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Phytohormones and plant defense

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Review paper

Abstract: Phytohormones, also known as plant growth regulators, regulate various physiological processes in plants, including germination, growth, and response to biotic and abiotic stresses. Plant diseases, caused by pathogens such as fungi, bacteria, and viruses, often alter hormonal pathways, leading to the simultaneous induction of antagonistic and synergistic hormones in plants. In resistant varieties, however, the hormonal responses follow a more sequential pattern. Plant hormone signaling pathways are primarily polarized along two antagonistic axes: the salicylic acid (SA) and jasmonic acid (JA) pathways on one side, and the ethylene pathway on the other. In addition to SA, JA, and ethylene, other growth regulators, such as auxins, brassinosteroids, cytokinins, and abscisic acid (ABA), also play significant roles in plant responses to biotic stress and are increasingly recognized for their importance in plant-pathogen interactions. Pathogens can modulate hormone biosynthesis and signaling to suppress plant defenses and alter the cellular environment, promoting their infection and proliferation. In this article, we will review the latest advances in understanding the function and regulation of plant hormones, the modulation of plant defense responses, and their synergistic and the crosstalk between phytohormones and defense pathways.

Keywords: Biotic stress, crosstalk, hormonal regulation, plant defense.

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Introduction

In nature, plants encounter a wide range of biological factors including fungi, bacteria, viruses, nematodes and other pathogens and pests that lead to various biotic stress responses.These factors, can cause diseases that lead to severe loss of crops productivity and quality. Their global reduction of agricultural productivity and economic losses threaten global food security and natural resources (Nawaz et al., 2023).

Therefore, understanding the natural defense mechanisms in plants to cope with stresses and controlling plant diseases is important for sustainable and eco-friendly exploitation of natural resources.The induction of defense responses to biotic and abiotic stresses through morphological, physiological, and biochemical mechanisms is regulated by plant hormones (Husen, 2021). Plants synthesize various hormones, including abscisic acid (ABA), gibberellic acid (GA), auxin, cytokinin (CK), salicylic acid (SA), jasmonic acid (JA), ethylene (ET), strigolactones (SL), and brassinosteroids (BR). Plant growth regulators, or phytohormones, are natural organic signaling molecules with low molecular weights (Husen, 2021). Phytohormones play a crucial role in regulating various growth and developmental processes, as well as controlling physiological responses, including defense mechanisms against stress in plants (Sutaoney et al., 2023).

The immune response activated by pathogen or insect attacks is regulated by the induced production of specific plant hormones. Salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and abscisic acid (ABA) are important regulators of inducible defense mechanisms (Dehkordi et al., 2018). The SA pathway is mainly induced by biotrophic pathogens and the JA pathway is mainly induced by necrotrophic pathogens and insect herbivores (Vos et al., 2013).

Some studies have highlighted the roles of abscisic acid (ABA), auxin, gibberellic acid (GA), cytokinin (CK), brassinosteroids (BR), and peptide hormones in plant defense signaling pathways (Bari and Jones, 2009; Nawaz et al., 2023).For an effective response to biological stresses, each hormone initiates a specific molecular pathway. These signaling pathways are integrated into a complex network of synergistic, antagonistic, and additive interactions, collectively referred to as hormonal crosstalk (Aerts et al., 2021). While the role of hormones in plant growth and their biosynthesis mechanisms is well established, this article aims to review recent advances in understanding the functions and regulation of plant hormones, their role in modulating plant defense responses, and the impacts of their synergistic and antagonistic interactions in various plant diseases.

Significance of Plant Defense Mechanisms

Plant health is a critical aspect of food security, yet it is constantly threatened by plant pathogens, which cause up to 40% of global crop production losses (Butt et al., 2020). The defense mechanisms of plants against pathogens are highly complex, relying on both innate immune systems and preformed defense structures.

The first line of defense in plants is passive and includes physical barriers such as the cuticle, wax, and trichomes, which serve to prevent the entry of pathogens and insects. Beyond these barriers, plants activate innate immune responses involving two levels of pathogen recognition (Checker et al., 2018). The first level involves pattern recognition receptors (PRRs) located on the plant cell surface. These receptors identify pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular patterns (MAMPs) (Saberi Riseh et al., 2022). This recognition triggers pattern-triggered immunity (PTI), which inhibits pathogen growth and colonization. However, some pathogens have evolved proteins capable of suppressing PTI, enabling further infection (Fu and Dong, 2013).

The second level of recognition relies on intracellular resistance (R) proteins, which can directly or indirectly detect specific pathogen effectors. This induces a more specialized and robust defense response known as effector-triggered immunity (ETI) (Saberi Riseh et al., 2022). ETI responses are faster and more potent than PTI and often lead to the formation of necrotic lesions at infection sites. These lesions restrict the pathogen's movement, effectively transforming a localized infection into a systemic defense response (Fu and Dong, 2013).

In general, both types of plant immune responses, PTI and ETI, activate similar defense mechanisms.

These include the production of reactive oxygen species (ROS), an increase in intracellular Ca^{2+} concentrations, activation of mitogen-activated protein kinases (MAPKs), upregulation of defense-related genes, and the production of antimicrobial compounds in damaged tissues (Checker et al., 2018).

Finally, the involvement of phytohormones in the regulation of plant biotic defense responses should not be ignored. ETI and PTI cause specific downstream signaling pathways, in which three phytohormones, SA, JA, and ET, are vital. SA pathways respond to biotrophic and hemibiotrophic pathogens and JA and ET pathways respond to necrotrophic agents and pests (De Vleesschauwer et al., 2014). SA provoke the SAR pathway that promotes the expression of PR genes, which confers tolerance to a wide range of pathogens (Dehkordi et al., 2018).

Phytohormones: Types and Functions

Phytohormones are biochemical compounds that exist in plants in very low concentrations. They play important regulatory roles in physiological processes, growth, plant development and plant response to biotic (Nawaz et al., 2023) and abiotic stresses (Haghpanah et al., 2024).

Phytohormones are traditionally divided into two groups: growth-stimulating and stress-related hormones. Growth stimulating hormones included gibberellins, cytokinins, auxins, brassinosteroids and strigolactones and stress/defense- related hormones included salicylic acid (SA), jasmonic acid (JA), ethylene (ET) and abscisic acid (ABA). However, in recent years, these divisions have become increasingly unclear, as more data become available indicating that the crosstalk between plant hormones during growth and stress responses is extensive, and that all hormones, regardless of their current name, play a role in defense of Plants (Gilroy and Breen, 2022).

Plant hormones also vary in their chemical nature and biological functions. In terms of chemical nature, they are derived from amino acids (IAA, ethylene, salicylic acid), lipids (jasmonic acid), isoprenoid (cytokinin, gibberellin, abscisic acid, brassinosteroids) (Madani et al., 2019) (Figure. 1).

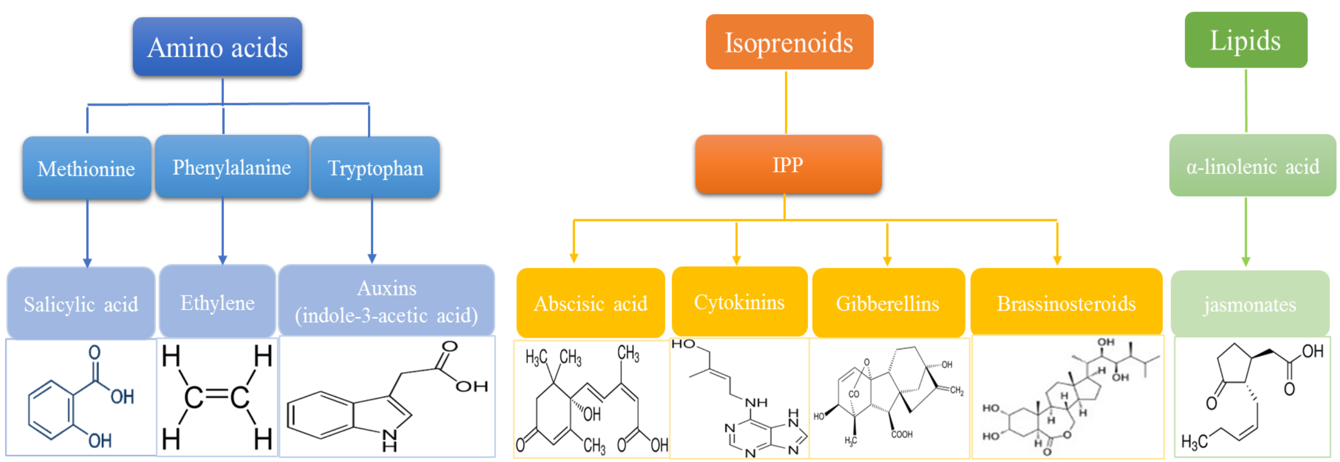

Figure 1. Types of phytohormones based on chemical structure and precursors of their biosynthesis (Base on Madani et al. 2019; Haghpanah et al. 2024 with some modifications).

Regulators of Plant Defense

Salicylic Acid (SA)

Salicylic acid (SA) is a crucial phytohormone involved in the regulation of plant immune responses, such as PTI, ETI, and systemic acquired resistance (SAR) (Kim et al., 2022; Li et al., 2022a). Upon pathogen attack, plants synthesize SA, which plays a central role in activating both local and systemic defense mechanisms. These defense responses include the synthesis of pathogenesis-related (PR) proteins, the accumulation of callose deposits, enzymatic and non-enzymatic antioxidants, and localized defense response (hypersensivity) that involves rapid, programmed cell death(Gomez‐Munoz et al., 2017).

SA's involvement in disease resistance is multifaceted. It regulates small interfering RNAs (siRNAs) and interacts with RNA silencing pathways to suppress viral replication, as seen in the resistance of sour orange to Citrus tristeza virus (Gomez‐Munoz et al., 2017). Additionally, mutations in the SA biosynthesis or signaling pathways can render plants more susceptible to viral infections, even in the presence of resistance (R) genes. On the other hand, overexpression of SA synthesis genes or exogenous SA application can enhance basal immunity by delaying viral infections (Li et al., 2022a).

SA's action is largely mediated by the NONEXPRESSOR OF PATHOGENESIS-RELATED GENES (NPR) family, with NPR1 being the key mediator of SA perception. Upon SA binding, NPR1 undergoes a conformational change, transitioning from an inactive oligomeric to an active monomeric form, which then translocates to the nucleus. There, NPR1 interacts with TGA transcription factors, activating defense-related genes, including those encoding PR proteins and WRKY transcription factors (Zhang and Li, 2019). Moreover, the regulation of SA signaling involves post-translational modifications, such as methylation and glycosylation, which can modulate its effects on plant immunity and growth (Vora et al., 2023).

Exogenous treatment with salicylic acid (SA) has been shown to enhance disease resistance by activating defense enzymes such as polyphenol oxidase, chitinase, and phenylalanine ammonia-lyase, while also boosting the expression of pathogenesis-related (PR) proteins. For instance, the application of SA in plants like tobacco has been shown to increase resistance to pathogens such as the tobacco mosaic virus (TMV) (Li et al., 2022a). However, the effect of SA on plant growth is concentration-dependent: lower concentrations promote growth, while higher concentrations inhibit it (Vora et al., 2023).

In summary, Salicylic acid (SA) is a key phytohormone in regulating plant immunity, playing an essential role in both local and systemic defense mechanisms. Upon pathogen attack, SA triggers the activation of immune responses, including the production of pathogenesis-related (PR) proteins, callose deposition, and hypersensitive responses, which restrict pathogen spread. SA mediates its effects through complex signaling pathways, primarily involving NPR1, TGA transcription factors, and siRNA pathways. Moreover, exogenous SA application has been shown to enhance disease resistance in plants such as tobacco, improving defense against pathogens like the *Tobacco mosaic virus* (TMV). However, its effects on plant growth are concentration-dependent, with lower concentrations promoting growth and higher concentrations inhibiting it. Understanding SA's role in plant immunity is crucial for developing strategies to improve crop protection and resistance against various pathogens (Gomez‐Munoz et al., 2017; Li et al., 2022a; Vora et al., 2023).

Jasmonic acid (JA):

Jasmonic acid (JA) is a key regulator in plant defense, particularly in response to biotic stressors such as herbivory and infections by necrotrophic pathogens. Upon wounding or insect attack, JA is synthesized and triggers various defense mechanisms, including the production of antimicrobial compounds. JA is known to function in antagonism to salicylic acid (SA)-mediated pathways, which are primarily involved in responses to biotrophic pathogens. This interaction between JA and SA helps plants to fine-tune their immune responses, ensuring an appropriate defense mechanism is activated depending on the nature of the pathogen or stress. Recent studies have highlighted the critical role of JA in modulating plant defenses and its crosstalk with other phytohormones, including SA, to enhance resistance to a broad range of threats (Vora et al., 2023).

For example, the response to wounding in tomato plants activates JA biosynthetic enzymes, leading to the expression of defense genes like proteinase inhibitors. This function is critical in establishing systemic induced resistance (SIR). JA promotes the synthesis of bioactive forms, such as jasmonyl-lisoleucine (JA-Ile), in both the damaged and healthy tissues of plants (Sutaoney et al., 2023; Vora et al., 2023). These hormones modulate the expression of resistance-related genes, initiating defense mechanisms through signaling pathways. The activation of JA responses is facilitated by proteins such as CORONATINE INSENSITIVE1 (COI1), JASMONATE ZIMDOMAIN (JAZ), and MYC2, which interact to regulate gene expression and activate defense systems by degrading JAZ repressors through the 26S proteasome pathway (Rubio et al., 2021; Li et al., 2022b).

Furthermore, jasmonic acid (JA) plays a key role in virus defense; its application during the early stages of viral infections, such as Potato virus Y (PVY) and Potato virus X (PVX), enhances resistance. However, in later stages of infection, JA may increase susceptibility, suggesting that the timing of JA application influences its effectiveness (García-Marcos et al., 2013). Additionally, research indicates that JA modulates the balance between its signaling and salicylic acid (SA) responses. Pretreatment with JA, followed by SA application, has been shown to enhance resistance to Tobacco mosaic virus (TMV) in Nicotiana benthamiana, although other studies suggest JA's indirect role in viral resistance, possibly by modulating SA-mediated resistance. This balance between JA and SA levels is crucial for determining the plant's resistance to various pathogens (García-Marcos et al., 2013; Zhu et al., 2014).

Furthermore, manipulation of JA signaling has been shown to influence pathogen dissemination in susceptible plant genotypes, highlighting the hormone's pivotal role in regulating plant defense mechanisms against both biotic and abiotic stresses.

Ethylene (ET):

Ethylene (ET) plays a critical role in plant immunity, particularly in the defense response to necrotrophic pathogens (Bürger and Chory, 2019). It is a central regulator of the plant immune signaling network, contributing to pattern-triggered immunity against biotrophic infections. ET also interacts with other hormones like auxin and jasmonic acid (JA), working together with JA to enhance defense responses against pathogens and herbivores (Ning et al., 2019). ET is perceived by several receptors, including ethylene response 1 (ETR1), ethylene response sensor 1 (ERS1), and ethylene insensitive 4 (EIN4), which are located in the endoplasmic reticulum (Vora et al., 2023). These receptors are histidine kinases that, upon activation, inhibit the downstream serine/threonine kinase, CONSTITUTIVE TRIPLE RESPONSE 1 (CTR1), and regulate ET signaling (Chen et al., 2021). Mutations in these receptors result in ET insensitivity and increased susceptibility to necrotrophic pathogens, highlighting the importance of ET in pathogen resistance.

Mutations in these receptors cause ET insensitivity and increase sensitivity to necrotrophic pathogens (Vora et al., 2023).

Ethylene influences plant defense mechanisms against various pathogens through both endogenous and exogenous pathways. During plant-pathogen interactions, a significant increase in endogenous ethylene synthesis occurs, activating defense-related genes such as L-PAL, 4-coumarate CoA ligase (4-CL), chalcone synthase (CHS), and hydroxyproline-rich glycoproteins (HRGP). Exogenous application of ET and its precursors has demonstrated a direct link between this volatile plant hormone and the activation of defense responses against pathogens (Sutaoney et al., 2023; Vora et al., 2023).

Modulators of Plant Defense

Abscisic acid (ABA):

ABA plays distinct roles in plant immunity depending on the infection stage and the pathogen involved. In the early stages of infection, ABA helps regulate plant defense by causing stomatal closure and inducing callose deposition. However, when activated at later stages, ABA can suppress ROS induction and inhibit SA or JA signaling pathways, thereby negatively affecting plant immunity (Bharath et al., 2021). ABA modulates plant immune responses and defense mechanisms depending on the type and lifestyle of the pathogen. For example, in *Arabidopsis thaliana*, ABA enhances resistance to the necrotrophic fungus *Alternaria brassicicola* but suppresses resistance to *Pseudomonas syringae* (Mohr and Cahill, 2003; García‐Andrade et al., 2011). Additionally, ABA increased resistance to *Cochliobolus miyabeanus* and enhanced susceptibility to *Magnaporthe oryzae* in Arabidopsis thaliana (Jiang et al., 2010). Studies have shown that interactions between *Tobacco mosaic virus* (TMV) and ABA affect ABA accumulation(Chen et al., 2021). Dehkordi et al. (2018) reported that ABA negatively influences the immune response in plants with resistance genes against viruses.

Cytokinin (CK):

Cytokinins play a significant role in enhancing resistance against biotrophic pathogens, often working in tandem with salicylic acid (SA) in its signaling pathway. The anti-biotrophic effect of cytokinins is reported to be both SA-dependent and dose-dependent. Various studies have highlighted the role of cytokinins in providing resistance against *Pseudomonas syringae* in Arabidopsis and tobacco (Choi et al., 2010). In contrast, research by Ma and Ma (2016) suggested that modulating the cytokinin pathway may actually suppress plant defense responses. Cytokinins are thus recognized as essential regulators in the complex interactions among plants, microbes, and insects, affecting both plant growth and defense mechanisms. Dehkordi et al. (2018) described, SA signaling is expected to activate the cytokinin response, potentially inducing resistance to *Plum pox* virus. The application of exogenous CK promoted the resistance against biotrophic and hemibiotrophic pathogens in rice and tobacco (Jiang et al., 2013).

Indole-3-acetic acid/Auxin

By interacting with other plant hormones, auxins play an important role in mediating responses to both biotic and abiotic stresses. While auxins generally promote plant growth, they have also been shown to weaken defense responses in certain situations. Studies indicate that exogenous application of auxins can exacerbate the severity of some plant diseases (Checker et al., 2018).

Auxin signaling interacts with various other phytohormone pathways, such as those of salicylic acid , jasmonic acid, and ethylene. Auxin and SA act in a mutually antagonistic manner, while auxin shares common functions with JA in plant defense mechanisms (Checker et al., 2018). Exogenous auxin treatments are known to increase pathogen severity and worsen disease outcomes. In the case of biotrophic pathogen infections, auxin signaling is typically suppressed, with the Aux/IAA repressor being stabilized by SA. This suppression is likely due to the synergistic role of auxin in enhancing JA-mediated resistance against necrotrophic pathogens (Vora et al., 2023).

Recent data highlight auxin's crucial role in the hormonal signaling network that governs plant defense against both biotrophic and necrotrophic infections. Auxin regulates the generation, degradation, and expression of genes involved in other hormone signaling pathways, in addition to developmental and defense responses (Gomes and Scortecci, 2021; Sutaoney et al., 2023). Interestingly, some pathogens themselves produce auxin or enhance its biosynthesis and accumulation during infection, influencing both plant defense and growth mechanisms (Checker et al., 2018).

Brassinosteroids (BRs):

Brassinosteroids play a role in controlling the plant's defense response against a wide range of microorganisms such as bacterial, viral and fungal diseases. BRs have long been known as a favorable modulator in plant resistance to disease, however, recent studies have shown different functions of BR in response to disease (Sutaoney et al., 2023). The use of these hormones in agriculture can increase productivity, improve resistance to plant diseases and reduce environmental stress.

BRs further regulate the antioxidant system by stimulating apoplastic H2O2 accumulation, thereby inducing stress tolerance in plants (Jiang et al., 2013). Application BR reduced the level of TMV and other biotrophs in tobacco plants (Hayat et al., 2011). Several pattern recognition receptors (PRRs) interact with receptor BRI1-associated kinase 1 (BAK1) in a ligand-dependent manner. BAK1 is known as a general regulator of plant immunity against some biotrophs and hemibiotrophs (Alazem and Lin, 2015). This group of hormones interacts with other phytohormones, especially auxin. A close relationship between BRs and auxin signaling has been seen. There is a strong synergy between auxins and BRs In addition, BRs are involved in the modulation of JA signaling and in JA-dependent plant defense response (Chaiwanon and Wang, 2015)

Crosstalk Between Phytohormones in Defense Pathways

When plants are simultaneously exposed to multiple pathogen stresses, hormone crosstalk becomes increasingly important. In recent decades, accumulating evidence has defined the role of various plant hormones in immunity and how they cooperate to coordinate the activation of the immune system through hormonal crosstalk. Hormone crosstalk is regulated at multiple levels, including protein stability, gene expression, transcriptional modification, protein modification, and hormone homeostasis (Ning et al., 2019; Aerts et al., 2021; Neil et al., 2021).

Phytohormones such as auxins, cytokinins, gibberellins, salicylic acid, jasmonic acid, ethylene , abscisic acid and brassinosteroids respond to stresses through crosstalk with signaling pathways (Figure. 2) (Checker et al., 2018; Aerts et al., 2021).

As the backbone of plant immune responses, plant signaling molecules SA, JA, and ET play a dominant role in inducible defense against microbial pathogens and herbivorous insects in a network of interconnected signaling pathways (Ning et al., 2019). While ABA, auxin, BR, GA, CK, and SL are involved in plant immune response through modulation.

Antagonistic interaction between the SA and JA pathways is the most common form and is studied, although large-scale additive and synergistic interactions have also been described (Hickman et al., 2019).

JA and SA signaling intersect negatively against necrotrophic pathogens and herbivores. NPR1 is a key intersecting in antagonistic crosstalk between SA and JA. SA and its functional analogs INA and BTH repress the expression of JA-responsive genes such as lipoxygenase 2 (LOX2), plant defensin 1.2, and vegetative storage protein (VSP), perhaps through inhibition of JA biosynthesis and action. The WRKY 70 transcription factor family also plays a prominent role in the antagonistic interactions of SA and JA. (Checker et al., 2018). Overexpression of the SA pathway, conferring resistance to a wide range of microbial pathogens can have deleterious effects on the JA/ET pathway. JA and ET have synergistic interactions and regulate the synthesis of genes encoding defense proteins, such as proteinase inhibitors and plant defensins.

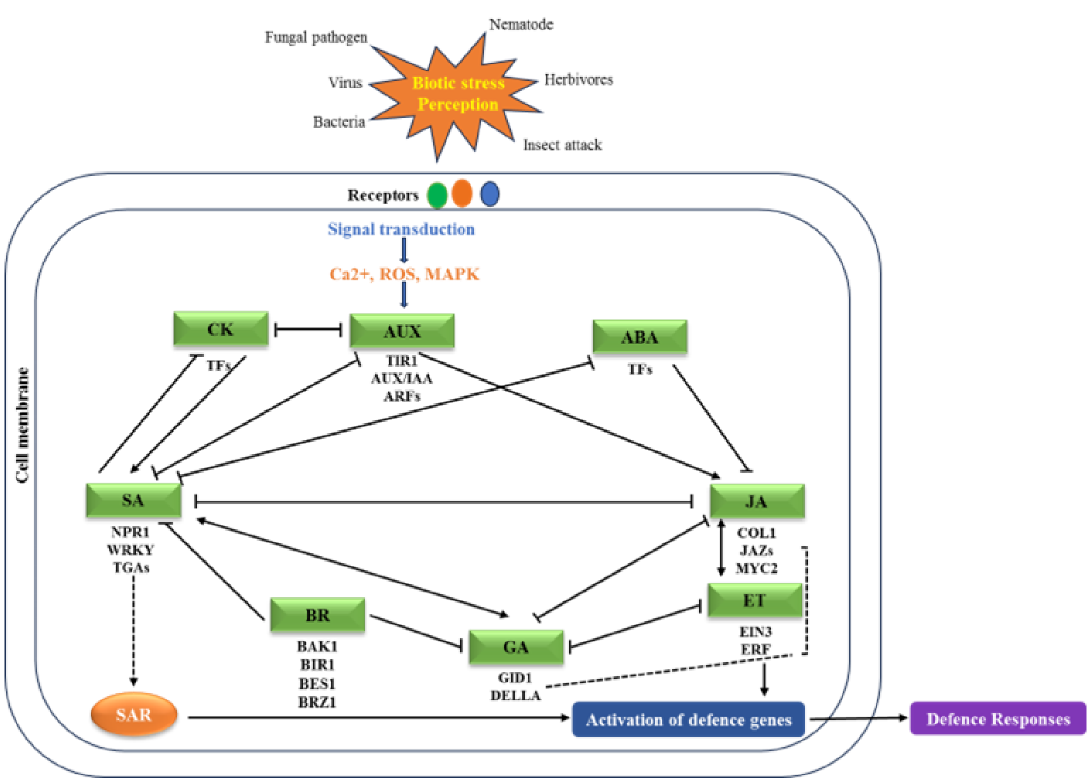

Figure 2. Scheme for plant hormone signaling networks and their crosstalk in stress responses (Shigenaga et al. 2017; Dehkordi-Nikbakht et al.2018).

In some cases, their cooperative action stimulates SA action, leading to increased PR gene (Checker et al., 2018). Studies have shown the key role of cytokinins in response to biotic stress. CK and SA signaling pathways converge to regulate plant defense, and SA defense responses are promoted by cytokinin-activated transcription factor (Reusche et al., 2013).

GA and JA also interact as DELLA proteins with key repressors of JA signaling, JAZ1, thereby preventing JA-mediated transcriptional repression. JA also regulates the expression of the GA1-3 (RGL3) suppressor, that positively regulates the JA-mediated response against necrotrophs by competing with MYC2 (Checker et al., 2018).

The crosstalk between pathways provides great regulatory potential to activate multiple resistance mechanisms in different combinations and may help the plant to prioritize the activation of a particular defense pathway over another. The effects of crosstalk between pathways may have a large impact on crop plants, providing better resistance against pathogens and insects in plants that are manipulated through genetic engineering of defense pathways or through the use of chemical plant protection agents that mimic the function of specific defense signaling molecules.Table 1 shows some of the antagonistic or synergistic interactions between plant hormones that contribute to plant immunity.

Table 1. Interactions between plant hormones that contribute to plant immunity.

Hormone Crosstalk	Interaction	Species	Reference
SA -JA/ET	Antagonistic	Various monocot and eudicot species	Thaler et al. 2012
SA-JA	Antagonistic	*Arabidopsis thaliana* wheat Maize *Oryza sativa*	Ding et al. 2016; Gorman et al. 2020, Huang et al. 2023; An et al. 2022
SA - CK	Synergistic	*Oryza sativa*	Jiang et al. 2013
ET- CK	Antagonistic	wheat	Veselova et al. 2021
JA-CK	Synergistic	*Oryza sativa*	Zhang et al. 2022
ABA -SA	Antagonistic	*Oryza sativa*	Xu et al. 2013
GA -JA/ET	Antagonistic	*Arabidopsis thaliana*	Hou et al. 2010
CK-AUX	Antagonistic	*Arabidopsis thaliana*	Naseem et al. 2014
BR-SA	Synergistic	*Arabidopsis*	Kim et al. 2022
BR-JA	Antagonistic	*Arabidopsis thaliana*	Liao et al. 2020
BR-ET	Synergistic	*Nicotiana benthamiana*	Xiong et al. 2020

Conclusion

Although chemical control agents can effectively combat plant pathogens, they pose severe environmental risks. Therefore, the use of efficient and effective solutions compatible with the environment and human health are promising alternatives to fight pathogens. One of the promising strategies for pathogen control is the use of plant hormones. The exogenous application of phytohormones significantly reduces the damage caused by various pathogens, both directly and through the activation of defense and antioxidant responses in different plant organs.

Over the past years, the understanding of the importance of hormonal regulation in plants under stress and hormonal signaling pathways has improved dramatically. Also, many efforts have been made to develop crops resistant to pathogenic agents and to understand different mechanisms of tolerance to these agents. However, more research is needed to elucidate the effect of different plant hormones on different crops and to better understand the complex molecular processes that control hormonal signaling and phytohormone-mediated defense responses to develop successful crop engineering programs for resistance against diseases and pests in the future tense. Due to their high level of complexity, many of the underlying molecular mechanisms by which phytohormones induce stress tolerance in crops are poorly understood and require further study. In addition, the crosstalk among the phytohormones and the basic mechanisms of the role of molecular components in hormonal crosstalk against stress are not yet fully understood due to their complexity and need further investigation. Since the crosstalk among phytohormones regulates the balance between plant growth and defense resistance, further molecular and genetic studies will expand our understanding of the underlying mechanisms of hormonal crosstalk in modulating plant growth and development under stress conditions.

In recent years, scientists have been trying to understand the mechanisms of resistance to pathogenic agents in plants through the exogenous application of phytohormones and genetic manipulation. Despite these important advances, some problems still need to be addressed, such as plant growth stage and cell metabolism during development, which are directly related to plant stress response under unfavorable conditions. Therefore, it is essential to investigate the crosstalk between plant growth stages and response to pathogen in hormonal biosynthesis and hormone signaling networks under stress conditions.

Supplementary Materials

No supplementary material is available for this article.

Author Contributions

Conceptualization; A.N.D and P.M.G., writing original draft, investigation, reviewing and editing; A.N.D, supervision; A.N.D All authors listed have made substantial, direct, and intellectual contributions to the work and have approved it for publication. All data were generated in-house, and no paper mill was used. All authors agree to be accountable for all aspects of work ensuring integrity and accuracy.

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Conflict of Interest Statement

The authors declare no conflict of interest.

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مقاله مروری

فیتوهورمون‌ها و دفاع گیاهی

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چکیده: هورمون‌های گیاهی فرآیندهای فیزیولوژیکی مختلفی را در گیاهان تنظیم می‌کنند، از جمله جوانه‌زنی، رشد و واکنش‌ها به تنش‌های زیستی و غیر زیستی. بیماری‌های گیاهی که توسط پاتوژن‌هایی همچون قارچ‌ها، باکتری‌ها و ویروس‌ها ایجاد می‌شوند، اغلب مسیرهای هورمونی گیاهان را تغییر داده و منجر به مهار و یا تقویت همزمان هورمون‌ها در گیاهان می‌شوند. در واریته‌های مقاوم، با این حال، واکنش‌های هورمونی الگوی با آرایش‌تری دارند. مسیرهای سیگنال‌دهی هورمون‌های گیاهی عمدتاً در دو سوی متفاوت برنامه ریزی شده‌اند: مسیرهای اسید سالیسیلیک (SA) و اسید جاسمونیک (JA) از یک طرف و مسیر اتیلن از طرف دیگر. علاوه بر سالیسیلیک، جاسمونیک و اتیلن، هورمون‌های دیگری همچون اکسین‌ها، براسینوستروئیدها، سیتوکینین‌ها و اسید آبسیزیک (ABA) نیز نقش‌های مهمی در واکنش‌های گیاه به تنش‌های زیستی ایفا می‌کنند و به طور فزاینده‌ای به دلیل اهمیت‌شان در تعاملات گیاه-پاتوژن شناخته شده‌اند. پاتوژن‌ها می‌توانند این مسیرهای هورمونی را دستکاری کرده تا دفاع‌های گیاهی را سرکوب کرده که این امر موجب تسهیل آلودگی و گسترش آن می‌شود. در این مقاله، آخرین پیشرفت‌ها در درک عملکرد و تنظیم هورمون‌های گیاهی، پاسخ‌های دفاعی گیاهان و آثار متقابل بین هورمون‌های گیاهی در مسیرهای دفاعی بررسی خواهد شد.

کلمات کلیدی: اثر متقابل، تنش زیستی، تنظیم هورمونی، دفاع گیاه.

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