

The Dual Role of Phytohormones Biosynthesis and Signalling in Growth Regulation and Stress Tolerance Mechanism

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Abstract

Plant growth hormones are also known as phytohormones, are naturally occurring signalling molecules that regulate a wide range of processes involved in plant growth, development, reproduction, and adaptation to environmental conditions. Their effects are produced at very low concentrations through coordinated interactions with cellular signalling pathways and gene-regulatory mechanisms. Among the major phytohormones, auxins and cytokinin have received considerable attention because of their important roles in cell division, cell enlargement, differentiation, root and shoot development, tissue culture, and plant regeneration. Gibberellins, abscisic acid, and ethylene further contribute to the regulation of plant growth, seed development, dormancy, stress responses, senescence, and other physiological processes.

This review focuses on the biological functions, biosynthesis, signalling mechanisms, and potential pharmaceutical and biotechnological applications of major plant growth hormones, with particular emphasis on auxins and cytokinin. Auxins, especially indole-3-acetic acid (IAA), regulate processes such as cell elongation, apical dominance, root initiation, vascular differentiation, and tropic responses. Cytokinin are primarily associated with cell division, shoot formation, nutrient mobilization, and regulation of plant developmental processes. The interaction between auxins and cytokinin is particularly important in plant tissue culture, where their relative concentration can influence the formation of roots, shoots, or undifferentiated callus tissue.

The review also discusses the relevance of plant hormone-regulated tissue culture and plant biotechnology to the pharmaceutical field, including the production and investigation of plant-derived bioactive compounds. Controlled manipulation of hormonal conditions can improve plant regeneration, micropropagation, biomass production, and the establishment of cultures used for the investigation of compounds with potential pharmacological activities such as antioxidant, antimicrobial, anti-inflammatory, and anticancer effects. In addition, the biosynthesis and signalling pathways of gibberellins, abscisic acid, and ethylene are discussed to provide a broader understanding of hormonal coordination in plants. Overall, understanding phytohormone biosynthesis, signalling, and interaction provides an important foundation for applying plant biotechnology in pharmaceutical research, sustainable production

of plant-derived materials, and the development of innovative approaches for obtaining biologically active compounds.

1. INTRODUCTION

Plant growth and development are controlled by a highly coordinated system in which internal chemical signals work together with environmental factors. These chemical signals are generally known as plant hormones or phytohormones. They are produced naturally within plant tissues and can regulate physiological activities even at very low concentrations. Unlike animals, plants do not have specialized endocrine glands for hormone secretion. Instead, plant hormones may be synthesized in one tissue and transported to another region where they influence cellular activities. Through these signalling molecules, plants coordinate important processes such as seed germination, cell division, cell enlargement, root and shoot development, flowering, fruit formation, senescence and adaptation to environmental conditions. The major classical groups include auxins, cytokinin, gibberellins, abscisic acid and ethylene, while several other signalling molecules have subsequently been recognized as important regulators of plant growth and stress responses [1, 2].

Among the different plant hormones, auxins and cytokinin occupy a central position in the regulation of plant growth. Auxin was one of the earliest plant hormones to be recognized experimentally. The early work of Charles and Francis Darwin on phototropic movement provided evidence that a growth-regulating signal could originate from the tip of a young plant. Later, Fritz Went demonstrated the presence of a diffusible growth-promoting substance using oat coleoptiles. These investigations contributed to the development of our present understanding of auxin biology. The principal naturally occurring auxin is indole-3-acetic acid (IAA), although other auxin-related compounds such as indole-3-butyric acid (IBA), phenylacetic acid and 4-chloro-IAA have also been identified in plants [3, 4]. Auxins influence a wide range of developmental events rather than producing only one particular growth response. They participate in cell division and elongation, vascular tissue differentiation, root initiation, apical dominance and directional growth responses. Their effect is strongly dependent on concentration, tissue type and developmental stage. IAA and IBA, for example, have been associated with lateral root formation, while auxin-mediated changes in cell-wall properties contribute to cell expansion. Auxin is also transported through the plant by regulated transport systems, including AUX/LAX influx carriers and PIN efflux proteins. This controlled movement creates local differences in auxin concentration, allowing different tissues to respond according to their developmental requirements [5, 6].

Cytokinin constitute another major group of plant growth regulators and are particularly associated with cell division and shoot development. The discovery of cytokinin activity emerged from observations that certain plant extracts and other biological materials could stimulate division of plant cells in culture. Kinetin was identified as an early cell-division-promoting compound, while zeatin was later recognized as a naturally occurring cytokinin. Other cytokinin and synthetic cytokinin-like compounds, including 6-benzylaminopurine (BAP) and thidiazuron (TDZ), have subsequently become important tools in plant tissue culture. Cytokinin influence cell-cycle progression, shoot differentiation, chloroplast development, nutrient mobilization and the maintenance of actively growing tissues. They can also delay leaf senescence, making them important in both basic plant biology and applied biotechnology [7, 8]. The biological effects of auxins and cytokinin cannot be understood completely by considering either hormone separately. Their relative balance and interaction are important for determining the developmental behaviour of plant tissues. Auxin generally has a strong influence on root initiation and organization,

parts of the plant. Even at very low concentrations, they can produce significant changes in cell division, cell expansion, differentiation, organ formation, senescence and responses to environmental conditions. The major groups traditionally include auxins, cytokinins, gibberellins, abscisic acid and ethylene, while several other signalling compounds are now recognized as important regulators of plant growth and adaptation [16].

Among these hormones, auxins occupy a central position because of their involvement in both basic plant development and plant biotechnology. Indole-3-acetic acid (IAA) is the principal naturally occurring auxin and has been associated with processes such as cell elongation, cell division, root formation, vascular differentiation, apical dominance and tropic responses. The biological response to auxin is not determined simply by its presence; it depends strongly on concentration, distribution, transport and the sensitivity of the particular tissue. Therefore, the same auxin can produce different responses in roots, shoots and cultured tissues [17]. The history of auxin research began with observations on the directional growth of plants. Charles Darwin and Francis Darwin investigated phototropic responses and proposed that a signal produced near the tip of the coleoptile was involved in bending towards light. Later investigations by other researchers provided experimental evidence for a diffusible growth-promoting substance. These studies ultimately contributed to the identification and characterization of auxin activity and established the foundation for modern plant hormone research. The development of auxin research is particularly important because it connected a simple physiological observation with the concept of chemical signalling in plants [18]. Natural auxins include compounds such as IAA and indole-3-butyric acid (IBA), while several synthetic compounds are widely used in plant propagation and tissue culture. Examples include 1-naphthaleneacetic acid (NAA) and 2,4-dichlorophenoxyacetic acid (2,4-D). Natural and synthetic auxins may differ in stability, transport, metabolism and biological effectiveness. Consequently, selection of an auxin for tissue culture is usually based on the plant species, explant type, required developmental response and culture conditions rather than simply selecting the most commonly used compound [19]. Auxin activity is closely associated with the development of the root system. IAA and IBA can stimulate lateral-root formation, although their effectiveness and mode of action may vary between plant species. Auxin also participates in adventitious root formation, vascular development and the establishment of developmental patterns. This property has considerable importance in plant biotechnology because successful rooting is an essential step during micropropagation of medicinal and economically important plants. Controlled auxin treatment can therefore improve the establishment of regenerated plantlets and support the multiplication of valuable plant material [20].

At the molecular level, auxin responses are regulated through a sophisticated signalling system involving TIR1/AFB receptors, Aux/IAA proteins and ARF transcription factors. In the absence of an adequate auxin signal, Aux/IAA proteins suppress the activity of ARFs. When auxin concentration increases, it promotes the interaction between the TIR1/AFB receptor complex and Aux/IAA proteins. The Aux/IAA proteins are then targeted for ubiquitination and degradation by the proteasome, allowing ARF proteins to regulate auxin-responsive genes. This pathway provides an important molecular explanation for how changes in auxin concentration can produce changes in cellular behaviour [21]. Auxin does not act independently of other plant hormones. One of its most important interactions is with cytokinin, particularly during the regulation of meristem activity and organ formation. The relative balance between auxin and cytokinin can influence whether cultured tissues develop roots, shoots or an undifferentiated callus. A relatively higher auxin influence generally favours rooting, whereas a stronger cytokinin influence can favour shoot development; an intermediate balance may support callus formation. However,

this relationship is not an absolute rule because the final response also depends on species, genotype, explant, hormone type, concentration and culture conditions [22].

Cytokinin form another major group of phytohormones and are particularly associated with cell division and shoot development. Naturally occurring cytokinins include zeatin and isopentenyl adenine derivatives, while kinetin, benzyladenine (BAP) and thidiazuron (TDZ) are commonly used in plant tissue culture. Cytokinins influence shoot multiplication, meristem activity, nutrient distribution, chloroplast development and leaf senescence. Their activity is also concentration-dependent, and excessive cytokinin exposure can sometimes result in abnormal or compact shoot development. Thus, cytokinin selection and concentration need to be optimized for each tissue-culture system [23].

The physiological importance of cytokinins extends beyond cell division. They participate in communication between roots and shoots and are influenced by nutrient availability, particularly nitrogen status. Cytokinin metabolism involves enzymes such as isopentenyl transferases and cytokinin oxidase/dehydrogenases, while conjugation can regulate the storage and activity of cytokinin molecules. These processes help plants adjust their developmental programmes according to internal nutritional conditions and external environmental signals [24].

The interaction between auxin and cytokinin becomes especially valuable in plant tissue culture and micropropagation. By adjusting the ratio and concentration of these hormones in a culture medium, researchers can guide cells through different developmental stages, including callus induction, shoot multiplication, rooting and plant regeneration. This approach is particularly useful for medicinal plants that are difficult to propagate conventionally or are required in large quantities for pharmacognostic and biotechnology studies. Hormone-mediated tissue culture can provide a controlled environment in which plant biomass and metabolite production can be investigated systematically [25].

The pharmaceutical importance of auxins and cytokinins is therefore mainly indirect rather than as conventional therapeutic drugs. Their major contribution is through pharmaceutical biotechnology, especially the controlled cultivation and multiplication of medicinal plants and the investigation of plant-derived bioactive compounds. Auxin-regulated callus, cell-suspension, root and hairy-root cultures can provide useful experimental systems for studying secondary metabolite production. Such systems allow researchers to investigate how culture conditions and hormone treatments influence the quantity and composition of compounds of pharmaceutical research [26]. Plant cell and tissue culture can also be combined with analytical and screening approaches for the discovery of potentially useful bioactive compounds. A general workflow may involve selection of a medicinal plant, explant preparation, surface sterilization, culture initiation, optimization of auxin and cytokinin concentrations, establishment of callus or specialized cultures, biomass or metabolite optimization, extraction, chromatographic analysis and biological activity testing. This creates a connection between plant physiology, microbiology, biotechnology, pharmacognosy and pharmaceutical research [27]. The concentration of auxin is particularly important in pharmaceutical biotechnology because hormonal treatment can influence not only plant growth but also the metabolic state of cultured cells. Changes in developmental status, stress responses and metabolic pathways may affect the accumulation of specialized metabolites. For this reason, hormone concentration should be considered together with other variables such as cytokinin concentration, culture medium composition, light, temperature, elicitors and culture age. The desired pharmaceutical or biochemical outcome should be confirmed through analytical measurement rather than assumed solely from increased biomass [28]. An additional area connecting plant hormones with microbiology is microbial production of auxins. Several plant-associated microorganisms are capable of producing IAA,

often using tryptophan-dependent pathways. Bacterial genera reported to produce IAA include *Pseudomonas*, *Azospirillum*, *Enterobacter*, *Streptomyces*, *Pantoea*, *Rhizobium*, *Azotobacter* and *Alcaligenes*. Microbial IAA can influence plant root architecture and thereby modify the interaction between plants and their associated microbial communities. This makes microbial auxin production an important subject for pharmaceutical microbiology and plant–microbe biotechnology research [29]. From a pharmaceutical biotechnology perspective, plant hormones may also be considered in relation to the production of plant-derived bioactive substances and biopharmaceutical products. Plant cell cultures and molecular farming systems have been investigated as platforms for producing recombinant proteins and other valuable biological products. In such systems, understanding plant growth regulation is important because cell growth, differentiation and metabolic activity influence the performance of the biological production platform. Auxin and cytokinin regulation can therefore become part of the broader strategy for establishing and maintaining productive plant cell [30]. There is also growing interest in the possible biological effects of phytohormones beyond their established functions in plants. Studies summarized in the literature have investigated interactions of compounds such as IAA and cytokinins with microbial, animal and mammalian systems. Some experimental findings have suggested possible bioactive effects, including effects related to cell growth and cancer-related processes. However, these observations remain an emerging research area and should not be interpreted as evidence that auxins or cytokinins are established human medicines. Further biochemical, toxicological and clinical investigation is required before therapeutic applications can be considered [31].

Overall, the study of plant growth hormones provides an important link between plant physiology, molecular biology, microbiology, tissue culture and pharmaceutical biotechnology. Auxins and cytokinins are especially significant because their controlled use can influence regeneration, rooting, shoot multiplication, cell proliferation and the metabolic behaviour of cultured plant tissues. Their interaction with microorganisms and their possible relationship with the production of valuable bioactive compounds further increases their research importance. Therefore, understanding the chemistry, physiological functions, signalling mechanisms, microbial interactions and biotechnological applications of auxins and cytokinins is essential for developing efficient plant-based research and production systems [32].

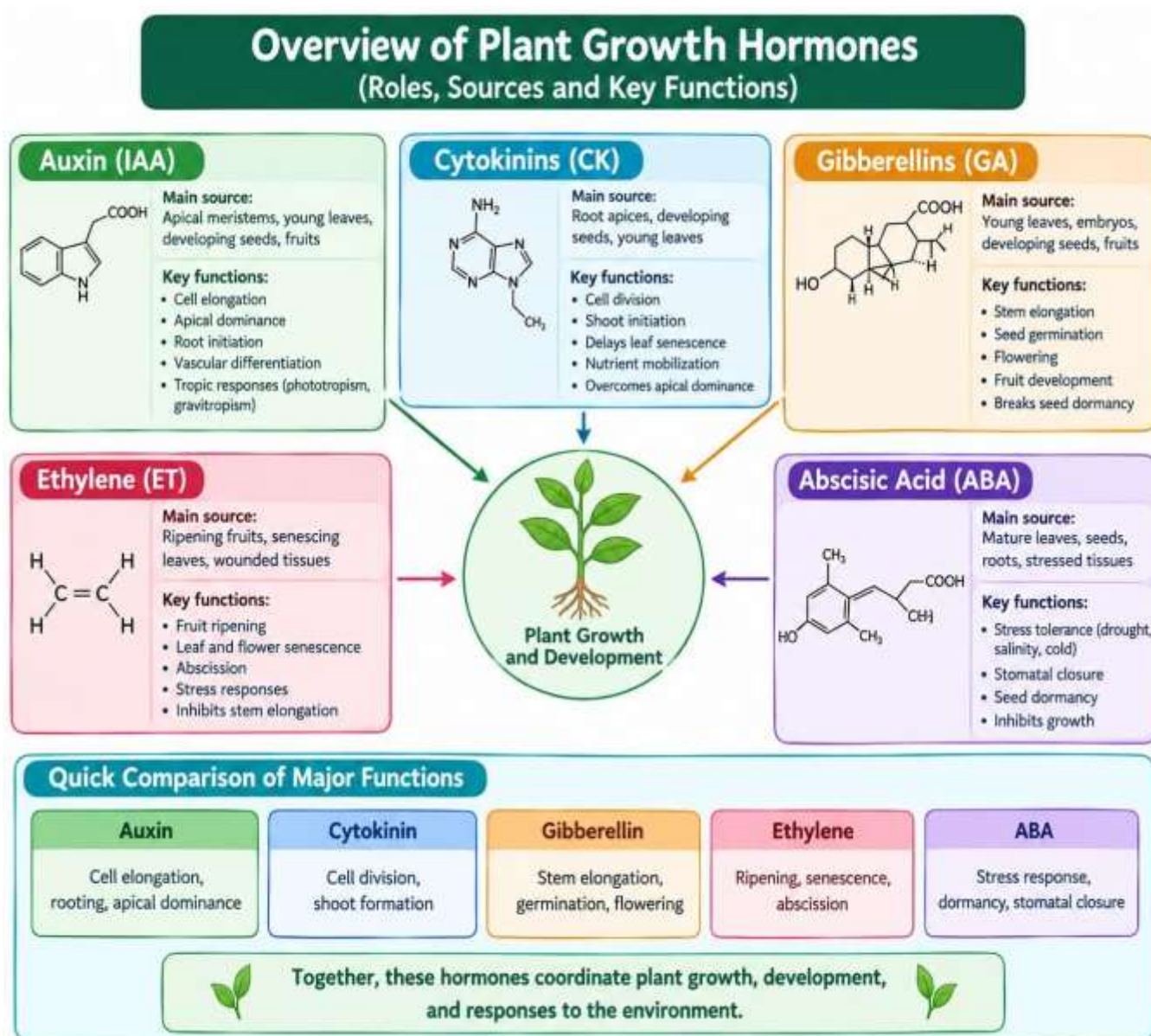


Figure 1. The physiological roles and chemical profiles of the five primary phytohormones- Auxins, Cytokinin, Gibberellin, Ethylene, Abscissic Acid (ABA).

2. Auxin synthesis and signalling cross talk

2.1 Auxin Synthesis

Auxin is one of the major plant hormones involved in regulating growth and development, and indole-3-acetic acid (IAA) is the principal naturally occurring auxin in higher plants. Although plants possess several routes for producing IAA, the best-characterized pathway is the tryptophan-dependent indole-3-pyruvic acid (IPyA) pathway. In this pathway, the amino acid tryptophan is first converted into indole-3-pyruvic acid by enzymes belonging to the TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA) and TAA-RELATED (TAR) families. IPyA is subsequently converted into IAA by the YUCCA (YUC) family of flavin-containing monooxygenases. The two-step TAA/YUC pathway is considered a major and highly conserved mechanism for IAA production in plants [33]. The first reaction of the

principal pathway involves the reversible conversion of tryptophan into IPyA. TAA1 and related TAR proteins catalyze this transamination reaction. The second reaction is catalyzed by YUCCA enzymes and converts IPyA into IAA through an oxidative decarboxylation reaction. YUC enzymes have an important regulatory position in the pathway because their activity strongly influences the amount of locally available auxin. Different YUC family members are expressed in particular tissues and developmental stages, allowing plants to establish auxin production at specific locations rather than producing the hormone uniformly throughout the plant [34]. Auxin synthesis is regulated spatially and temporally according to the developmental requirements of the plant. Local auxin production can contribute to the formation of auxin maxima and gradients that are necessary for processes such as embryogenesis, root development, vascular differentiation, lateral root formation and reproductive development. Therefore, the amount of auxin present in a particular tissue is determined not only by its biosynthesis but also by its transport, conjugation, storage and degradation. This coordinated regulation allows plants to maintain an appropriate concentration of biologically active IAA according to cellular requirements [35]. Apart from the IPyA pathway, plants possess additional tryptophan-dependent routes involving intermediates such as indole-3-acetamide, tryptamine and indole-3-acetaldoxime. However, the biochemical details and relative contribution of some of these pathways can vary among plant species and tissues. The presence of multiple routes provides flexibility in maintaining auxin homeostasis under changing developmental and environmental conditions. Consequently, auxin metabolism is better understood as a regulated network rather than as a single linear biochemical pathway [36]. Once IAA is produced, its concentration can be controlled through reversible conjugation and irreversible degradation. GH3 family enzymes can attach amino acids to IAA, generating conjugated forms that generally reduce the pool of free active auxin. IAA can also undergo oxidative degradation involving dioxygenase for auxin oxidation (DAO). These mechanisms are important because excessive accumulation of free IAA can disturb normal development, while insufficient auxin can also lead to developmental abnormalities. Thus, biosynthesis, conjugation and degradation work together to maintain auxin homeostasis [37].

2.2 Auxin Transport and Formation of Auxin Gradients

Following its synthesis, auxin is distributed throughout plant tissues through both passive movement and regulated transport systems. The major families involved in auxin transport include AUX1/LAX influx carriers, PIN-FORMED (PIN) efflux carriers and ABCB transport proteins. The asymmetric localization of PIN proteins on cell membranes is particularly important because it determines the direction in which auxin moves from one cell to another. Consequently, polar auxin transport contributes to the establishment of local auxin maxima and gradients that provide positional information during plant development [38]. Auxin gradients are important because plant cells can respond differently to different local concentrations of the hormone. The combination of local biosynthesis and polar transport allows auxin to accumulate in particular regions, where it can regulate cell division, cell elongation and differentiation. Therefore, auxin transport and biosynthesis are closely connected processes. Changes in either process can modify the distribution of IAA and consequently alter developmental patterns [39].

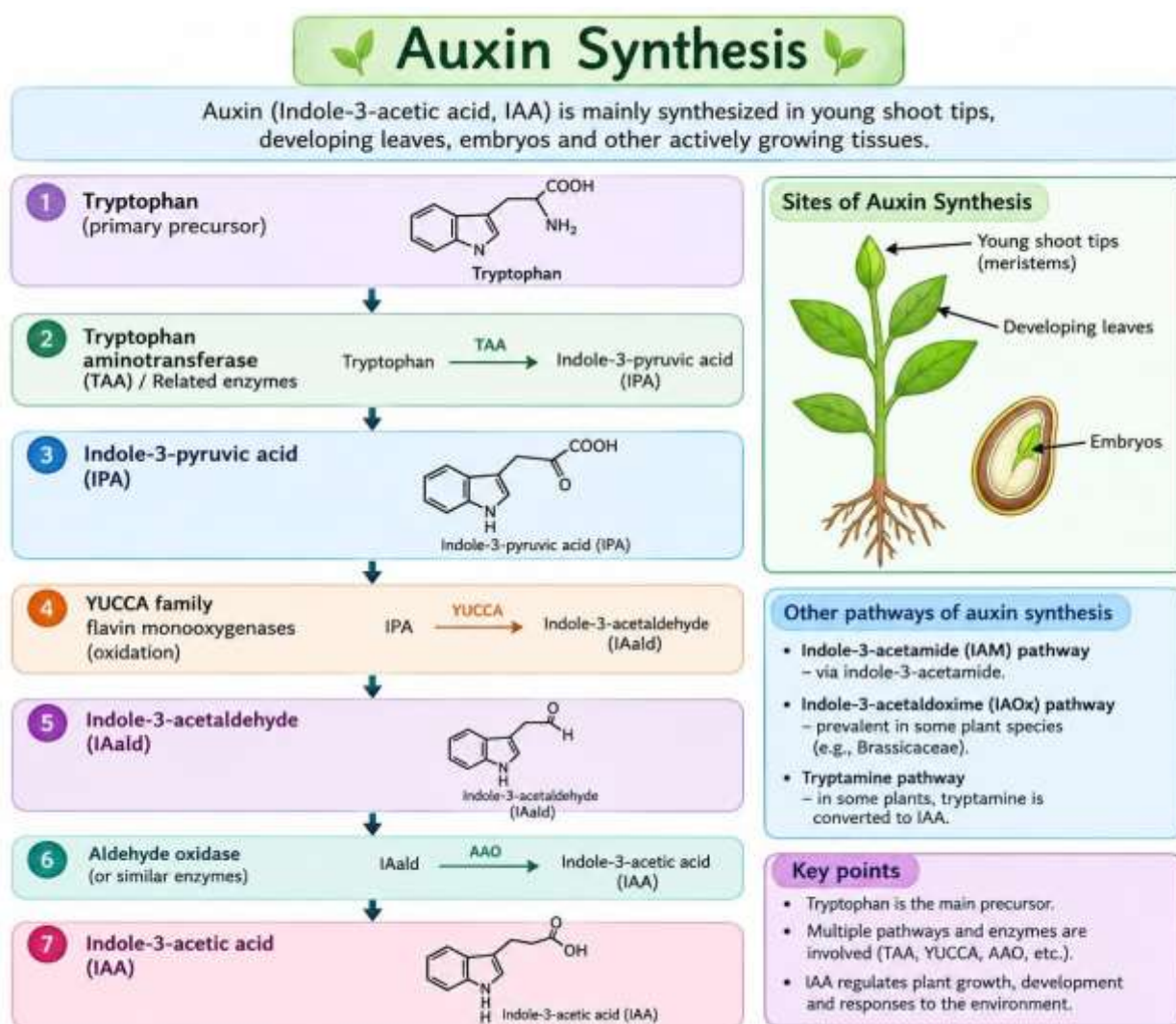


Figure 2. A detailed biochemical flowchart detailing the multi-step enzymatic synthesis of the plant hormone Auxin (Indole -3-acetic acid).

2.3 Auxin Signalling

Auxin signalling begins when IAA is perceived by specific receptor proteins. The best-characterized mechanism involves the TIR1/AFB family of auxin receptors, which function as F-box components of the SCF ubiquitin-ligase complex. In the absence of sufficient auxin, Aux/IAA proteins act as transcriptional repositories and inhibit the activity of auxin response factors (ARFs). When auxin binds to the TIR1/AFB receptor, it promotes the interaction between the receptor and Aux/IAA proteins. The Aux/IAA proteins are then ubiquitinated and targeted for degradation by the proteasome, releasing ARF transcription factors from repression and allowing the expression of auxin-responsive genes [40]. The TIR1/AFB–Aux/IAA–ARF system provides a rapid molecular mechanism through which changes in auxin concentration can be converted into changes in gene expression. After Aux/IAA degradation, ARF proteins can regulate target genes involved in cell expansion, root development, vascular differentiation and other developmental processes. Different combinations of TIR1/AFB receptors, Aux/IAA proteins and ARF transcription factors are expressed in different tissues. This molecular diversity helps explain why the same hormone can generate different responses depending on the tissue, developmental stage and cellular context [41].

Auxin signalling is not restricted to transcriptional regulation in the nucleus. Research has also demonstrated rapid auxin responses involving membrane-associated mechanisms. Auxin perception associated with ABP1/TMK signalling has been linked with rapid changes at the plasma membrane, including regulation of proton pumps and changes in cell-surface conditions. These rapid responses can contribute to processes such as cell expansion and changes in cellular physiology. Thus, auxin action involves interconnected nuclear and rapid cellular signalling mechanisms rather than a single pathway [42]. Recent findings have further expanded the classical model of auxin signalling. A 2025 study reported that TIR1/AFB receptors possess adenylate cyclase activity and that auxin-induced production of cyclic AMP (cAMP) can contribute to transcriptional auxin responses. This work suggests that the established model based mainly on Aux/IAA degradation may not represent the entire mechanism by which auxin perception is converted into developmental responses. The finding introduces cAMP as an additional component requiring consideration in current models of auxin signalling and highlights that auxin biology continues to develop as new molecular mechanisms are identified [43]. auxin synthesis, transport and perception are integrated. Local production of IAA provides the hormone, transport establishes its distribution, and receptor-mediated signalling converts the hormone concentration into cellular and developmental responses [44].

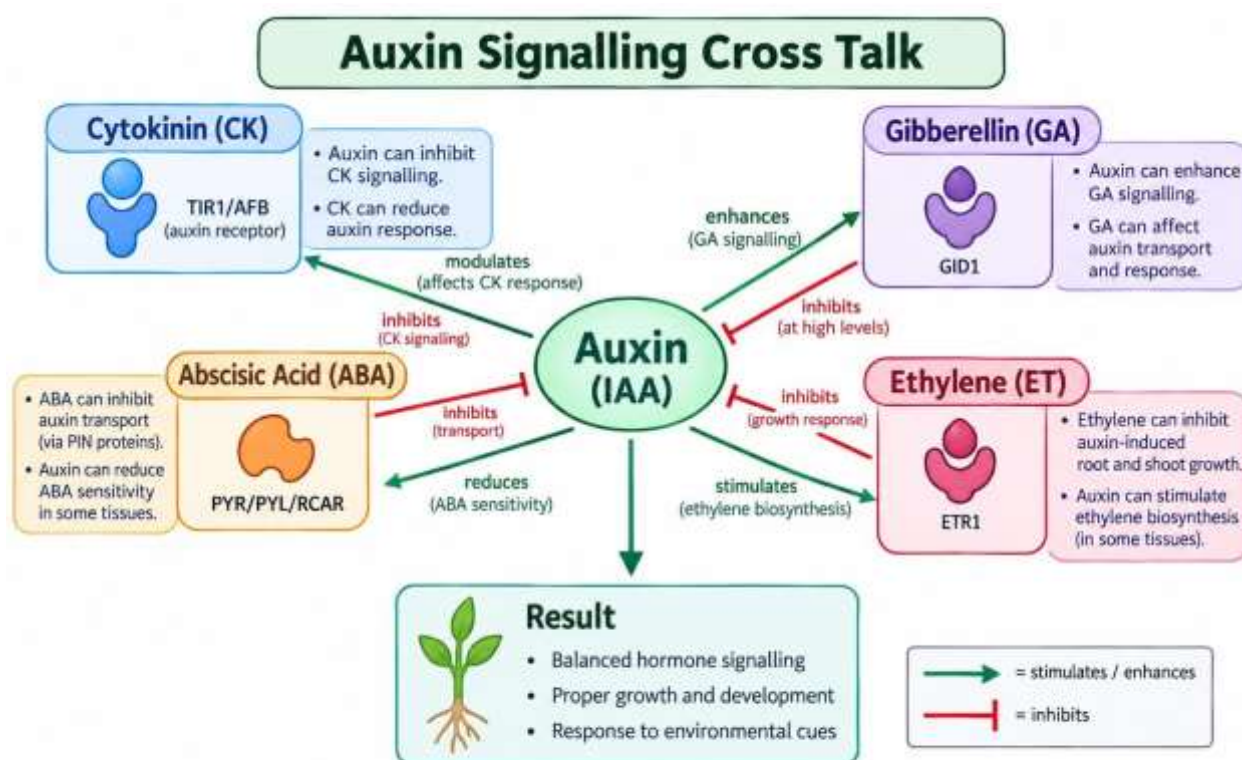


Figure 3. A conceptual biochemical pathway map detailing hormone cross talk, centered around Auxin (IAA). Auxins provides regulatory network, interacting with multiple other plant hormones

3. Gibberellins-synthesis and signalling cross talk

Gibberellins (GAs) are a group of diterpenoid plant hormones that regulate several important aspects of plant growth and development. They are particularly associated with stem and internode elongation, seed

germination, leaf expansion, flowering, fruit development and reproductive growth. Among the numerous gibberellins identified in plants, GA₁ and GA₄ are considered important biologically active forms in many plant species. Gibberellin activity is determined not only by its biosynthesis but also by metabolic inactivation and cellular sensitivity. The balance between active and inactive GAs allows plants to coordinate growth according to developmental stage and environmental conditions [45].

3.1 Biosynthesis of Gibberellins

Gibberellin biosynthesis begins from geranylgeranyl diphosphate (GGDP), a precursor of diterpenoid compounds. The initial reactions take place mainly in plastids, where GGDP is converted into ent-kaurene through the activities of ent-copalyl diphosphate synthase (CPS) and ent-kaurene synthase (KS). Ent-kaurene is subsequently oxidized through reactions involving cytochrome P450 monooxygenases, producing intermediates that ultimately lead to the formation of gibberellin precursors. These early reactions establish the basic carbon skeleton required for the subsequent production of biologically active GAs [46]. Following the formation of ent-kaurene, a series of oxidation reactions converts it into ent-kaurenoic acid and subsequently into GA₁₂, which represents an important branching point in the gibberellin biosynthetic pathway. Further reactions occur mainly in the endoplasmic reticulum and cytosol and involve enzymes such as GA 20-oxidases (GA20ox) and GA 3-oxidases (GA3ox). GA20ox enzymes catalyze successive modifications of GA precursors, while GA3ox enzymes convert inactive precursors into biologically active forms such as GA₁ and GA₄. The coordinated action of these enzymes determines the amount of active gibberellin available in plant tissues [47].

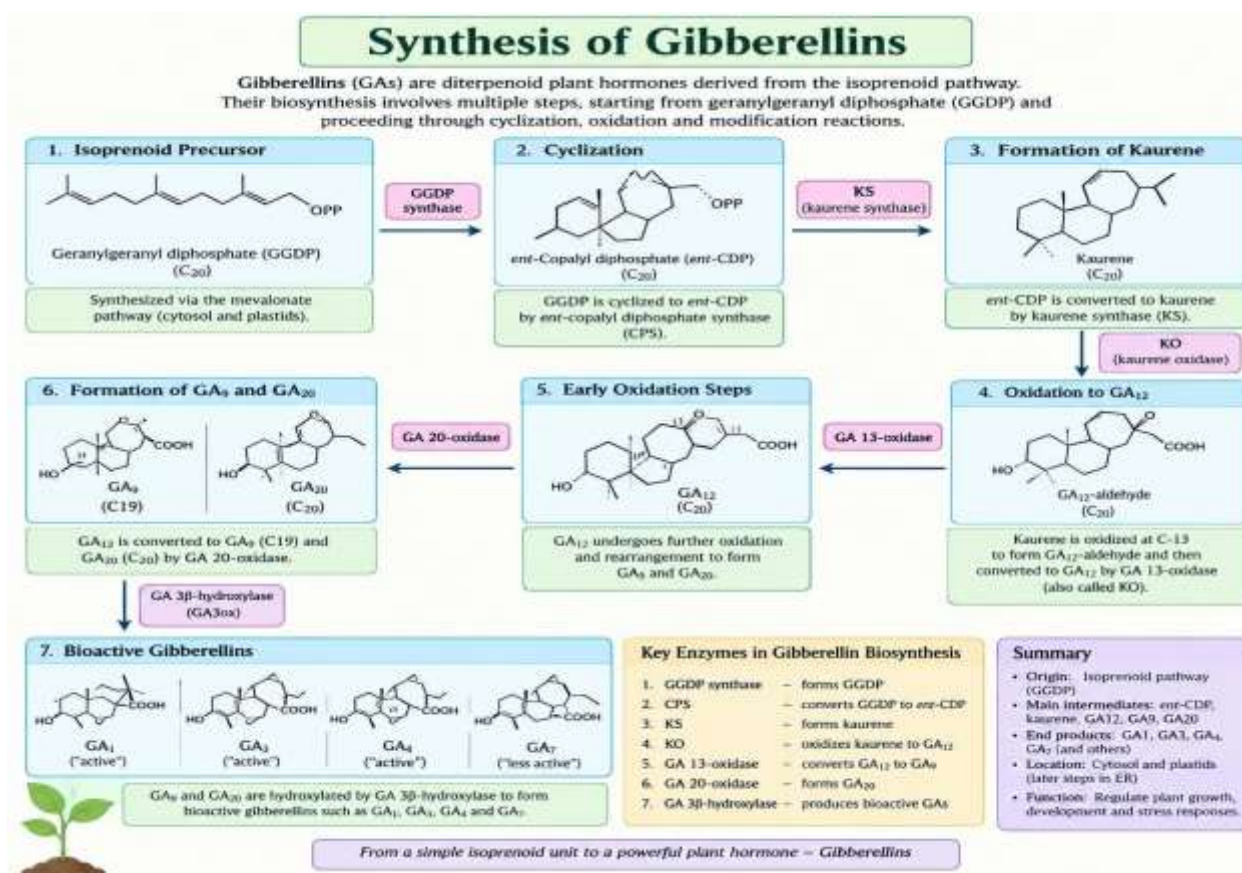


Figure 4. Illustrate the complete biosynthetic pathway of Gibberellins (Gas), a crucial class of diterpenoid plant hormones.

Gibberellin concentration is also controlled by deactivation pathways. GA 2-oxidases (GA2ox) convert active GAs or their immediate precursors into less active or inactive compounds. This degradation pathway is essential for maintaining hormonal balance because excessive GA activity can cause abnormal elongation and developmental changes. Plants can therefore regulate growth by adjusting the relative activities of GA20ox, GA3ox and GA2ox enzymes. Environmental factors such as light, temperature and nutritional status can influence these enzymes and consequently modify the endogenous GA level [48]. The regulation of gibberellin biosynthesis is closely connected with plant developmental requirements. During seed germination, for example, an increase in active GA promotes the transition from a dormant state to active growth. In elongating stems, GAs stimulates cell expansion and division, resulting in increased internode length. Conversely, reduction of active GA through enhanced catabolism or decreased biosynthesis can produce dwarf or semi-dwarf phenotypes. This relationship demonstrates that the physiological effect of gibberellins is strongly dependent on the balance between synthesis and degradation rather than simply on the presence of the hormone [49].

3.2 Gibberellin Signalling

Gibberellin signalling is primarily mediated through the soluble receptor GIBBERELLIN INSENSITIVE DWARF1 (GID1). When an active gibberellin binds to GID1, the hormone–receptor complex interacts with DELLA proteins, which function as important negative regulators of GA responses. In the absence of sufficient GA, DELLA proteins remain relatively stable and restrict the activity of several growth-promoting transcriptional regulators. When GA binds to GID1, the resulting complex facilitates recognition of DELLA proteins by an SCF-type E3 ubiquitin ligase complex, leading to their ubiquitination and subsequent degradation by the 26S proteasome [50]. The degradation of DELLA proteins represents a central step in gibberellin signalling. Once DELLA-mediated repression is removed, transcription factors and other regulatory proteins can activate gene-expression programs associated with growth and development. Through this mechanism, gibberellin perception at the receptor level is translated into physiological responses such as stem elongation, seed germination, flowering and reproductive development. The GID1–DELLA module is therefore considered a major molecular switch controlling GA-dependent growth [68]. DELLA proteins do not simply function as passive inhibitors of growth. They interact with numerous transcription factors and regulatory proteins involved in different developmental pathways. Consequently, changes in DELLA abundance can influence several processes simultaneously. The interaction between DELLA proteins and other signalling networks also allows gibberellin responses to be integrated with signals from other plant hormones and environmental conditions. This provides plants with a flexible mechanism for adjusting growth according to internal developmental programs and external stimuli [51].

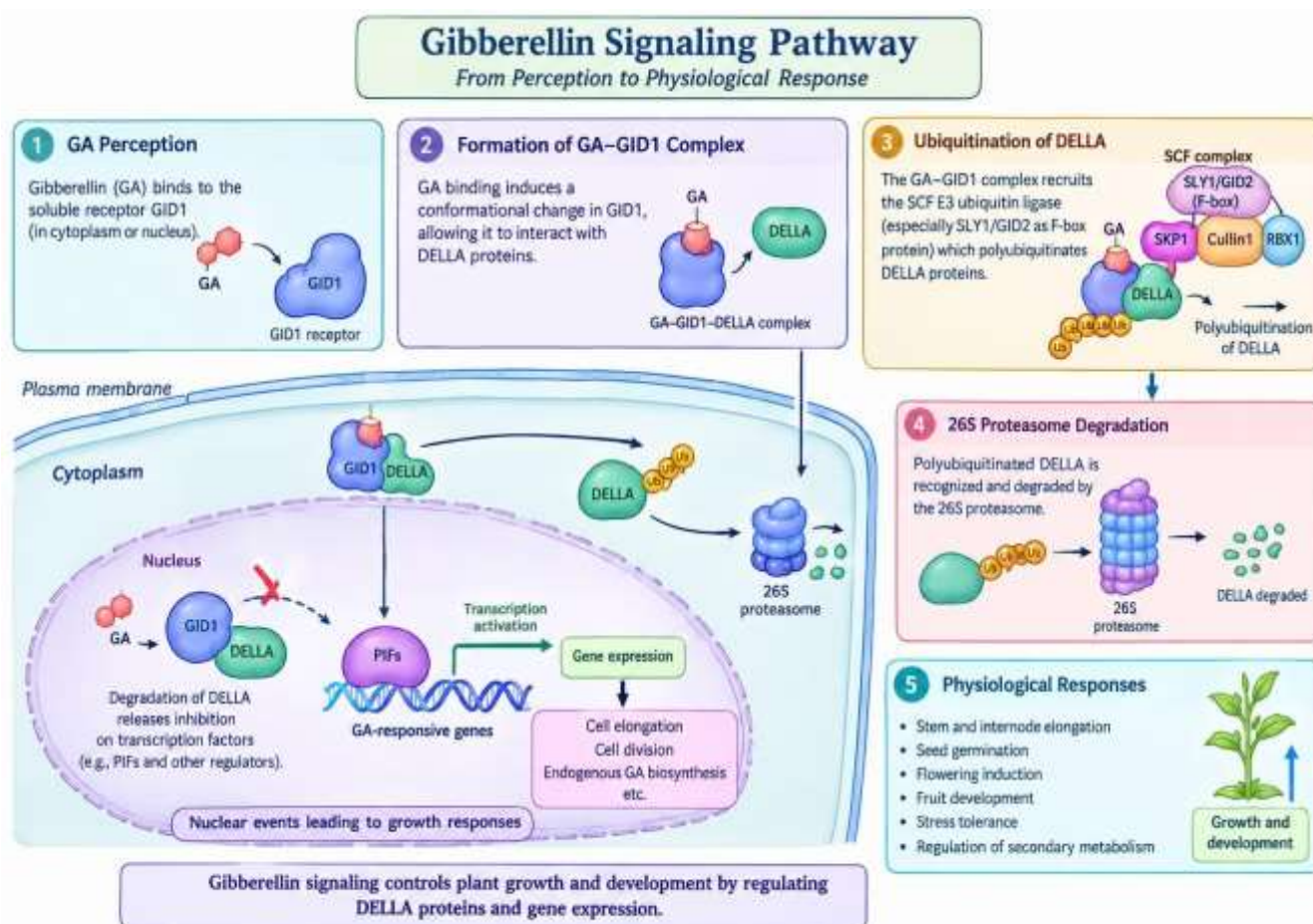


Figure:5 Illustrates the multi-step Gibberellin (GA) signalling pathway, detailing the molecular transcription from hormone perception to physiological responses in plants

3.3 Gibberellins in Seed Germination

Gibberellins have a major role in breaking seed dormancy and promoting germination in many plant species. Following suitable environmental conditions, GA biosynthesis increases in the embryo and surrounding tissues. The resulting increase in active GA promotes cellular growth and stimulates the production of hydrolytic enzymes in certain seeds. In cereal grains, GA signalling in the aleurone layer contributes to the synthesis and secretion of enzymes such as α -amylase, which helps convert stored starch into soluble sugars. These nutrients provide energy for the developing embryo and support early seedling growth. [52]

The relationship between gibberellins and abscisic acid (ABA) is particularly important during the transition between seed dormancy and germination. ABA generally promotes dormancy, whereas GA promotes germination and subsequent growth. The physiological outcome depends on the relative activities of these two hormonal systems. Gibberellin signalling through GID1 and DELLA degradation therefore forms part of a larger hormonal network that determines whether a seed remains dormant or proceeds toward germination. [53]

3.4 Gibberellins and Pharmaceutical Biotechnology

Although gibberellins are primarily studied as regulators of plant growth, their significance extends to biotechnology because manipulation of GA biosynthesis and signalling can influence biomass production,

plant architecture and the cultivation of economically important medicinal plants. Controlled regulation of plant growth can be useful in tissue culture and in the establishment of efficient plant-production systems. In pharmaceutical biotechnology, such systems may support the propagation of medicinal plants that serve as sources of pharmacologically valuable secondary metabolites [54]. Gibberellins can also be produced by microorganisms, including certain fungi and bacteria. Microbial production of gibberellic acid has attracted industrial interest because fermentation can provide a controlled approach for obtaining GA products. Gibberellic acid (GA₃) is particularly well known for its commercial applications in agriculture and plant biotechnology. The ability of microorganisms to synthesize biologically active gibberellins establishes an important connection between plant hormone biology, industrial microbiology and bioprocess technology [55]. gibberellin action can be viewed as a coordinated sequence beginning with precursor biosynthesis and ending with hormone-dependent changes in gene expression. The balance between GA20ox/GA3ox-mediated synthesis and GA20ox-mediated inactivation determines the availability of active GAs, while the GID1–DELLA signalling module translates GA levels into developmental responses. This integrated mechanism allows plants to adjust growth according to their developmental stage and environmental conditions [56].

4. Cytokinin synthesis and signalling

4.1 Cytokinin synthesis

Cytokinins are a group of naturally occurring N⁶-substituted adenine derivatives that function as important regulators of plant growth and development. Major naturally occurring cytokinins include isopentenyl adenine (iP), trans-zeatin (tZ), cis-zeatin (cZ), and dihydrozeatin (DHZ). Cytokinin biosynthesis occurs in different plant tissues, particularly in actively growing regions such as root and shoot meristems. The cellular concentration of active cytokinin is determined by a coordinated balance between biosynthesis, conversion, transport, conjugation and degradation. Therefore, cytokinin homeostasis is essential for maintaining appropriate hormone levels during different stages of plant development [57]. The major pathway for cytokinin biosynthesis begins with the prenylation of adenine nucleotides. The enzyme isopentenyl transferase (IPT) transfers a dimethylallyl group from dimethylallyl diphosphate (DMAPP) to ATP, ADP or AMP, producing cytokinin nucleotide precursors. These products can subsequently undergo further modification to generate different cytokinin forms. IPT enzymes therefore have an important regulatory role in controlling the initial rate of cytokinin production. The expression of IPT genes is tissue-dependent, allowing plants to increase cytokinin production at particular developmental sites according to their physiological requirements [58].

A major branch of the pathway involves the formation of trans-zeatin-type cytokinins. The cytokinin nucleotides generated through IPT activity can be hydroxylated by the cytochrome P450 enzymes CYP735A1 and CYP735A2. These enzymes convert isopentenyl-type cytokinin nucleotides into trans-zeatin-type nucleotides. This step is particularly important because trans-zeatin is one of the biologically active cytokinin forms involved in regulating shoot development, vascular processes and other developmental responses. The spatial expression of CYP735A genes contributes to the formation of tissue-specific cytokinin profiles [59]. The final activation of cytokinin nucleotides is strongly associated with the enzyme LONELY GUY (LOG). LOG proteins are cytokinin riboside-5'-monophosphate phosphoribohydrolases that convert cytokinin nucleotides directly into biologically active free bases. This reaction provides an important point of control because free-base cytokinins are readily available for receptor-mediated signalling. Consequently, LOG activity can determine where and when active cytokinin

responses occur. Studies of LOG genes have demonstrated that localized cytokinin activation is particularly important in meristematic tissues and organ development [60]. Cytokinins can also originate through pathways associated with tRNA metabolism. Certain tRNAs contain prenylated adenine residues, and degradation of these modified tRNAs can contribute to the production of cis-zeatin-type cytokinin. Thus, cytokinin metabolism is connected not only with a dedicated biosynthetic pathway but also with normal cellular nucleic-acid metabolism. The relative contribution of different pathways can vary according to plant species, tissue and developmental stage, contributing to the chemical diversity of cytokinin found in plants [61].

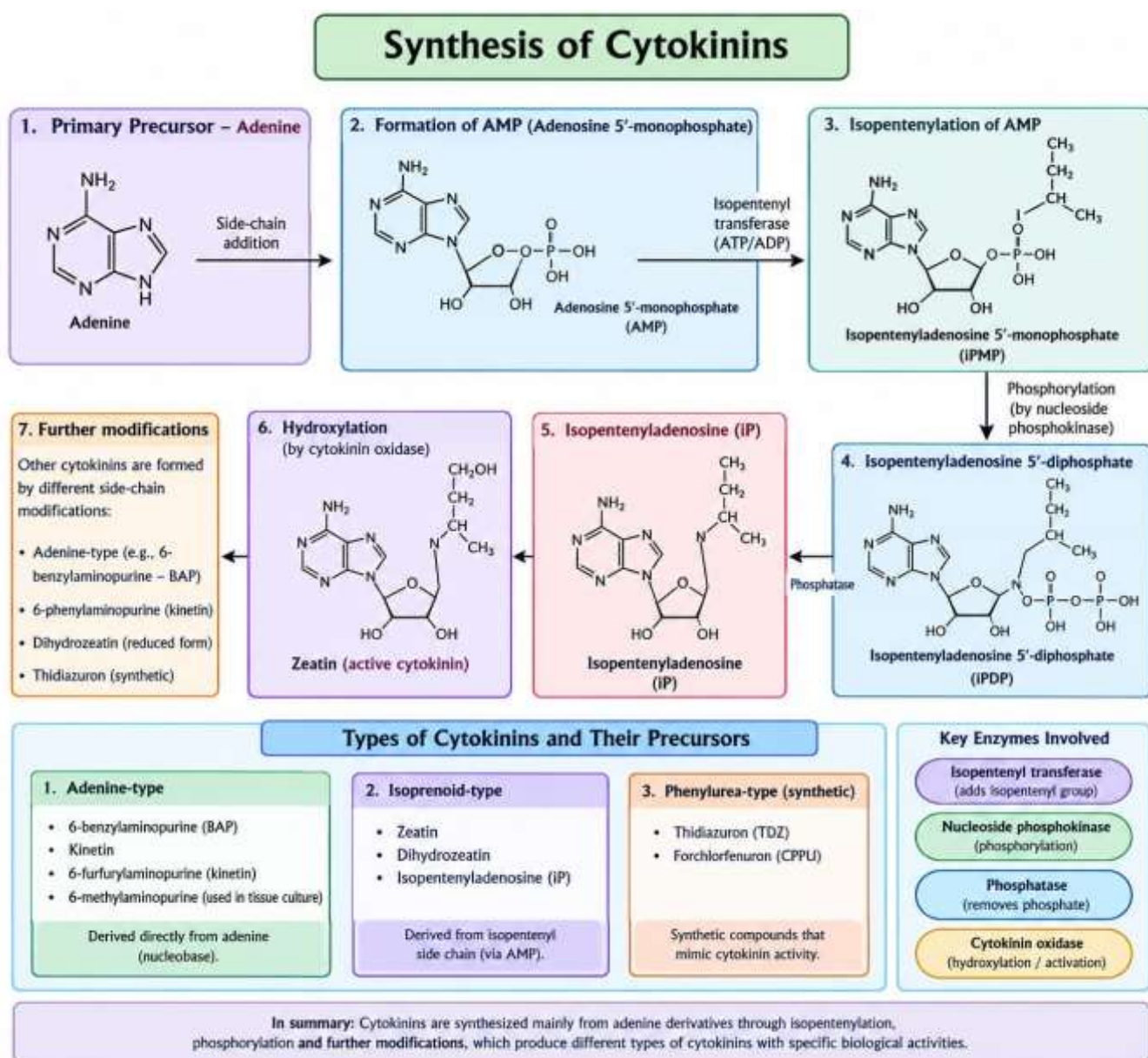


Figure 6. Illustrates the step-by-step formation of cytokinin starting from the primary precursor adenine, through intermediates like AMP, up to active form like Zeatin.

4.2 Cytokinin degradation and homeostasis

The concentration of active cytokinins is controlled not only through synthesis but also through metabolic

inactivation. One of the major enzymes involved in irreversible cytokinin degradation is cytokinin oxidase/dehydrogenase (CKX). CKX enzymes cleave the cytokinin side chain and thereby reduce the amount of biologically active hormone available to cells. In addition, cytokinins can undergo conjugation reactions, including glucosylation, which may produce storage or inactive forms. Through these processes, plants can rapidly adjust cytokinin concentration when developmental or environmental conditions change [62]. The balance between IPT-mediated synthesis and CKX-mediated degradation is therefore an important component of cytokinin homeostasis. Increased cytokinin biosynthesis can promote cell division and shoot development, whereas increased degradation can reduce cytokinin activity. This balance is particularly important in meristems, where relatively small changes in hormone concentration can influence cell proliferation and organ formation. Such metabolic control also provides plants with flexibility to modify their growth in response to nutrients, environmental stresses and developmental signals [63].

4.3 Cytokinin signalling

Cytokinin signalling differs from the classical auxin signalling mechanism and is primarily based on a two-component phosphorelay system. Cytokinin molecules are perceived by membrane-associated histidine kinase receptors, mainly AHK2, AHK3 and AHK4/CRE1 in Arabidopsis. Binding of cytokinin to these receptors activates their histidine kinase activity and initiates a phosphorylation cascade. This mechanism resembles two-component signalling systems found in bacteria and demonstrates the evolutionary conservation of this type of cellular communication [64].

Following cytokinin perception, the phosphoryl group is transferred from the activated receptor to histidine phosphotransfer proteins (AHPs). AHP proteins function as mobile signalling components and can transport the signal toward the nucleus. Within the nucleus, AHPs transfer the phosphoryl group to response regulators (ARRs). This sequence—receptor activation, AHP phosphorylation and ARR activation—forms the central cytokinin phosphorelay pathway [65].

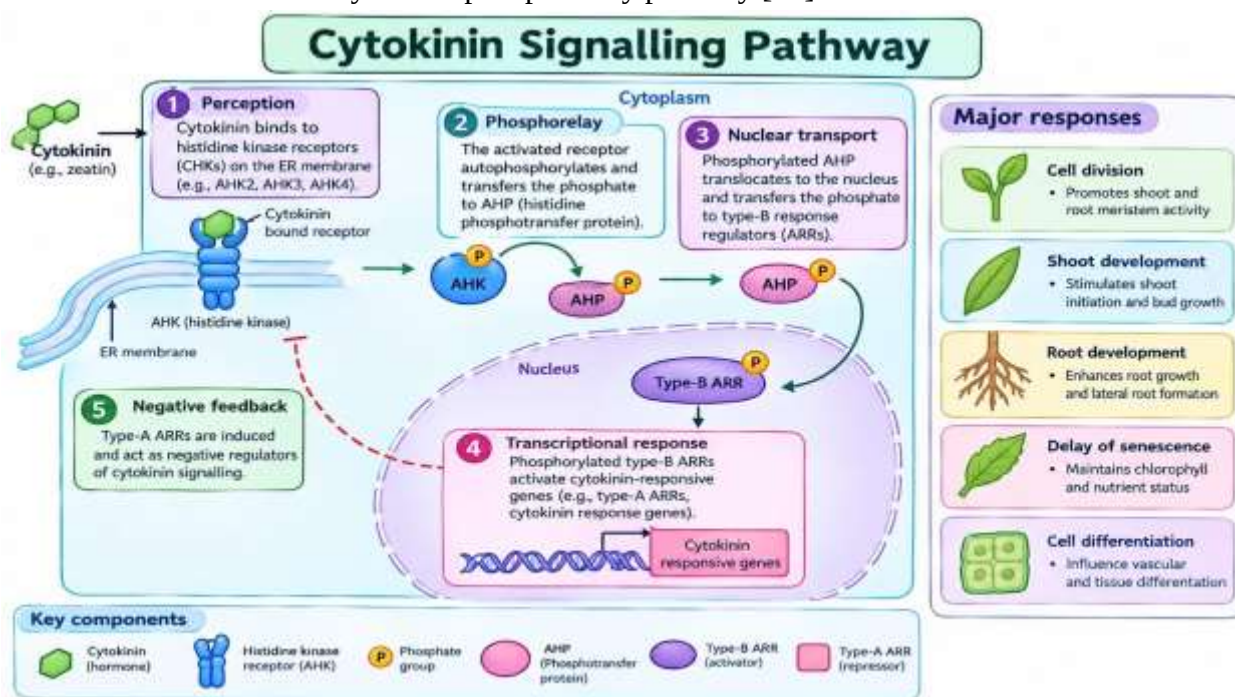


Figure 7. Illustrates the central cytokinin signalling pathway, which operates via a multi-step phosphor-relay system moving from the endoplasmic reticulum (ER) membrane to the nucleus.

The response regulators are broadly divided into type-A and type-B ARR. Type-B ARRs function mainly as transcriptional regulators and activate the expression of cytokinin-responsive genes. Type-A ARRs are generally involved in negative-feedback regulation and can reduce the intensity or duration of cytokinin responses. This arrangement provides a self-regulating signalling system in which cytokinin can rapidly activate a response while simultaneously inducing mechanisms that prevent excessive signalling [66]. Cytokinin signalling does not operate independently of other plant hormones. In particular, the interaction between cytokinin and auxin is fundamental for controlling the balance between root and shoot development. Cytokinin generally promotes shoot meristem activity, whereas auxin has important roles in root initiation and development. Their reciprocal regulation of biosynthetic and signalling components allows plants to establish developmental patterns and determine the fate of dividing cells. This hormonal interaction is also highly important in plant tissue culture, where changing the auxin-to-cytokinin ratio can influence callus formation, shoot regeneration and root development [67].

4.4 Cytokinins in plant biotechnology

The ability of cytokinins to regulate cell division and shoot formation makes them particularly important in plant tissue culture and micropropagation. Synthetic cytokinin-like compounds such as 6-benzylaminopurine (BAP), kinetin and thidiazuron (TDZ) are frequently used to stimulate shoot multiplication and regeneration. The response depends on the plant species, explant type, cytokinin concentration and interaction with auxins. Consequently, optimization of cytokinin concentration is an important step when developing tissue-culture protocols for medicinal and economically valuable plants [68]. Cytokinin action is controlled through a coordinated relationship between biosynthesis, activation, degradation, transport and signal transduction. IPT enzymes initiate cytokinin production, CYP735A enzymes contribute to trans-zeatin formation, and LOG proteins generate active free-base cytokinins. Active cytokinins are then perceived by AHK receptors, which initiate an AHP-mediated phosphorelay leading to ARR-dependent gene regulation. This integrated pathway enables cytokinins to regulate cell division, meristem maintenance, shoot development, nutrient responses and interactions with other plant hormones [69].

5. Ethylene Synthesis and Signalling

Ethylene is a unique gaseous phytohormone that regulates several stages of plant growth, development and responses to environmental conditions. Unlike most other plant hormones, ethylene is produced in the gaseous state and can readily diffuse through plant tissues. It participates in fruit ripening, leaf and flower senescence, organ abscission, seed germination, root development and responses to mechanical injury, flooding, pathogen attack and other stresses. The biological effect of ethylene depends on both the amount produced and the sensitivity of the receiving tissues [70].

5.1 Biosynthesis of Ethylene

The biosynthesis of ethylene begins with the amino acid methionine. Methionine is converted into S-adenosyl-L-methionine (SAM) by SAM synthetase. SAM is then converted into 1-aminocyclopropane-1-carboxylic acid (ACC) by the enzyme ACC synthase (ACS). ACC is the immediate precursor of ethylene and is subsequently oxidized by ACC oxidase (ACO) to produce ethylene. Carbon dioxide and cyanide are also generated during this reaction, while the cyanide formed is detoxified through plant metabolic pathways. This relatively short biosynthetic pathway is nevertheless highly regulated at transcriptional and post-translational levels [71]. The ACS step represents a major regulatory point in ethylene production. Different ACS genes are expressed in response to developmental signals and environmental

stimuli, allowing plants to alter ethylene production according to their physiological requirements. Wounding, flooding, pathogen attack, mechanical stress, fruit maturation and other conditions can stimulate changes in ACS activity. ACO also contributes to the regulation of ethylene production, and its activity is influenced by factors such as oxygen availability and developmental stage. Therefore, ethylene biosynthesis is controlled through coordinated regulation of both its precursor formation and final conversion [72]. Ethylene biosynthesis is closely connected with the Yang cycle, which enables plants to recycle the sulfur-containing portion of methionine metabolism. During the conversion of SAM to ACC, 5'-methylthioadenosine (MTA) is generated. MTA is subsequently metabolized through the Yang cycle, allowing methionine to be regenerated and reused for further ethylene synthesis. This recycling mechanism is important because it allows continuous ethylene production without requiring a proportionate increase in the cellular methionine pool. Thus, ethylene synthesis is integrated with primary sulfur and methionine metabolism [73].

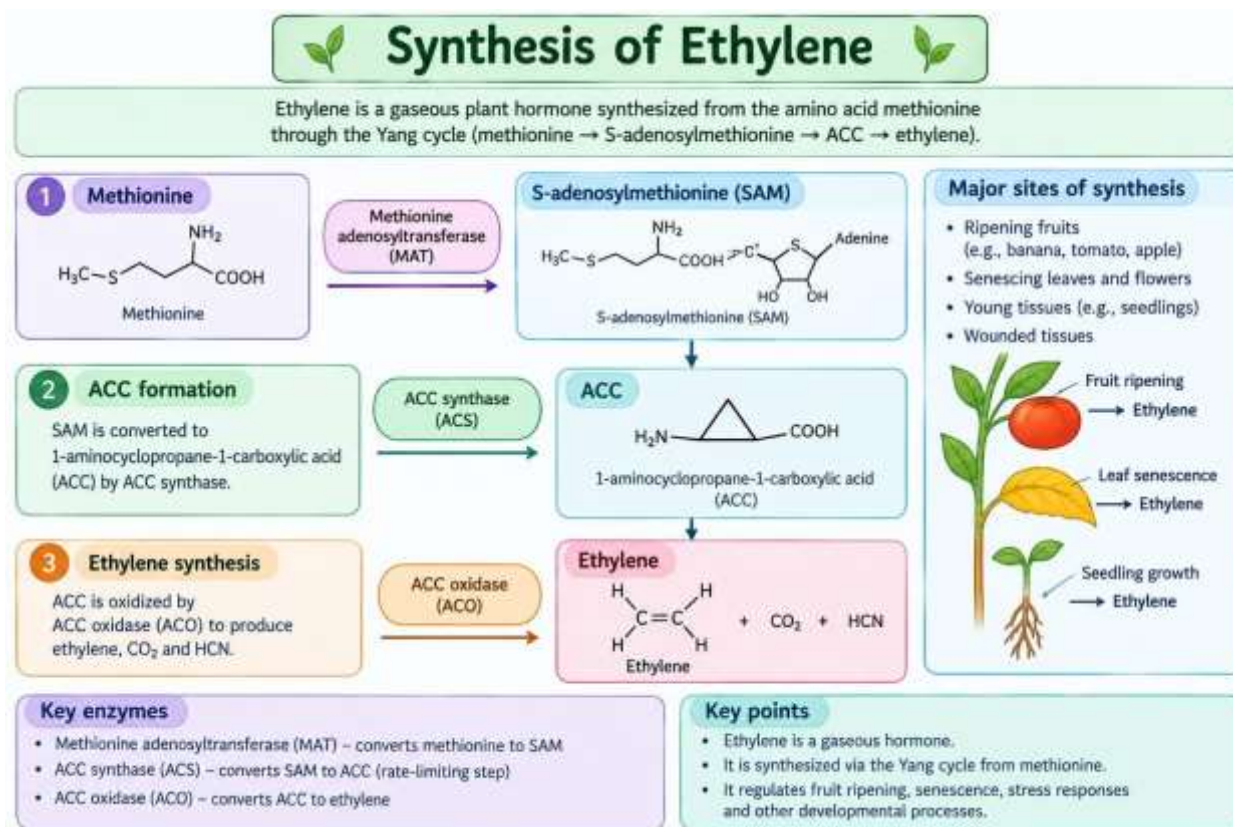


Figure 8. Illustrate the biosynthetic pathway of ethylene, a crucial gaseous plant hormone responsible for fruit ripening and developmental processes.

An additional level of regulation occurs through the metabolism and transport of ACC. ACC can be conjugated into inactive forms or metabolized through alternative pathways. Some plant-associated microorganisms produce ACC deaminase, which converts ACC into compounds other than ethylene and can consequently influence the amount of ethylene produced by plants. This interaction provides an important link between ethylene metabolism and plant–microbe interactions. Microbial regulation of ACC availability is therefore of interest in agricultural and plant–biotechnology research, particularly in studies of plant growth under stress [74].

5.2 Ethylene Perception and Signalling

Ethylene signalling begins with its perception by a family of membrane-associated receptors, including ETR1, ETR2, ERS1, ERS2 and EIN4 in Arabidopsis. These receptors are mainly associated with the endoplasmic reticulum membrane and contain a metal cofactor, particularly copper, that is important for ethylene perception. Unlike many hormone receptors in which ligand binding directly activates a positive signalling pathway, ethylene receptors and their downstream regulator CTR1 function predominantly as negative regulators of ethylene responses [75]. In the absence of ethylene, the receptors maintain an active state and stimulate CONSTITUTIVE TRIPLE RESPONSE1 (CTR1), a Raf-like serine/threonine protein kinase. Active CTR1 suppresses the activity of ETHYLENE INSENSITIVE2 (EIN2), thereby preventing activation of downstream ethylene-responsive genes. At the same time, transcription factors such as EIN3 and EIL1 are maintained at relatively low levels through regulated protein degradation. This arrangement keeps the ethylene response pathway in an inactive state when the hormone is not present [76]. When ethylene is present, it binds to the receptors and changes their signalling state, resulting in inhibition of CTR1 activity. The reduction in CTR1-mediated suppression allows EIN2, a key positive regulator of ethylene signalling, to become activated. The C-terminal region of EIN2 is then processed and contributes to signalling toward the nucleus. This provides the molecular connection between ethylene perception at the membrane and changes in nuclear gene expression [77].

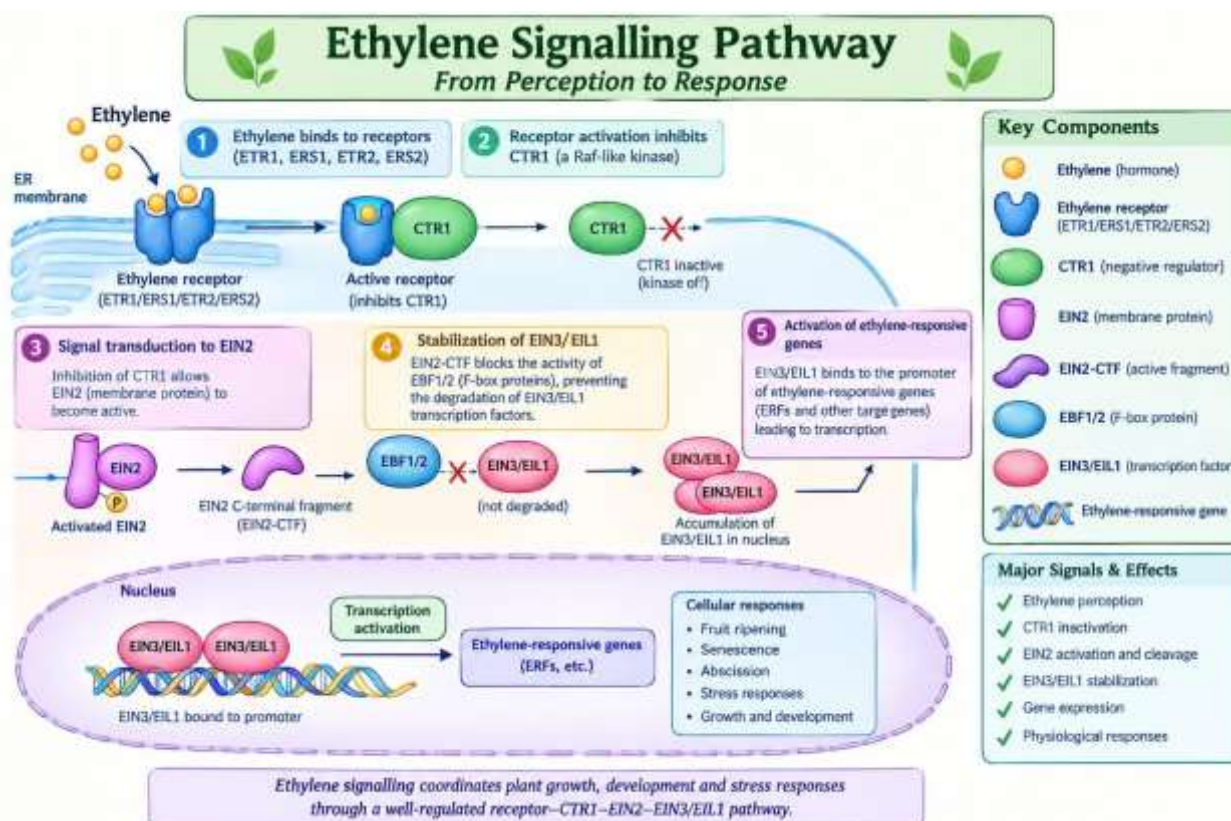


Figure 9. illustrates the ethylene signalling pathway in plants, detailing the molecular mechanism from hormone perception to gene expression.

The downstream transcription factors EIN3 and EIL1 are central regulators of the nuclear ethylene response. Following activation of the EIN2-dependent pathway, EIN3/EIL proteins accumulate and

regulate the expression of target genes. One important group of downstream targets is the ethylene response factor (ERF) family. ERFs regulate additional sets of genes involved in growth, development and responses to environmental stresses. Therefore, the ethylene signalling cascade can be summarized as receptor perception followed by CTR1 inhibition, EIN2 activation, EIN3/EIL stabilization and ERF-dependent transcriptional regulation [78].

5.3 Ethylene and Plant Development

Ethylene has diverse effects on plant development depending on the tissue, developmental stage and concentration of the hormone. In young seedlings, ethylene contributes to the characteristic triple response, which includes reduced elongation, increased radial expansion and exaggerated apical-hook formation. These changes help seedlings growing through soil adjust their growth pattern when they encounter mechanical resistance. Ethylene also influences root-hair formation and root architecture, demonstrating that its effects are not restricted to above-ground tissues [79]. One of the most economically important functions of ethylene is its involvement in fruit ripening. In climacteric fruits, increased ethylene production is associated with major biochemical and physiological changes, including softening, pigment changes, aroma formation and alterations in carbohydrate and organic-acid metabolism. Ethylene signalling activates transcriptional programs that coordinate these processes. Consequently, regulation of ethylene synthesis or perception is an important strategy in post-harvest biotechnology for controlling fruit maturation and extending storage life [80]. Ethylene also participates in senescence and organ abscission. During leaf and flower ageing, changes in ethylene production and sensitivity can activate gene-expression programs associated with cellular degradation and nutrient redistribution. Ethylene signalling can also interact with other hormones, including auxin, jasmonates, abscisic acid and cytokinins. These interactions enable plants to integrate developmental and environmental signals rather than responding to ethylene in isolation [81].

5.4 Ethylene in Stress Responses and Biotechnology

Ethylene production commonly increases when plants experience environmental stress, including flooding, wounding, pathogen attack, extreme temperatures and mechanical damage. Through EIN2, EIN3/EIL and ERF-dependent signalling, ethylene can regulate genes associated with defence, oxidative stress management and adaptation. The hormone therefore functions as an important communication signal that connects stress perception with changes in gene expression and plant physiology [82]. From a biotechnology perspective, manipulation of ethylene biosynthesis and signalling has applications in fruit storage, crop improvement, stress management and post-harvest technology. Reduction of ethylene synthesis or interference with ethylene perception can delay certain ripening and senescence processes, whereas controlled ethylene application can be used to synchronize or promote ripening in appropriate crops. Understanding the ACS–ACO biosynthetic pathway and the ETR–CTR1–EIN2–EIN3/EIL–ERF signalling pathway therefore provides a molecular basis for developing strategies to regulate ethylene-dependent plant processes [83]. Ethylene regulation involves a comparatively simple core biosynthetic pathway but a highly controlled signalling network. ACS and ACO determine ethylene production, while the ETR–CTR1–EIN2–EIN3/EIL–ERF cascade converts ethylene perception into changes in gene expression. The integration of ethylene with other hormonal and environmental signalling pathways enables plants to coordinate growth, maturation, senescence and stress adaptation [84].

6. Biosynthesis and Physiological Effects of Absciscic Acid

6.1 Biosynthesis of Absciscic Acid

Absciscic acid (ABA) is an important plant hormone mainly associated with seed maturation, dormancy and adaptation to environmental stress. Unlike some other plant hormones, ABA is derived from carotenoid precursors. Its biosynthesis is closely regulated according to the developmental stage of the plant and environmental conditions such as drought, salinity and water deficiency. The concentration of ABA in plant tissues depends on the balance between its synthesis, transport, conjugation and degradation [85]. The biosynthetic pathway begins with carotenoid compounds present in plastids. All-trans- β -carotene is converted through a series of reactions into oxygenated carotenoids. The pathway proceeds through compounds such as zeaxanthin, antheraxanthin and violaxanthin, followed by formation of 9-cis-epoxycarotenoids. A major regulatory step is catalysed by 9-cis-epoxycarotenoid dioxygenase (NCED), which cleaves the 9-cis epoxycarotenoid precursor and produces xanthoxin. NCED activity is particularly important because it can strongly influence ABA accumulation during stress conditions [86]. After its formation in plastids, xanthoxin is converted into abscisic aldehyde. This intermediate subsequently undergoes oxidation to form active abscisic acid (ABA). The final oxidation step is associated with abscisic aldehyde oxidase (AAO). Therefore, the overall pathway can be summarized as carotenoid precursor $\rightarrow$ xanthophyll derivatives $\rightarrow$ xanthoxin $\rightarrow$ abscisic aldehyde $\rightarrow$ ABA. Regulation at different stages allows the plant to increase or decrease ABA production according to its physiological requirements [87].

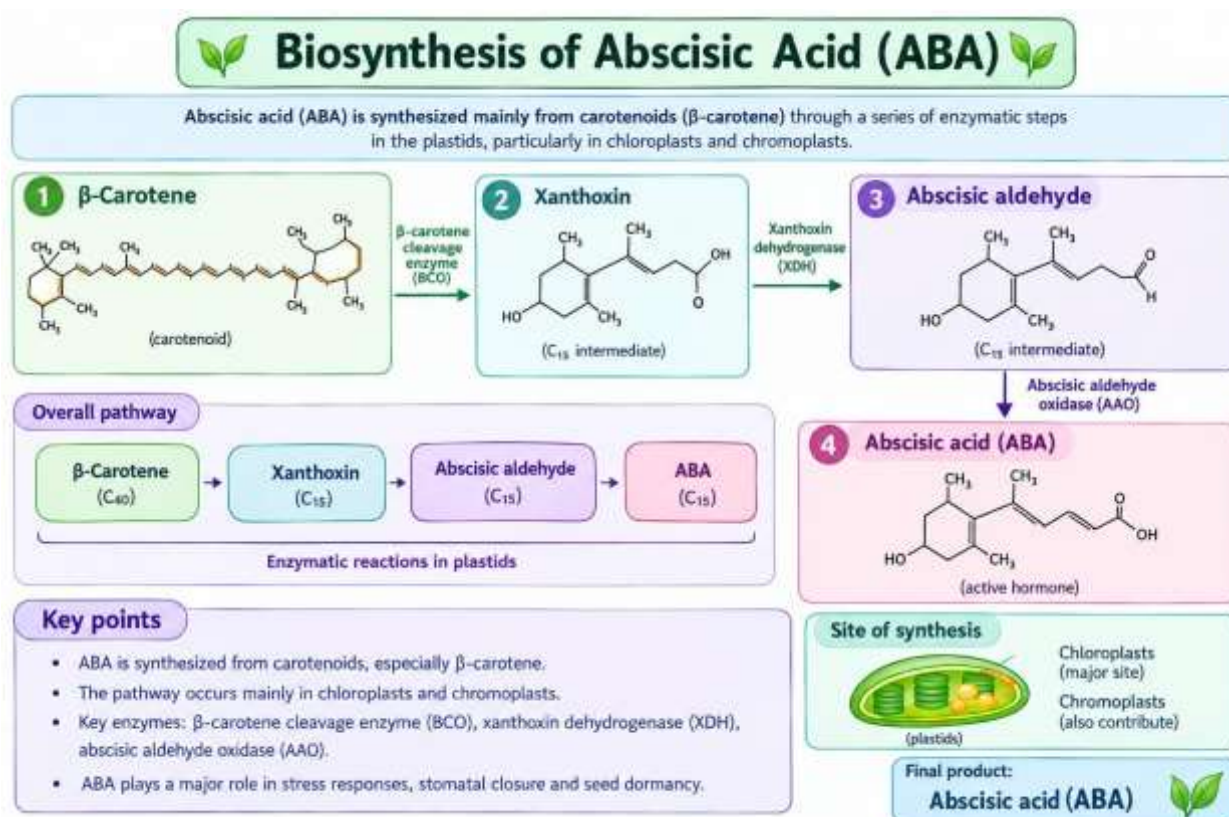


Figure 10. Illustrate the biosynthesis pathway of Absciscic Acid (ABA), a vital plant hormone. It out-line the step-by-step chemical conversion from carotenoids into the active hormone.

6.2 Regulation and Signalling of ABA

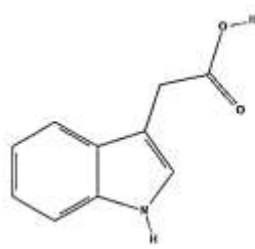
ABA production increases when plants experience environmental conditions such as drought, high salinity and water deficit. Increased ABA concentration allows plants to respond rapidly to stress by activating specific signalling pathways. ABA is perceived mainly by the PYR/PYL/RCAR family of receptors. When ABA binds to these receptors, they interact with type 2C protein phosphatases (PP2Cs) and inhibit their activity. This releases the suppression of SnRK2 protein kinases, allowing them to become active and phosphorylate downstream target proteins [88]. Activated SnRK2 kinases regulate several downstream proteins, including transcription factors involved in ABA-responsive gene expression. This signalling mechanism changes the expression of genes associated with stress tolerance, water conservation and developmental regulation. ABA signalling also interacts with calcium-dependent pathways, ion channels and other cellular signalling systems, particularly in guard cells. These coordinated responses allow plants to modify their physiology rapidly when environmental conditions become unfavourable [89].

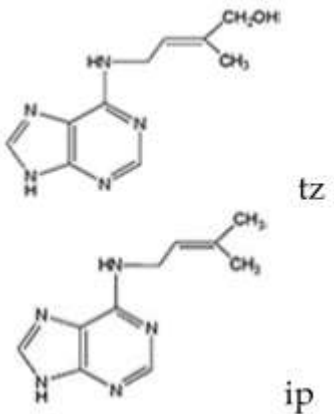
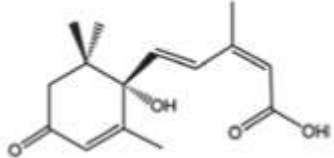
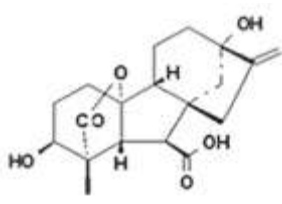
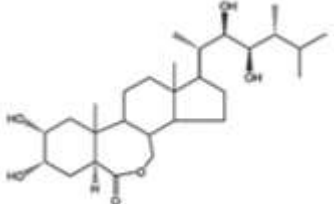
6.3 Physiological Effects of Absciscic Acid

One of the most important physiological functions of ABA is the regulation of stomatal closure. During water deficit, ABA accumulates in guard cells and activates signalling mechanisms that alter ion movement across the guard-cell membrane. Loss of ions and water from guard cells reduces their turgor, causing stomata to close. This reduces transpiration and helps the plant conserve water during drought conditions [90]. ABA also plays a major role in seed maturation, seed dormancy and germination control. Increased ABA activity during seed development promotes maturation and helps prevent premature germination. During unfavourable environmental conditions, ABA-mediated responses contribute to the maintenance of dormancy until conditions become suitable for germination. Thus, ABA provides an important connection between plant development and environmental adaptation. In addition to controlling water balance and seed behaviour, ABA participates in broader stress-adaptation responses. It regulates the expression of stress-responsive genes and contributes to plant responses to drought and salinity. ABA can also influence growth and development, allowing plants to balance growth with survival under unfavourable conditions. Therefore, ABA functions not simply as a growth inhibitor but as a central regulatory hormone that coordinates developmental processes with environmental stress responses [91].

Conclusion

Table 1. Summary of phytohormones, their functions, and effects on nitrogen uptake.

Hormone	Year of Discovery	Key Plant Parts	Effect on Nitrogen Uptake	Molecular Structure
Auxin (IAA)	1930s	Roots, stems, leaves, flowers, seeds	Enhances nitrogen uptake under low-nitrogen conditions, affects ammonium utilization	

Hormone	Year of Discovery	Key Plant Parts	Effect on Nitrogen Uptake	Molecular Structure
Cytokinin	1950s	Roots, shoots, leaves	Increases nitrogen use efficiency by regulating nitrogen distribution and metabolism	
ABA	1960s	Roots, leaves, seeds	Enhances nitrogen uptake by regulating root development and nitrogen transporter expression	
Ethylene	Early 1900s	Roots, shoots, leaves	Promotes root growth and increases nitrogen uptake under high planting density and nitrogen deficiency	
Gibberellins	1920s	Stem tip, young leaves, immature seeds, root system	Enhance nitrogen accumulation under sub-low temperature conditions and promote energy and carbon skeleton supply	
Brassinosteroids	1970s	Pollen, seeds, fruits, stem tips, young internodes, roots	Regulates nitrogen transport genes in collaboration with other hormones (such as auxin)	

Plant growth hormones are essential regulatory molecules that coordinate plant growth, development, reproduction, adaptation, and responses to environmental conditions. The present review demonstrates that phytohormones do not function independently; instead, their biosynthesis, transport, metabolism,

signalling pathways, and interactions with other hormones collectively determine the developmental response of plant tissues. Auxins, cytokinins, gibberellins, abscisic acid, and ethylene therefore form an interconnected regulatory network rather than acting as isolated growth-promoting or growth-inhibiting substances.

Among the hormones discussed, auxins and cytokinins have particular importance in plant biotechnology because of their central roles in cell division, differentiation, root formation, shoot development, callus induction, and plant regeneration. Auxin, particularly indole-3-acetic acid (IAA), regulates developmental processes through coordinated biosynthesis, polar transport, cellular perception, and gene regulation. The TIR1/AFB–Aux/IAA–ARF signalling system provides an important molecular basis for understanding auxin responses, while recent findings indicate that additional signalling mechanisms may also contribute to auxin action.

Cytokinins mainly contribute to cell proliferation, shoot development, meristem activity, nutrient responses, and tissue regeneration. Their activity is regulated through coordinated biosynthesis, activation, degradation, and receptor-mediated signalling. The cytokinin phosphorelay involving AHK receptors, AHP proteins, and ARR regulators demonstrates how hormonal signals are converted into changes in gene expression and plant development.

An important finding from the reviewed information is that the auxin–cytokinin relationship is a major determinant of plant tissue behaviour. Manipulation of their relative concentrations can be used to influence callus formation, shoot multiplication, rooting, and regeneration. However, these responses are not governed by a fixed hormone ratio alone; plant species, genotype, explant type, hormone concentration, culture conditions, and tissue sensitivity can all modify the final outcome.

The review also highlights the importance of plant growth hormones in micropropagation and medicinal-plant biotechnology. Controlled hormonal conditions can support the multiplication and regeneration of valuable medicinal plants and provide relatively controlled biological material for subsequent phytochemical investigation. Tissue-culture systems can further be combined with extraction, chromatographic analysis, and biological screening to investigate plant-derived compounds with potential antioxidant, antimicrobial, anti-inflammatory, and anticancer activities. These applications establish a clear connection between plant physiology, microbiology, pharmacognosy, biotechnology, and pharmaceutical research.

The review further indicates that microorganisms are an important component of phytohormone research. Plant-associated bacteria and fungi can produce or modify hormones such as auxins and cytokinins, while microbial production of IAA can influence plant root architecture and plant–microbe interactions. This provides opportunities for studying microbial hormone production, fermentation-based approaches, plant growth-promoting microorganisms, and biological systems for biotechnology.

Gibberellins, abscisic acid, and ethylene broaden the understanding of hormonal regulation beyond auxin and cytokinin. Gibberellins participate particularly in stem elongation, seed germination, flowering, and reproductive development through the GID1–DELLA signalling mechanism. Ethylene regulates processes including fruit ripening, senescence, abscission, development, and stress responses through the ETR–CTR1–EIN2–EIN3/EIL–ERF pathway. ABA is primarily associated with seed dormancy, maturation, and environmental stress adaptation. Together, these pathways demonstrate the complexity of hormonal coordination in plants.

From a pharmaceutical biotechnology perspective, the major significance of plant hormones is currently indirect rather than as established therapeutic drugs. Their value lies mainly in controlling plant growth,

regeneration, biomass production, tissue-culture systems, medicinal-plant propagation, and the investigation of plant-derived bioactive compounds. Although some studies have explored biological effects of phytohormones beyond plants, these findings remain an emerging research area and require further biochemical, toxicological, mechanistic, and clinical investigation before therapeutic applications can be established.

Overall, the reviewed evidence supports the view that understanding phytohormone biosynthesis, signalling, metabolism, hormonal crosstalk, and plant–microbe interactions can strengthen the development of controlled plant biotechnology platforms. Future research should focus on optimizing hormone combinations for specific medicinal plants, improving metabolite production in plant cell and tissue cultures, investigating microbial production and biotransformation of phytohormones, and establishing reliable links between hormonal manipulation and the quantity and quality of bioactive metabolites. Such approaches may contribute to more controlled, reproducible, and sustainable strategies for plant-based pharmaceutical and biotechnological research.

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