The Dynamics of Auxin in Plant Growth

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Abstract

Auxin, a paramount plant hormone, holds pivotal importance in orchestrating fundamental aspects of plant growth and development. Its influence spans critical functions such as cell elongation, root and shoot patterning, vascular differentiation, and tropic responses. The significance of auxin lies in its ability to regulate gene expression, thereby governing diverse physiological processes essential for plant life. At the core of auxin signalling is the intricate interplay between the auxin receptor complex TIR1/AFB, the Aux/IAA transcriptional repressors, and the ARF transcription factors. This cascade of events culminates in genome-wide transcriptional responses, dictating the plant's response to environmental stimuli and shaping its architectural framework. The context-specificity of auxin responses, governed by diverse TIR1/AFB co-receptor pairs, underscores its crucial role as a master regulator in the dynamic landscape of plant biology.

Keywords: Auxin, Plant hormone, Cell elongation, Tropism, Signaling.

1. Introduction

Darwin (1880) hypothesized the presence of a signal that was carried from the tip of the coleoptile to the bending regions lower down, at the time when he made his initial observations on the phototropism of grass

coleoptiles. Went in the Netherlands was eventually able to isolate the chemical by diffusion from coleoptile tips into agar blocks after multiple workers further characterized the signal's movement. These blocks, when replaced on the tips of decapitated coleoptiles, stimulated the growth of the decapitated coleoptiles and caused them to bend when placed asymmetrically on these tips. This revealed the presence of a growth-promoting substance that was produced at the tips of the coleoptiles, transported basipetally, and, when dispersed asymmetrically, caused the coleoptile to bend away from the side where the concentration was higher. Went originally gave this material the name *Wuchsstoff*, which was eventually altered to *auxin*. The substance was ultimately determined to be the straightforward chemical indoleacetic acid, or IAA, after several incorrect identifications (Wildman 1997).

The relevance of auxin is highlighted by the fact that it is involved in virtually every cellular decision made during plant development as well as reactions to environmental factors, abiotic stress, and growth tropisms. Auxin biology has advanced significantly in recent years, especially with regard to *Arabidopsis thaliana*, and the elements and mechanisms of auxin sensing and response have been largely clarified. (Abel and Theologis 2010).

2. Biosynthesis

Auxins are low molecular weight organic acids with an aromatic ring and a carboxyl group that must be 0.55 Å apart in order for them to be active. IAA is the most prevalent endogenous auxin and can perform the majority of auxin functions necessary for plant development and environmental response. Only three other naturally occurring chemicals with auxin activity have been identified in plants, namely phenylacetic acid (PAA), 4-chloroindole-3-acetic acid (4-Cl-IAA), and indole-3-butyric acid (IBA).

These molecules complement IAA. They have been found in conjugated and free acid forms (Sauer et al. 2013).

Over the past few years, genetic, biochemical and molecular studies have greatly advanced our understanding of auxin biosynthesis. Indole-3-acetic acid (IAA), plant auxin, is essential for the growth and development of plants. The Trp-dependent (TD) and Trp-independent (TI) pathways are the two main methods suggested for plants to synthesise IAA. Indole-3-acetamide, indole-3-pyruvic acid, tryptamine, and indole-3-acetaldoxime are the four TD routes that have been theorised, identified, and widely researched. Auxin production pathways in some bacteria are remarkably comparable to those in plants, showing conserved biosynthetic mechanisms (Di et al. 2016).

Auxin plays a pivotal role in regulating crucial aspects of plant growth and development, encompassing cell division, elongation, tropisms, apical dominance, senescence, blooming, and stress response (Yang et al. 2014). The three primary auxins in plants are IAA, 4-Cl-IAA, and PAA, with IAA being the most abundant and significant (Simon and Petrasek 2011). Maintaining auxin homeostasis is vital for normal plant development, achieved through the control of auxin transport, production, and conversion. Plant species employ both tryptophan-dependent (TD) and tryptophan-independent (TI) pathways for auxin biosynthesis, including the IAM, IPyA, TAM, and IAOx pathways (Woodward and Bartel 2005; Chandler 2009). Abiotic factors such as temperature and wounding cooperatively regulate free IAA levels, while recent research has identified enzymes and regulators, particularly in the IPyA pathway, contributing to the active regulation of auxin biosynthesis (Reverberi et al. 2005).

2.1 L-Trp biosynthesis pathway in plants

Plant cells synthesize Trp from chorismate via indole-3- glycerol phosphate (IGP) in the chloroplast (Radwanski and Last 1995). This process includes six critical steps. Anthranilate synthase (AS), a rate-limiting step in Trp biosynthesis, is catalysed by the WEI2/ASA1 and WEI7/ASB1 genes in *Arabidopsis thaliana*. AS catalyses the conversion of chorismate to anthranilate. While the β subunit transfers an amino group from glutamine, the α subunit attaches to chorismate and catalyses its aromatization. Anthranilate is converted to 1-(O-carboxylphenylamino)-1-deoxyribulose-5-phosphate, which is also called CdRP by phosphoribosylanthranilate transferase (PAT1) and phosphoribosylanthranilate isomerase (PAI1/2/3). CdRP is then catalyzed by indole glycerol phosphate synthase (IGS) into IGP. IGP is a branch point that can lead to TI auxin synthesis directly from indole (Mano and Nemoto 2012). IGP is converted by the Trp synthase to make trp (Last et al. 1991).

2.2 Trp-dependent IAA biosynthesis pathways

The IAM pipeline, IPyA pathway, IAOx pathway, and TAM pathway are the four currently recognised TD pathways of IAA biosynthesis. Genes involved in the manufacture of Trp derivatives and well-known intermediary metabolites define these pathways.

2.2.1 The indole-3-acetamide (IAM) pathway

The IAM (Indole-3-Acetamide) route, initially identified in *Pseudomonas* and other bacteria associated with plants, involves the conversion of L-Trp to IAM by tryptophan monooxygenase in bacteria

(Casanova et al. 2005). In the subsequent step, indole acetamide hydrolase catalyzes IAM to synthesize IAA (Indole-3-Acetic Acid) (Pollmann et al. 2003). Previously believed exclusive to bacteria, the discovery of IAM's metabolic conversion to IAA in Arabidopsis revealed a plant-centered IAM route, likely distinct from bacterial processes. The enzyme Acylamidohydrolases (AMI1) facilitates the IAM pathway's second step, transforming IAM into IAA. Evidence supporting the significance of the IAM pathway includes its detection in seaweeds, algae, and various plants, along with genetic and molecular studies affirming its presence across the plant kingdom (Lehmann et al. 2010).

2.2.2 The indole-3-pyruvic acid (IPyA) pathway

The IPyA (Indole-3-Pyruvic Acid) route is a common pathway in bacteria, notably in *Enterobacter cloacae* and *Azospirillum brasilense*, fostering plant root growth. In this route, L-Trp is converted to IPyA by tryptophan aminotransferase (AT) in bacteria. Indole-3-pyruvate decarboxylase (IPDC) transforms indole-3-acetaldehyde (IAD) from IPyA, and IAD is oxidized by indole-3-acetaldehyde oxidase (IAO) to produce IAA (Zhao 2014). TAA1, a key enzyme, catalyzes IPyA formation from L-Trp in plants, influencing various aspects of plant growth. TAA1 and YUC regulate IPyA homeostasis, with transcription factors like SHORT-INTERNODES 1/STYLISH 1 (SHI1/STY1) controlling their expression. YUC's mechanism for catalyzing IPyA to IAA involves NADPH and O2 (Stepanova et al. 2008). The IPyA pathway represents the first fully elucidated IAA biosynthesis pathway in plants (Dai et al. 2013).

2.2.3 The tryptamine (TAM) pathway

The role of tryptamine (TAM) in plant growth is debated, despite its similar properties to IAA. Present in species like tomato, rice, Arabidopsis, barley, and pea, TAM's significance is uncertain, as it may exist non-specifically or at levels inconsistent with a discrete signal (Quittenden et al. 2009). TAM is not the primary precursor of IAA, and they arise from separate Trp pools. Tryptophan decarboxylase (TDC) is believed to convert L-Trp into TAM, followed by YUC catalysis to produce hydroxytryptamine (HTAM). IAOx is then synthesized from HTAM, leading to IAA (Zhao et al. 2001). While the TAM pathway's role in IAA biosynthesis is not firmly supported, it remains a potential precursor, with instances of TAM conversion to IAA in specific plant tissues, suggesting a variable existence across plant species and organs (Brumos et al. 2014; Tivendale et al. 2014).

2.2.4 The indole-3-acetaldoxime (IAOx) pathway

Although isolated over 40 years ago, the precise biosynthesis mechanism of IAOx (Indole-3-Acetaldehyde Oxime) remains unknown (Sugawara et al. 2009). In Arabidopsis, IAOx synthesis from L-Trp involves cytochrome P450 enzymes CYP79B2 and CYP79B3. CYP79B2 overexpression leads to an IAA-overproduction phenotype. Studies suggest that both IAM and IAN are downstream intermediates of IAOx, with CYP71A13 converting IAOx to IAN. The conversion of IAN to IAA is unclear, but nitrilases (NITs) may be involved. However, IAOx-dependent IAA production appears non-standard, likely functioning selectively in specific settings or developmental stages, as observed in Arabidopsis but not in tomato, rice, maize, pea, or tobacco (Vorwerk et al. 2001; Nafisi et al. 2007).

2.4 Trp-independent pathway

The TI (Tryptophan-Independent) pathway, documented in maize, *Arabidopsis*, carrot, *Lemna gibba, Nicotiana tabacum*, and tomato, functions alongside the TD (Tryptophan-Dependent) pathway to regulate auxin homeostasis (Epstein et al. 2002). While the TD pathway maintains high IAA levels for cell division, the TI pathway is suggested to sustain basal auxin levels. Developmental stages and tissue types influence the pathways' contributions to auxin content. In plants, both pathways are active, with the TI circuit exhibiting feedback inhibition. Trp's significance in IAA biosynthesis is debated, and an indole-synthesizing TI route has been discovered (Ribnicky et al. 2002). Challenges in identifying TI pathway mutants or intermediate metabolites may arise from the dominance of the TD pathway, metabolite similarity, or the use of unsuitable model plants like Arabidopsis and rice (Wang et al. 2015).

3. Functions of auxin

Plants in the angiosperm family go through various stages of life cycle transitions. For the development of plants, these many transition periods are essential. These changes are influenced by both internal and external cues, such as phytohormones and environmental conditions. An essential component of plant morphogenesis, auxin is a traditional phytohormone that is involved in a number of physiological processes, including phototropism, cell differentiation, cell expansion, floral opening, organ abscission, and seed germination (Wu et al. 2020).

Research has shown that phytohormones generated from chorismate, such as auxin, melatonin and SA, not only have a common precursor but also

are crucial for controlling fruit ripening and growth. They interact with other phytohormones in a spatiotemporal manner to exchange functional and metabolic signals that carefully control the development of climacteric and non-climacteric fruits. It is evident from the variations in dynamics between climacteric and non-climacteric fruits that the reaction of hormones generated from chorismate is very species-specific rather than universal. Moreover, phytohormones generated from chorismate regulate the build-up of bioactive substances, which affects the quality of the fruit (Pérez-Llorca et al. 2019).

3.1 Auxin and stem cell elongation

Auxin plays a pivotal role in promoting rapid cell elongation in plant stems and coleoptiles. This response is marked by a swift and dramatic increase in growth rate, initiated within 10 minutes of auxin application, resulting in a 5–10 times boost in cell length, lasting for hours or days. The process of auxin-induced cell expansion involves two interconnected mechanisms: the extension of the existing cell wall fuelled by turgor-induced stress and the osmotic uptake of water driven by a water potential gradient.

Energy, specifically ATP synthesis, is crucial for auxin-induced growth, as demonstrated by the inhibition of growth within minutes when ATP synthesis is blocked. Auxin-induced development is a tissue response, where all connected cells collectively elongate or not based on shared cell walls. While auxin primarily targets exterior cell layers (collenchyma and epidermis) in dicot stems, it can also influence interior cells in certain situations.

Auxin enhances wall extensibility rapidly, requiring continuous auxin availability, ATP, active ATPases, protein synthesis, and turgor. To induce cell elongation, auxin must bind to receptors either inside the cell or at the plasma membrane, leading to wall loosening outside the cell. Protons, released into the apoplastic solution in response to auxin, play a crucial role in acidifying the wall and triggering the activity of wall-loosening enzymes. These enzymes, called wall loosening proteins (WLP), are believed to cleave load-bearing bonds in hemicelluloses, particularly xyloglucan in dicot walls, facilitating cell expansion. The exact identity of these bonds and enzymes remains a subject of ongoing research (Cleland 2004).

3.2 Function of auxin in tropisms

Research on the regulation of plant tropisms has always been closely related to efforts to uncover the processes behind polar auxin transport in higher plants. Charles Darwin proposed a theory as early as the nineteenth century, speculating that directed plant growth could be regulated by a transmissible signal in response to external stimuli. Auxin was discovered by plant physiologists to be a potential chemical that might mediate tropic growth responses much later. But it wasn't until the development of *Arabidopsis* genetics and cutting-edge molecular methods at the close of the 20th century that auxin-signalling pathways could be identified, leading to mechanistic understanding of the regulation of polar auxin transport and its relevance for plant tropisms (Retzer et al. 2014).

Adaptive development of plants to variations in light and gravity vectors necessitates an intricate signal transduction pathway. Auxin is associated with both gravitropism and phototropism, albeit many of the specifics of the mechanisms by which these divergent growth responses are

caused remain unclear. More specifically, it has been found and demonstrated that this mechanism requires the redistribution of auxin throughout tissues triggered by light or gravity. Auxin has been linked to tropisms through a variety of methods, such as the isolation of mutants with altered gravitropic or phototropic response resulting from changes in auxin transport or response, the identification of auxin gradients using radiolabelled auxin and auxin-inducible gene reporter systems, and the application of auxin transport inhibitors that prevent gravitropism and phototropism. Proteins that transport auxin have been identified and the mechanisms which determine auxin transport polarity have been explored. Finally, the data in support of several hypotheses for mechanisms by which auxin transport could be differentially regulated during gravitropism are examined (Muday 2001).

Auxin is essential in phototropic signal transduction, which involves the movement of auxin within plant tissues. The presence of indole-3-acetic acid (IAA), a form of auxin, is confirmed in various plant materials, including coleoptiles of oats and maize. PIN1, an auxin efflux carrier, is investigated for its cellular localization in the hypocotyl. Phototropic stimulation disrupts the basal localization of PIN1 more on the shaded side, and this response is absent in a phot1-deficient mutant, indicating the involvement of auxin transport in phototropism.

The NPH4 gene, encoding the auxin-regulated transcriptional activator ARF7, is linked to severe defects in both phototropism and gravitropism. Mutants of auxin-regulated genes, such as AUX/IAA19, also contribute to phototropism by influencing auxin-mediated growth asymmetry. These findings underscore the integral role of auxin in regulating

plant growth responses to light stimuli, emphasizing its significance in shaping plant development and behavior. Auxin is also implicated in the negative phototropism of plant roots and the phototropic curvature of *Phaseolus* leaf pulvinus. Phototropism, the response to light, in *Arabidopsis* primary roots involves signaling components NPH3 and RPT2, while in rice primary roots, CPT1 participates in this process. PIN3, a putative auxin efflux carrier, may also play a role in root phototropism. Additionally, the phototropic curvature of the *Phaseolus* leaf pulvinus is driven by turgor-dependent changes, where cells on the irradiated side shrink and those on the shaded side swell. This phenomenon, coupled with the observation that pulvinar protoplasts swell in response to applied auxin (IAA), suggests that lateral auxin redistribution might contribute to the turgor-driven phototropic curvature. Overall, auxin appears to be involved in the molecular and physiological processes underlying root and leaf phototropism.

3.3 Regulation of senescence and floral organ abscission by auxin

Transcription factors known as auxin response factors (ARFs) mediate reactions to the plant hormone auxin. Ellis at al. (2005) looked at Arabidopsis lines with T-DNA insertions in the ARF2 and AUXIN RESPONSE FACTOR1 (ARF1) genes. They discovered that ARF2 facilitates changes in Arabidopsis development from one stage to another. Arf2 mutant plants showed delays in a number of aging-related processes, such as floral organ abscission, rosette leaf senescence, silique ripening, and the start of flowering. Senescing leaves were shown to express ARF2. Independent of the ethylene and cytokinin response pathways, ARF2 controlled the senescence of leaves and the abscission of floral organs. ARF1 functions partially redundantly with ARF2, as evidenced by the enhancement

of numerous arf2 abnormalities by arf1 mutations. An arf1 mutation, on the other hand, enhanced transcription of Aux/IAA genes in Arabidopsis flowers, in contrast to arf2 mutations, validating earlier biochemical investigations (Fig. 1).

(I) (II)

Figure 1. (I) Natural senescence in wild-type and arf2 rosette leaves. Leaves and inflorescences from 8-week-old plants are laid out in order of emergence. (II) Effects of arf gene mutations on flower development. Stage 13 Columbia (A) and arf2-8 flowers (E). Primary inflorescences of Columbia (B), Ws-0 (C) arf1-5 arf2-8 (F) and arf1-4 dsARF2 (G) plants. Abscission zones of Columbia (D) and arf1-5 arf2-8 (H) floral organs. St, stamen; P, petal; Se, sepal. Arrowheads indicate the abscission zone (Ellis at al. 2005).

3.4 Auxin-mediated embryo patterning and control of cell division

The process of embryo growth in seed plants that starts with ovule fertilisation is known as embryogenesis. Following germination, this procedure will establish the general architecture of the newly formed plant. The final size and shape of the seed, which in turn affects the overall quality

and quantity of seed production, are determined by the coordinated growth of embryonic tissues (Han et al., 2019). Auxin allows proper polarity and patterning of the developing embryo through its distribution, which is maintained by a local auxin production together with well-coordinated transport. The auxin signalling pathway interprets these auxin maxima into proper developmental programs (Locascio et al. 2014; Schlereth et al. 2010).

Auxin plays a pivotal role in embryo patterning by influencing formative cell divisions and cell specification during embryo development. Coordinated cell divisions create distinct cell layers by orienting the division plane, and auxin disrupts the default geometric division rule, compelling cells to choose an alternative division wall. This control exerted by auxin is crucial for pattern formation in embryo morphogenesis. The influence of auxin on division plane orientation is achieved through its impact on the orientation of cortical microtubule arrays (CMAs), with a well-established link between CMA orientation and division plane orientation. Auxin-mediated stability of microtubules, along with factors such as cell shape and reduced edge catastrophe, governs CMA orientation, predicting division plane orientation and facilitating oriented cell division during early embryonic stages. Additionally, auxin's role extends to cell polarization relative to body axes, influencing division orientation during multicellular development. The SOSEKI proteins, particularly SOK1, are implicated in this process, with SOK1 expression being transcriptionally regulated by ARF5/MP. SOK1 is localized in specific regions of the embryo and its misexpression leads to altered cell division orientations across cell types. Despite these findings, the detailed cellular mechanisms underlying SOK1's activity in division plane orientation remain to be determined (Yoshida et al. 2014; Chakrabortty et al. 2018).

3.5 Contribution of auxin during seed germination

In *Arabidopsis thaliana*, abscisic acid (ABA) suppresses postgerminative growth and seed germination. Both auxin and jasmonic acid (JA) increase the activity of ABA. In a study conducted by Mei et al. (2023) demonstrate how exogenous auxin and JA complement one another to strengthen the ABA-induced delay in seed germination. For JA-promoted ABA responses, auxin production, perception, and signalling are essential. The auxin-dependent transcription factors ARF16 and AUXIN RESPONSE FACTOR10 (ARF10) interact with the JA signalling repressors known as JASMONATE ZIM-DOMAIN (JAZ). Combined ABA and JA treatment partially rescues the hyposensitive phenotype of JAZ-accumulating plants with impaired JA signalling, as ARF10 and ARF16 positively regulate JA-increased ABA responses. Moreover, ABI5, a crucial regulator of ABA signalling, is physically associated with ARF10 and ARF16. This means that ABI5 is primarily responsible for ARF16's capacity to elicit JA-mediated ABA responses. The transcriptional activity of ABI5 is stimulated by ARF10 and ARF16, while JAZ repressors counteract their effects. Altogether, the findings showed that auxin plays a role in the synergistic modulation of JA on ABA signalling and provide an explanation for how ARF10/16 collaborates with JAZ and ABI5 to integrate the pathways involved in auxin, JA, and ABA signalling in seed germination.

3.6 Initiation of apicobasal polarity: Emphasis on auxin

Auxin plays a crucial role in early embryonic patterning by influencing the initial separation of apical and basal cells after the first zygotic division. This separation establishes a foundation for subsequent patterning events, with fate decisions relying on the differential expression of

WUSCHEL-related homeobox (WOX) transcription factors along the apicobasal axis. Specifically, WOX2, WOX8/STPL, and WOX9 are expressed in different regions of the eight-celled embryo. Auxin response mediated by ARF5/MP is essential for these expression dynamics, as observed in arf5/mp and iaa12/bdl mutants, where the shift in WOX9 expression is compromised. WOX2 emerges as a key regulator in the WOX gene cascade, orchestrating embryonic shoot patterning. The interplay between WOX genes and auxin is evident in wox8 wox9 double mutants, where reduced PIN1 expression suggests the necessity of WOX8/WOX9 for normal PIN1 activity and localized auxin response maxima. Moreover, a genetic interaction between WOX2, WOX8, and ARF5/MP underscores their collective role in regulating PIN1 expression during cotyledon development, emphasizing the intricate connection between WOX genes, auxin-mediated responses, and potentially other auxin-independent factors in embryo patterning (Haecker et al. 2004; Breuninger et al. 2008).

3.7 Role of auxin in initiating SAM

In the process of initiating the Shoot Apical Meristem (SAM), auxin, the plant hormone, plays a crucial role. Initially, stem cells are specified between presumptive cotyledons in the globular embryo. During apical patterning, a shift from radial to bilateral symmetry occurs with the development of cotyledon primordia. The proper separation of cotyledon primordia is essential for SAM establishment (Lie et al. 2012).

SAM development and cotyledon separation are controlled by a network of genes, including CUP-SHAPED COTYLEDON1 (CUC1), CUC2, CUC3, and SHOOT MERISTEMLESS (STM). Three key factors in the auxin transport and response pathway—PIN1, PINOID (PID), and

ARF5/MP—regulate the expression of CUC1 and CUC2, contributing to cotyledon separation and bilateral symmetry. PIN1 and PID work together to promote auxin accumulation in cotyledon primordia, inhibiting the expression of CUC1 and CUC2. This process, facilitated by auxin, is crucial for the establishment of bilateral symmetry (Vroemen et al. 2003).

Furthermore, the WOX2 module, which includes WOX2, WOX8, WOX1, WOX3, and WOX5, is essential for the initiation of the embryonic apical meristem. This module promotes the development of a three-layered shoot meristem by regulating cell division patterns, including the presumptive SAM region. By promoting PIN1 expression, the WOX2 module prevents auxin accumulation in the SAM region. Additionally, the WOX2 module enhances the expression of HD-ZIP III genes, known regulators of embryonic apical fate, suggesting that HD-ZIP III TFs act downstream of the WOX2 module in the same genetic pathway to regulate stem cell initiation during embryonic apical patterning. In summary, auxin, through the PIN1-mediated pathway, helps establish the bilateral symmetry necessary for SAM formation, and the WOX2 module, in coordination with auxin and cytokinin pathways, contributes to stem cell initiation and protects them from differentiation, ensuring correct specification of the SAM region in the apical domain (Zhang et al. 2017).

3.8 Role of Auxin in Embryonic Root Formation

In embryonic root formation, auxin has a significant role in initiating the Root Apical Meristem (RAM). The asymmetric division of the hypophysis, marked by the initiation of RAM at the globular stage, is essential. The specification of the hypophysis and subsequent RAM development are dependent on auxin signaling. Mutants with disrupted auxin

signaling, such as MP and BDL, exhibit a rootless phenotype. Auxin transporters, including AUX1, LAX2, and PIN1, are targets of the MP/BDL signaling pathway, guiding an auxin flow toward the hypophysis (Capron et al. 2009).

MP, a transcription factor, directly targets genes such as TMO5 and TMO7, crucial for RAM specification. TMO7 acts as an intercellular signal in the hypophysis for RAM initiation. Additionally, NTT, WIP4, and WIP5, also direct targets of MP, promote the asymmetric division marking RAM initiation (Weijers et al. 2006). The PLT genes, including PLT1 and PLT2, form an indispensable gene network regulating RAM establishment. PLT genes act downstream of auxin response, and their expression depends on MP/ARF5 and NPH4/ARF7. PIN-mediated auxin accumulation in the basal domain is crucial for initiating and establishing RAM by transcriptionally regulating PLT genes (Crawford et al. 2015).

Furthermore, PLT genes are implicated in vascular regeneration, modulating auxin biosynthesis and directly regulating CUC2 expression. This intricate mechanism, observed in leaves, may also exist in the embryo, highlighting the multifaceted role of auxin in embryonic root formation (Radhakrishnan et al. 2020).

4. Signal transduction of auxin

Clarifying the molecular pathways behind hormone function is one of the numerous difficulties facing plant hormone research. Auxin signal transduction pathway's present working model is primarily derived from hormone response pathways that have been reported in other systems. It is believed that auxin is recognised and bound by receptors within cells as well

as on the cell surface with a high affinity. Following receptor binding, a sequence of biochemical and molecular processes would take place, eventually resulting in physiological growth responses that are visible, like cell elongation, division, and/or differentiation. Because of the identification of several crucial regulatory elements of the pathway, we now have a far better knowledge of the molecular mechanisms governing auxin action than we had ten years ago (Hagen et al. 2004).

Auxin can cause both specialised and general transcriptional reactions when it is perceived in the nucleus. Auxin/INDOLE-3-ACETIC ACID (Aux/IAA) transcriptional repressors, AUXIN RESPONSE FACTOR (ARF) transcription factors, and F-box TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALLING F-BOX PROTEIN (TIR1/AFB) auxin co-receptors are the three protein families that comprise the essential elements of the auxin signalling machinery. Auxin stimulates TIR1/AFB and Aux/IAA protein interaction, which leads to ARF repression being released and the Aux/IAAs being degraded (Salehin et al. 2015).

Auxin regulates gene expression through a complex pathway involving transcriptional responses mediated by Auxin Response Factors (ARFs) and Aux/IAA transcriptional repressors. At low auxin levels, Aux/IAAs inhibit ARF activity. However, in the presence of auxin, TIR1/AFB proteins bind to Aux/IAAs, leading to their degradation. This process triggers rapid induction of auxin-responsive genes, forming negative-feedback loops. Aux/IAAs have three functional domains: a leucine repeat EAR motif for repression, an internal domain II with a degron motif for interaction with TIR1/AFBs, and a C-terminal PB1 domain for interactions and self-dimerization. The degron motif determines Aux/IAA

stability, and other sequences outside domain II contribute to TIR1/AFB binding and degradation. This intricate mechanism highlights auxin's role in finely regulating gene expression for plant growth and development (Wang et al. 2016).

Auxin perception initiates ARF-mediated transcriptional responses after the degradation of Aux/IAA transcriptional repressors. ARF factors bind to auxin-responsive gene promoters through cis-regulatory AuxREs, often containing the core element TGTC. Structural analyses reveal specific motifs (e.g., TGTCCG) preferred by different ARFs. ARFs, characterized as transcriptional activators or repressors, possess an N-terminal DNA-binding domain, a variable middle region, and a C-terminal PB1 dimerization domain. ARFs can form dimers, influencing transcriptional responses, and their interactions with Aux/IAAs are vital for efficient ARF repression. Structural studies uncover a PB1 domain facilitating various dimerizations and oligomerizations, offering insights into the intricate regulation of auxin-responsive gene expression (Wang and Estelle 2014).

Auxin-mediated gene repression involves ARFs recruiting Aux/IAAs to target gene promoters, inducing chromatin modifications that decrease gene accessibility. Aux/IAAs interact with corepressor proteins TPL and TPR, engaging histone deacetylases for transcriptional repression. A novel auxin-mediated chromatin switch was revealed, where ARF5 interacts with BRM and SYD, subunits of the SWI/SNF complex, promoting gene activation in flower primordia. This interaction enhances DNA accessibility to transcription factors, facilitating target gene induction. Aux/IAAs prevent BRM and SYD association with gene promoters, allowing the dynamic

switch between gene repression and activation orchestrated by auxin and Aux/IAA degradation (Kagale and Rozwadowski 2011; Wu et al. 2015).

5. Conclusion

Plant hormone auxin is engaged in an incredibly wide range of biological processes. These span from fundamental biological functions like endocytosis, cell polarity, and cell cycle regulation to specialized reactions like cell elongation and differential growth, as well as large-scale occurrences like embryogenesis, tissue patterning, and organ de novo development. Despite the fact that auxin study dates back more than a century, a thorough understanding of how auxin controls such a broad spectrum of responses remains a long way off. The auxin molecule itself may hold some of the answers to this query. There are compounds that resemble auxins that occur naturally, and these molecules may be involved in particular cellular and developmental processes. Moreover, auxin is intracellularly compartmentalised, actively changed, and metabolised, all of which can significantly affect its availability and action.

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