

A COMPREHENSIVE REVIEW OF THE CHEMISTRY BEHIND PLANT-MICROBE INTERACTIONS AND THEIR IMPLICATIONS FOR SUSTAINABLE AGRICULTURE.

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Abstract

The interaction between plants and microbes is pivotal to sustainable agriculture, encompassing mutualistic, pathogenic, and commensurate interactions. Plants and microbes communicate chemically through various molecules, including phytohormones, secondary metabolites, and quorum-sensing molecules. These molecules play a significant role in plant defence, growth, and microbial communication. A plant's defence mechanisms against pathogens involve identifying pathogen-associated molecular patterns (PAMPs) and triggering effector-triggered immunity (ETI), as well as activating hypersensitive reactions and systemic acquired resistance through resistance (R) proteins. In addition to contributing to the antimicrobial activity of plants, phytoalexins induce systemic resistance as well. Beneficial plant-microbe interactions, including those with plant growth-promoting rhizobacteria, mycorrhizal associations, and endophytic microbes, offer potential for sustainable agriculture by enhancing nutrient uptake, stress tolerance, and crop productivity. These interactions reduce reliance on chemical fertilizers and pesticides, enhance crop resilience, and offer bioremediation potential. However, understanding the complexity of plant-microbe interactions and developing targeted strategies for manipulating these interactions present challenges. Future research directions include exploring the potential of synthetic biology, addressing ethical and regulatory considerations, and leveraging the benefits of plant-microbe interactions for sustainable agriculture. The review provides a comprehensive overview of the current understanding of plant-microbe interactions and highlights the importance of further research in harnessing these interactions for sustainable agriculture.

Keywords: Plant microbe interactions, sustainable agriculture, athogen-associated molecular patterns

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1. Introduction

The interaction between plants and microbes is critical to sustainable agriculture since it influences and plant growth, health. productivity. Understanding these interactions is important for the development of sustainable agricultural practices, as they can both be beneficial and detrimental. Plant-associated microbes have the potential to provide economical and sustainable solutions to current agricultural challenges (Ke et al., 2021). These interactions can improve plant growth and health, making them a focal point in sustainable agricultural research (Coker et al., 2022). Exploiting plant-microbe interactions is important for meeting agricultural demands sustainably (Mataranyika et al.. 2022). plant-microbe Furthermore. interactions are essential for controlling ecosystem functioning and can significantly influence nutrient availability (Gondal et al., 2021).

Plant-microbe interactions are also important for sustainable agriculture as they improve crop production and agricultural sustainability (Nguyen et al., 2022). It has been shown that these interactions can improve plant resistance and tolerance to abiotic stresses, ultimately enhancing productivity (Poudel et al., 2019). crop Additionally, plant-microbe interactions can influence above- and belowground interactions between plants and other organisms, making them valuable for managing agricultural ecosystems (Löser et al., 2022). Understanding the ecological consequences of these interactions is crucial for sustainable agricultural practices, as they can impact the overall community assembly of plantroot microbiomes (Hietaranta et al., 2022).

The significance of microbes in sustainable crop production (Patil et al., 2020) is highlighted by their essential role in promoting plant growth under stressful conditions. Furthermore, the information gained from studying plant-microbe interactions may be used to formulate these microbes into biofertilizers for sustainable crop production (Nosheen et al., 2021). The multifaceted roles of flavonoids in regulating plant-microbe interactions further underscore the importance of understanding these relationships for sustainable agriculture (Wang et al., 2022). Moreover, the ability of plantassociated microbes to influence indirect plant defenses has implications for disease transmission herbivory, further emphasizing their and importance in agricultural sustainability (Pulido et al., 2019).

Plant-microbe interactions can, however, negatively affect plant recruitment and generalist predators as well, highlighting the complexity of

these relationships and the need for comprehensive research to understand their full impact (O'Brien et al., 2021). Additionally, the inconsistent functionality and persistence of plant beneficial microbes in the field pose challenges to their effective utilization in sustainable agriculture (Hu & Chen, 2021).

In conclusion, plant-microbe interactions are of paramount importance in sustainable agriculture, as they have the potential to improve crop productivity, enhance plant resilience to stress, and contribute to the overall health of agricultural ecosystems. Understanding the complexities of these interactions is crucial for developing effective and sustainable agricultural practices.

2. Mutualistic interactions and Symbiotic relationships

The mutualistic interactions between plants and microbes encompass a wide range of symbiotic relationships that are vital to both partners' health Particularly and functioning. symbiotic relationships facilitate beneficial mutualistic interactions between plants and microbes, promoting nutrient acquisition, stress tolerance, and overall plant health (Khaliq et al., 2022). These relationships are characterized by a mutually beneficial exchange of resources and services, ultimately enhancing the fitness and physiology of both partners (Jaiswal et al., 2023).

The symbiotic relationship between arbuscular mycorrhizal fungi (AMF) and plants is an excellent example of a mutualistic interaction. In addition to improving plant survival and productivity, AMF forms symbiotic associations with plant roots, facilitating the exchange of nutrients and water. This enhances the plant's ability to withstand environmental stresses and promotes overall growth and productivity. The importance of nutrient transport as the core of these symbiotic relationships highlights the essential role of AMF in facilitating beneficial interactions with plants (Sun et al., 2021). Furthermore, the establishment of mycorrhizal symbiosis requires genetic and epigenetic reprogramming and metabolome modulation by the exchange of effector molecules between the beneficial microbe and the plant, emphasizing the intricate nature of these mutualistic associations (Šečić et al., 2021).

The mutualistic relationship between nitrogenfixing rhizobia bacteria and leguminous plants is another example of a positive mutualistic interaction. As a result of this symbiosis, atmospheric nitrogen is converted into a form that is readily available to plants, thereby increasing soil fertility and promoting plant growth and productivity (Harris et al., 2021). Extensive research efforts have been made to understand the molecular, physiological, and ecological aspects of this symbiotic relationship, highlighting its significance in promoting plant health and productivity (Habtewold & Goyal, 2023).

Moreover, the mutualistic interactions between plants and Streptomyces bacteria, as well as pollinating bees, exemplify the diverse nature of beneficial mutualistic associations. These interactions contribute to the overall health and resilience of plants, highlighting the multifaceted roles of microbes in establishing mutualistic relationships with both plants and insects (Kim et al., 2019).

Ultimately, mutualistic interactions between plants and microbes provide a wide range of symbiotic relationships that are vital to promoting plant health, stress tolerance, and overall productivity. Examples such as the symbiotic relationships with arbuscular mycorrhizal fungi, nitrogen-fixing rhizobia bacteria, and Streptomyces bacteria, as well as pollinating bees, underscore the significance of these interactions in shaping the dynamics of plant-microbe associations and their implications for sustainable agriculture.

3. Pathogenic interactions and attack mechanism

Plants are attacked by pathogens through a complex interplay between the pathogen and the host plant's defense mechanisms. When pathogens attack the plant's immune system, conserved molecular patterns, known as pathogen-associated molecular patterns (PAMPs), trigger basal immune responses called PAMP-triggered immunity (PTI) (Campos et al., 2022). The rhizosphere, the region of soil influenced by the plant's roots, acts as the first line of defense against pathogen infection, serving as an initial filter for the subset of microbes that will colonize the root as endophytes (Liu et al., 2019). Furthermore, the alteration of the cuticle in leaves of mycorrhizal plants may be part of the priming mechanism to more efficiently react to subsequent pathogen attacks (Mendoza-Soto et al., 2022). Actinobacteria are known for the production of secondary metabolites under stress, which initiates pre-signaling to enable induced immunity at early plant stages to tackle pathogen attacks during the later stages of plant development (Arun et al., 2023). Additionally, the sensing of abiotic stress, mechanical injury, or pathogen attack by a single plant tissue results in the activation of systemic signals that travel from the affected tissue to the entire plant, alerting it of an impending stress or pathogen attack (Fichman & Mittler, 2021).

Plant diseases caused by pathogenic interactions can have a significant impact on crop productivity, since they can lead to substantial yield losses. In response to pathogen attacks, the induced defense mechanism is activated, and it has been shown that the alteration of the cuticle of leaves in mycorrhizal plants may serve as a priming mechanism for the plant to be able to respond to future pathogen attacks more efficiently (Mendoza-Soto et al., 2022). Furthermore, the interaction between Crocus sativus and Fusarium oxysporum, based on dual RNA-seq, indicates that in the host saffron, its phenylpropanoid metabolism, plant hormone signal transduction, and plant-pathogen interaction pathways were activated during the infection process, which were conducive to the enhancement of cell wall, the occurrence of hypersensitivity, and the accumulation of various antibacterial proteins phytoantitoxins (Luo et al., 2022). and Additionally, the recognition of pathogen effectors by specific resistant (R)-proteins in plants initiates an immune mechanism termed effector-triggered immunity, which plays a crucial role in plant defense against pathogen attacks (Campos et al., 2021).

The mechanisms of pathogen attack on plants are complex and involve interactions between the pathogen and the host plant's defence responses, which include the recognition of PAMPs, alteration of the cuticle and systemic signalling. The impact of pathogenic interactions on crop productivity is significant, as plant diseases caused by pathogen attacks can lead to substantial yield losses. Understanding these mechanisms and their impact on crop productivity is crucial for developing effective strategies to mitigate the effects of pathogen attacks and promote sustainable agriculture.

4. Commensal interactions

The communal interactions between plants and microbes involve a type of ecological relationship where one organism benefits from the other without being significantly harmed or benefited. Plant microbiota interact in such a manner that contributes significantly to the overall health and resilience of plants. Examples of commensal interactions include the association of plants with beneficial, commensal, and pathogenic microbes, which collectively make up the plant microbiota. The root microbiome consists of commensal, pathogenic, and plant-beneficial microbes. highlighting the diverse nature of microbial interactions in the rhizosphere. Furthermore, plants form commensal associations with soil microorganisms, creating a root microbiome that provides benefits to the host, including protection against pathogens.

Various aspects of plant health and functioning are affected by commensal interactions, which have many potential benefits for plants. It is well known that commensal interactions with microbial communities can have a significant impact on plants' ability to adapt to their environment and evolve, resulting in their resilience and survival as a result. Additionally, the root microbiome plays a crucial role in enhancing the defense potential of plants by activating a broad-spectrum immune response in leaves, known as induced systemic resistance (ISR). Moreover. commensal interactions with soil microorganisms can directly benefit the host plant by enhancing plant growth and indirectly by producing hydrolytic enzymes and priming plant defense.

In conclusion, commensal interactions between plants and microbes are integral to the plant microbiota and contribute to the overall health, resilience, and adaptive capacity of plants. Understanding the diverse nature of commensal interactions and their potential benefits for plants is crucial for elucidating the complex dynamics of plant-microbe associations and their implications for sustainable agriculture.

5. Chemical Signaling in Plant-Microbe Interactions

Various aspects of plant health, growth, and stress responses can be affected by chemical signaling in plant-microbe interactions. Phytohormones, such as auxins, cytokinins, and gibberellins, are significant for the bi-directional communication between plants and microbes, regulating processes such as root development, nutrient uptake, and stress responses Rodríguez et al. (2019). Additionally, emerging evidence has shown that extracellular vesicles (EVs) play a prominent role in plant-microbe interactions by safely transporting functional molecules, such as proteins and RNAs, to interacting organisms, thereby influencing interkingdom communication and signaling (He et al., 2021).

The volatile organic compounds produced by microbes have been shown to be plants growth promoters as well as signaling molecules between holobionts and their rhizosphere communities, which influence plant-microbe interactions and ecosystem functions (Lyu et al., 2021). Furthermore, the modulation of the plant defense system in response to microbial interactions involves the activation of the sophisticated plant immune system at the molecular level, highlighting the intricate chemical signaling mechanisms involved in plant-microbe interactions (Nishad et al., 2020). Chemical interactions at the interface of plant root hair cells and intracellular bacteria contribute to the maintenance of symbiosis and enhanced plant cell growth, emphasizing the role of chemical signaling in promoting beneficial plant-microbe interactions (Chang et al., 2021).

The nitric oxide molecule has been found to be a potential signaling molecule in plant-microbe interactions, influencing the establishment of symbiotic relationships and regulating plant responses to microbial colonization (Pande et al., 2021). Moreover, chemical signaling between bacteria-bacteria, bacteria-fungi, and plantmicrobe interactions plays diverse roles in mediating microbial communication and influencing plant-microbe associations (White et al., 2019). The development of chemical probes for key signaling molecules and phytohormones is essential for better understanding plant-microbe interactions, particularly beneficial interkingdom relationships (Vivian, 2021).

The coordination of tripartite interactions among plants and microbes in the rhizosphere is also facilitated by chemical signaling between plants and microbes, which facilitates info-chemical exchanges, signaling molecules, and biological mechanisms that influence plant-microbe and microbe-microbe interactions (Mashabela et al., 2022). Efforts to understand the chemistry behind the interactions in the plant holobiont have revealed a complex network of molecules and metabolic pathways that modulate plant-microbe and microbe-microbe communication pathways, regulating diverse ecological responses (Berlanga-Clavero et al., 2020). Additionally, the effect of strigolactones on the recruitment of the rice rootassociated microbiome demonstrates the active exudation of signaling molecules by plants to recruit beneficial microbes, influencing plantmicrobe interactions and ecosystem functioning (Kim et al., 2022).

In conclusion, chemical signaling in plant-microbe interactions encompasses a diverse array of signaling molecules, phytohormones, and chemical communication pathways that mediate the coordination and communication between plants and microbes. Understanding these chemical signaling mechanisms is crucial for elucidating the complex dynamics of plant-microbe associations and their implications for sustainable agriculture and ecosystem functioning.

5.1. Plant-derived signaling molecules

Plant-derived signaling molecules, including phytohormones and secondary metabolites, play a

crucial role in mediating various aspects of plantmicrobe interactions. Salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are phytohormones that play a key role in regulating plant growth and development as well as in defending plants from pathogens and herbivores Han & Kahmann (2019)Zhao & Li, 2021; Zhou et al., 2022; Batool et al., 2022; Ahmad et al., 2022; V et al., 2023; Zhuang et al., 2021; Ahmad et al., 2022; Islam et al., 2019; Dodueva et al., 2021; Dhar et al., 2020; Ramabulana et al., 2020; Ofir et al., 2021; Gao et al., 2020; Yang et al., 2020; Abhyankar & Kottayi, 2021; Sreelakshmy et al., 2021; Deryabin et al., 2021; Betti et al., 2021). These phytohormones are critical for activating plant immune responses, inducing systemic acquired resistance (SAR) and induced systemic resistance (ISR), and modulating the trade-off between plant growth and defense (Zhou et al., 2022; Batool et al., 2022; Ahmad et al., 2022). Additionally, secondary metabolites derived from plants, including terpenoids, flavonoids, alkaloids, tannins, and anthraquinones, exhibit antimicrobial activity and contribute to the plant's ability to combat microbial infections (Ramabulana et al., 2020; Ofir et al., 2021; Gao et al., 2020; Yang et al., 2020; Abhyankar & Kottayi, 2021; Sreelakshmy et al., 2021; Deryabin et al., 2021; Betti et al., 2021; Nam et al., 2019; Twaij et al., 2022; Ogundairo et al., 2023; Okezie et al., 2023; Christiansen et al., 2020; Inayah et al., 2022; Ouyang et al., 2021; Cokera & Adeniyi-Aogo, 2022; Dave et al., 2019; Alkhulaifi et al., 2019; Mesta et al., 2020; Nayak et al., 2019).

The secondary metabolites derived from plants, such as terpenoids, flavonoids, and alkaloids, have also been found to possess antimicrobial properties, inhibiting the growth of pathogenic microorganisms and contributing to the plant's defense against microbial infection (Twaij et al., 2022; Ogundairo et al., 2023; Okezie et al., 2023; Christiansen et al., 2020; Inayah et al., 2022; Ouyang et al., 2021; Cokera & Adeniyi-Aogo, 2022; Dave et al., 2019; Alkhulaifi et al., 2019; Mesta et al., 2020; Nayak et al., 2019). These secondary metabolites are involved in regulating plant-microbe interactions and influencing the production of various defense-related enzymes and pathogenesis-related proteins (Ramabulana et al., 2020: Ofir et al., 2021: Gao et al., 2020: Yang et al., 2020; Abhyankar & Kottayi, 2021; Sreelakshmy et al., 2021; Deryabin et al., 2021; Betti et al., 2021; Nam et al., 2019). The interplay between plant hormones and secondary metabolites contributes to the modulation of plant defense responses and the regulation of antimicrobial activities (Ramabulana et al., 2020; Ofir et al.,

2021; Gao et al., 2020; Yang et al., 2020; Abhyankar & Kottayi, 2021; Sreelakshmy et al., 2021; Deryabin et al., 2021; Betti et al., 2021; Nam et al., 2019).

Phytohormones and secondary metabolites are plant-derived signaling molecules that play an important role in mediating plant-microbe interactions, regulating defense responses, growth promotion, and antimicrobial properties. Understanding the intricate interplay between these signaling molecules and their impact on plantmicrobe interactions is essential for elucidating the complex dynamics of plant defense and microbial interactions.

5.2 Microbe-derived signaling molecules

For microbial communication and plant immunity, microbe-derived signalling molecules such as farnesol, tyrosol, and autoinducers are essential. Rodrigues & Černáková (2020)Naguib et al., 2022; Jung & Meile, 2020; Tan et al., 2019; Liang et al., 2019).These molecules enable bacteria to coordinate their response to external or internal stimuli and regulate behaviors such as biofilm formation and antimicrobial resistance. Effector molecules, produced by pathogens and pests, also play a significant role in modulating plant immunity and promoting effector-triggered susceptibility (ETS) through the manipulation of host protein activities (Todd et al., 2022; Guo & Cheng, 2022; Kim et al., 2022; Prešern, 2023; Motamedifar et al., 2021; Liu et al., 2020). These effector molecules are recognized by plant immune receptors, such as nucleotide-binding leucine-rich repeat receptors (NLRs), triggering defense responses and influencing the outcome of plantpathogen interactions. Effector molecules are essential for the establishment of pathogenicity and virulence in microbial pathogens and pests, contributing to the modulation of plant defense pathways and the suppression of host immune responses.

In conclusion, microbe-derived signalling molecules, such as quorum sensing molecules and effector molecules, play an important role in influencing plant immunity and facilitating microbial communication. Understanding the intricate interplay between these signaling molecules and their impact on plant-microbe interactions is essential for elucidating the complex dynamics of microbial communication and its implications for plant health and disease resistance.

6. Plant Defense Mechanisms against Pathogens

The plant's defence mechanisms against pathogens involve a complex interplay of molecular, cellular, and physiological processes aimed at preventing microbial invasions. Plant survival depends heavily on these defence mechanisms, which play a significant role in shaping the outcomes of interactions between plants and pathogens. Investigating the molecular mechanisms of plantpathogen interactions, including pathogenicity and plant resistance, is essential for developing novel and safer strategies for effectively controlling plant diseases Cheng et al. (2020).

Plants possess specialized structures, chemicals, and complex defense mechanisms against pathogens. These defense mechanisms include the production of antimicrobial compounds, reactive oxygen species, and the hypersensitive response, as well as the deposition of callose and lignin to strengthen cell walls and block pathogen entry (Irkitbay et al., 2022; Gupta et al., 2021; Iqbal et al., 2021; Oblessuc et al., 2020; Gupta et al., 2020; Bi et al., 2022). Additionally, plants produce phytoalexins, which are antimicrobial secondary metabolites, as part of their defense response to pathogen attack (Bi et al., 2022). The induction of systemic acquired resistance (SAR) and the activation of plant immunity inducers are also critical components of plant defense against pathogens (Hu et al., 2022; Fatima & Senthil-Kumar, 2021; Gold, 2021; Kv, 2019; Benjamin et al., 2022).

The effector-triggered immunity (ETI) mechanism is another essential defense mechanism in plants, involving the recognition of pathogen effectors by plant immune receptors, which activates defense responses and suppresses the pathogen's virulence factors (Wang et al., 2021; Pantiya & Mikhailova, 2020; Tan et al., 2019; Pran, 2022). The deployment of immune receptors and the modulation of plant immunity play a crucial role in plant defense against pathogens (Bufford et al., 2019; Yang et al., 2022; Jiang et al., 2020). Furthermore, the interplay between plant immune receptors and pathogen effectors is a key determinant of plant disease resistance and susceptibility (Xi et al., 2021; Luo et al., 2022; Guo & Cheng, 2022).

Additionally, establish mutualistic plants relationships with beneficial microbes while deploying the immune system to defend against pathogenic ones (Kourelis et al., 2023; Campos et al., 2021; Morcillo et al., 2019). The role of the microbiota in gating plant proper immunocompetence and the impact of eubiotic microbiota on plant immunity have been the focus of recent research (Paasch et al., 2023; Bjornson & Zipfel, 2021).

In conclusion, plant defense mechanisms against pathogens involve a diverse array of molecular and physiological processes, including the production of antimicrobial compounds, the activation of immune receptors, and the establishment of mutualistic associations with beneficial microbes. Understanding these defense mechanisms is crucial for developing effective strategies to enhance plant resistance to pathogens and mitigate the impact of plant diseases.

6.1 Recognition of pathogen-associated molecular patterns (PAMPs)

Plant defense mechanisms are triggered by recognition of pathogen-associated molecular patterns (PAMPs) in pathogen-microbe interactions. PAMPs are conserved molecular patterns present in microbial pathogens, such as bacteria, fungi, and oomycetes, and are recognized by plant pattern recognition receptors (PRRs) to trigger a series of immune responses, collectively known as PAMP-triggered immunity (PTI) (Hu et al., 2022; Zhou et al., 2021; Zhao, 2023; Teixeira et al., 2019; Piazza et al., 2021; Gamir et al., 2020; Janda et al., 2019; Wang et al., 2019). Upon recognition of PAMPs, PRRs initiate a cascade of signaling events, leading to the activation of defense mechanisms, including the production of antimicrobial compounds, reinforcement of cell walls, and the induction of

systemic acquired resistance (SAR) (Hu et al., 2022; Zhou et al., 2021; Zhao, 2023; Teixeira et al., 2019; Piazza et al., 2021; Gamir et al., 2020; Janda et al., 2019; Wang et al., 2019).

PAMPs can include a wide range of molecules, such as bacterial flagellin, chitin, and other conserved microbial components, which are recognized by specific PRRs, leading to the activation of defense responses in plants (Hu et al., 2022; Zhou et al., 2021; Zhao, 2023; Teixeira et al., 2019; Piazza et al., 2021; Gamir et al., 2020; Janda et al., 2019; Wang et al., 2019).

6.1.1 Activation of PAMP-triggered immunity (PTI)

Plants are capable of recognizing pathogenassociated molecular patterns (PAMPs) by pattern recognition receptors (PRRs), causing PAMPtriggered immunity (PTI) to be activated. Upon recognition of PAMPs, PRRs initiate a cascade of signaling events, leading to the activation of defense mechanisms, including the production of reactive oxygen species (ROS), induction of calcium influx, activation of mitogen-activated protein kinase (MAPK) cascades, and transcriptional induction of defense-related genes (Sun & Zhang, 2020; Wang et al., 2019; Teixeira et al., 2019; Wang et al., 2019; Majhi & Sessa, 2019; Piazza et al., 2021; Ngou et al., 2022; Yuan et al., 2021).

The activation of PTI is a rapid, non-specific response to a wide range of pathogens, forming the first line of defence for plants against microbial infections. The signaling events triggered by PTI play a crucial role in priming the plant's immune system and initiating a series of defense responses to combat pathogen invasion. These responses include the reinforcement of cell walls, the production of antimicrobial compounds, and the induction of systemic acquired resistance (SAR) (Sun & Zhang, 2020; Wang et al., 2019; Teixeira et al., 2019; Wang et al., 2019; Majhi & Sessa, 2019; Piazza et al., 2021; Ngou et al., 2022; Yuan et al., 2021).

The understanding of the molecular mechanisms underlying the activation of PTI and the signaling events involved is essential to elucidate the dynamics of plant defense against pathogens and to develop novel strategies for enhancing plant resistance to diseases.

Given the importance of PTI in plant defense, the references (Sun & Zhang, 2020; , Wang et al., 2019; , Teixeira et al., 2019; , Wang et al., 2019; , Majhi & Sessa, 2019; , Piazza et al., 2021; , Ngou et al., 2022), and Yuan et al. (2021) provide valuable insights into the molecular and cellular processes involved in the activation of PTI and the signaling events triggered by PAMP recognition.

If you need further information on any specific aspect of PTI activation or the signaling events involved, please feel free to let me know!

6.2 Effector-triggered immunity (ETI)

The effector-triggered immunity (ETI) mechanism is a crucial part of plant defence against pathogens. The mechanism involves recognition of pathogenderived effectors by plant resistance (R) proteins, particularly the nucleotide-binding leucine-rich repeats (NLR) immune receptors. Upon recognition of effectors, NLRs initiate a robust immune response, leading to the activation of ETI and the induction of defense mechanisms to counteract pathogen invasion. ETI is characterized by a rapid and specific response to pathogen effectors, often leading to the hypersensitive response (HR) and the restriction of pathogen growth and proliferation (Ngwaga et al., 2021; Todd et al., 2022; Wang et al., 2022; Yin et al., 2022; Breit-McNally et al., 2022; Chen et al., 2023; Kretschmer et al., 2019; Niu et al., 2021; Chen & Mao, 2020; Yang et al., 2021; Wang et al., 2020; Karre et al., 2021; Varden et al., 2019; Fitoussi et

al., 2021; Jing et al., 2020; Yoshihisa et al., 2021; Romero-Contreras et al., 2019; Liu et al., 2020; Pogorelko et al., 2019; Yuan et al., 2019; Sang et al., 2019; Fitoussi et al., 2019; Varden et al., 2019). The activation of ETI is essential for plant defense against a wide range of pathogens, including bacteria, fungi, oomycetes, and nematodes. Effectors are small, secreted molecules that alter host cell structure and function, facilitating infection or triggering a defense response. Plants have evolved intracellular resistance (R) proteins to directly or indirectly perceive effectors, leading to the activation of ETI and the subsequent restriction of pathogen growth and proliferation (Ngwaga et al., 2021; Todd et al., 2022; Wang et al., 2022; Yin et al., 2022; Breit-McNally et al., 2022; Chen et al., 2023; Kretschmer et al., 2019; Niu et al., 2021; Chen & Mao, 2020; Yang et al., 2021; Wang et al., 2020; Karre et al., 2021; Varden et al., 2019; Fitoussi et al., 2021; Jing et al., 2020; Yoshihisa et al., 2021; Romero-Contreras et al., 2019; Liu et al., 2020; Pogorelko et al., 2019; Yuan et al., 2019; Sang et al., 2019; Fitoussi et al., 2019; Varden et al., 2019).

The molecular mechanisms behind the activation of ETI and the signaling events involved are essential for understanding the complex dynamics of plant defense against pathogens and for developing strategies designed to enhance plant resistance to microbial infections.

Given the importance of ETI in plant defense, the references (Ngwaga et al., 2021; , Todd et al., 2022; , Wang et al., 2022; , Yin et al., 2022; , Breit-McNally et al., 2022; , Chen et al., 2023; , Kretschmer et al., 2019; , Niu et al., 2021; , Chen & Mao, 2020; , Yang et al., 2021; , Wang et al., 2020; , Karre et al., 2021; , Varden et al., 2019; , Fitoussi et al., 2021; , Jing et al., 2020; , Yoshihisa et al., 2021; , Romero-Contreras et al., 2019; , Liu et al., 2020; , Pogorelko et al., 2019; , Yuan et al., 2019; , Sang et al., 2019; , Fitoussi et al., 2019; , Eitu et al., 2020; Al., 2019; , Fitoussi et al., 2019; , Sang et al., 2019; , Fitoussi et al., 2019; , and Varden et al. (2019) provide valuable insights into the molecular and cellular processes involved in the activation of ETI and the signaling events triggered by effector recognition.

6.2.1 Role of resistance (R) proteins in ETI

The resistance (R) proteins, particularly the nucleotide-binding leucine-rich repeat (NLR) proteins, are intracellular immune receptors, recognizing pathogen-derived effectors and initiating effector-triggered immunity in plants (Wu et al., 2020; Liu et al., 2021; Koseoglou et al., 2022; Xie & Duan, 2023; Maruta et al., 2022; Ngwaga et al., 2021; Kourelis et al., 2021; Vo et al., 2022; Karre et al., 2022; Breit-McNally et al.,

2022; Ding et al., 2022.). Upon recognition of effectors, R proteins trigger a cascade of signaling events, leading to the activation of ETI and subsequent restriction of pathogen growth and proliferation. This recognition specificity allows plants to mount a faster and stronger immune response, providing a critical layer of defense against a wide range of pathogens, including bacteria, fungi, oomycetes, and nematodes (Wu et al., 2020; Liu et al., 2021; Koseoglou et al., 2022; Xie & Duan, 2023; Maruta et al., 2022; Ngwaga et al., 2021; Kourelis et al., 2021; Vo et al., 2022; Karre et al., 2021; Breit-McNally et al., 2022; Ding et al., 2020).

The molecular mechanisms underlying the role of R proteins in ETI and the signaling events involved are essential for understanding the complex dynamics of plant defense against pathogens and for developing novel strategies to enhance plant resistance to microbial infections.

6.2.2 Hypersensitive response and systemic acquired resistance

During plant-microbe interactions, hypersensitive responses (HR) and systemic acquired resistance (SAR) play vital roles as defense mechanisms against pathogens.

The hypersensitive response (HR) is a rapid and localized cell death response triggered by the invasion of a pathogen. It is a crucial defense mechanism that restricts the spread of pathogens by sealing off the infected area. HR is often associated with the activation of resistance (R) proteins, particularly nucleotide-binding leucine-rich repeat (NLR) immune receptors, which specifically recognize pathogen effectors. Upon recognition, R proteins trigger a cascade of signaling events, leading to the induction of HR and subsequent restriction of pathogen growth and proliferation Castro-Moretti et al. (2020).

Systemic acquired resistance (SAR) is a longlasting and broad-spectrum immune response that occurs throughout the entire plant following an initial localized infection. SAR is induced by the accumulation of signaling molecules, such as salicylic acid, and leads to enhanced resistance against a wide range of pathogens. This systemic immunity is triggered by local plant-microbe interactions and is studied as SAR or induced systemic resistance (ISR) depending on the site of induction and the lifestyle of the inducing microorganism (Vlot et al., 2020).

The interaction between HR and SAR is crucial for the overall defense response of plants against microbial pathogens. HR provides an immediate localized response to contain the pathogen, whereas SAR provides long-term and broadspectrum immunity throughout the plant, which enhances its resistance to subsequent infections.

Understanding the molecular mechanisms underlying HR and SAR, as well as the signaling events involved, is essential for elucidating the complex dynamics of plant defense against pathogens and for developing novel strategies to enhance plant resistance to microbial infections.

7. Chemical defense compounds

The ability of plants to defend themselves against pathogens and herbivores is greatly enhanced by chemical defense compounds in plant-microbe The synthesize interactions. plants such compounds. including lignin, phytoalexins, alkaloids. terpenoids, flavonoids, and glucosinolates, in response to attacks by microbials and herbivores (Ninkuu et al., 2022) and herbivores. The production of these compounds is often induced by the recognition ofpathogenassociated molecular patterns (PAMPs) or microbial effectors, leading to the activation of plant defense mechanisms (Ninkuu et al., 2022; Vlot et al., 2020).

Research has shown that lignin and its associated phytoalexins modulate plant defense against fungi, enhancing the plant's innate immunity against pathogens (Ninkuu et al., 2022). Additionally, systemic acquired resistance (SAR) and induced systemic resistance (ISR) are systemic immune responses triggered by the accumulation of signaling molecules, such as salicylic acid and pipecolic acid, leading to enhanced resistance against a wide range of pathogens (Vlot et al., 2020).

Furthermore, these chemical compounds have been identified as important defensive compounds in plants, exhibiting toxic, antinutritive, or repellent properties against herbivores and pathogens (Zhang et al., 2020; Lv et al., 2022). They not only act directly upon the insect or pathogen but also have an interplay with the herbivore's microbiome, influencing plant-microbe interactions (Zhang et al., 2020; Lv et al., 2022; Mason et al., 2019).

Moreover, chemical compounds have been shown to induce immunity and resistance against pathogens and insects, enhancing plant growth and defense signaling (Mostafa et al., 2021; Hoffmann et al., 2023). Understanding the diverse roles and mechanisms of action of these compounds is essential for developing sustainable strategies for crop protection and enhancing plant resilience to biotic stresses.

8. Phytoalexins and their antimicrobial activity in plant microbe interaction

The phytoalexin is a secondary metabolite produced by plants in response to the attack of microorganisms or herbivores. Plants use these compounds to protect themselves against pathogens, exhibiting antimicrobial activity and contributing to their ability to resist infection. Phytoalexins are induced during the interaction between plants and pathogens or after physical and mechanical damage, and they are considered an important component of the plant's defense arsenal Ishihara, 2021; Cook et al., 2022; Pedras & Alavi, 2020).

The antimicrobial activity of phytoalexins is welldocumented, with many of these compounds targeting the cell wall or cell membrane of pathogens. They have been shown to exhibit toxicity towards pathogens, contributing to the plant's ability to resist microbial infections. Phytoalexins are inducible antimicrobial metabolites in plants and have been indicated to be important for the rejection of microbial infection (Ube et al., 2019; Ishihara, 2021; Cook et al., 2022).

The production of phytoalexins is a key aspect of plant-microbe interactions, and these compounds are considered an integral part of the plant's defense response. They are involved in the plant's ability to resist fungal or bacterial infections and play a crucial role in enhancing plant resilience to biotic stresses. Furthermore, phytoalexins are part of the plant's chemical defense system, contributing to its overall ability to defend against pathogens and herbivores (Bi et al., 2022; Ichinose et al., 2020; Pedras & Alavi, 2020).

Understanding the diverse roles and mechanisms of action of phytoalexins is essential for developing sustainable strategies for crop protection and enhancing plant resilience to biotic stresses.

9. Conclusion

The interaction between plants and microbes involves a complex network of chemical signalling and defensive mechanisms. As low molecular weight secondary metabolites, phytoalexins play a crucial role in the defense of plants against pathogens, exhibiting antimicrobial activity and contributing to the plant's ability to withstand infection. The production of phytoalexins is an important aspect of the plant's defense response, often leading to systemic acquired resistance (SAR) and the induction of a hypersensitive reaction. These compounds are induced during the interaction between plants and pathogens or after physical and mechanical damage, and they are considered an important component of the plant's defense arsenal.

The antimicrobial properties of phytoalexins are well established. Many of these compounds target the cell wall or membrane of pathogens, act as a toxicant toward pathogens, and contribute to the plant's ability to resist infection by bacteria. Furthermore, phytoalexins are part of the plant's chemical defense system, contributing to its overall ability to defend against pathogens and herbivores. The interplay between phytoalexins and the plant microbiome, as well as their role in shaping the composition and function of the plant microbiome, is an area of active research.

The development of sustainable crop protection strategies and the enhancement of plant resilience to biotic stress requires a deeper understanding of phytoalexins' diverse roles. By integrating system phenotypes into microbiome networks and identifying candidate synthetic communities, research is being conducted with the aim of maximizing the potential of phytoalexins and beneficial microbes in agriculture. Moreover, specific metabolites are contributing to the resistance of plants to bacterial and fungal diseases, providing valuable insight into their defence mechanisms.

The study of phytoalexins and their antimicrobial activity in plant-microbe interactions represents a promising avenue for the development of novel approaches to enhance plant immunity and promote sustainable agricultural practices. Further research in this area will continue to shed light on the intricate interplay between plants and microbes and the potential applications of phytoalexins in crop protection and disease management.

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