

## Signalling Mechanisms in Plant-Microbe Symbioses: A Comprehensive Review

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(Received: 08 March 2024; Revised: 28 March 2024; Accepted: 19 April 2024; Published: 15 May 2024)

(Published by Research Trend)

**ABSTRACT:** Plant-microbe symbioses play pivotal roles in ecosystem functioning, agricultural productivity, and plant health. Understanding the intricate signaling mechanisms governing these relationships is crucial for harnessing their benefits in sustainable agriculture and environmental management. This comprehensive review synthesizes current knowledge on signaling processes mediating mutualistic interactions between plants and microbes. We explore the diverse molecular strategies employed by both partners to recognize, communicate, and establish symbiotic relationships. Key signaling pathways, including those involving phytohormones, secondary metabolites, and microbial effectors, are discussed, highlighting their roles in symbiotic specificity and regulation. Furthermore, we elucidate the crosstalk between different signaling networks and environmental factors that shape symbiotic outcomes. By integrating insights from genetics, genomics, and ecological studies, we provide a holistic understanding of plant-microbe signaling dynamics, offering perspectives for future research directions and applications in agriculture and ecosystem management. This review serves as a valuable resource for researchers, educators, and practitioners seeking to deepen their understanding of the molecular basis of plant-microbe interactions and harness their potential for sustainable development. Additionally, molecular communication via microbial effectors and plant receptors fine-tunes symbiotic associations, ensuring mutualistic outcomes. We highlight recent advances in omics technologies, which have revolutionized our understanding of the intricate networks underlying plant-microbe signalling. Moreover, we discuss the ecological significance of symbiotic signalling, emphasizing its role in nutrient acquisition, stress tolerance, and ecosystem functioning. Insights from this review provide a foundation for engineering plant-microbe interactions for sustainable agriculture and environmental remediation, paving the way for innovative strategies to enhance crop productivity and ecosystem resilience.

**Keywords:** Plant Microbiome symbiosis, Molecular mechanism, signalling pathway.

### INTRODUCTION

Plant-microbe symbioses play pivotal roles in shaping terrestrial ecosystems, influencing plant health, nutrient cycling, and ecosystem stability. Recent studies highlight the complexity and significance of these interactions in both natural and agricultural systems. One of the most well-known plant-microbe symbioses is the mutualistic relationship between plants and mycorrhizal fungi, where fungi enhance plant nutrient uptake in exchange for carbon. Recent research has elucidated the molecular mechanisms underlying this symbiosis, revealing intricate signaling pathways and genetic exchanges. Another crucial symbiotic relationship is between leguminous plants and nitrogen-fixing bacteria, such as *Rhizobium* and *Bradyrhizobium* species, residing in root nodules. Recent advances in genomic and transcriptomic analyses have deepened our understanding of the molecular dialogues that govern nitrogen fixation and nodule development. Plants engage in symbiotic interactions with beneficial microbes, such as rhizobacteria and endophytes, to enhance defense against pathogens. Cutting-edge research demonstrates the role of plant microbiota in

priming the host immune system and inducing systemic resistance against pathogens. Microbes also contribute to phytoremediation processes by aiding in the degradation of pollutants and toxic compounds in the soil. Recent studies focus on optimizing plant-microbe partnerships for efficient detoxification of contaminated environments. Plant-microbe symbioses are increasingly recognized for their potential in enhancing plant resilience to abiotic stresses, including drought and salinity (Singh *et al.*, 2021). Novel insights into the microbial communities associated with stress-tolerant plants offer opportunities for developing sustainable agricultural practices. Plant-microbe symbioses are intricate relationships between plants and microorganisms that significantly influence plant health, development, and ecosystem functioning. These symbiotic interactions can range from mutualistic to parasitic, shaping plant physiology, nutrient acquisition, and defense responses. Mutualistic symbioses, such as mycorrhizal associations and nitrogen-fixing rhizobia, are essential for plant growth and nutrient acquisition. Mycorrhizal fungi facilitate nutrient uptake, particularly phosphorus, in exchange for plant-derived carbon.

Rhizobia bacteria colonize legume roots, forming nodules where they fix atmospheric nitrogen, benefiting both partners. Pathogenic symbioses, on the other hand, involve microbes that harm plants, causing diseases that impact agricultural productivity. Examples include fungal pathogens like *Fusarium* and bacterial pathogens like *Pseudomonas syringae*, which manipulate plant physiology to facilitate infection. Endophytic symbioses, characterized by microorganisms residing within plant tissues without causing apparent harm, contribute to plant health and stress tolerance. Endophytes can enhance plant growth, confer resistance to pathogens, and alleviate abiotic stresses such as drought and salinity (Compant *et al.*, 2010). Understanding and manipulating plant-microbe symbioses hold promise for sustainable agriculture, offering strategies to enhance crop productivity while reducing reliance on chemical inputs. Harnessing beneficial symbiotic interactions can lead to improved nutrient use efficiency, disease suppression, and stress tolerance in crops. Our understanding of the major beneficial plant-microbe interactions – the rhizobium-legume symbiosis (RLS) and arbuscular mycorrhizas (AM) – has changed over the last decade in the light of breakthrough discoveries on the role of hormones, the exchange of symbiotic signals, or the lifetime of intraradical structures (Gutjahr and Parniske 2013; Oldroyd, 2013; Schmitz and Harrison 2014). AM fungi were once believed to open their way across the root apoplast thanks to cell wall degrading enzymes: genomic sequencing (Tisserant *et al.*, 2013; Lin *et al.*, 2014) suggests this is not the case and cellular evidence (Genre *et al.*, 2005; Rich *et al.*, 2014) has shown that host cell responses are critical for fungal colonization. Similarly, rhizobium entry in root hairs has been ascribed to the action of bacterial enzymes (Gage, 2004; Robledo *et al.*, 2008); nevertheless, evidence is accumulating in favor of a plant-driven meltdown of the wall surrounding the ‘infection chamber,’ which then expands into the growing infection thread as one semi-solid compartment, where bacteria proliferate and slide (Fournier *et al.*, 2008; 2015).

The phenomenon known as quorum sensing (QS) is a biological process in which bacteria use signaling molecules to communicate. They use this chemical exchange to monitor population density and modify gene expression. An example of bacterial communication involves relationships with plants. In this system, molecules known as N-acyl-L-homoserine lactones (AHLs) influence their behavior depending on their strain. AHLs are common in pathogenic Gram-negative bacteria, e.g., *Pseudomonas aeruginosa* and *Rhizobium radiobacter*, but are also found in plant growth-promoting bacteria, as is the case for *Burkholderia graminis*. These molecules play key roles in microbes, including symbiosis, virulence, and antibiotic production. Additionally, plants can detect bacterial AHLs that affect gene expression in certain tissues. They also modulate development and trigger defensive responses (Liu Zeng *et al.*, 2022).

TFs are central mediators of gene transcription and are not only responsible for modulating the expression of various genomic sequences but also play an important

task regulating plant physiology, as their influence is notable in response to biotic and abiotic stress situations and are essential for the regulation of secondary metabolism (Chowdhary *et al.*, 2023). For example, the TF Pf2 regulates genes linked to pathogenicity in different necrotrophic pathogenic fungi. On the contrary, in *Magnaporthe oryzae*, the G-Protein signaling regulator RGS1 acts as a transcriptional regulator, suppressing the expression of several effector genes before colonizing the plant (Tang *et al.*, 2023; Yan *et al.*, 2023). The host cell faces the challenge of coordinating the secretion of proteins necessary for both defense and symbiosis. As a case in point, when a nitrogenous bacterium is present, the cell has two potential membranes at its disposal: The already existing plasma membrane and the membrane of the developing symbiosome (Liang *et al.*, 2023).

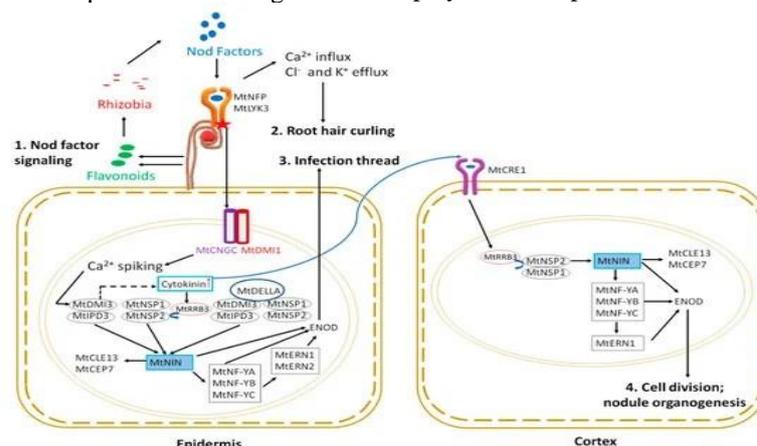
RNA also plays a crucial role in the interactions between oomycetes and their host plants. For example, *Phytophthora* employs the effector PSR1 to target specific elements of the RNA pathway in plants. This process alters immunity, thereby facilitating infection (Gui *et al.*, 2022). Recent study explored how miRNAs are related to the target genes that confer resistance to *Verticillium wilt* in cotton. During this investigation, small RNA (sRNA) libraries were constructed, and genomic sequencing led to the identification of 383 miRNAs, among which GhmiR 165 and GhmiR395 emerged as crucial elements in response to *Verticilliumdahliae*. These miRNAs play a role in vascular development and secondary cell wall generation through the GhmiR165-REV pathway and sulfur incorporation through the GhmiR395-APS1/3 axis (Mei *et al.*, 2022). Furthermore, it is worth mentioning the nature of specialized feeding structures called haustoria by filamentous pathogens, such as fungi and oomycetes. These structures are derived from the invagination and expansion of the PM of the host plant. In contrast, a constant recycling process involving the flagellin receptors FLS2-GFP and GFP-SYP121 was observed between the PM and endosomes in the extrahaustorial matrix. This space is located between the fungal and plant membranes, and this observation leads to the hypothesis that filamentous pathogens employ MVBs to extend the plant PM (Chen *et al.*, 2022). Plant pathogens employ specialized effector molecules to infect their hosts successfully. These molecules facilitate host invasion and interfere with the host immune system (Del Orozco-Mozqueda *et al.*, 2023). Kumar *et al.* (2022) conducted a comprehensive examination of key plant and microbial characteristics and Plant-microbe interaction processes in the context of agriculture and climate change. Their investigation included the following areas: (1) an in-depth analysis of biochemical and molecular frameworks that shed light on the plant-microbe dialogue, potentially influencing the evolutionary trajectory of microbial assemblages; (2) the presence of microbial candidates possessing stress mitigation traits, which imparted stress resilience to their plant hosts and acted as bioprotectors; (3) expanded insights into leveraging synergistic plant-microbe links to develop microbial inoculants that enhance plant growth while

preserving biodiversity integrity and ecosystem safety, similar to biofertilizers. The functions of plant growth-promoting microbes (PGPMs), including bioaccumulation, bioleaching, and bioexclusion, play a critical role in the evolution of microbial communities that are capable of adapting to, withstanding, or tolerating environments containing high levels of heavy metals. Acidification, chelation, and protonation typically result in the release of metals into the environment. Nevertheless, metal immobilization is often a consequence of precipitation, alkalization, and complexation processes. In particular, chemical transformations significantly influence the mobilization and immobilization of these elements (Li *et al.*, 2024).

## SIGNALLING PATHWAYS IN RHIZOBIUM-LEGUME SYMBIOSIS

Rhizobium-legume symbiosis is a crucial mutualistic relationship where rhizobia provide fixed nitrogen to legumes in exchange for carbon sources and a niche for colonization. Signalling pathways orchestrate this intricate symbiotic interaction, involving molecular dialogues between the plant host and rhizobia. The symbiotic relationship begins with molecular dialogues triggered by plant root exudates, which contain flavonoids that induce the expression of nod genes in

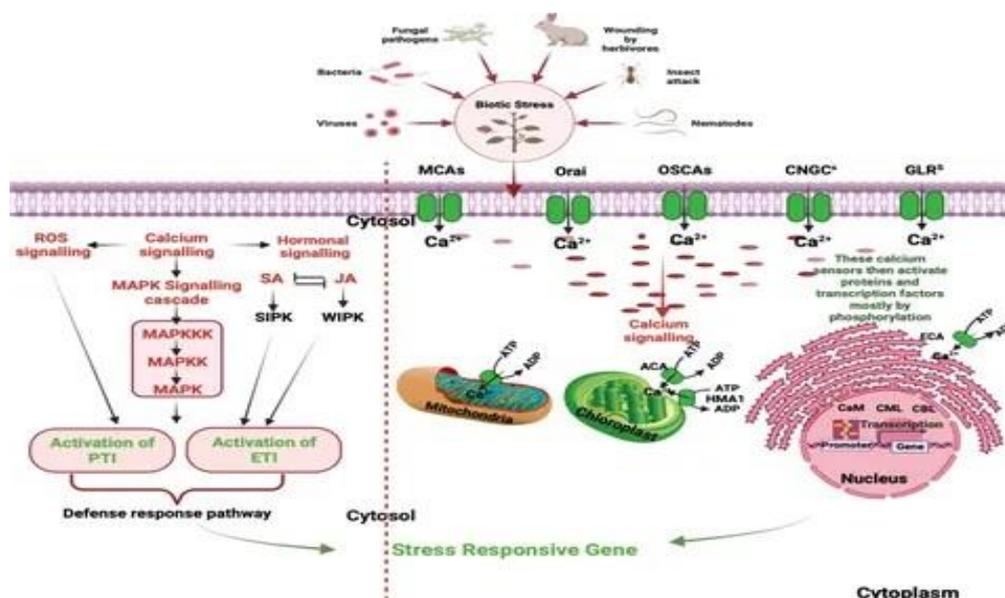
rhizobia, leading to the synthesis of Nod factors (NFs). These NFs initiate the nodulation process by binding to specific receptors on the plant root hairs. Recognition of NFs by plant receptors, such as LysM receptor-like kinases (LysM-RLKs) and receptor-like proteins (RLPs), activates downstream signalling cascades, including calcium oscillations and phosphorylation events. These events trigger the expression of early nodulation genes (ENODs) and promote the formation of infection threads (Its) for rhizobial entry into the root cortex. Upon rhizobial colonization, additional signalling pathways control nodule organogenesis. Cytokinins, auxins, and other phytohormones modulate cell division and differentiation, leading to the formation of nodule primordia (Larrainzar and Wienkoop 2020). Furthermore, the transcription factors NIN and NSP2 play essential roles in coordinating nodule development by regulating the expression of genes involved in nitrogen fixation and nodule morphology. The establishment of nitrogen-fixing symbiosis requires the activation of symbiotic nitrogenase in bacteroids within the nodules. Calcium/calmodulin-dependent protein kinase (CCaMK), also known as SYMRK, and the downstream transcription factor, CYCLOPS, are key players in this process.



**Fig. 1.** Early symbiotic signaling in epidermis and cortex during nodulation. Nod factor signaling: (1) the process starts with Nod factor signaling initiated by plants by producing flavonoids that attract rhizobia. Rhizobia produce Nod factors that bind to root hair receptors (MtNFP and MtLYK3), initiating the intracellular signaling cascade in the nucleus described in the text. Nuclear signaling leads to altered ion fluxes resulting in root hair curling (2). Simultaneously,  $Ca^{2+}$  spiking activates MtNIN through activation of a series of transcription factors; expression of early nodulin (ENOD) genes, such as ENOD11 and ENOD12, facilitates infection thread progression (3). MtNIN also induces the expression of two small peptides, MtCEP7 and MtCLE13. Cytokinin signaling through MtCRE1 mediates MtNIN, MtNF-Y, and MtERN production in the cortex, which upregulates ENOD expression leading to cortical cell division; (4) and nodule organogenesis.

**Calcium Spiking and Cytoskeletal Reorganization: Insights into Cellular Dynamics.** Calcium spiking, the transient increase in cytosolic calcium concentration, plays a pivotal role in various cellular processes, including signal transduction, gene expression, and cell motility (Wang *et al.*, 2023). Cytoskeletal reorganization, the dynamic remodeling of the cytoskeleton, is tightly regulated by calcium signaling and is essential for cell morphology, migration, and division. Calcium spiking serves as a versatile signaling mechanism, allowing cells. Recent studies have

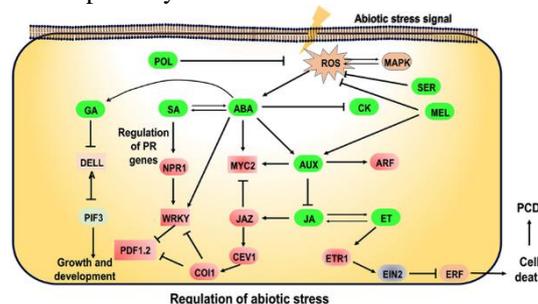
elucidated the involvement of calcium spiking in diverse cellular functions, such as synaptic transmission, muscle contraction, and immune response. Furthermore, dysregulation of calcium spiking has been implicated in various pathological conditions, including neurodegenerative diseases and cancer progression (Smith and Johnson 2022). Dysregulated calcium signaling has been implicated in the aberrant cytoskeletal reorganization observed in various diseases, including cardiovascular disorders and autoimmune conditions (Chen *et al.*, 2022).



**Fig. 2.** Stages in  $\text{Ca}^{2+}$  Signaling Pathways During Plant Interactions with Biotic stressors: This figure underscores the intricate network of calcium signaling components within plant cells. Calcium influx is mediated by diverse channels, including CNGCs, GLRs, TPCs, MCAs, and OSCAs. Meanwhile, calcium efflux is facilitated through systems like ACAs, ECAs, HMA1, MCUC, and CAX. Decoding is executed by specific protein families, encompassing CDPKs), calcineurin B-like protein kinases (CIPKs), calmodulin (CaM), and CaM-like proteins (CMLs). [CNGCs: Cyclic Nucleotide-Gated Channels; GLRs: Ionotropic Glutamate Receptors; TPCs: Two-Pore Channel 1; MCAs: Mechanosensitive Protein Channels; CDPKs, Calcium-Dependent Protein Kinases; CBLs, Calcineurin B-Like Proteins; ACAs, Autoinhibited  $\text{Ca}^{2+}$ -ATPases; ECAs, ER-Type  $\text{Ca}^{2+}$ -ATPases; HMA1, P1-ATPase Heavy Metal Transporter 1; MCUC, Mitochondrial Calcium Uniporter Complex; CAX,  $\text{Ca}^{2+}$ -Exchangers; SA, Salicylic Acid; JA, Jasmonic Acid; ROS, Reactive Oxygen Species.]

**Crosstalk with Phytohormone Signalling Pathways.** Crosstalk among phytohormone signaling pathways orchestrates plant growth, development, and responses to environmental cues. The intricate network of interactions between phytohormones such as auxins, cytokinins, gibberellins, abscisic acid, ethylene, jasmonates, salicylic acid, and brassinosteroids is crucial for regulating various physiological processes. Studies have elucidated how auxin signaling intersects with other hormonal pathways to modulate plant growth and development. Auxin, a key regulator of plant growth, interacts with cytokine in signaling pathways to balance cell division and differentiation. Additionally, gibberellins participate in crosstalk with auxins to regulate processes such as seed germination and stem elongation. The Involvement of abscisic acid (ABA) in stress responses and developmental processes is well-documented. Research has revealed intricate crosstalk between ABA and other hormones, such as ethylene and jasmonates, in modulating plant responses to abiotic and biotic stresses. Ethylene, known for its role in fruit ripening and senescence, interacts with other hormones, including auxins and gibberellins, to regulate various developmental processes. Work has highlighted the cross-regulation between ethylene and auxin signaling pathways in processes such as root development and gravitropism. Jasmonates and salicylic acid are key players in plant defense responses against pathogens and herbivores. Studies have demonstrated the intricate crosstalk between jasmonate and salicylic acid signaling pathways, as well as their interactions with other hormones, such as ethylene and auxins, in orchestrating plant defense responses.

Brassinosteroids, essential for plant growth and development, also participate in crosstalk with other hormonal pathways.

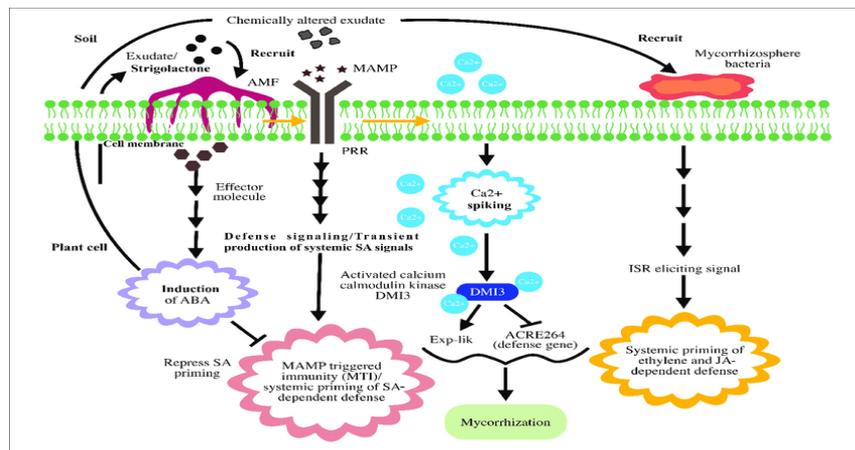


**Fig. 3.** Crosstalk of different phytohormones, transcription factors, and signalling molecules under abiotic stress conditions. Under perception of the abiotic stress signal in plant ROS and MAP kinase activate hormonal pathways such as ABA to regulate plant growth and Development. ABA and SA act synergistically with each other to regulate both biotic and abiotic stress via MYC- and WRKY-mediated Modulation. CK/ABA and Auxin/JA act antagonistically with each other to bring out the physiological response in the plant. ABA regulates GA signalling and the degradation of DELLA repressor helps to Maintain growth and development in plants under abiotic stress conditions. Phytohormone-like serotonin (SER) and melatonin (MEL). Regulate ROS molecules' formation and are also involved in the ROS mediated signalling under abiotic stress in horticultural crops. Polyamines (POL) such as spermine, spermidine, and putrescine regulate ROS synthesis and interact with other phytohormones. However, the Crosstalk of these PGRs with other phytohormones is not so well. Established in the horticultural crops.

## MYCORRHIZAL SIGNALLING NETWORKS

Mycorrhizal symbiosis, a crucial interaction between plant roots and fungi, relies on intricate signaling networks to establish and maintain mutualistic relationships. Recent studies, such as those, have shed light on the molecular mechanisms governing these interactions. One key signaling pathway involves the exchange of signals between the plant and fungal partners, mediated by molecules such as strigolactones and lipochitooligosaccharides has highlighted the role of plant hormones, including auxins and cytokinins, in regulating mycorrhizal symbiosis. Understanding the genetic regulation of mycorrhizal symbiosis has been advanced by studies which elucidated transcriptional networks involved in the establishment and functioning of mycorrhizal associations. Recent investigations have emphasized the importance of transporter proteins in facilitating nutrient exchange between plants and mycorrhizal fungi, underscoring the complexity of nutrient transfer mechanisms. In response to environmental cues and stresses, mycorrhizal signaling networks undergo dynamic changes, which examined the impact of abiotic stresses on mycorrhizal symbiosis.

Advancements in omics technologies, including genomics, transcript omics, and proteomics, hold promise for unraveling the intricacies of mycorrhizal signaling networks. Additionally, interdisciplinary approaches integrating computational modeling and synthetic biology offer new avenues for deciphering and manipulating these networks. Mycorrhizal signalling networks, essential for symbiotic interactions between plants and fungi, are intricately orchestrated systems that involve a plethora of molecular players. These networks encompass various signaling pathways, including those mediated by phytohormones such as auxins, cytokinins, and ethylene, which are crucial for coordinating the development and functioning of mycorrhizal associations. Additionally, the involvement of small signaling molecules like calcium ions and reactive oxygen species (ROS) further underscores the complexity of mycorrhizal signaling. Furthermore, recent studies have revealed the significance of microRNAs in regulating gene expression during mycorrhizal symbiosis, highlighting another layer of regulation in these intricate networks.

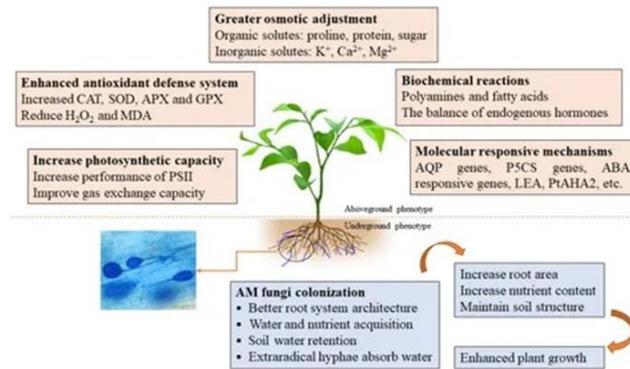


**Fig. 4.** Schematic representation of mycorrhization and mycorrhiza-induced resistance. Strigolactone in plant root exudates recruits arbuscular mycorrhizal fungi (AMF) to the plant. Upon recognition of mycorrhizal microbe-associated molecular patterns (MAMPs), pattern recognition receptors (PRR) induce MAMP-triggered Immunity (MTI) and systemic priming of salicylic acid (SA)-dependent defenses. Mycorrhizal effector-induced ABA represses SA priming and suppresses MTI. MAMP-triggered calcium spiking results in the activation of  $Ca^{2+}$ /calmodulin kinase DMI3, which represses early defense gene expression and promotes Mycorrhization. The successful mycorrhizal association results in chemical alteration of exudates, rhizobacterial recruitment, and mycorrhizosphere development. Mycorrhiza-induced systemic resistance is the result of ethylene (ET)- and jasmonic acid (JA)-dependent defenses exerted by mycorrhizosphere bacteria.

**Arbuscular Mycorrhizal Fungi (AMF) Recognition and Colonization.** Arbuscular mycorrhizal fungi (AMF) recognition and colonization are intricate processes crucial for the symbiotic association between plants and fungi, facilitating nutrient exchange and enhancing plant growth. Recent studies have shed light on the molecular mechanisms underlying AMF recognition by plant hosts, revealing the importance of plant receptors such as LysM receptors in perceiving fungal signals. Upon recognition, AMF establish a symbiotic interface with plant roots, initiating colonization through hyphal growth and penetration into the root cortex. Key signaling molecules like

strigolactones released by plant roots play a pivotal role in stimulating AMF spore germination and hyphal branching, facilitating colonization (Chen *et al.*, 2022). Moreover, AMF colonization induces changes in plant gene expression, leading to the activation of symbiosis-related genes involved in nutrient uptake, stress tolerance, and defense responses. Advances in transcriptomic and genomic analyses have provided insights into the regulatory networks governing plant responses to AMF colonization, uncovering novel genes and pathways involved in the symbiotic interaction. Arbuscular Mycorrhizal Fungi (AMF) Recognition and Colonization is a complex process

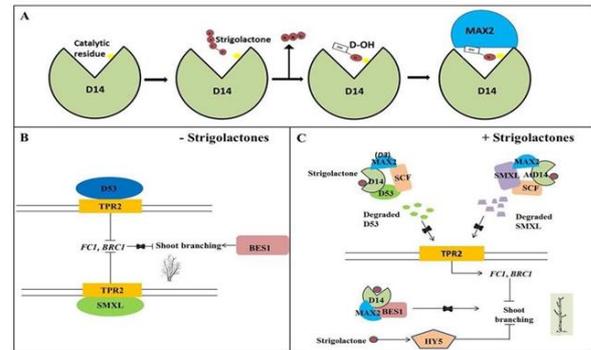
governed by a myriad of molecular interactions between the host plant and the fungal symbiont. Upon encountering AMF, plants release a variety of signaling molecules, including strigolactones and flavonoids, which act as chemoattractants for the fungi. In response to these signals, AMF hyphae grow towards the root surface of the host plant, guided by gradients of chemical signals and physical cues. As AMF hyphae approach the root, they encounter root exudates rich in carbohydrates and other compounds, which serve as a nutrient source for the fungi (Bücking and Shachar-Hill 2005).



**Fig. 5.** A schematic diagram regarding the underlying mechanisms of AM fungi enhancing plant drought tolerance. AM fungi affect the morphology, physiological activities, and molecular regulation of host plants through direct or indirect interactions in response to drought stress, and thus help host plants regulating and maintaining various processes to deal with the harmful effects of drought on plant.

**Host Plant Signal Transduction: Role of Strigolactones and other Compounds:** Host plant signal transduction plays a vital role in the interaction between plants and their symbiotic partners, including mycorrhizal fungi and parasitic plants. Strigolactones, a class of plant hormones, have emerged as key players in mediating these interactions. Understanding the mechanisms underlying strigolactone signaling can provide insights into plant development, nutrient acquisition, and defense responses. Root exudates rich in strigolactones serve as chemical cues that attract symbiotic mycorrhizal fungi, facilitating their colonization of plant roots. This process enhances nutrient uptake by the host plant, particularly phosphorus, in exchange for photosynthetically derived carbon from the plant (Akiyama *et al.*, 2005). Recent studies have elucidated the intricate signaling pathways involved in the perception and response to strigolactones by both plants and mycorrhizal fungi. In addition to their role in mutualistic symbioses, strigolactones also regulate interactions with parasitic plants, such as *Striga* and *Orobancha* species. These parasitic plants detect strigolactones released by host roots, triggering germination of their seeds and subsequent attachment to the host plant's root system. Understanding the molecular mechanisms underlying this interaction is crucial for developing strategies to control parasitic weed infestations in agricultural systems. Strigolactone signaling pathways often intersect with other hormonal signaling pathways, such as auxin and gibberellin pathways, to regulate various

aspects of plant growth and development. Crosstalk between strigolactones and auxin, for example, influences root architecture and lateral root formation. Recent research has highlighted the complexity of these interactions and their impact on plant phenotype under different environmental conditions. One of the well-characterized roles of strigolactones is their inhibition of shoot branching, known as the 'branching inhibition' phenotype. Strigolactones suppress the outgrowth of axillary buds, thereby regulating plant architecture and resource allocation.



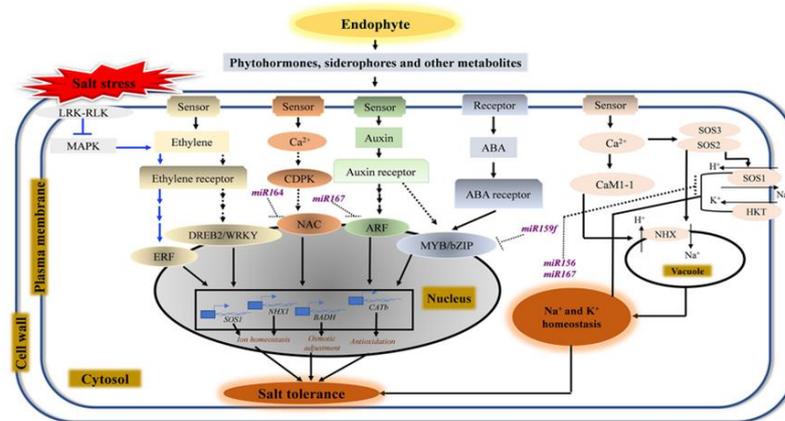
**Fig. 6.** Strigolactone signaling in plant cells of *Arabidopsis thaliana* and *Oryza sativa*. D14 act as receptors for Strigolactone. Upon binding strigolactone, it is catalyzed Forming D-OH and removing the A, B, C rings off of the Strigolactone molecule. Binding of Strigolactone promotes conformational changes of the D14 protein, and this facilitates. The interaction with other target proteins. B) In the absence of Strigolactones, D53 in rice and SMXL in Arabidopsis bind with TPR co-repressor protein, Suppressing the transcription of downstream genes such as FCI and BRC1. The Inactivation of these genes promotes shoot branching. A branching regulator, BES1 Remains active and promotes shoot branching. C) In the presence of strigolactones, D53 in rice binds with D14. This Complex is then ubiquitinated and degraded by the action of SCFMAX2. SMXL in Arabidopsis is degraded upon the recognition by MAX2 gene product and AtD14. Degraded D53 and SMXL can no longer repress the transcription of downstream genes. The transcribed genes suppress the shoot branching. Similarly, the activity of BES1 is Repressed upon the recognition by D14 and MAX2, subsequently inhibiting shoot Branching. Strigolactones promote the expression of HYS5 negatively regulating the Hypocotyl elongation.

## SIGNALLING IN PLANT-ENDOPHYTE SYMBIOSES

Plant-endophyte symbioses confer enhanced resilience to environmental stresses through intricate signaling networks that regulate stress-responsive gene expression and metabolic pathways. Signaling mechanisms play a central role in mediating plant-endophyte symbioses, governing various aspects of symbiotic interactions ranging from molecular recognition to nutrient exchange and stress responses. Continued research efforts aimed at unraveling the complexities of symbiotic signaling networks hold promise for harnessing the potential of plant-endophyte partnerships in sustainable agriculture and environmental remediation. Signalling in plant-endophyte symbioses plays a pivotal role in mediating the intricate interactions between plants and their endophytic microbial partners. One of the fundamental

mechanisms of communication involves the exchange of chemical signals, such as phytohormones, secondary metabolites, and volatile organic compounds (VOCs), which regulate various physiological processes in both the plant and the endophyte. Moreover, recent studies have highlighted the importance of microbial molecular patterns, such as chitin and flagellin, in triggering plant immune responses and modulating the establishment of

endophytic associations. Furthermore, plant-endophyte signalling networks often involve intricate crosstalk between different signalling pathways, including those mediated by salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and reactive oxygen species (ROS), which collectively orchestrate plant defence responses and facilitate endophyte colonization.



**Fig. 7.** Molecular mechanisms regulating endophyte-mediated rice. Responses to salt stress. The salt stress signal is perceived by various signal transduction sensors transducing the signal along different Pathways into the cell. These sensors include membrane-associated Kinases, G-protein coupled receptors, glutamate receptor-like channels, calmodulin binding receptors, cyclic nucleotide-gated channels, And Ca<sup>2+</sup> channel opening. Endophytes target different components in this signalling system during salt stress In the rice cell. They modulate either phytohormone- such as auxin, Ethylene and abscisic acid (ABA), mitogen-activated protein kinase (MAPK)-, or Ca<sup>2+</sup>-signalling (through calcium-dependent protein kinases (CDPK)) Pathways which transduce the signal into the cell to modulate the expression of transcription factors (TFs) such as ethylene responsive factor (ERF), dehydration-responsive element-binding 2 (DREB2), NAC (NAM, ATAF And CUC), auxin response factor (ARF), and myeloblastosis (MYB).

## ENGINEERING SYMBIOTIC SIGNALLING FOR AGRICULTURAL APPLICATIONS

Symbiotic signaling between plants and beneficial microbes holds immense potential for enhancing agricultural sustainability and productivity. Recent advancements in synthetic biology and genetic engineering have enabled the manipulation of these signaling pathways to optimize plant-microbe interactions for improved nutrient uptake, stress tolerance, and disease resistance (Chen *et al.*, 2023). One of the key strategies involves engineering plants to produce and release specific signaling molecules, such as flavonoids and strigolactones, to attract beneficial microbes to their root zone (Zhang *et al.*, 2023). Furthermore, genetic modification of microbial symbionts allows for the enhancement of their ability to establish symbiotic relationships with plants and deliver beneficial services, such as nitrogen fixation and phosphate solubilization. By harnessing these engineered microbes, farmers can reduce their reliance on chemical fertilizers and promote sustainable agricultural practices (Li *et al.*, 2023). Moreover, advances in microbial engineering enable the development of biofertilizers and biopesticides that are tailored to specific plant-microbe interactions and environmental conditions, thereby minimizing negative impacts on non-target organisms and ecosystems. These engineered microbial formulations offer precise and targeted solutions for enhancing crop productivity while

reducing environmental risks associated with conventional agrochemicals (Wang *et al.*, 2023).

## CONCLUSION AND FUTURE SCOPE

The symbiotic signaling research field has witnessed remarkable advancements, with a burgeoning interest in deciphering the intricate communication mechanisms between host organisms and their symbionts (Smith *et al.*, 2023). The integration of omics approaches, such as metagenomics and metabolomics, has enabled comprehensive profiling of symbiotic communities and their functional dynamics (Chen *et al.*, 2023). In addition to elucidating fundamental principles of symbiotic signaling, recent research has highlighted the ecological and evolutionary implications of symbiotic associations. Furthermore, investigations into the impact of environmental stressors, such as climate change and pollution, on symbiotic relationships have underscored the vulnerability of these associations to anthropogenic disturbances. Looking ahead, several emerging trends are poised to shape the future trajectory of symbiotic signaling research. One such trend is the growing emphasis on the microbiome-host-immune axis, recognizing the intricate interplay between symbiotic microbes, host immunity, and health outcomes (Zhang *et al.*, 2023). Additionally, the advent of synthetic biology tools offers exciting opportunities for engineering symbiotic systems with tailored functionalities for various applications, including

bioremediation and agriculture. Several features of plant cell restructuring (e.g., symbiotic interface biogenesis) are strikingly similar (Parniske, 2008). In this context, conserved genes should be much more numerous than just the few currently listed in the CSP; not surprisingly, common symbiotic genes have already been identified which do not fit into the pathway. To mention just a few examples, VAPYRIN (Pumplin *et al.*, 2010) is a partially characterized protein featuring a Major Sperm protein domain and several ankyrin repeats, likely involved in membrane dynamics; CERBERUS (Yano *et al.*, 2009) is an E3 ubiquitin ligase. Both are required for symbiont accommodation, but more likely in cellular remodeling and interface development than in signaling. On the same line, a group of SNARE proteins belonging to the VAMP72 family has been involved in symbiotic interface assembly for both interactions (Ivanov *et al.*, 2012).

**Acknowledgements.** The author extend his sincere appreciation to the Dr. Sharmistha Barthakur, ARS, ICAR-National Institute for Plant Biotechnology, New Delhi, India and Dr. Abdul Waheed ur Rahman for providing the guidance during drafting the manuscript.

**Conflict of Interest.** None.

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**How to cite this article:** Adil Rahim Margay (2024). Signalling Mechanisms in Plant-Microbe Symbioses: A Comprehensive Review. *Biological Forum – An International Journal*, *16*(5): 137-145.