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MOLECULAR INSIGHTS INTO PLANT HORMONE SIGNALING UNRAVELING THE GENETIC FOUNDATIONS OF GROWTH, DEVELOPMENT, AND STRESS RESPONSES UNDER CLIMATE CHANGE

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Abstract *Intricate biological signaling systems control vegetation growth, progress, and reactions to ecological stressors. This review intends to thoroughly delve into our existing comprehension concerning the molecular processes and genetic factors involved in these pathways, including various plant hormones. Significant attention will be accorded to critical hormones such as auxins, gibberellins, cytokinins, abscisic acid, ethylene, and jasmonates. It explores how these routes intersect and collaborate for managing physiological aspects of plants like growth efficiency or resilience against unfavorable conditions, which is also covered here. We can now amplify this by using recent developments in genetics, gene atlas, and cell biology, which have unveiled complicated operations linked with hormone reception, hormone-transmitted signal mechanisms, and following gene stimulation activities seen after that. This review will explore these advances and highlight the interplay between these processes. The emerging role of small regulatory RNAs and epigenetic modifications in modulating hormone responses will also be discussed. Understanding these complex molecular mechanisms is significant for sustainable agriculture, climate resilience, and overall plant well-being. By unraveling these processes, researchers can potentially manipulate plant traits to enhance productivity, improve stress tolerance, and contribute to developing more resilient crops. This knowledge will have implications for addressing global challenges such as food security and climate change.*

Keywords: *hormones; epigenetic modifications, molecular mechanisms, food security, climate change*

1. Introduction

Recently, there has been growing concern about food security and nutrition, primarily due to the challenges posed by changing climatic conditions and the need to sustain a rapidly expanding global population (Abbas et al., 2015). As a result, there is a pressing need to understand better various plant metabolic processes to enhance their yield (Hasanuzzaman et al., 2020). Abiotic stresses, driven by climate variations, have emerged as critical factors affecting crop productivity. These stresses encompass a wide range of adverse conditions, including salinity, drought, heavy metal toxicity, nutrient imbalances, and temperature fluctuations, all of which significantly disrupt plants' normal physiology, development, and yield. Abiotic stressors disrupt various physiological processes in plants and their overall metabolic well-being, leading to a substantial increase in the production of reactive oxygen species (ROS), which can damage proteins, lipids, and ultimately result in cell death (Mittler, 2002). While plants have evolved several defense mechanisms to cope with different abiotic stresses, prolonged exposure to such stress conditions can overwhelm these protective pathways. Consequently, alternative resistance mechanisms are being explored, including applying specific substances externally to enhance a plant's ability to tolerate stress (Grassmann et al., 2002).

Vital growth control, development regulation and environmental response in plants are largely guided by plant hormones (Ryu & Cho, 2015). These hormones function through complex signaling networks encompassing hormone perception, signal transduction, and transcriptional regulation (Razem et al., 2006). This article aims to provide an overview of recent advancements in understanding of the molecular intricacies of major plant hormone pathways. Through recent advancements in genetics, researchers have made significant progress in unraveling the interplay between hormone perception, signal transduction, and downstream gene expression (Chen et al., 2005). Moreover, emerging research has highlighted the role of small regulatory RNAs (Irfan et al., 2023) and epigenetic modifications in modulating hormone responses (Yamamuro et al., 2016). Understanding these intricate molecular mechanisms is of utmost importance for various applications in agriculture (Sami et al., 2024). By deciphering the complexities of hormone pathways, scientists can harness plant traits vital for sustainable agriculture, climate resilience, and overall plant well-being (A Sami, MZ HAIDER, MW MEERAN, et al., 2023). In conclusion, plant hormones act as pivotal regulators of growth, development, and responses to environmental cues (Slovak et al., 2016). Recent advancements in genetics, genomics, and molecular biology have highlighted the intricate molecular mechanisms underlying major plant hormone pathways. Unraveling these mechanisms holds great potential for improving sustainable agriculture, enhancing climate resilience, and promoting overall plant health (Backer et al., 2018).

2. Auxin Signaling

2.1. Auxin Perception

Process commences with the acknowledgment of auxin through dedicated receptors. The major auxin receptor group in plants is the TIR1/AFB group (Transport Inhibitor Response 1/Auxin Signaling F-Box Proteins). These receptors form a crucial component of the SCF (SKP1-Cullin-F-box) E3 ubiquitin ligase complex (Quint & Gray, 2006).

2.2. Auxin Binding and Co-receptor Interaction

Auxin forms a connection with the receptor proteins TIR1/AFB in the presence of auxin. This connection enables the interaction between the TIR1/AFB receptor and the AUX/IAA (Auxin/Indole-3-Acetic Acid) proteins, which act as transcriptional repressors. AUX/IAA proteins continuously suppress the activity of genes responsive to auxin.

2.3. Proteasomal Degradation of AUX/IAA Repressors

When the auxin-bound receptor engages with the AUX/IAA proteins, it triggers the polyubiquitination of the AUX/IAA proteins through the SCF complex. This ubiquitination signals the degradation of the AUX/IAA repressors through the 26S proteasome.

2.4. Release of Auxin Response Factors (ARFs)

The degradation of AUX/IAA proteins relieves their repression on Auxin Response Factor (ARF) transcription factors. ARFs are key regulators of auxin-responsive gene expression. Upon derepression, ARFs can activate or repress the expression of target genes involved in various auxin-mediated processes (Hayashi, 2012).

2.5. Activation of Gene Expression

Activated ARFs bind to auxin response elements (AuxREs) within the promoters of target genes. This binding leads to the activation or repression of gene transcription, depending on the specific ARF and the context of the target gene (Dharmasiri & Estelle, 2004).

2.6. Auxin Transport and Polar Transport

In the realm of plant biology, a hormone called auxin holds significant power over the growth and development of plants. Auxin can exert its influence through the complex workings of polar auxin transport, which involves PIN proteins and ABCB transporters. This hormone has a hand in a multitude of plant processes, including cell division and elongation, the establishment of root architecture, the suppression of lateral bud growth in favor of the main shoot tip (known as apical dominance), and the control of tropisms such as phototropism and gravitropism. But auxin's reach extends even further, as it is also crucial for tasks like vascular tissue differentiation, embryonic development, the initiation of organs, and the growth and ripening of fruit. And as if that wasn't enough, auxin interacts with other plant hormones like cytokinins, gibberellins, abscisic acid, ethylene, and jasmonates, further adding to its role in the intricate processes that govern plant growth and development (Zerrouk et al., 2020).

3. Gibberellin Signaling

Gibberellins regulate diverse processes, such as seed germination, stem elongation, and flower development.

3.1. Gibberellin Biosynthesis

Gibberellins are initially synthesized in plastids from geranylgeranyl diphosphate (GGDP), a precursor of the terpenoid pathway. The key enzyme in gibberellin biosynthesis is ent-kaurene synthase (KS), which converts GGDP to ent-kaurene. This precursor molecule is then modified through several steps to produce various active gibberellins (Hartweck, 2008).

3.2. Gibberellin Perception

Gibberellin signaling begins with the perception of active gibberellins by a class of receptor proteins called GID1 (Gibberellin Insensitive Dwarf 1). GID1 proteins are soluble receptors located in the cytoplasm. When gibberellins bind to GID1, it induces a conformational change in the receptor (AHMAD et al., 2023a).

3.3. Destruction of DELLA Repressors

The conformational change in GID1 upon gibberellin binding allows it to interact with DELLA proteins, which are negative regulators of gibberellin signaling. DELLA proteins suppress growth and development by interacting with transcription factors and inhibiting their activity. When gibberellin-bound GID1 interacts with DELLA proteins, it triggers the ubiquitination and subsequent degradation of DELLA proteins via the proteasome pathway (Wu et al., 2021).

3.4. Activation of Transcription Factors

With the removal of DELLA repressors, the transcription factors inhibited by DELLA proteins are now free to activate downstream gene expression. These transcription factors are part of the basic leucine zipper (bZIP) family, known as the Growth-Regulating Factors (GRFs) (Middleton et al., 2012).

3.5. Expression of Gibberellin-Responsive Genes

The activated GRFs induce the expression of gibberellin-responsive genes involved in various physiological processes. These genes include those related to cell expansion, division, elongation, and differentiation (Richards et al., 2001).

4. Cytokinin Signaling

Cytokinin signaling is a crucial biochemical process in plants that involves the transmission of signals triggered by cytokinin hormones. Cytokinins are a class of plant growth regulators or hormones that play a necessary role in plant development and growth, including cell division, shoot initiation, leaf senescence, nutrient uptake, and more (Ferreira & Kieber, 2005).

4.1. Cytokinin Perception

Cytokinin receptors are typically histidine kinases that are located on the plasma membrane. When a cytokinin molecule binds to its receptor, it triggers autophosphorylation of the receptor's histidine.

4.2. Histidine Phosphotransfer

The phosphorylated receptor transfers the phosphoryl group to a histidine-containing phosphotransfer protein (HPt).

4.3. Histidine-Containing Phosphotransfer Protein (HPt)

HPt proteins act as molecular messengers, shuttling the phosphoryl group from the cytokinin receptor to the next component in the pathway.

4.4. Response Regulator (RR) Activation

The phosphoryl group is ultimately transferred to a response regulator protein (RR), typically located in the nucleus. Phosphorylation of the response regulator reflects a conformational change that allows it to work as a transcription factor (Hutchison et al., 2006) (HUSSAIN et al., 2023).

4.5. Gene Expression Regulation

Once activated, the phosphorylated response regulator translocates into the nucleus and binds to specific DNA sequences in the promoter regions of target genes. This binding influences the transcription of these target genes, leading to changes in various cellular processes.

4.6. Downstream Effects

The altered gene expression patterns triggered by cytokinin signaling lead to various physiological responses, such as cell division, differentiation, shoot growth, root development, and stress (Greenboim-Wainberg et al., 2005).

5. Abscisic Acid (ABA) Signaling

Abscisic acid (ABA) is an elemental constituent in facilitating stress reactions, monitoring seed dormancy, and governing stomatal regulation. Our investigation investigates understanding ABA discernment utilizing PYR/PYL/RCAR receptor implements alongside subsequent protein phosphatases. The interactional discourse intertwining ABA with various hormones during periods necessitating abiotic stress adaptation commands significant consideration (Zhang, 2014).

5.1. ABA Perception

ABA receptors, known as PYRABACTIN RESISTANCE1 (PYR1)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR), are located in the cytoplasm.

In the absence of ABA, PP2Cs (Type 2C protein phosphatases) are active and maintain SnRK2 (sucrose non-fermenting 1-related protein kinase 2) kinases in an inactive state (Guo et al., 2011).

5.2. ABA Binding and Inhibition of PP2Cs

When ABA is present, it binds to the ABA receptors (PYR/PYL/RCAR proteins), leading to a conformational change in the receptors. This conformational change allows the receptors to bind to and inhibit PP2Cs, negative regulators of the ABA signaling pathway. Inhibition of PP2Cs releases the repression of SnRK2 kinases (Hirayama & Umezawa, 2010).

5.3. Activation of SnRK2 Kinases

SnRK2 kinases are activated through autophosphorylation in response to the inhibition of PP2Cs. Activated SnRK2 kinases become phosphorylated and can then phosphorylate downstream target proteins.

5.4. ABF/AREB Transcription Factors Phosphorylation

One of the main targets of activated SnRK2 kinases is the ABF/AREB family of transcription factors (ABA-responsive element-binding factors).

SnRK2-mediated phosphorylation activates ABF/AREB transcription factors, allowing them to bind to ABA-responsive elements (ABREs) in the promoters of target genes (Muñiz García et al., 2012) (Haider et al., 2023).

5.5. Gene Expression Regulation

ABF/AREB transcription factors bound to ABREs in gene promoters activate the transcription of various ABA-responsive genes.

These genes encode proteins that are involved in stress responses, including enzymes, osmolyte biosynthesis, protective proteins, ion transporters, and other reagents that help the plant withstand stress conditions (Tang et al., 2012) (AHMAD et al., 2023b).

5.6. Stomatal Closure and Osmotic Regulation

ABA signaling plays a key role in regulating stomatal closure. ABA-induced activation of SnRK2 kinases leads to stomata closure to reduce water loss through transpiration.

ABA also triggers the accumulation of osmolytes, such as proline, and other compatible solutes that help maintain cellular osmotic balance during stress (Adnan Sami et al., 2023)

5.7. Other Physiological Responses

ABA influences growth and development by modulating root growth, seed germination, and leaf senescence. It regulates seed dormancy, inhibiting germination until conditions are favorable for seedling establishment. ABA can also induce expression of LEA (late embryogenesis abundant) proteins involved in desiccation tolerance (A Sami, MZ Haider, M Imran, et al., 2023).

5.8. Crosstalk with Other Signaling Pathways

ABA signaling interacts with other hormone pathways, such as those involving auxins, cytokinins, and gibberellins, to integrate responses to different environmental stimuli.

6. Ethylene Signaling

Ethylene controls senescence, fruit ripening, and responses to biotic stress. Our review examines the ethylene receptor family and the intricate regulation of EIN3/EIL transcription factors. We discuss how ethylene interacts with other hormones, such as jasmonates, to coordinate defense responses (Cao et al., 2008).

6.1. Ethylene Perception

Ethylene, an aerosol plant hormone, plays a crucial part in multiple facets of the vegetative growth cycle and its defensive response to strain. This perception of Ethylene initiates with binding operations between ethylene itself and related receptors - these essential components of proteins are ensconced within the cell's endoplasmic reticulum membrane (He et al., 2022).

6.2. Activation of CTR1 Kinase

Active ethylene receptors inhibit the function of the constitutive triple response 1 (CTR1) kinase, an important factor that controls the ethylene signaling pathway. Without ethylene present, CTR1 phosphorylates and hampers the activity of the ethylene response factor (ERF) transcription factors (Stepanova & Ecker, 2000).

6.3. Inactivation of CTR1 Kinase

When ethylene binds to its receptors, CTR1 kinase activity is inhibited, initiating the subsequent steps of the signaling pathway.

6.4. Degradation of EIN2 Proteins

The inactivation of CTR1 results in the accumulation of the EIN2 protein (ethylene insensitive 2), which is normally targeted for proteasomal degradation by CTR1. The accumulation of EIN2 is a key step in transmitting the ethylene signal (Muñiz García et al., 2012.

6.5. Release of EIN2 and Activation of EIN3/EIL Transcription Factors

EIN2 acts as a positive regulator by preventing EIN3/EIL (ethylene insensitive 3/ethylene insensitive-like) transcription factors from degrading. EIN3/EIL transcription factors are stable and accumulate in the nucleus in response to ethylene signaling.

6.6. Gene Expression Regulation

EIN3/EIL transcription factors function as master regulators of ethylene-responsive gene expression. They bind to specific DNA sequences in the promoters of target genes known as ethylene response elements (EREs). The binding of EIN3/EIL to EREs leads to the activation of a wide range of ethylene-responsive genes, including those involved in the ethylene-induced triple response, stress responses, senescence, and fruit ripening (A Sami, MZ Haider, M Imran, et al., 2023).

6.7. Physiological Responses

The ethylene-induced triple response is a classic ethylene response that includes shortening and thickening of stems, radial swelling of the root, and curvature of the apical hook in seedlings. Ethylene also regulates various developmental processes, such as root hair development, fruit ripening, leaf senescence, and flower development.

6.8. Interplay with Other Hormones

Ethylene signaling interacts with other hormonal pathways, including auxins, gibberellins, and abscisic acid, coordinate plant responses to different environmental cues.

6.9. Feedback Regulation

Ethylene signaling is subject to negative feedback regulation to prevent excessive ethylene responses. EIN3/EIL transcription factors induce the expression of genes encoding ethylene biosynthetic enzymes, reducing ethylene production when the response is initiated.

7. Jasmonate Signaling

Jasmonates regulate defense against herbivores and pathogens, as well as reproductive processes. We delve into jasmonate perception, involving COI1 receptors and downstream transcriptional regulation through JAZ repressor proteins. The interplay between jasmonates and other hormones, such as salicylic acid, is explored (Zhang, 2014).

8. Conclusion

By unraveling the genetic foundations of plant hormone signaling, we pave the way for innovative strategies to enhance crop yield, stress resilience, and sustainable agriculture. Integrating molecular insights from diverse hormonal pathways holds promise for addressing global agricultural challenges and ensuring food security in a changing climate. The review synthesizes how plant hormone pathways intersect and collaborate, enabling plants to fine-tune their responses to complex environments. Hormonal debate, including antagonistic and synergistic interactions, is determined in the context of growth, development, and stress response. Recent insights into the role of epigenetic modifications and small regulatory RNAs in shaping hormone responses are discussed. We highlight the impact of chromatin remodeling and microRNAs on hormone-related gene expression.

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Declaration

Conflict of interest

The researchers affirm that there were no financial or commercial ties that might be seen as a potential conflict of interest throughout the research's execution.

Data Availability statement

All data generated or analyzed during the study have been included in the manuscript.

Ethics approval and consent to participate

These aspects are not applicable in this research.

Consent for publication

Not applicable

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