant health and productivity. Understanding how plants recruit and assemble their microbiomes is another crucial area of research (Backer et al., 2018). Plants actively shape their rhizosphere microbiome by secreting substrates that vary between plant species (Özyiğit & Doğan, 2014) (Lebeis, 2015). These substrates can selectively attract or repel specific microbes, influencing the composition and function of the plant microbiome. Identifying the plant genes and signaling pathways that control microbiome assembly will enable the development of strategies to engineer plants that selectively recruit beneficial microbes.

Nanotechnology presents innovative solutions for improving agricultural practices, particularly in enhancing plant-microbe interactions, by optimizing nutrient delivery to plants (Singh et al., 2019). Nano sensors could also be employed to monitor crop health, soil conditions, and environmental parameters, providing real-time feedback for optimizing agricultural practices (Iavicoli et al., 2017). Nanomaterials are expected to accumulate primarily in agricultural soils, either through direct release or as by-products (Cota-Ruiz et al., 2020). These materials have the potential to revolutionize various aspects of agricultural production, including agrochemical delivery, seed germination, plant growth and protection, and pathogen and pesticide residue detection (Martins et al., 2020). However, the potential risks of nanomaterials to plants, soil organisms, and human health must be carefully evaluated before widespread adoption (Iavicoli et al., 2017) (Hong et al., 2013). The development of nano-enabled fertilizers and pesticides can improve nutrient use efficiency and reduce the environmental impact of agriculture.

Future studies should focus on assessing the long-term effects of nanomaterials on soil health, plant physiology, and the composition and function of the soil microbiome (Iavicoli et al., 2017) (Hong et al., 2013).

CONCLUSION

In summary, signalling cascades in plant-microbe interactions form the molecular foundation of plant immunity, growth, and environmental adaptation. The complex processes, beginning with the identification of microbial signals and concluding with transcriptional reprogramming and hormonal regulation, allow plants to distinguish between pathogens and beneficial bacteria, therefore customising their responses accordingly. Key regulators, such as WRKY transcription factors, phytohormones, and humic chemicals, are vital in governing these interactions. Investigating the deep complexity of these signalling networks offers substantial potential for the advancement of next-generation agricultural technologies. Future efforts may include altering signalling components to promote plant resilience, employing synthetic biology to develop beneficial microbial consortia, and utilising bio-stimulants such as humic chemicals to naturally improve plant performance. The amalgamation of omics technologies (genomics, transcriptomics, metabolomics) with systems biology and machine learning may augment precision agriculture, foster sustainable crop production while minimise chemical inputs.

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Conflict of interest: The authors declare that they have no competing interests.

Ethics approval: Not Applicable. The research work and the report were made in an ethical and responsible manner.

Availability of data and Material: The datasets used and analysed during the current study are available from the authors on reasonable request. The datasets generated and used in our present study are included in this article.

Authors' contributions: JSH, MAD supervised and design conceptualisation. HDS& NGN search review literature and data acquisition and also contributes in analysing datas and manuscript preparation.

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