Signalling: Growth Promoters and Inhibitors

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

Review Article

ABSTRACT

Plant growth and development are intricately regulated by a multitude of signaling pathways that respond to internal and external cues. Central to these regulatory mechanisms are the signaling pathways of growth promoters and inhibitors. Various growth-promoting hormones, including auxins, cytokinins, gibberellins, and brassinosteroids, stimulate cell division, elongation, and differentiation, playing vital roles in shaping plant architecture and influencing various developmental processes. The pathways of these growth promoters involve specific receptors and transcription factors that orchestrate growth in response to dynamic signals. In contrast, growth inhibitors, represented by hormones like abscisic acid, ethylene, jasmonic acid, and salicylic acid, act as crucial checkpoints that restrict growth during stress, pathogen attacks, or other adverse conditions. These signaling pathways trigger growth inhibition and activate defense mechanisms, enabling plants to adapt to challenging environments. Balancing the interplay between growth promoters and inhibitors allows plants to allocate resources efficiently and ensure their survival under changing circumstances. Understanding these signaling pathways is not only fundamental to plant biology but also essential for applications in agriculture, horticulture, and environmental management. This abstract provides a concise overview of these essential processes. This

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knowledge enables us to manipulate plant growth and development for improved crop yields, disease resistance, and stress tolerance. Ongoing research continues to unravel the complexities of these pathways, offering valuable insights into how plants delicately balance growth promotion and inhibition to thrive in an ever-evolving world.

Keywords: Auxin; brassinosteroids; cytokinin; ethylene; gibberellin; salicylic acid.

1. INTRODUCTION

Plant growth and development are tightly controlled by a diverse set of signalling molecules, which are including regulators and inhibitors. These chemicals are critical in coordinating many parts of plant life, including germinating and cell elongation through blooming, fruit development, and stress response. Plants can adapt and grow in ever-changing settings due to the dynamic interaction of these chemicals. Plant growth hormones, commonly referred to as phytohormones, are chemical messengers that have a significant impact on several developmental processes within plants. These hormones are synthesized in certain tissues and delivered to specific locations to influence growth and development. Auxins, gibberellins, cytokinin's, abscisic acid, ethylene, and brassinosteroids are some of the primary plant growth hormones, each with its own particular role in forming the plant's architecture. Plant growth inhibitors, on the other hand, serve to restrict or inhibit specific components of plant development, as the name implies. While this may appear to be counterproductive, inhibitors are necessary for preserving plant equilibrium. They, for example, aid in the prevention of excessive growth and the regulation of responses to environmental stimuli. Abscisic acid is a well-known inhibitor during drought circumstances, Jasmonic acid in response to herbivory or pathogen assault, and salicylic acid during specific stress reactions. In plants the roles and quantities of these growth hormones and inhibitors are carefully regulated to respond to the plant's individual demands, developmental stage, and environmental difficulties. This sophisticated regulatory network lets plants adapt to light, gravity, temperature, and other environmental conditions, guaranteeing their survival and successful reproduction. Recognizing the application of hormones that stimulate plant growth and inhibitors is critical for horticulturalists agriculturists, and other professionals who want to boost the productivity of crops, boost stress tolerance, and regulate plant development for a variety of reasons. It demonstrates the plant kingdom's extraordinary intricacy and flexibility,

as these molecular messengers choreograph a complex pattern of development and evolution in order to maintain the plant's general well-being. "In actuality, these hormones exert many of their effects via a complicated chain of interactions with other hormones and signaling molecules. PGRs, also known as biostimulants or bio inhibitors, function inside plant cells to stimulate or inhibit certain enzymes or enzyme systems, therefore aiding in the regulation of plant metabolism" [1]. "Botanical hormones are biological chemical messengers that regulate the maturation and growth of plants as well as reactions to stresses caused by abiotic and biotic factors, allowing plant homeostasis and adaptability to environmental changes" [2]. "Temperature is an environmental component that has a significant impact on the plant's development program. It is crucial in modulating the degree of dormancy experienced by the seeds" [3]. Plant hormones have powerful, seemingly independent effects on plant development as well as growth. Auxin stimulates growth in general; cytokinin's delay leaf senescence and impact cell division; abscisic acid causes bud hibernation and promotes stomatal closure; gibberellins aid in the sprouting of seeds.

2. CROSSTALK IN PHYTOHORMONAL SIGNALING IN PLANT GROWTH AND DEVELOPMENT

2.1 Signaling of Auxin

Initially, auxin signaling molecules were explored by studying the effects of exogenous administration of hormone combinations on plant proliferation or morphology [4]. "Hormones, as endogenous variables, are critical in controlling developmental processes. Hormonal control of development is a complicated process including interactions between numerous hormones at the transcriptional, translational, and cellular levels" [5]. "Furthermore, auxin is a key player in the current hormonal crosstalk that influences several developmental phases" [6,5,7] Fig. 1. It regulates cell division, elongation, and programmed cell death, hence influencing embryonic and post-embryonic development [8]
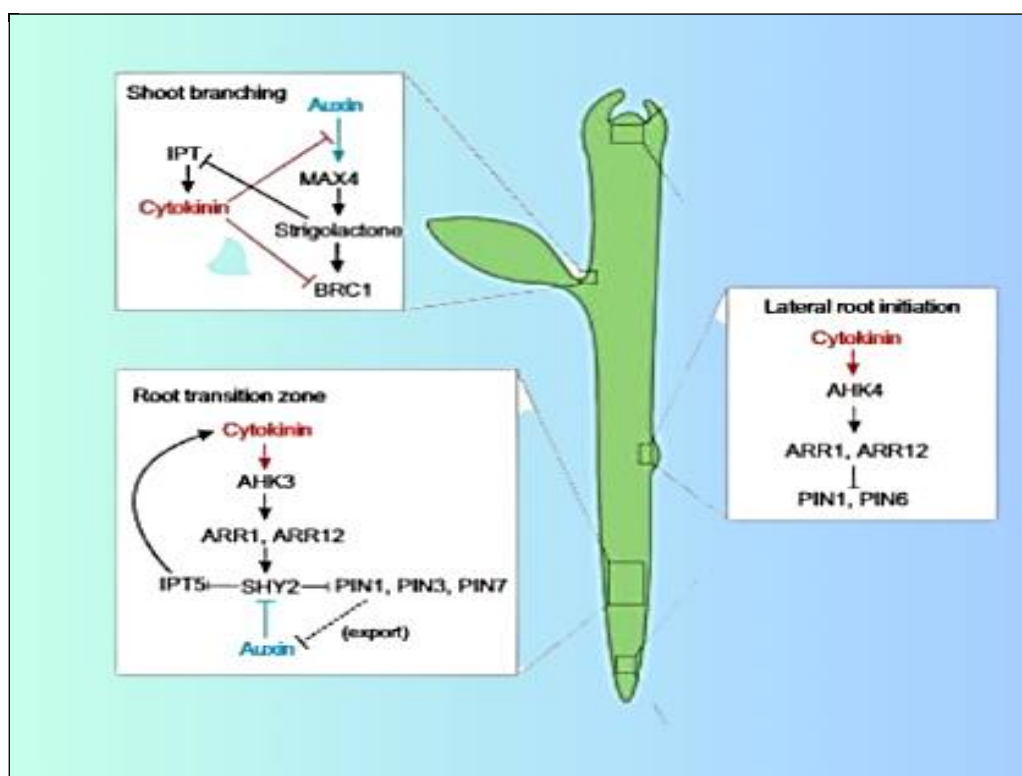
Fig. 1. hormonal crosstalk controlling the proliferation of plants and development, with auxin at the centre

"Auxin's impact is cell type dependent: at the same dose, indole-3-acetic acid (IAA) boosts hypocotyl elongation, suppresses main root development, initiates lateral root initiation, and stimulates root hair creation" [2]. "Auxin and cytokinin have been demonstrated to have both synergistic and antagonistic effects on shoot and root growth" [6,9]. "Auxin and ethylene are two other hormones that interact in a traditional and complicated way. In regulating various developmental processes such as apical hook formation, root and shoot extension, root and shoot gravitational attraction, lateral root formation, root hair initiation and elongation, hypocotyl phototropism, and leaf abscission, they exhibit both synergistic and antagonistic interactions" [10]. "Gibberellin (GA) and auxin have been shown to regulate pea stem elongation and senescence by [6] populus lateral root development, and Arabidopsis apical dominance, inflorescence, and root development" [11]. "Brassinoide (BR) combines with auxin to control cell elongation in roots, shoots, and tropisms" [12].

"Jasmonic acid (JA) and auxin work together to govern root growth, lateral root development, and flowering, but also work against each other to control coleoptile elongation" [5]. "According to recent research, ABA and auxin interact to regulate lateral root formation" [13]. "Auxin is distinctive among plant hormones in that it can travel both long and small distances. Short-distance movement is slower, happens cell-to-cell, and is controlled by influx and exhaust carrier proteins" [10]. "Auxin distribution in the root is more complicated, having two different polarity" [14]. "Through the outer layers of root cells, IAA flows in the opposite way towards the shoot. IAA shootward migration is controlled by AUX1, PIN2, and ABCB4. Auxin and cytokinin (CK) are phytohormones that regulate important cell specification processes, drive growth, and are present during embryogenesis and establishing seedlings" [15,16]. There are several sites where the mechanisms of auxin and cytokinin networks interact. In addition to the inter-hormonal interconnections revealed, both hormones control their own metabolism and perception, which adds to the pathways' complexity. Many critical elements of plant growth rely on interactions between auxins and cytokinin (e.g., shoot branching, the tip of the shoot meristem, the root transition zone, lateral root initiation, and the root meristem [17] Fig. 2.
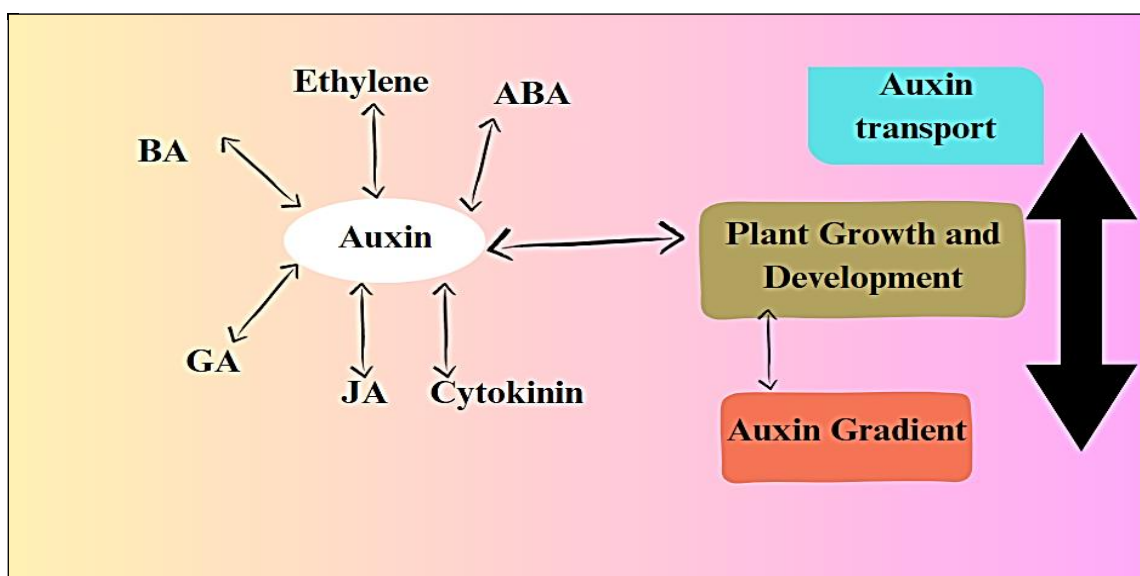
**Fig. 2. Auxin interacts with cytokinin in various development stages**

The auxin and cytokinin pathways interact in a variety of ways[17].[9] proposed a model in which the size of the meristem of the root is determined by enmity between auxin and cytokinin in the vascular evolution zone; this antagonistic effect is mediated by battling legislation of SHY2, which in turn interferes with cytokinin biosynthesis while suppressing auxin transport and signalling (Fig. 2) demonstrated that auxin initiates the activation of two type A ARRs, ARR7 and ARR15, blocking cytokinin signalling [18] (Fig. 2)). The Aux/IAA SHORT HYPOCOTYL2 (SHY2) gene, a regulator of auxin signalling, plays an important role in meristem growth and development [19]. Liu et al. [20] show in this work that ethylene-auxin cross-talk requires a dynamic relationship among ERF.B3 and IAA27. The evidence they provide to support this is that overexpression of an important inhibitor form of ERF.B3 results in modified auxin sensitivity, root development, and impaired chlorophyll accumulation, similar to the phenotypes of lines with downregulated IAA27 expression.

2.2 Signalling of Gibberellin

Gibberellins have a significant impact on germination, the advancement of plants in general (mostly through cell expansion), floral development, and blooming duration. They regulate seed germination, leaf growth, stem elongation, and blooming. The manner of GA activity in planta is yet unknown, as it is influenced by various both positive and negative synergistic relationships with other domestic and environmental signals [21] (Fig. 3). Several genes that encode GA signalling components involved in the initiation of seed germination have also been identified [22]. RGL2 inhibits GA responses that predominantly affect how quickly seeds germinate [23]. SPY, another Arabidopsis gene, is a negative control of GA signalling. However, unlike RGL2, it also governs all other GA-related developmental processes. SPY is also a cytokinin signalling pathway activator [24].

GAs controls a variety of developmental activities in plants throughout their life cycle, from allowing seeds to germinate through the broadening of leaves, stem elongation, flower induction, and seed formation [25]. Because GA interactions with other hormones include components of the GA biosynthesis and reaction networks [25]. of several developmental processes. Unlike GA, which promotes germination, development, and blooming, ABA suppresses these activities. Furthermore, the antagonistic interaction and ratio among these two hormones control the transition from morphogenesis to seed viability. Several mechanisms have been discovered to underpin this antagonistic interplay in several developmental phases (Fig 3). GA and auxin functions overlap in terms of cell growth and tissue differentiation control. Auxin influences both GA signalling and GA biosynthesis (Fig. 3). GA promotion of root elongation in Arabidopsis has been demonstrated to need auxin. The ablation of the shoot apex, which is a significant source of auxin, decreased GA-induced root growth, and this effect was restored by auxin administration.
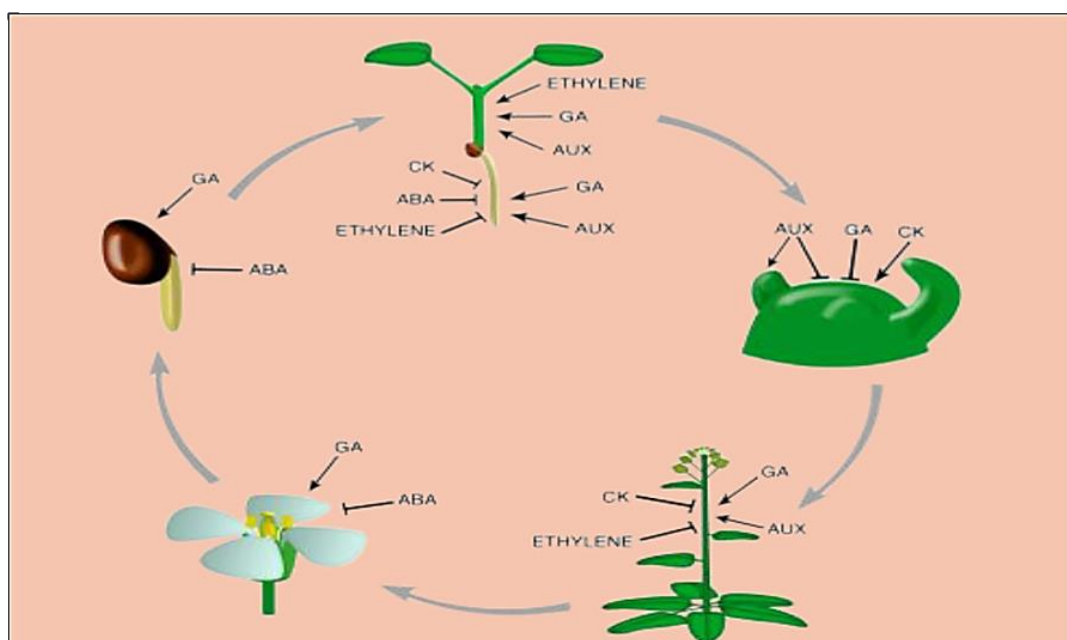
Fig. 3. throughout the plant's life cycle, ga interacts both positively and adversely with other plant hormones

Ethylene suppresses proliferation in a GA-antagonistic way has demonstrated that the DELLA proteins mediate at least some of the inhibitory impact of ethylene on development and it cooperates with GA in this respectt [26]. In Arabidopsis, GA increases seedling root elongation, which is blocked by ethylene. In water-soluble rice and R. palustris, submergence stimulates ethylene and GA production, and GA promotes ethanol-induced internode extension [27]. In Arabidopsis, GAs are intrinsic regulators of hypocotyl development via cellular elongation via DELLA protein degradation.

Ethylene inhibits GA production or decreases GA responses by stabilising DELLA. GA and ethylene interact in a network of positive and negative interactions. Ethylene inhibits GA production or decreases GA responses by stabilising DELLA.GA stimulates ethylene responses in seedlings cultivated in the dark and in the light (apical hook development in the dark and the elongation of the hypocotyl in the light). In deepwater rice and R. palustris, submergence encourages ethylene and GA production, and GA enhances ethylene-induced internode elongation.

2.3 Signalling of Cytokinin's

Cytokinin's are a kind of plant hormone that is involved in many aspects of plant development,

including organ formation, apical dominance, and leaf senescence [17]. Cell division, dominance of the apical layer, chloroplast biogenesis, nutrient mobilisation, leaf senescence, vascular differentiation, thereby photomorphogenic development, shoot differentiation, and anthocyanin production are all regulated by cytokinin's (CKs) [28,8]. The modulation of the type A ARRs ARR5, ARR7, and ARR15, which play a role in freezing tolerance, is influenced by cytokinin and ethylene signalling. Cytokinin also boosts ethylene production by enhancing the stability of ACS proteins, which catalyse the rate-limiting step in ethylene biosynthesis. CKs are frequently regarded as ABA inhibitors and auxin antagonists/synergists in a variety of plant activities [29]. Strigolactones, which were discovered in Arabidopsis thaliana, Pisum sativa, and other plants as branching mutants, are assumed to be synthesised mostly in the roots and carried upwards in the xylem to restrict bud expansion [30,31]. The mechanics of cytokinin transport are poorly understood, while possible efflux and influx transporters have been found [32]. A His-Asp phosphorelay comparable to that seen in bacterial two-component signalling systems, which are the primary means by which bacteria perceive and respond to environmental stimuli, is involved in the cytokinin signal transduction pathway [33]. Increased strigolactone levels in pea and Arabidopsis result in lower cytokinin levels in the xylem sap, but not

in the shoot. Cytokinin interacts with strigolactones to control the formation of axillary buds. In addition to blocking the transcription factor BRC1, which operates downstream of strigolactones, cytokinin's hinder auxin-mediated regulation of the strigolactone biosynthetic gene MAX4.Strigolactones, in turn, suppress cytokinin production via IPT1. Cytokinin degradation is mediated by enzymes encoded by the CYTOKININ OXIDASE (CKX) gene family. The cytokinin signalling pathway interacts with ABA, controlling salinity and drought response. ABA inhibits multiple CKX genes, while AHK2 and AHK3 inhibit several ABA responsive genes. Cytokinin is a phytohormone that influences several agriculturally significant activities, including growth, nutritional responses, and exposure to both abiotic and biotic stresses. Plant cytokinin levels are controlled by manufacturing and inactivation mechanisms. Cytokinin's are recognized by membrane-localized histidine kinase receptors and transduced to the nucleus via a His-Asp phosphorelay to promote the expression of a family of transcription factors [34]. Cytokinins are plant hormones that play a crucial role in regulating various aspects of plant growth and development, including cell division, shoot initiation, leaf senescence, and more. The signaling pathway of cytokinins involves a complex network of components. Cytokinins are perceived by membrane-bound receptor proteins called cytokinin receptors. In Arabidopsis thaliana, there are three major cytokinin receptors: AHK2 (ARABIDOPSIS HISTIDINE KINASE 2), AHK3 (ARABIDOPSIS HISTIDINE KINASE 3), and AHK4/CRE1 (CYTOKININ RESPONSE 1). These receptors have histidine kinase activity and are involved in cytokinin perception [35]. Upon cytokinin binding to the receptors, a phosphorylation cascade involving histidine phosphotransfer proteins (AHPs) is initiated. AHPs transfer phosphate groups between proteins in the pathway [36]. Cytokinins activate a family of transcription factors known as type-B Arabidopsis response regulators (ARRs) through phosphorylation by AHPs. These type-B ARRs then control the expression of target genes involved in various cytokinin responses [37]. Cytokinin signaling leads to a range of physiological responses, including enhanced cell division, shoot branching, delayed leaf senescence, and more, which contribute to plant growth and development [28].The cytokinin signalling pathway is tightly regulated by negative feedback loops, including the type-A ARRs that act as negative regulators of cytokinin

signalling [36].Understanding the cytokinin signalling pathway is crucial for elucidating the mechanisms by which cytokinins control plant growth and development.

2.4 Signalling of Brassinosteroid (BRs)

Brassinosteroids (BRs) are a type of polyhydroxylated steroidal hormone that plays important roles in plant growth and development, including cell elongation, cell division, senescence, vascular differentiation, reproduction, photomorphogenesis, and stress responses [38]. Brassinosteroids have been detected in nearly all plant tissues, with the largest concentrations observed in seeds, pollen, and young developing tissues [7]. Brassinosteroids have strong impacts on overall plant growth via cell [39]. Recent detailed analyses revealed that BRs are involved in many aspects of root development, including meristem size maintenance, root hair formation, lateral root initiation, gravitropic response, mycorrhiza formation, and nodulation in legume species [40]. In comparison to the auxin route, Brassinosteroid perception is a more traditional signalling paradigm. Exogenous Brassinosteroid application, as well as brassinosteroid-deficient and brassinosteroid-insensitive mutants, have all resulted in a thorough functional model of brassinosteroid activity in plants Fig 4.Brassinosteroids (BRs) are a class of plant hormones that play essential roles in various aspects of plant growth and development. They are involved in processes such as cell elongation, cell division, vascular differentiation, and responses to environmental stimuli. The first step in the BR signalling pathway involves the perception of brassinosteroids by a cell surface receptor. The primary receptor for BRs in plants is the receptor kinase complex, which consists of the brassinosteroid insensitive 1 (BRI1) and BRI1-associated kinase 1 (BAK1). BRI1 is a leucine-rich repeat receptor kinase, and BAK1 is a co-receptor that interacts with BRI1 upon BR binding [41]. Upon binding of BRs to the BRI1-BAK1 receptor complex, a signal is transduced into the cell. This involves a cascade of phosphorylation events, leading to the activation of downstream components. The key transcription factors in the BR signalling pathway are the brassinazole-resistant 1 (BZR1) and BRI1-EMS-suppressor 1 (BES1) proteins. Activated BZR1 and BES1 transcription factors regulate gene expression by binding to specific target genes. They control the expression of genes involved in cell expansion, differentiation,

and other processes, leading to the physiological responses associated with BRs. The changes in gene expression triggered by the activation of BZR1 and BES1 lead to various physiological responses. These responses can include increased cell elongation, root growth, and resistance to stress conditions, among other effects. It's important to note that the BR signalling pathway is highly interconnected with other signalling pathways, allowing plants to integrate multiple signals and respond appropriately to environmental conditions.

2.5 Signalling of Salicylic Acid (SA)

Salicylic acid (SA) is a phytohormone that acts as a signal molecule in the immune and plant development pathways [42,43,44]. SA is produced in plants by two separate processes: the isochorismate (IC) and the phenylalanine (PA) ammonia-lyase (PAL) pathways [45,46]. Plants with changed endogenous SA levels exhibit aberrant growth characteristics [44,47]. A high amount of endogenous SA causes growth retardation. Many Arabidopsis mutants with over accumulating SA, such as has accelerated cell death 6 (acd6), permanent expresser of PR gene 5 (cpr5), and the SAP and MIZ domain protein gene 1 (siz1), present the dwarf plant morphology with a shorter stem, smaller leaves, and/or floral organs compared to the wild type

[48,49,50]. The Arabidopsis SA-deficient mutant sid2 and the SA-depleted NahG transgenic line, on the other hand, display increased leaf biomass as compared to WT [51].

It is worth mentioning that the effects of SA may vary depending on the plant type or organ. Aim1 rice mutants with lower endogenous SA levels, for example, have weaker seedling and spore-producing roots than the original wild type [52]. It has been shown that overexpression of NahG can decrease the cell multiplication and expansion defects produced by siz1 [50], suggesting that SA suppresses these two processes in the cells. However, SA buildup in a different situation might have a distinct effect on the development of cells control. Vanacker et al. [53] discovered that elevated SA levels stimulate cell proliferation and growth in acd6-1 leaves. SA may influence plant growth by either negatively or positively influencing cell division and expansion. Some evidence suggests that SA has a deleterious influence on the two cellular processes in Arabidopsis leaves. For example, SA-deficient NahG transgenic plants grew faster than WT plants and had a 1.7-fold increase in leaf rosette biomass at the early stage of propagation [51]. This higher growth effect on NahG transgenic plants was more noticeable at low temperatures and was caused by greater increase in cell size of rosette leaves.
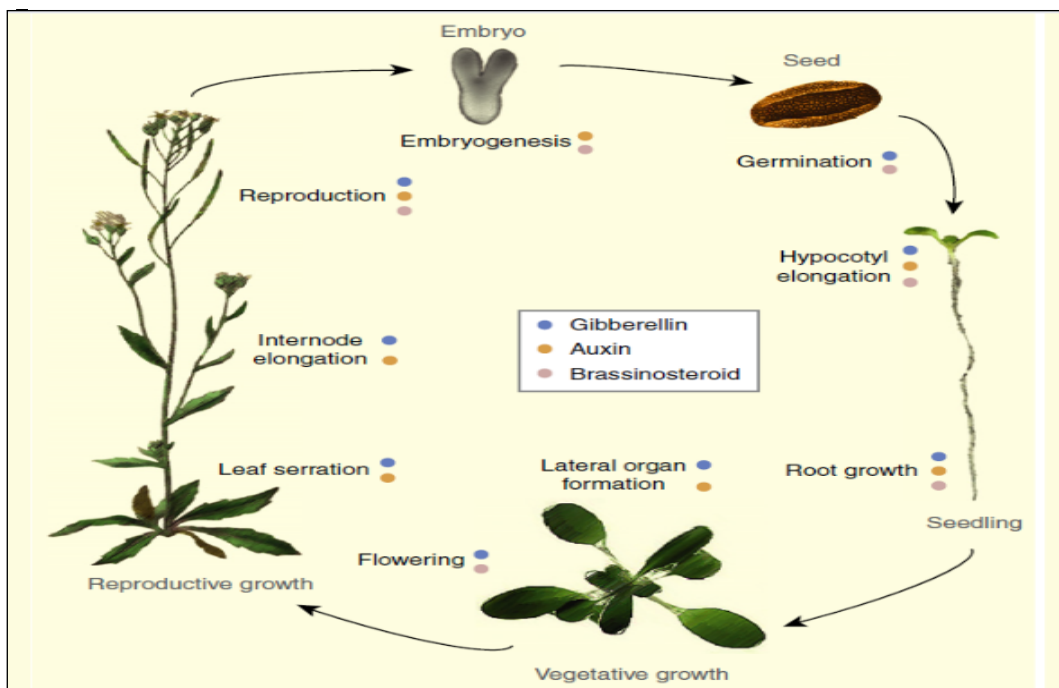

Fig. 4. Brassinosteroids have a role in plant development throughout the life cycle

SA signalling during plant immunological responses has been extensively studied, and NPR1 has been identified as a critical player in this process. NPR1 also plays a role in SA-mediated growth regulation by controlling cell division and expansion [53,54,55]. Arabidopsis npr1-1 mutant leaves contained fewer cells and more DNA, showing that NPR1 promotes cell division and inhibits endoreduplication in leaves [53]. Fujikura et al. [54] discovered that the xs2 mutant accumulated high SA levels and inhibited cell growth, creating smaller cells than the WT. Interestingly, the xs2 mutant's severe impairment in cell size was repaired in the xs2 npr1 double mutant. These findings suggest that the inhibition of cell growth in xs2 was mediated by an NPR1-dependent signalling pathway. Furthermore, the SA-over accumulating Arabidopsis mutant cad1 boosted QC cell division, which was rescued by mutations in SID2 or NPR1, demonstrating that the cad1 mutant promotes QC cell division via an NPR1-dependent SA signalling pathway [55]. To govern plant and organ growth, SA interacts with other hormones involved in the regulation of cell division and expansion, such as auxin, GA, and ethylene (ET) [56,57,58,47]. Auxin is a significant growth hormone that regulates these cellular activities, particularly in roots [59,60,61,62], and SA can influence root development by influencing auxin accumulation and transit. Pasternak et al. [63] shown that exogenous SA has a concentration-dependent effect on the root tip meristem in Arabidopsis.

2.6 Signalling of Abscisic Acid (ABA)

Because of their regulatory action on abscission and dormancy, these were previously known as Dormin or Abscisin. This hormone is widely distributed in higher plants and can be detected in a variety of organs and tissues (both old and young). ABA causes abscission of the leaves of many plants as well as the fruits of some plant species. ABA appears to be an intrinsic component that induces dormancy in at least some temperature zone woody plant buds. ABA also slows or delays seed germination. ABA suppresses the growth of several plant tissues and organs, including leaves, coleoptiles, stems, hypocotyls, and roots. It accelerates senescence by causing leaf abscission, degeneration of excised leaves, and accelerating chlorophyll breakdown. Recent research has shown that ABA accelerates leaf senescence and abscission in the absence of ethylene [64,65].

Several ABA auxotrophic maize mutants, termed vp2, vp5, vp7, and vp9, have been found by genetic screening of viviparous mutants [66]. Plastids catalyse the conversion of zeaxanthin (C40) to xanthoxin (C15) (Fig5). Catabolism of ABA occurs via the conversion of ABA to phaseic acid (PA), which is catalysed by a P450 encoded by CYP707As [67]. PA is subsequently catalysed to dihydrophaseic acid (DPA) and DPA4ODglucoside (DPAG) by PA reductase (PAR), ABH2, and glycosyltransferase (GT) [68]. PA has been shown to preferentially activate a subset of ABA receptor PYLs (Fig 5) [68]. Abscisic acid occurs naturally in plants in both anionic (ABA) and protonated (ABAH) forms. ABA can diffuse passively via the plasma membrane, and ABA diffusion decreases with cytoplasmic alkalinization, which rises during osmotic stressors [67,69,70]. When plants are exposed to a variety of environmental circumstances, they rapidly acquire ABA.

The maintenance of a basal level of free ABA consistent with different tissues in diverse settings is critical to the overall plant's appropriate growth and development states. As a result, ABA catabolism is strictly regulated by both ABA conjugation and catalytic hydroxylation. A UDPglucosyltransferase (UGT) encoded by UGT71C5 can glycosylate ABA. ABAGE, or ABA glucose ester, is an inactive version of ABA [71]. When the environment changes, AtBG1 and AtBG2 encode glucosidases that rapidly convert ABAGE to active ABA, which is released from the endoplasmic reticulum and vacuole [23,52]. By quickly activating and inactivating ABA, the conjugation cycle established by glucosyltransferase and glucosidase allows plants to phenotypically adjust to their environment via ABA mediated responses. Catabolism of ABA occurs via the conversion of ABA to phaseic acid (PA), which is catalysed by a P450 encoded by CYP707As (Kushiro et al. 2004). PA is subsequently catalysed to dihydrophaseic acid (DPA) and DPA4ODglucoside (DPAG) by PA reductase (PAR), ABH2, and glycosyltransferase (GT) [68]. PA has been shown to preferentially activate a subset of ABA receptor PYLs (Fig 5) [68].
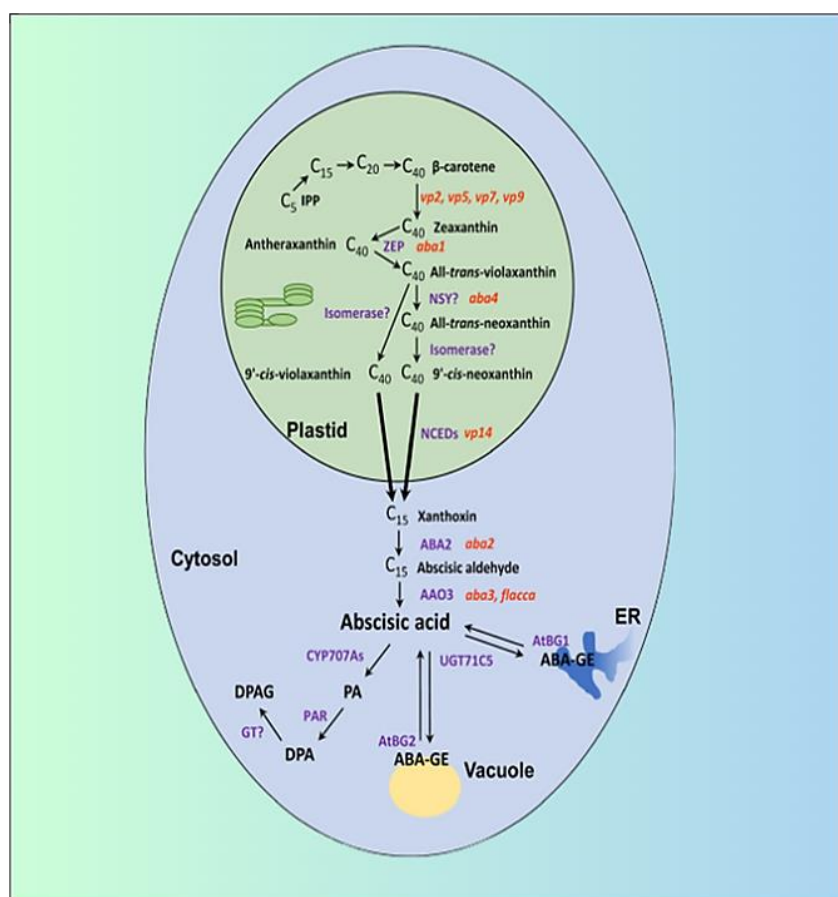
Fig. 5. plant abscisic acid (aba) the process of biosynthesis breakdown, and (de)conjugation

Pathogen infection, for example, can influence ABA homeostasis in host plants. Some biotrophic infections, such as wheat rust fungus, can induce ABA elevations that lead to increased cytoplasmic sugar accumulation by increasing TaSTP6 expression. In Arabidopsis, when infected with the necrotrophic disease Botrytis cinereal, the transcription factor WRKY33 increases ABA production by upregulating the transcription of NCED3 and NCED5 [20] The tomato NAC transcription factor LeJA2 (for jasmonic acid 2) stimulates the production of ABA, which can inhibit pathogen entrance through stomata. Hormone crosstalk also has a role in ABA homeostasis. Auxin and GA, for example, influence endogenous ABA levels in forest strawberry (Fragaria vesca) through influencing the regulatory loops of FveCYP707As and FveNCEDs [71]. Furthermore, JA accumulation is essential for ABA accumulation in Arabidopsis roots following dehydration treatment [72].

Future research would offer insight on the relationship between global ABA content regulation and different biological processes. All of these systems work together to fine-tune the amount of ABA at various developmental stages and in response to diverse environmental variables. More signalling factors that function upstream of ABA accumulation, as well as the processes that coordinate the dynamic control of ABA content and biological activity, remain unknown. Protein phosphorylation and dephosphorylation are critical for maintaining an adequate balance of ABA-mediated growth regulation depending on the plant's environmental situation [73,74]. Protein phosphatases can interact with and inhibit SnRK2s, SnRK1s, SnRK3s, and even mammalian AMPKs, all of which play important roles in abiotic stress, ABA, and energy signalling [75,73].

2.7 Signalling of Ethylene

Ethylene is a gaseous plant hormone that exerts a profound influence on various aspects of plant growth, development, and responses to environmental stimuli. It is often referred to as

the "ripening hormone" because of its central role in fruit ripening. However, ethylene's significance extends far beyond fruit ripening, affecting processes ranging from seed germination to leaf senescence. This article introduces ethylene, summarizing its biosynthesis, signaling pathway, and diverse physiological effects, with references to key studies that have advanced our understanding of this essential plant hormone.

2.7.1 Biosynthesis of ethylene

Ethylene is synthesized from the amino acid methionine through a series of enzymatic reactions. The two key enzymes in ethylene biosynthesis are ACC synthase (ACS), which converts methionine to 1-aminocyclopropane-1-carboxylic acid (ACC), and ACC oxidase (ACO), which transforms ACC into ethylene. This biosynthesis pathway is tightly regulated and can be influenced by various internal and external factors [76].

2.7.2 Ethylene receptors

Ethylene signals are perceived by membrane-bound receptors, such as Ethylene Response Sensor 1 (ERS1) and Ethylene Response Sensor 2 (ERS2), in association with Constitutive Triple Response 1 (CTR1). Upon ethylene binding, the receptors inactivate CTR1, initiating a signaling cascade. This cascade ultimately leads to the activation of transcription factors, such as Ethylene-Insensitive 3 (EIN3) and Ethylene-Insensitive 3-Like 1 (EIL1), which regulate the expression of ethylene-responsive genes [77].

2.7.3 Physiological Effects of ethylene

Ethylene exerts diverse effects on plant growth and development. It is responsible for the "triple response" in seedlings, which includes a thickened stem, an exaggerated apical hook, and inhibited root elongation. Ethylene also plays a critical role in fruit ripening, leaf and flower senescence, abiotic and biotic stress responses, apical dominance, root development, and abscission, among other processes [78]. Understanding the multifaceted roles of ethylene in plant physiology is essential for crop management, post-harvest handling, and horticultural practices. Moreover, ethylene's significance in stress responses and environmental adaptations makes it a subject of ongoing research in the field of plant biology. Ethylene is a gaseous plant hormone that plays a significant role in regulating various aspects of plant growth and development, as well as responses to environmental cues. Here is an overview of ethylene, its biosynthesis, and its effects on plants:
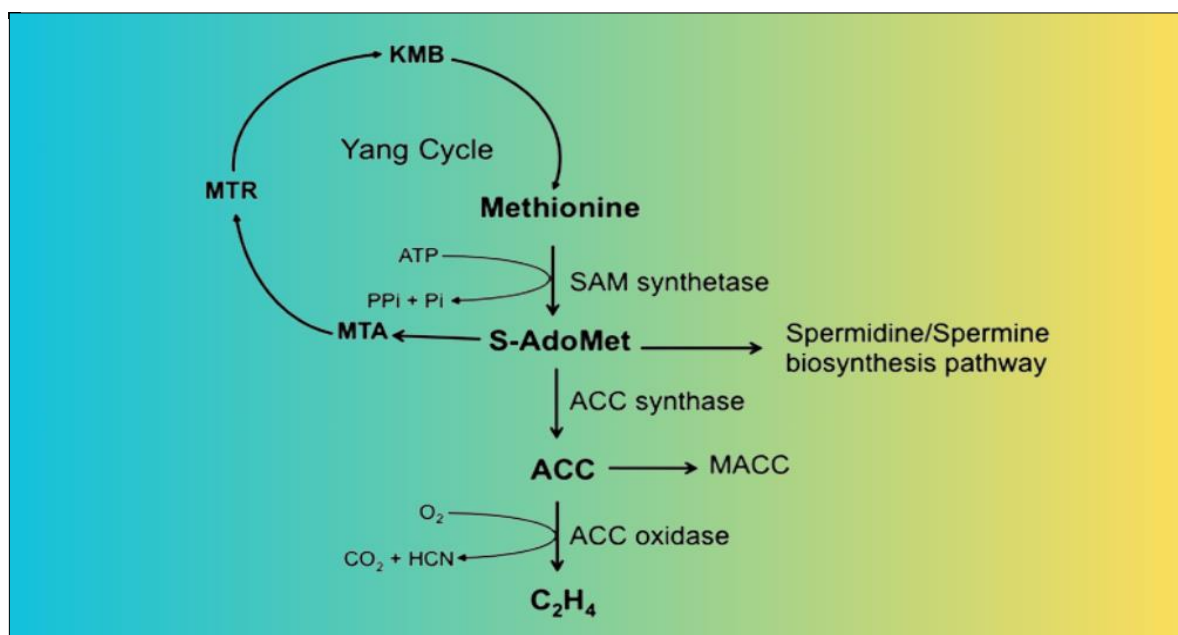

Fig. 6. pictural representation of ethylene biosynthesis

Ethylene Biosynthesis:(Fig 6)

1. Methionine Conversion: Ethylene is synthesized from the amino acid methionine. The first step involves the conversion of methionine to S-adenosylmethionine (SAM) by the enzyme methionine adenosyltransferase.
2. SAM to ACC: SAM is then converted to 1-aminocyclopropane-1-carboxylic acid (ACC) by ACC synthase (ACS).
3. ACC to Ethylene: ACC is subsequently converted to ethylene through the action of ACC oxidase (ACO).

2.7.4 Ethylene receptors

Ethylene signals are perceived by a family of membrane-bound receptors, primarily Ethylene Response Sensor 1 (ERS1) and Ethylene Response Sensor 2 (ERS2), which function in association with Constitutive Triple Response 1 (CTR1).

In the presence of ethylene, the receptors are activated, leading to inactivation of CTR1 through phosphorylation. Inactivation of CTR1 allows for the de-repression of Ethylene-Insensitive 2 (EIN2). Active EIN2 acts as a positive regulator of ethylene signaling, promoting the cleavage and nuclear translocation of the Ethylene-Insensitive 3 (EIN3) and Ethylene-Insensitive 3-Like 1 (EIL1) transcription factors. EIN3 and EIL1 subsequently activate the expression of ethylene-responsive genes.

2.7.5 Effects of ethylene

Ethylene induces the "triple response" in seedlings, which includes a thickening and shortening of the stem, an exaggerated curvature of the apical hook, and inhibition of root elongation. Ethylene is well-known for its role in fruit ripening. It promotes the ripening process and can be used for the controlled ripening of fruits. Ethylene also accelerates the senescence of leaves and flowers, leading to their wilting and decay. Ethylene is involved in responses to various stresses, such as pathogen infection and environmental stressors like drought and flooding. Ethylene is implicated in apical dominance, regulating the growth of lateral branches and buds. Ethylene can affect root development, promoting root hair elongation and controlling root architecture. Ethylene triggers leaf and fruit abscission, allowing for the shedding of older leaves and ripe fruit.

Understanding the role of ethylene in plant physiology is essential for various applications in agriculture, horticulture, and the mitigation of crop losses. Ethylene is also a key target for research in the field of plant biology and stress responses. Ethylene is a versatile plant hormone with a wide range of applications in agriculture, horticulture, and post-harvest management. Its effects on plant growth and development make it a valuable tool for various purposes. Ethylene is widely used to initiate and control the ripening of climacteric fruits, such as tomatoes, bananas, apples, and pears. Ethylene gas is applied to unripe fruit to trigger the ripening process, allowing for better timing of harvest and distribution. Ethylene is involved in the regulation of flower senescence. Controlling ethylene exposure can extend the vase life of cut flowers, making them last longer in floral arrangements.

Ethylene promotes seed germination in some plant species. Pre-treating seeds with ethylene gas can enhance germination rates and uniformity. Ethylene plays a role in apical dominance, influencing the growth of lateral branches and buds. Controlling ethylene levels can affect branching patterns in plants. Ethylene can stimulate the formation of root hairs and influence root architecture. It is used in some cases to enhance root development in crops. Ethylene triggers the abscission of leaves and fruits. This property is harnessed for defoliation in cotton farming and for the controlled shedding of ripe fruit. Ethylene is involved in plant responses to various stresses, such as drought, flooding, and pathogen attack. Understanding ethylene signaling can help in developing stress-tolerant crops. Ethylene can affect the flavor and aroma of certain fruits, influencing their taste and scent. Ethylene is used in post-harvest management to regulate fruit ripening and control storage conditions. It can extend the shelf life of some fruits and vegetables when managed properly. Ethylene is a valuable tool for researchers studying plant biology and physiology. It can be applied to investigate the effects of ethylene on various aspects of plant growth and development. Ethylene interacts with other plant hormones, such as auxins and cytokinins, to regulate plant responses to different stimuli. Understanding these interactions is essential for plant manipulation. Ethylene management is also important in enclosed environments, such as greenhouses and storage facilities, to prevent unwanted effects on plant growth and maintain optimal conditions for crops. Ethylene has industrial applications outside of agriculture,

including its use in the production of plastics, chemicals, and fuel. The controlled application of ethylene is a valuable strategy in modern agriculture and horticulture, enabling growers to optimize crop yield, quality, and post-harvest handling. Its diverse effects on plant growth and development make it a versatile tool for various purposes in the plant science and agricultural industries. The signaling pathway of ethylene in plants involves a complex network of components that regulate various physiological responses. Ethylene signals are perceived by a family of membrane-bound receptors, including Ethylene Response Sensor 1 (ERS1) and Ethylene Response Sensor 2 (ERS2). These receptors are part of a family of ethylene receptors that can form heterodimers with Constitutive Triple Response 1 (CTR1), an ethylene signaling negative regulator [79]. In the absence of ethylene, CTR1 functions as a negative regulator of ethylene signaling. However, when ethylene binds to the receptors, CTR1 is inactivated, leading to the de-repression of Ethylene-Insensitive 2 (EIN2). EIN2 acts as a positive regulator of ethylene signaling and serves as a critical node in the pathway [80]. Active EIN2 promotes the cleavage and nuclear translocation of the transcription factors Ethylene-Insensitive 3 (EIN3)and Ethylene-Insensitive 3-Like 1 (EIL1). These transcription factors regulate the expression of ethylene-responsive genes involved in various physiological processes, including those associated with growth, development, and stress responses [81]. The activation of ethylene-responsive genes leads to a wide range of physiological responses, including the "triple response" in seedlings, which includes a thickening and shortening of the stem, an exaggerated curvature of the apical hook, and inhibition of root elongation. Ethylene also plays a key role in processes like fruit ripening, leaf and flower senescence, and responses to abiotic and biotic stresses [82]. The ethylene signaling pathway is a complex and finely regulated system that governs various aspects of plant growth and development, as well as responses to environmental cues. The references cited above provide insights into the molecular and biochemical aspects of ethylene signaling in plants. For more detailed and up-to-date information, consult recent research articles and reviews in the field. The signaling pathway of ethylene in plants is a well-studied process that involves a complex network of components. Ethylene signals are perceived by a family of membrane-bound receptors known as ethylene receptors. In Arabidopsis thaliana, the receptors include Ethylene Response Sensor 1 (ERS1) and Ethylene Response Sensor 2 (ERS2). These receptors are part of the family of ethylene receptors responsible for sensing ethylene gas [83]. In the absence of ethylene, the receptors are bound to Constitutive Triple Response 1 (CTR1), which functions as a negative regulator of ethylene signaling. When ethylene is present, it binds to the receptors, leading to the inactivation of CTR1 and allowing Ethylene-Insensitive 2 (EIN2) to be de-repressed [84]. EIN2 acts as a positive regulator of ethylene signaling and plays a pivotal role in the pathway. It promotes the cleavage and nuclear translocation of the transcription factors Ethylene-Insensitive 3 (EIN3) and Ethylene-Insensitive 3-Like 1 (EIL1). These transcription factors, in turn, regulate the expression of ethylene-responsive genes that control various physiological processes [85]. The activation of ethylene-responsive genes results in a broad spectrum of physiological responses in plants, including the "triple response" in seedlings, control of fruit ripening, leaf and flower senescence, and responses to abiotic and biotic stresses [82]. The ethylene signaling pathway is a crucial regulatory system governing various aspects of plant growth and development. The references provided here offer insights into the molecular and biochemical components of the ethylene signaling pathway.

3.CONCLUSION

The signaling pathways of growth promoters and inhibitors play pivotal roles in regulating plant growth and development. Auxins, such as indole-3-acetic acid (IAA), are essential growth promoters that regulate cell elongation, apical dominance, phototropism, and root development. The auxin signaling pathway primarily involves the transport protein PIN1, which regulates auxin distribution, and the auxin response factors (ARFs) that control gene expression. Cytokinins are hormones that promote cell division and shoot initiation. The signaling pathway of cytokinins includes receptor kinases and transcription factors like type-B Arabidopsis response regulators (ARRs).In conclusion, the signaling pathways of growth promoters and inhibitors are intricate and interconnected, allowing plants to fine-tune their growth and development in response to internal and external cues. These pathways enable plants to adapt to changing environmental conditions, optimize resource allocation, and defend against stress

and pathogens. A comprehensive understanding of these signaling pathways is crucial for agricultural and horticultural practices, as well as for advancing our knowledge of plant biology and stress responses. Ongoing research continues to uncover the complexities of these pathways, providing insights into how plants balance growth promotion and inhibition to thrive in diverse environments.

The intricate signaling pathways of growth promoters and inhibitors are pivotal mechanisms that govern the dynamic and adaptable nature of plant growth and development. Growth inhibitors, including abscisic acid, ethylene, jasmonic acid, and salicylic acid, serve as crucial regulators that restrain growth under unfavorable conditions or in response to stress. These pathways are activated in times of stress, pathogen attack, or other challenges, leading to growth inhibition and the activation of defense mechanisms. By balancing growth promotion and inhibition, plants can strategically allocate resources and adaptd to changing circumstances to ensure their survival. Understanding the complexities of these signaling pathways is not only fundamental for plant biology but also critical for various applications, including agriculture, horticulture, and environmental management. It allows us to manipulate plant growth and development for improved crop production, disease resistance, and stress tolerance. Ongoing research continues to unravel the intricate details of these pathways, offering new insights into how plants achieve the delicate balance between promoting growth and limiting it when necessary. This knowledge is invaluable for addressing the growing challenges of food security, environmental sustainability, and climate resilience in the face of a change.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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