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Review

Calcium signaling: Unveiling its role in disease control in plants

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Abstract: Calcium signaling is a fundamental regulatory mechanism in plants, governing a myriad of physiological processes crucial for growth, development, and responses to environmental stimuli, including biotic stresses such as pathogen attack. Over the past decades, research into the intricate network of calcium signaling pathways has revealed its pivotal role in orchestrating plant defense mechanisms against a diverse array of pathogens. This review comprehensively examines the multifaceted roles of calcium ions in modulating plant immune responses, elucidating the molecular mechanisms underlying calcium-mediated signal transduction and its integration with other defense signaling pathways. We delve into the intricate crosstalk between calcium signaling and various hormonal pathways, reactive oxygen species (ROS) signaling, and secondary metabolite biosynthesis, highlighting the interconnectedness of these regulatory networks in shaping plant defense strategies. Furthermore, we explore the potential applications of calcium-based strategies for sustainable disease management in agriculture, including the use of calcium channel blockers, calcium chelators, and calcium-rich compounds as novel antimicrobial agents and priming agents for enhancing plant immunity. Challenges and future directions in the field are also discussed, aiming to advance our understanding of calcium signaling in plant-pathogen interactions and harness its potential for developing innovative approaches to combat plant diseases and ensure global food security. This review provides a comprehensive overview of the current state of knowledge regarding calcium signaling in plant disease control, offering valuable insights and perspectives for future research endeavors in this rapidly evolving field.

Keywords: calcium signaling; plant defense; pathogen attack; immune responses; signal transduction; hormonal pathways; reactive oxygen species (ROS); secondary metabolites; disease management; antimicrobial agents; priming agents; sustainable agriculture; plant-pathogen interactions; food security

1. Introduction

Plants, being sessile organisms, have evolved sophisticated defense mechanisms to protect themselves against various biotic stresses, including pathogens, pests, and herbivores [1]. Among these defense mechanisms, calcium signaling emerges as a crucial player in orchestrating plant immune responses. Calcium ions (Ca^{2+}) serve as versatile second messengers that transmit extracellular signals to intracellular targets, thereby initiating a cascade of defense responses tailored to combat invading pathogens [2]. The intricate interplay between calcium signaling pathways and downstream defense mechanisms underscores the importance of understanding the role of calcium in plant defense.

Recent advancements in molecular and cellular biology have shed light on the intricacies of calcium signaling networks in plants [3]. Key components of calcium signaling, including calcium-permeable channels, calcium sensors, and calcium-binding proteins, have been identified and characterized [4]. These components function in concert to perceive pathogen-derived signals and elicit appropriate defense responses, such as the production of reactive oxygen species (ROS), activation of defense-related genes, and reinforcement of cell wall barriers [5]. Furthermore, calcium signaling is intimately intertwined with phytohormone signaling pathways, such as salicylic acid (SA), jasmonic acid (JA), and ethylene, forming a complex regulatory network that fine-tunes plant immune responses [6].

Understanding the molecular mechanisms underlying calcium-mediated defense signaling holds immense potential for improving crop resistance to diseases and pests [7]. By deciphering the intricacies of calcium signaling pathways in model plants such as Arabidopsis thaliana, researchers can identify conserved signaling components that are applicable across diverse plant species [3]. Moreover, emerging evidence suggests that manipulating calcium signaling components through genetic engineering or exogenous elicitor treatments can enhance plant immunity without compromising growth and development [8]. Harnessing the power of calcium signaling in crop plants offers a promising avenue for sustainable agriculture practices that minimize reliance on chemical pesticides and promote environmental sustainability.

In this review, we aim to provide a comprehensive overview of the current understanding of calcium signaling in plant defense. We will discuss the molecular mechanisms underlying calcium-mediated immune responses, highlight the crosstalk between calcium signaling and other defense pathways, and explore the potential applications of calcium-based strategies for crop protection. By synthesizing recent research findings and identifying future research directions, we seek to elucidate the pivotal role of calcium signaling in shaping plant defense responses and advancing agricultural sustainability.

2. The role of calcium signaling in plant immunity

Plant immunity, a complex network of defense mechanisms, relies on calcium signaling as a central regulatory hub to orchestrate responses against invading pathogens. This multifaceted process involves the perception of pathogen-derived signals, activation of signaling cascades, and deployment of defense mechanisms to mitigate pathogen invasion and spread.

At the forefront of plant immunity are pattern recognition receptors (PRRs), which detect conserved pathogen-associated molecular patterns (PAMPs) and initiate a rapid influx of calcium ions into the cytosol [9]. This calcium influx serves as a primary signaling event, triggering a cascade of downstream responses that culminate in the activation of defense genes and the production of antimicrobial compounds. Calcium-dependent protein kinases (CDPKs) are key players in this process, phosphorylating target proteins to regulate various defense processes, including reactive oxygen species (ROS) production, ion fluxes, and transcriptional reprogramming [10].

In addition to PAMP-triggered immunity (PTI), plants possess a second layer of defense known as effector-triggered immunity (ETI), which is activated upon the recognition of pathogen effectors by plant resistance (R) proteins [11]. ETI is associated with a rapid and robust calcium signaling response, leading to the activation of defense mechanisms such as the hypersensitive response (HR) and systemic acquired resistance (SAR). Calcium-mediated signaling events integrate with other defense signaling pathways, including those mediated by salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), to coordinate an effective immune response tailored to the specific pathogen encountered.

Recent advances in calcium imaging techniques have revolutionized our understanding of the spatiotemporal dynamics of calcium signaling during plant-pathogen interactions. High-resolution imaging studies have revealed the formation of calcium gradients and oscillations in response to pathogen perception, highlighting the complexity and specificity of calcium-mediated immune signaling [3].

Furthermore, calcium signaling intersects with other cellular processes, such as growth and development, to regulate plant responses to biotic stresses. Crosstalk between calcium signaling and hormonal pathways modulates immune responses, allowing plants to fine-tune their defense strategies in response to changing environmental conditions.

Overall, calcium signaling serves as a cornerstone of plant immunity, integrating various signaling inputs to coordinate an effective defense response against invading pathogens. A deeper understanding of calcium-mediated immune pathways holds immense potential for the development of novel strategies to enhance crop resilience and mitigate the impact of plant diseases on global food security.

2.1. Molecular mechanisms of calcium signaling in plant immunity

Calcium signaling plays a pivotal role in orchestrating plant immune responses against various pathogens. At the molecular level, calcium ions serve as secondary messengers, relaying signals from pathogen recognition receptors (PRRs) and other immune sensors to downstream signaling components. One of the well-studied pathways is the activation of mitogen-activated protein kinase (MAPK) cascades upon pathogen perception, leading to the activation of defense-related genes and physiological responses [4]. Additionally, calcium-dependent protein kinases (CDPKs) have emerged as central players in plant immunity, integrating calcium signals with phosphorylation events to regulate immune responses [12]. Furthermore, calcium-binding proteins such as calmodulins and calmodulin-like proteins act as molecular switches, modulating the activity of target proteins in response to changes in calcium levels [13].

The activation of calcium channels and pumps also contributes to the spatiotemporal dynamics of calcium signals during immune responses. For instance, transient receptor potential (TRP) channels have been implicated in calcium influx across the plasma membrane upon pathogen recognition [13,14]. Similarly, intracellular calcium release from organelles such as the endoplasmic reticulum (ER) and vacuole further amplifies calcium signaling and regulates immune signaling pathways [14].

Understanding the molecular mechanisms governing calcium signaling in plant immunity is essential for engineering crop plants with enhanced disease resistance. By elucidating the intricate interplay between calcium signaling components and immune regulators, researchers can develop novel strategies to bolster plant defenses against pathogens and mitigate crop losses due to diseases.

2.2. Calcium signaling-mediated regulation of defense-related genes

Calcium signaling plays a pivotal role in orchestrating the expression of defense-related genes involved in plant immunity. Upon pathogen perception or stress induction, calcium spikes and oscillations trigger a cascade of downstream signaling events, ultimately leading to the activation of transcription factors and the modulation of gene expression profiles. Several key defense-related genes have been identified as targets of calcium signaling, highlighting the central role of calcium in regulating plant defense responses.

One group of defense-related genes regulated by calcium signaling encodes pathogenesis-related (PR) proteins, which serve as molecular markers of plant defense and play diverse roles in combating pathogens. Calcium-dependent signaling pathways have been implicated in the induction of PR gene expression following pathogen infection or treatment with defense elicitors [15]. For example, the expression of PR1, a marker gene for salicylic acid-mediated defense responses, is positively regulated by calcium signaling cascades involving calcium-dependent protein kinases (CDPKs) [16].

In addition to PR proteins, calcium signaling modulates the expression of genes involved in the biosynthesis of antimicrobial compounds and cell wall reinforcement, further enhancing plant resistance to pathogens. Genes encoding enzymes responsible for the synthesis of phytoalexins, antimicrobial peptides, and cell wall-associated proteins are under the control of calcium-dependent transcriptional regulators [17]. Calcium-responsive transcription factors such as WRKY, MYB, and bZIP proteins have been implicated in the regulation of these defense-related genes, highlighting the diverse mechanisms by which calcium signaling regulates plant immunity [18].

Furthermore, calcium signaling influences the expression of genes involved in reactive oxygen species (ROS) metabolism and programmed cell death (PCD), which are integral components of plant defense responses. Calcium influx activates NADPH oxidases and other ROS-generating enzymes, leading to the accumulation of ROS and initiation of PCD in infected or stressed cells [17]. The fine-tuned regulation of ROS production and PCD by calcium signaling ensures effective defense against pathogens while minimizing collateral damage to healthy tissues.

Understanding the regulatory role of calcium signaling in defense-related gene expression is essential for deciphering the molecular basis of plant immunity. Manipulating calcium signaling pathways and their downstream targets holds promise for engineering crop plants with enhanced resistance to pathogens and improved stress tolerance.

2.3. Calcium signaling crosstalk with hormonal pathways in plant defense

Calcium signaling intersects with hormonal signaling pathways to coordinate plant defense responses against pathogens and environmental stresses. Cross-talk between calcium and phytohormones, such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and abscisic acid (ABA), modulates the amplitude and duration of defense signaling cascades, fine-tuning the plant's response to different biotic and abiotic stresses.

Salicylic acid (SA), a key signaling molecule in plant defense against biotrophic pathogens, interacts with calcium signaling to regulate defense gene expression and establish systemic acquired resistance (SAR). Calcium influx activates SA biosynthesis and induces the expression of SA-responsive genes, leading to the accumulation of pathogenesis-related proteins and the establishment of defense priming [19]. Conversely, SA-mediated defense responses can feedback on calcium signaling by modulating the activity of calcium-dependent protein kinases (CDPKs) and calmodulin-binding proteins, thereby amplifying defense signal transduction pathways [20].

Jasmonic acid (JA) and its derivatives, known as jasmonates, mediate plant defense against necrotrophic pathogens and herbivorous insects. Calcium signaling interacts with the JA signaling pathway to regulate the expression of JA-responsive genes involved in defense and stress responses. Calcium-dependent protein kinases (CPKs) phosphorylate transcription factors such as MYC2, a master regulator of JA signaling, to modulate JA-responsive gene expression and enhance plant resistance to herbivores and necrotrophic pathogens [6]. Conversely, JA signaling can influence calcium signaling by regulating the expression and activity of calcium channels and pumps, thereby modulating calcium influx and downstream signaling events [14].

Ethylene (ET) is another phytohormone that interacts with calcium signaling to regulate plant defense responses, particularly in response to necrotrophic pathogens and environmental stresses. Calcium influx activates ET biosynthesis and induces the expression of ET-responsive genes, leading to the production of defense-related metabolites and the activation of defense pathways [21]. ET signaling, in turn, can modulate calcium signaling by regulating the expression and activity of calcium-binding proteins and ion channels, thereby modulating calcium fluxes and downstream signaling cascades [22].

Abscisic acid (ABA), a stress hormone involved in plant responses to drought, salinity, and other abiotic stresses, also interacts with calcium signaling to regulate plant defense. Calcium influx triggers ABA biosynthesis and activates ABA-responsive genes involved in stress tolerance and defense modulation. ABA signaling can influence calcium signaling by regulating the expression and activity of calcium transporters and sensors, thereby modulating calcium homeostasis and stress responses [23].

Understanding the intricate crosstalk between calcium signaling and hormonal pathways is essential for unraveling the complexity of plant defense regulation. Manipulating the interplay between calcium and hormonal signaling pathways holds promise for engineering crop plants with enhanced resilience to diverse stresses and improved agricultural productivity.

2.4. Calcium signaling-mediated regulation of defense gene expression

Calcium ions serve as versatile secondary messengers that regulate the expression of defense-related genes in response to pathogen infection and environmental stresses. Calcium signaling pathways modulate the activity of transcription factors, chromatin modifiers, and epigenetic regulators to orchestrate the transcriptional reprogramming required for plant defense.

Upon perception of pathogen-associated molecular patterns (PAMPs) or damage-associated molecular patterns (DAMPs) by pattern recognition receptors (PRRs), calcium influx is rapidly induced, triggering downstream signaling events leading to the activation of defense gene expression[5]. Calcium-dependent protein kinases (CDPKs) and calcineurin B-like proteins (CBLs), in conjunction with their interacting partners, phosphorylate and regulate the activity of transcription factors such as WRKY, MYB, and ERF, which are key regulators of defense gene expression [3,24]. These transcription factors bind to cis-regulatory elements in the promoters of defense genes, activating or repressing their transcription in response to calcium signals.

In addition to direct regulation of transcription factors, calcium signaling influences defense gene expression through epigenetic mechanisms involving histone modifications and DNA methylation. Calcium-dependent histone kinases phosphorylate histone proteins, leading to alterations in chromatin structure and accessibility, thereby modulating the expression of defense-related genes [25]. Moreover, calcium signaling regulates the activity of DNA methyltransferases and demethylases, influencing the methylation status of defense gene promoters and their transcriptional regulation [26]. These epigenetic modifications serve as molecular switches that fine-tune the responsiveness of defense genes to calcium signals and integrate them with other signaling pathways to optimize plant defense responses.

Understanding the intricate mechanisms by which calcium signaling regulates defense gene expression is crucial for engineering crop plants with enhanced resistance to pathogens and environmental stresses. Manipulating calcium signaling components and their downstream targets holds promise for developing novel strategies to improve crop yield and quality under challenging growing conditions.

2.5. Calcium signaling modulation by environmental stimuli

Environmental stimuli play a crucial role in modulating calcium signaling pathways in plants, thereby influencing their defense responses against various biotic and abiotic stresses. Abiotic factors such as light, temperature, water availability, and nutrient status, as well as biotic factors including pathogen infection and herbivore attack, can trigger changes in cytosolic calcium concentrations and the activation of calcium-dependent signaling cascades.

Light perception by photoreceptors such as phytochromes, cryptochromes, and phototropins initiates calcium signaling events that regulate various physiological processes, including stomatal movement, photomorphogenesis, and defense responses [27]. Calcium influx into guard cells mediates stomatal closure in response to blue light, thereby limiting pathogen entry and water loss from leaves. Moreover, light-induced calcium signals activate defense-related genes involved in the synthesis of secondary metabolites and antimicrobial proteins, enhancing plant resistance to pathogens.

Temperature fluctuations also influence calcium signaling dynamics in plants, with both heat stress and cold stress eliciting transient increases in cytosolic calcium levels. Calcium-dependent protein kinases (CDPKs) and calcium-binding proteins such as calmodulins and calmodulin-like proteins (CMLs) are implicated in temperature stress responses, regulating the expression of heat shock proteins and other stress-responsive genes to mitigate cellular damage [28]. Similarly, water deficit conditions induce calcium-dependent signaling pathways that mediate stomatal closure and the activation of stress-responsive transcription factors such as DREB and AREB, which regulate the expression of drought-responsive genes involved in water conservation and osmotic adjustment.

Pathogen infection and herbivore attack trigger rapid changes in cytosolic calcium concentrations, serving as secondary messengers that amplify defense signaling pathways. Calcium influx into the cytoplasm upon recognition of pathogen-associated molecular patterns (PAMPs) by pattern recognition receptors (PRRs) activates downstream immune responses, including the production of reactive oxygen species (ROS), the activation of defense-related genes, and the reinforcement of cell wall barriers [3]. Similarly, herbivore-induced calcium signals modulate the expression of defense genes and the biosynthesis of specialized metabolites that deter herbivory and attract natural enemies of herbivores.

Overall, the modulation of calcium signaling by environmental stimuli is central to the coordination of plant defense responses against diverse biotic and abiotic stresses. Understanding the molecular mechanisms underlying these interactions will facilitate the development of strategies to enhance plant resilience and productivity in changing environmental conditions.

3. Discussion

The elucidation of calcium signaling mechanisms in plant immunity has provided profound insights into the molecular basis of plant defense responses against pathogens and pests. By integrating calcium signaling with other signaling pathways and cellular processes, plants orchestrate a sophisticated defense strategy to combat biotic stresses. In this discussion, we delve into the implications of calcium signaling in plant immunity, highlighting its multifaceted roles and potential applications in crop protection and sustainable agriculture.

3.1. Role of calcium signaling in plant defense

Calcium signaling plays a pivotal role in plant defense responses against diverse pathogens, including bacteria, fungi, viruses, and nematodes. Upon pathogen recognition, plants activate calcium influx channels and calcium sensors, leading to rapid changes in cytosolic calcium levels and the initiation of downstream signaling cascades. Calcium-dependent protein kinases (CDPKs), calmodulins (CaMs), and calmodulin-like proteins (CMLs) are key components of calcium signaling pathways that regulate defense gene expression, reactive oxygen species (ROS) production, and programmed cell death (PCD) [29].

Furthermore, calcium signaling intersects with hormonal pathways, such as salicylic acid (SA), jasmonic acid (JA), ethylene, and abscisic acid (ABA), to coordinate plant immune responses. Crosstalk between calcium signaling and hormonal pathways fine-tunes defense gene expression, phytohormone biosynthesis, and stomatal closure, providing plants with flexibility and specificity in mounting defense responses tailored to different types of pathogens and environmental conditions [12].

3.2. Potential applications in crop protection

Understanding the intricacies of calcium signaling in plant immunity holds significant implications for crop protection and disease management strategies. Harnessing calcium signaling pathways through genetic engineering or exogenous elicitor treatments offers promising avenues for enhancing plant resistance to pathogens and pests. By modulating the expression of calcium sensors, ion channels, and downstream signaling components, researchers can engineer crops with improved disease resistance and stress tolerance [6].

Moreover, the identification of calcium channel blockers and calcium signaling inhibitors provides valuable tools for manipulating plant immune responses and mitigating the impact of biotic stresses on crop productivity. Targeted delivery of calcium antagonists or elicitor molecules to infected tissues or vulnerable plant organs can disrupt pathogen-induced calcium signaling events, thereby attenuating disease progression and minimizing yield losses [30].

4. Challenges and future directions

Despite significant progress in unraveling the complexities of calcium signaling in plant immunity, several challenges remain to be addressed. The elucidation of calcium signaling networks in non-model crops and under field conditions presents a formidable task due to the inherent complexities of agricultural ecosystems and the diverse array of interacting biotic and abiotic factors. Additionally, the potential pleiotropic effects of manipulating calcium signaling components on plant growth, development, and stress responses necessitate comprehensive risk assessment and optimization strategies to ensure the efficacy and safety of engineered crops.

Future research directions in this field may focus on exploring novel calcium signaling components and regulatory mechanisms underlying plant immune responses, as well as developing innovative biotechnological approaches for targeted manipulation of calcium signaling pathways in crops. Integration of omics technologies, advanced imaging techniques, and computational modeling will facilitate systems-level understanding of calcium signaling dynamics in planta and enable predictive modeling of plant-pathogen interactions under diverse environmental scenarios.

In conclusion, calcium signaling emerges as a central hub in plant immunity, orchestrating a myriad of defense responses to safeguard plant health and productivity. By unraveling the intricacies of calcium signaling networks and harnessing their potential for crop protection, researchers can pave the way for sustainable agriculture practices that promote food security and environmental resilience in the face of emerging biotic challenges.

5. Conclusion

In conclusion, calcium signaling plays a fundamental role in orchestrating plant immune responses against a diverse range of pathogens and pests. Through the activation of calcium-dependent signaling pathways, plants are able to perceive and respond to biotic stresses with precision and specificity. The integration of calcium signaling with hormonal pathways and other defense mechanisms provides plants with a sophisticated defense arsenal to combat pathogen invasion and minimize yield losses.

Furthermore, the elucidation of calcium signaling networks in plants has significant implications for crop protection and sustainable agriculture. By harnessing the potential of calcium signaling pathways through genetic engineering, exogenous elicitor treatments, and targeted delivery of calcium antagonists, researchers can develop novel strategies to enhance crop resistance to diseases and pests. These advancements hold promise for improving agricultural productivity, reducing dependency on chemical pesticides, and ensuring global food security in the face of evolving biotic challenges.

However, challenges such as understanding calcium signaling in non-model crops, assessing the potential pleiotropic effects of manipulating calcium signaling components, and optimizing biotechnological approaches for field application remain to be addressed. Future research endeavors should focus on unraveling novel calcium signaling components, elucidating regulatory mechanisms underlying plant immune responses, and developing innovative biotechnological solutions for crop protection.

In essence, the elucidation of calcium signaling pathways in plant immunity represents a cornerstone in the quest for sustainable agriculture practices that promote resilience, productivity, and environmental stewardship. By harnessing the power of calcium signaling, researchers can pave the way for a future where crops are better equipped to withstand biotic stresses, ensuring the stability and security of global food systems.

Conflict of interest: The authors declare no conflict of interest.

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