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RECENT ADVANCEMENTS OF PHYTOHORMONE-MEDIATED PLANT IMMUNITY AGAINST BIOTIC STRESSES

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Plants are continuously exposed to a variety of biotic stresses, including pathogenic microorganisms such as bacteria, fungi, viruses, and nematodes. To counter these threats, plants have evolved complex immune systems that allow them to recognize pathogens and trigger defense mechanisms. Central to this immune response is the regulation and coordination of various **phytohormones**—signaling molecules that play key roles in plant growth, development, and stress responses. Phytohormones, including salicylic acid (SA), jasmonic acid (JA), ethylene (ET), abscisic acid (ABA), auxin, gibberellin (GA), brassinosteroids (BR), and cytokinin (CK), participate in plant immune responses by regulating signaling networks and modulating gene expression. Recent advancements in the understanding of phytohormone-mediated defense mechanisms have highlighted the dynamic crosstalk among these signaling pathways. This viral narrative provides an overview of the role of various phytohormones in plant immunity against biotic stresses and discusses recent discoveries in the field.

Phytohormone Signaling in Plant Immunity

Phytohormones regulate plant immunity through two major mechanisms:

- **Pattern-triggered immunity (PTI):** The recognition of pathogen-associated molecular patterns (PAMPs) by plant cell-surface receptors, which results in basal defense responses.
- **Effector-triggered immunity (ETI):** The recognition of pathogen effectors by plant intracellular receptors, leading to a stronger and often faster immune response.

Salicylic Acid (SA) and Systemic Acquired Resistance (SAR)

SA plays a pivotal role in plant defense, particularly in resistance to biotrophic pathogens that rely on living host cells for nutrients. The SA signaling pathway is strongly associated with the establishment of **systemic acquired resistance (SAR)**, a long-lasting defense response activated by localized pathogen infection.

- **SA biosynthesis** is primarily initiated through the isochorismate pathway, with *Isochorismate synthase 1* (ICS1) being a key enzyme in its production.
- Once synthesized, SA activates transcription factors like **NPR1 (Non expressor of Pathogenesis-Related genes 1)**, which in turn induces the expression of pathogenesis-related (PR) genes.
- The defense response associated with SA is effective against many biotrophic and hemibiotrophic pathogens by promoting the accumulation of reactive oxygen species (ROS) and inducing localized cell death (the hypersensitive response, HR).

Recent studies have shed light on how SA interacts with other phytohormones such as JA and ABA. For example, SA often antagonizes the JA pathway, leading to enhanced defense against biotrophs while suppressing responses to necrotrophs (pathogens that kill host cells). This antagonism ensures that resources are allocated effectively to the appropriate defense mechanism based on the type of pathogen.

Jasmonic Acid (JA) and Ethylene (ET): Defense Against Necrotrophs and Herbivores

Jasmonic acid and ethylene play crucial roles in defense against necrotrophic pathogens and insect herbivores. Unlike biotrophs, necrotrophs kill host cells and feed on the dead tissue, so the plant's defense strategy involves strengthening cell walls, promoting tissue repair, and producing antimicrobial compounds.

- **JA signaling** is initiated when JA binds to the receptor **COI1 (Coronatine Insensitive 1)**, leading to the degradation of the repressor JAZ proteins, thereby activating JA-responsive genes.
- Ethylene, often in synergy with JA, triggers defense responses by activating specific transcription factors such as **ERF1 (Ethylene Response Factor 1)**, which upregulates the expression of genes involved in pathogen defense and insect resistance.

Recent advancements have revealed how JA and ET signaling pathways interact with SA, forming a regulatory network that allows plants to fine-tune their responses to different types of pathogens. For example, JA-ET signaling is often antagonistic to SA-mediated responses, and this balance determines whether a plant will prioritize defenses against necrotrophs or biotrophs.

Abscisic Acid (ABA): The Stress Hormone

ABA is traditionally known for its role in abiotic stress responses, particularly in regulating stomatal closure during drought. However, its role in biotic stress responses has gained attention in recent years. ABA can modulate plant immunity both positively and negatively, depending on the pathogen and environmental context.

- In some cases, ABA has been shown to **suppress defense responses**, particularly against necrotrophs and certain bacterial pathogens, by interfering with SA and JA signaling. For example, ABA inhibits SA-mediated defenses by inducing the expression of the repressor gene **WRKY40**, which negatively regulates immune responses.
- Conversely, ABA can enhance resistance to certain pathogens by promoting callose deposition at infection sites, which strengthens cell walls and restricts pathogen invasion.

Recent research has revealed that ABA signaling interacts with other stress-related pathways, including **calcium signaling** and **ROS production**, contributing to a nuanced and flexible immune response that integrates both abiotic and biotic signals.

Auxins, Gibberellins, Brassinosteroids, and Cytokinins: Modulators of Immunity

Other phytohormones, including auxins, gibberellins, brassinosteroids, and cytokinins, also play significant roles in modulating plant immunity. While their primary functions relate to plant growth and development, they can influence immune responses through complex signaling crosstalk.

- **Auxins (e.g., indole-3-acetic acid, IAA)**: Auxins are known to promote growth, but they can also modulate immune responses. Pathogens, particularly bacteria, often hijack auxin signaling to enhance virulence. For example, some bacterial pathogens produce auxin-like molecules that suppress SA-dependent defenses.
- **Gibberellins (GAs)**: GAs are growth-promoting hormones that can inhibit immune responses by destabilizing DELLA proteins, which are important repressors of growth and defense. However, DELLA proteins can also enhance JA signaling, creating a trade-off between growth and defense.
- **Brassinosteroids (BRs)**: BRs are primarily growth regulators, but recent studies have shown that they can enhance resistance to certain pathogens. BR signaling interacts with

both SA and JA pathways, indicating a role in fine-tuning immune responses.

- **Cytokinins (CKs)**: CKs are involved in cell division and differentiation but also play a role in defense. They can enhance resistance to certain pathogens by promoting the expression of defense-related genes.

Crosstalk Among Phytohormones: Fine-Tuning Immunity

A major theme in recent research on phytohormone-mediated plant immunity is the **crosstalk** between different signaling pathways. Phytohormones rarely act in isolation; instead, they form an intricate network of signaling interactions that allow plants to respond flexibly to diverse and often simultaneous stresses.

- **SA-JA Crosstalk**: As mentioned, SA and JA often act antagonistically, with SA promoting resistance to biotrophs and JA being more effective against necrotrophs and herbivores. The balance between these two pathways is crucial for determining the type of immune response.
- **ABA-JA Interaction**: ABA can suppress JA-mediated defenses in some cases, particularly under drought stress. This trade-off highlights how plants integrate signals from both abiotic and biotic stressors to optimize survival.
- **Hormonal Priming**: Recent research has focused on how plants "prime" their immune system through hormonal signaling. For example, exposure to low levels of certain phytohormones can prepare plants to mount a faster and stronger defense response upon subsequent pathogen attack.

Recent Advancements in Phytohormone-Mediated Immunity

Recent breakthroughs in molecular biology and genomics have led to significant advancements in our understanding of phytohormone-mediated plant immunity. Key developments include:

- **Transcriptomics and Proteomics**: High-throughput sequencing technologies have revealed the dynamic changes in gene expression and protein levels during phytohormone-mediated immune responses. These studies have identified new regulatory genes and signaling molecules involved in hormone crosstalk.
- **Gene Editing Technologies**: CRISPR/Cas9 and other gene-editing tools have enabled precise manipulation of phytohormone pathways, allowing researchers to dissect their roles in immunity and identify potential targets for improving disease resistance in crops.
- **Chemical Biology**: The use of small molecules to modulate phytohormone signaling pathways has opened new avenues for enhancing plant immunity. Synthetic analogs of SA, JA, and other hormones are being explored for their potential to prime plants for better resistance against pathogens.

Phytohormones are central to the regulation of plant immunity against biotic stresses, acting through a complex network of signaling pathways that interact with each other to fine-tune defense responses. Recent advancements in molecular biology, genomics, and chemical biology have deepened our understanding of these processes and opened new possibilities for enhancing crop resistance to pathogens. As research continues to uncover the intricacies of phytohormone crosstalk and signaling, it holds great promise for the development of more resilient agricultural systems capable of withstanding the challenges posed by biotic stressors.

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