

Review Article

SIGNALLING: GROWTH PROMOTERS AND INHIBITORS

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. This abstract provides a concise overview of these essential processes. 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 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.

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Keywords: Abscisic acid, Auxin, Brassinosteroids, Cytokinin, Ethylene, Gibberellin, Growth promoter, Hormones, Inhibitors, Jasmonic acid, Salicylic acid.

1. INTRODUCTION

Plant growth and development are tightly controlled by a diverse set of signalling molecules, which are included 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

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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, agronomists, 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 (Nancy A. Eckardt, 2015). 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 (Bisht, T. S *et al.*, 2019).

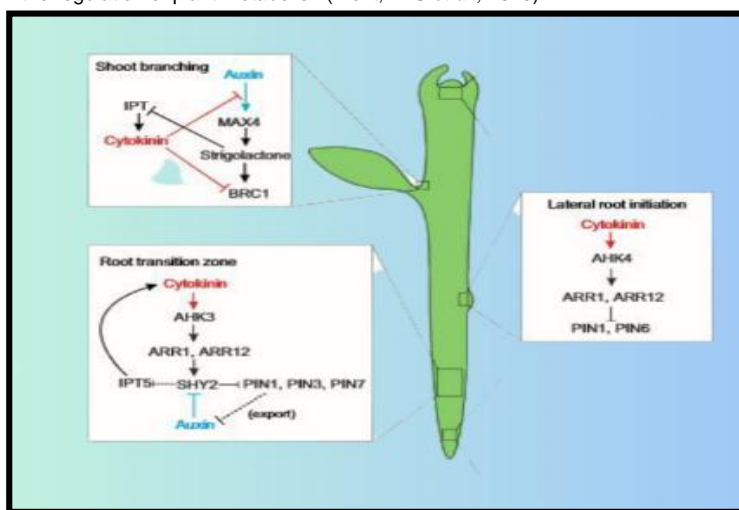


Fig. 1. hormonal crosstalk controlling the proliferation of plants and development, with auxin at the centre.

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 (Yeshitila, M., & Gobena, A. 2020). 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 (Koorneef *et al.*, 2002). 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 (Skoog and Miller, 1957). 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 (Chandler, 2009). Furthermore, auxin is a key player in the current hormonal crosstalk that influences several developmental phases (Swarup *et al.* 2002, Chandler 2009, Depudyt and Hardtke 2011) Fig 1. It regulates cell division, elongation, and programmed cell death, hence influencing embryonic and post-embryonic development (Davies, 2004).

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 (Yeshitila, M., &

Gobena, A. 2020). Auxin and cytokinin have been demonstrated to have both synergistic and antagonistic effects on shoot and root growth (Swarup et al. 2002, Dello loio et al. 2008). 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 (Muday et al. 2012). Gibberellin (GA) and auxin have been shown to regulate pea stem elongation and senescence by (Swarup et al. 2002), populus lateral root development (Gou et al. 2010), and Arabidopsis apical dominance, inflorescence, and root development (Silverstone et al. 1997, Willige et al. 2011). Brassinoides (BR) combines with auxin to control cell elongation in roots, shoots, and tropisms (see Hardtke et al. 2007). 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 (for a review, see Chandler 2009). According to recent research, ABA and auxin interact to regulate lateral root formation (Shkolnik-Inbar and Bar-Zvi 2010). 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 (Muday and Rahman 2008). Auxin distribution in the root is more complicated, having two different polarity (Abidur Rahman, 2013). 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 (Peer et al. 2011). Auxin and cytokinin (CK) are phytohormones that regulate important cell specification processes, drive growth, and are present during embryogenesis and establishing seedlings (Bennett and Scheres, 2010; Perilli et al., 2010). 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 (Sedeer El-Shawk et al, 2013) Fig 2.

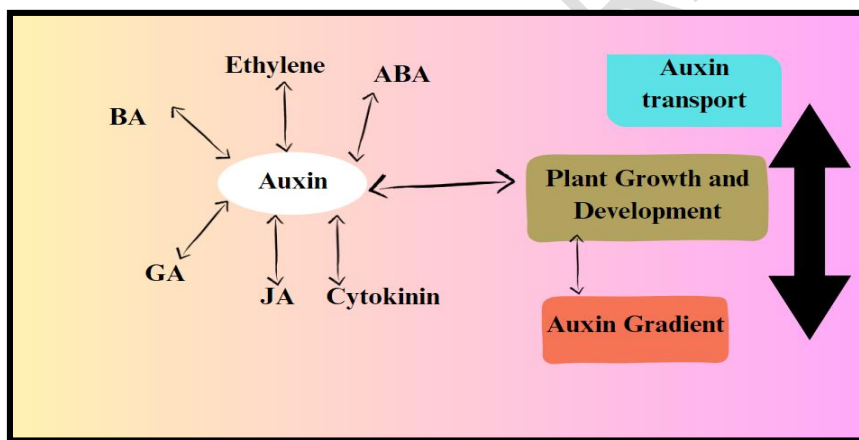


Fig:2.in numerous developmental content, auxin interacts with cytokinin.

The auxin and cytokinin pathways interact in a variety of ways (Sedeer El-Shawk et al. 2013). (Dello loio et al. 2008) 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). Müller and Sheen (Müller and Sheen, 2008) demonstrated that auxin initiates the activation of two type A ARRs, ARR7 and ARR15, blocking cytokinin signalling (Zhang et al., 2011 (Fig. 2)). The Aux/IAA SHORT HYPOCOTYL2 (SHY2) gene, a regulator of auxin signalling, plays an important role in meristem growth and development (Elena Pacifici et al., 2015). Liu et al. (2018) 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 (Magome et al., 2004). 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 (Nemhauser et al.,

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2006) (Fig. 3). Several genes that encode GA signalling components involved in the initiation of seed germination have also been identified (Tyler *et al.*, 2004). RGL2 inhibits GA responses that predominantly affect how quickly seeds germinate (Lee *et al.*, 2002). SPY, another Arabidopsis gene, is a negative control of GA signalling. However, unlike RGL2, it also governs all other GA-related developmental processes (Izhaki *et al.*, 2001). SPY is also a cytokinin signalling pathway activator (Greenboim-Wainberg *et al.*, 2005).

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 (Sun and Gubler, 2004). Because GA interactions with other hormones include components of the GA biosynthesis and reaction networks (Sun TP, Gobbler, 2004) 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 (Razem *et al.*, 2006). 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.

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 respect (Achard *et al.*, 2007). 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 (Benschop *et al.*, 2006). In Arabidopsis, GAs are intrinsic regulators of hypocotyl development via cellular elongation via DELLA protein degradation (de Lucas *et al.*, 2008).

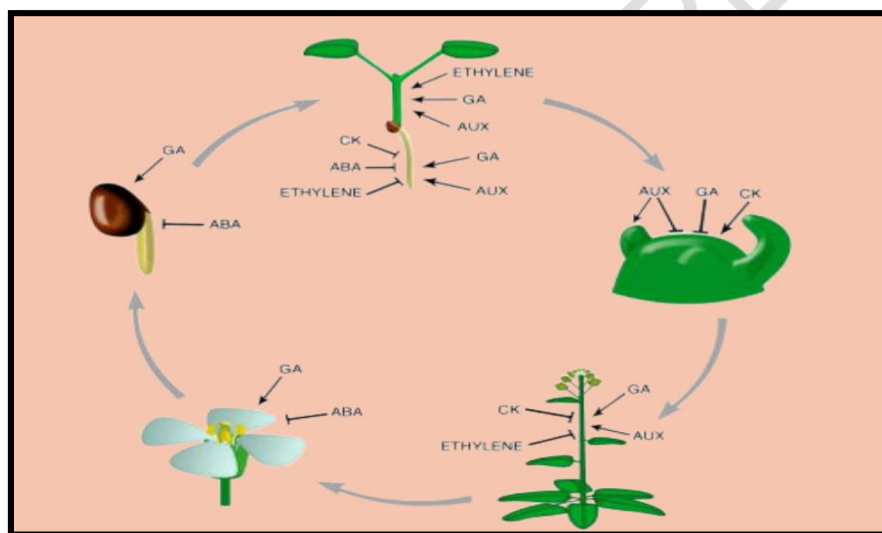


Fig:3. throughout the plant's life cycle, ga interacts both positively and adversely with other plant hormones.

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 (Sedeer El-Showk, 2013). 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) (Mok and Mok, 2001; Davies, 2004). 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 (Chae *et al.*, 2003). CKs are

frequently regarded as ABA inhibitors and auxin antagonists/synergists in a variety of plant activities (Pospisilova, 2003). 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 (Beveridge, 2006; Kohlen *et al.*, 2011). The mechanics of cytokinin transport are poorly understood, while possible efflux and influx transporters have been found (Duran-Medina *et al.*, 2017). 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 (Cheung and Hendrickson, 2010; Stock *et al.*, 2000). Increased strigolactone levels in pea and *Arabidopsis* result in lower cytokinin levels in the xylem sap, but not in the shoot (Foo *et al.*, 2007). 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 (Dun *et al.*, 2009). Cytokinin degradation is mediated by enzymes encoded by the CYTOKININ OXIDASE (CKX) gene family (Schmullig *et al.*, 2003). 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 (Jeon *et al.*, 2010). 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 (Kieber, J. J., and Schaller, G. E. 2018). 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 signalling 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 (Inoue, T., *et al.*, 2001). 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 (J. P., Haberer, *et al.*, 2004). Cytokinins activate a family of transcription factors known as type-B *Arabidopsis* response regulators (ARRs) through phosphorylation by AHPs. These type-B ARR then control the expression of target genes involved in various cytokinin responses (Rashotte, A. M., *et al.*, 2003). 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 (Mok, D. W., & Mok, M. C. 2001). The cytokinin signalling pathway is tightly regulated by negative feedback loops, including the type-A ARR that act as negative regulators of cytokinin signalling. (J. P., Haberer, *et al.* 2004). 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 (Clouse and Sasse, 1998; Divi and Krishna, 2009). Brassinosteroids have been detected in nearly all plant tissues, with the largest concentrations observed in seeds, pollen, and young developing tissues (Stephen Depuydt and Christian S. Hardtke, 2011). Brassinosteroids have strong impacts on overall plant growth via cell (Pacifci *et al.*, 2015). 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 (Wei Z. and Li J, 2016). 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 (Wang, X., Chory, J. 2006). 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.

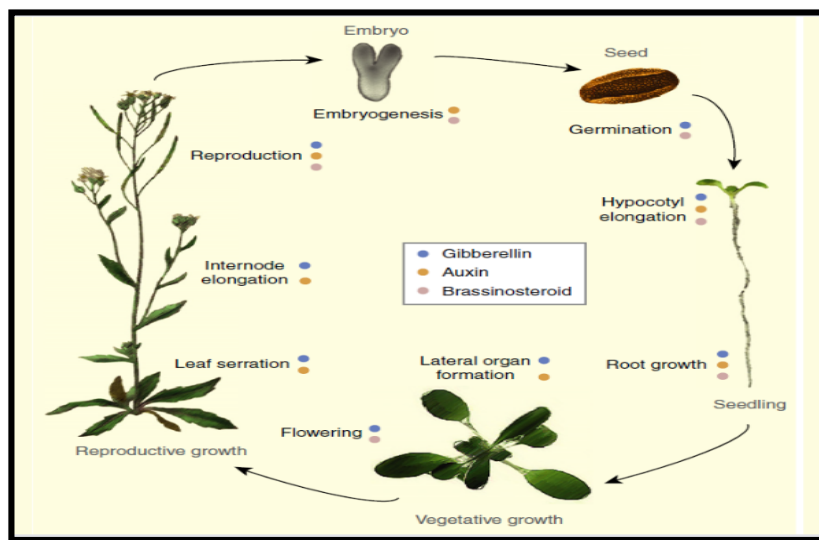


Fig.4. Brassinosteroids have a role in plant development throughout the life cycle.

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 (Hayat et al., 2007; Vlot et al., 2009; Rivas-San Vicente and Plasencia, 2011). SA is produced in plants by two separate processes: the isochorismate (IC) and the phenylalanine (PA) ammonia-lyase (PAL) pathways (Serino et al., 1995; Zhang and Li, 2019). Plants with changed endogenous SA levels exhibit aberrant growth characteristics (Rivas-San Vicente and Plasencia, 2011; Pokotylo et al., 2021). 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 (WT; Bowling et al., 1997; Rate et al., 1999; Miura et al., 2010). 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 (Scott et al., 2004; Abreu and Munné-Bosch, 2009). 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 (Xu et al., 2017). It has been shown that overexpression of NahG can decrease the cell multiplication and expansion defects produced by *siz1* (Miura et al., 2010), 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. 2001) 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 (Abreu and Munné-Bosch, 2009). 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 (Scott et al., 2004; Xia et al., 2009).

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 (Vanacker et al., 2001; Fujikura et al., 2020; Wang et al., 2021). *Arabidopsis npr1-1* mutant leaves contained fewer cells and more DNA, showing that NPR1 promotes cell division and inhibits endoreduplication in leaves (Vanacker et al., 2001). (Fujikura et al. 2020) 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 (Wang *et al.*, 2021). 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) (Ari *et al.*, 2020; Emamverdian *et al.*, 2020; Mazzoni-Putman *et al.*, 2021; Pokotylo *et al.*, 2021). Auxin is a significant growth hormone that regulates these cellular activities, particularly in roots (Perrot-Rechenmann, 2010; Barbeza *et al.*, 2017; Huang *et al.*, 2019; Seo *et al.*, 2021), and SA can influence root development by influencing auxin accumulation and transit. (Pasternak *et al.* 2019) 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 (Ogawa *et al.* 2009; Zhao *et al.* 2016).

Several ABA auxotrophic maize mutants, termed *vp2*, *vp5*, *vp7*, and *vp9*, have been found by genetic screening of viviparous mutants (Reid 1990). 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 (Kushiro *et al.* 2004). PA is subsequently catalysed to dihydrophaseic acid (DPA) and DPA4ODglucoside (DPAG) by PA reductase (PAR), ABH2, and glycosyltransferase (GT) (Weng *et al.* 2016). PA has been shown to preferentially activate a subset of ABA receptor PYLs (Fig 5) (Weng *et al.* 2016). 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 alkalization, which rises during osmotic stressors (Wilkinson and Davies 1997; Karuppanapandian *et al.* 2017). 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 (Liu *et al.* 2015b). 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 (Lee *et al.* 2006; Xu *et al.* 2012). 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) (Weng *et al.* 2016). PA has been shown to preferentially activate a subset of ABA receptor PYLs (Fig 5) (Weng *et al.* 2016).

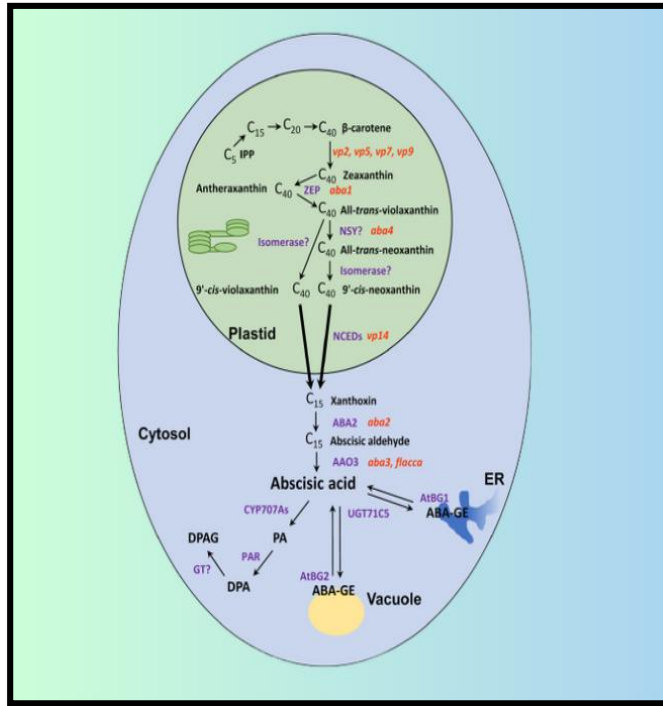


Fig.5. plant abscisic acid (aba) the process of biosynthesis breakdown, and (de)conjugation.

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 (Huai *et al.* 2019). In Arabidopsis, when infected with the necrotrophic disease *Botrytis cinerea*, the transcription factor WRKY33 increases ABA production by upregulating the transcription of NCED3 and NCED5 (Liu *et al.* 2015a). The tomato NAC transcription factor LeJA2 (for jasmonic acid 2) stimulates the production of ABA, which can inhibit pathogen entrance through stomata (Du *et al.* 2014). 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 (Liao *et al.* 2018). Furthermore, JA accumulation is essential for ABA accumulation in Arabidopsis roots following dehydration treatment (de Ollas *et al.* 2015).

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 (Zhu 2016; Shi *et al.* 2018; Yang and Guo 2018). 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 (Sanders *et al.* 2007; Zhu 2016).

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 (Yang, S. F., & Hoffman, N. E. 1984).

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 (Johnson, P. R., & Ecker, J. R. 1998).

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 (Abeles, F. B. *et al.*, 1992). 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:

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).

2.7.3 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.

2.7.4 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.

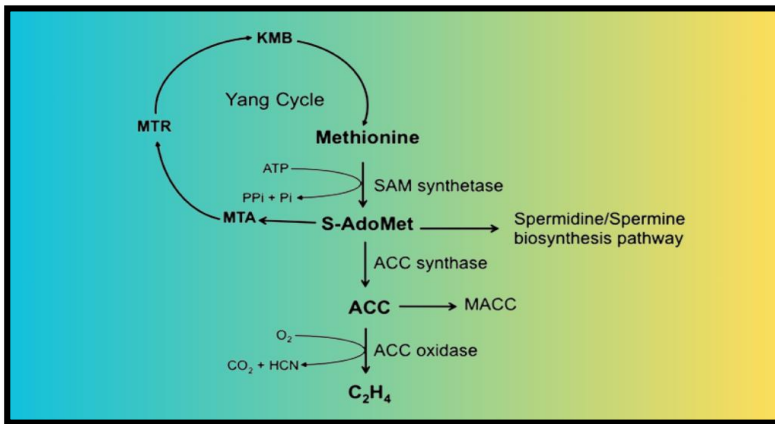


Fig.6. pictural representation of ethylene biosynthesis

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 (Hua, J., *et al.*, 1995). 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 (Qiao, H., *et al.*, 2009). 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 (Solano, R., *et al.*, 1998). 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 (Guo, H., Ecker, J. R. 2003). 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 (Chang, C., *et al.*, 1993). 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 (Kieber, J. J., *et al.*, 1993). 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 (Ju, C., Yoon, *et al.*, 2012). 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 (Guo, H., Ecker, J. R. 2003). 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 adapt 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.

REFERENCES

- [1] Abeles, F. B., Morgan, P. W., & Saltveit, M. E. (1992). *Ethylene in Plant Biology* (2nd ed.). Academic Press.
- [2] Abidur Rahman 2013. Auxin: a regulator of cold stress response *Physiologia Plantarum* 147: 28–35.
- [3] Abreu, M. E., and Munné-Bosch, S. (2009). Salicylic acid deficiency in NahG transgenic lines and *sid2* mutants increases seed yield in the annual plant *Arabidopsis thaliana*. *J. Exp. Bot.* 60, 1261–1271. doi: 10.1093/jxb/ern363.
- [4] Achard P, Gong F, Cheminant S, Alioua M, Hedden P, Genschik P 2008. The cold-inducible CBF1 factor-dependent signaling pathway modulates the accumulation of the growth repressing DELLA proteins via its effect on gibberellin metabolism. *Plant Cell* ; 20:2117-29.

- [5] Ari, Y., Sam, F., Siddiqui, H., Bajguz, A., and Hayat, S. (2020). Salicylic acid in relation to other phytohormones in plant: A study towards physiology and signal transduction under challenging environment. *Environ. Exp. Bot.* 175:104040. doi: 10.1016/j.envexpbot.2020.104040.
- [6] Barbeza, E., Dünserb, K., Gaidoraa, A., Lendl, T., and Buscha, W. (2017). Auxin steers root cell expansion via apoplastic pH regulation in *Arabidopsis thaliana*. *P. Natl. Acad. Sci. U. S. A.* 114, E4884–E4893. doi: 10.1073/pnas.1613499114
- [7] Bennett T, Scheres B. 2010. Root development—two meristems for the price of one? *Current Topics in Developmental Biology* 91, 67–102.
- [8] Benschop JJ, Bou J, Peeters AJM, Wagemaker N, Gu hl K, Ward D, Hedden P, Moritz T, Voeselek LACJ 2006. Long-term submergence-induced elongation in *Rumex palustris* requires abscisic acid-dependent biosynthesis of gibberellin. *Plant Physiol* 141: 1644–1652.
- [9] Beveridge CA. 2006. Axillary bud outgrowth: sending a message. *Current Opinion in Plant Biology* 9, 35–40.
- [10] Bisht, T. S., Rawat, L., Chakraborty, B., & Yadav, V. (2018). A Recent Advances in Use of Plant Growth Regulators (PGRs) in Fruit Crops-A Review.
- [11] Bowling, S. A., Clarke, J. D., Liu, Y., Klessig, D. F., and Dong, X. (1997). The *cpr5* mutant of *Arabidopsis* expresses both NPR1-dependent and NPR1-independent resistance. *Plant Cell* 9, 1573–1584. doi: 10.1105/tpc.9.9.1573.
- [12] Chang, C., Kwok, S. F., Bleecker, A. B., & Meyerowitz, E. M. (1993). *Arabidopsis* ethylene-response gene *ETR1*: similarity of product to two-component regulators. *Science*, 262(5133), 539-544
- [13] Chandler, J.W.; Werr, W. 2009 . Cytokinin–auxin crosstalk in cell type specification. *Trends Plant Sci. Chem.* 276, 26405–26410.
- [14] Cheung, J. and Hendrickson, W. A. (2010). Sensor domains of two-component regulatory systems. *Curr. Opin. Microbiol.* 13, 116-123.
- [15] Clouse, S. D., Sasse, J. M. (1998). BRASSINOSTEROIDS: Essential Regulators of Plant Growth and Development. *Annual Review of Plant Physiology and Plant Molecular Biology*, 49(1), 427-451.
- [16] Davies, P. J. 2004. *Plant Hormones: Biosynthesis, Signal Transduction Action*: (Kluwer Academic).
- [17] Dello Iorio, R., et al. 2008 . A genetic framework for the control of cell division and differentiation in the root meristem. *Science*. 322, 1380–1384 dependent auxin distribution. *Plant Cell* 19: 2197– 2212.
- [18] de Ollas C, Arbona V, Gómez-Cadenas A (2015) Jasmonoyl isoleucine accumulation is needed for abscisic acid build-up in roots of *Arabidopsis* under water stress conditions. *Plant Cell Environ* 38: 2157–2170
- [19] Du M, Zhai Q, Deng L, Li S, Li H, Yan L, Huang Z, Wang B, Jiang H, Huang T, Li CB, Wei J, Kang L, Li J, Li C (2014) Closely related NAC transcription factors of tomato differentially regulate stomatal closure and reopening during pathogen attack. *Plant Cell* 26: 3167–3184
- [20] Duran-Medina, Y., Diaz-Ramirez, D. and Marsch-Martinez, N. (2017). Cytokinin on the Move. *Front. Plant Sci.* 8, 146.
- [21] Elena Pacifici , Laura Polverari* and Sabrina Sabatini 2015 . Plant hormone cross-talk: the pivot of root growth *Journal of Experimental Botany*, Vol. 66, No. 4 pp. 1113–1121, 2015 doi:10.1093/jxb/eru534.
- [22] Emamverdian, A., Ding, Y., and Mokherdoran, F. (2020). The role of salicylic acid and gibberellin signaling in plant responses to abiotic stress with an emphasis on heavy metals. *Plant Signal. Behav.* 15:1777372. doi: 10.1080/15592324.2020.1777372.
- [23] Fujikura, U., Kazune, E., Horiguchi, G., Seo, M., Yuri, K., Yuji, K., et al. (2020). Suppression of class I compensated cell enlargement by *xs2* mutation is mediated by salicylic acid signaling. *PLoS Genet.* 16:e1008873. doi: 10.1371/journal.pgen.1008873
- [24] Greenboim-Wainberg Y, Maymon I, Borochoff R, Alvarez J, Olszewski N, Ori N, Eshed Y, Weiss D. 2005. Crosstalk between gibberellin and cytokinin: the *Arabidopsis* GA response inhibitor *SPINDLY* plays a positive role in cytokinin signaling. *The Plant Cell* 17, 92–102.
- [25] Guo, H., Ecker, J. R. (2003). Plant responses to ethylene gas are mediated by SCF(EBF1/EBF2)-dependent proteolysis of EIN3 transcription factor. *Cell*, 115(6), 667-677.
- [26] Hardtke CS, Dorcey E, Osmond KS, Sibout R 2007. Phytohormone collaboration: zooming in on auxin-brassinosteroid interactions. *Trends Cell Biol* 17: 485–492.
- [27] Hayat, S., Ali, B., and Ahmad, A. (2007). "Salicylic acid: biosynthesis, metabolism and physiological role in plants," in *SALICYLIC ACID: A Plant Hormone*. eds. S. Hayat and A. Ahmad (Netherlands: Springer), 1–14.
- [28] Huang, R. F., Zheng, R., He, J., Zhou, Z. M., Wang, J. C., Xiong, Y., et al. (2019). Noncanonical auxin signaling regulates cell division pattern during lateral root development. *P. Natl. Acad. Sci. U. S. A.* 116, 21285–21290. doi: 10.1073/pnas.1910916116.
- [29] Hua D, Wang C, He J, Liao H, Duan Y, Zhu Z, Guo Y, Chen Z, Gong Z (2012) A plasma membrane receptor kinase, *GHR1*, mediates abscisic acid- and hydrogen peroxide- regulated stomatal movement in *Arabidopsis*. *Plant Cell* 24: 2546–2561.
- [30] Hua, J., Chang, C., Sun, Q., & Meyerowitz, E. M. (1995). Ethylene insensitivity conferred by *Arabidopsis* *ERS* gene. *Science*, 269(5231), 1712-1714.

- [31] Inoue, T., Higuchi, M., Hashimoto, Y., Seki, M., Kobayashi, M., Kato, T., ... & Kakimoto, T. (2001). Identification of CRE1 as a cytokinin receptor from Arabidopsis. *Nature*, 409(6823), 1060-1063.
- [32] Johnson, P. R., & Ecker, J. R. (1998). The ethylene gas signal transduction pathway: A molecular perspective. *Annual Review of Genetics*, 32(1), 227-254.
- [33] J. P., Haberer, G., Ferreira, F. J., Deruère, J., Mason, M. G., Schaller, G. E., ... & Kieber, J. J. (2004). Type-A Arabidopsis response regulators are partially redundant negative regulators of cytokinin signaling. *The Plant Cell*, 16(3), 658-671.
- [34] Ju, C., Yoon, G. M., Shemansky, J. M., Lin, D. Y., Ying, Z. I., Chang, J., ... & Ecker, J. R. (2012). CTR1 phosphorylates the central regulator EIN2 to control ethylene hormone signaling from the ER membrane to the nucleus in Arabidopsis. *Proceedings of the National Academy of Sciences*, 109(47), 19486-19491.
- [35] J. X., Gendron, J. M., Yang, Y., Li, J., Wang, Z. Y. (2002). The GSK3-like kinase BIN2 phosphorylates and destabilizes BZR1, a positive regulator of the brassinosteroid signaling pathway in Arabidopsis. *Proceedings of the National Academy of Sciences*, 99(15), 10185-10190.
- [36] Karuppanapandian T, Geilfus CM, Muhling KH, Novak O, Gloser V (2017) Early changes of the pH of the apoplast are different in leaves, stem and roots of *Vicia faba* L. under declining water availability. *Plant Sci* 255: 51–58.
- [37] Kieber, J. J., Rothenberg, M., Roman, G., Feldmann, K. A., & Ecker, J. R. (1993). CTR1, a negative regulator of the ethylene response pathway in Arabidopsis, encodes a member of the raf family of protein kinases. *Cell*, 72(3), 427-441.
- [38] Kieber, J. J., & Schaller, G. E. (2018). Cytokinin signaling in plant development. *Development*, 145(4), dev149344.
- [39] Kohlen W, Charnikhova T, Liu Q, Bours R, Domagalska MA, Beguerie S, Verstappen F, Leyser O, Bouwmeester H, RuyterSpira C. 2011. Strigolactones are transported through the xylem and play a key role in shoot architectural response to phosphate deficiency in nonarbuscular mycorrhizal host Arabidopsis. *Plant Physiology* 155, 974–987
- [40] Koornneef, M., Bentsink, L., & Hilhorst, H. (2002). Seed dormancy and germination. *Current opinion in plant biology*, 5(1), 33-36.
- [41] Kushihiro T, Okamoto M, Nakabayashi K, Yamagishi K, Kitamura S, Asami T, Hirai N, Koshihara T, Kamiya Y, Nambara E (2004) The Arabidopsis cytochrome P450 CYP707A encodes ABA 8'-hydroxylases: Key enzymes in ABA catabolism. *EMBO J* 23: 1647–1656.
- [42] Lee KH, Piao HL, Kim HY, Choi SM, Jiang F, Hartung W, Hwang I, Kwak JM, Lee IJ, Hwang I (2006) Activation of glucosidase via stress-induced polymerization rapidly increases active pools of abscisic acid. *Cell* 126: 1109–1120.
- [43] Liao X, Li M, Liu B, Yan M, Yu X, Zi H, Liu R, Yamamoto C (2018) Interlinked regulatory loops of ABA catabolism and biosynthesis coordinate fruit growth and ripening in woodland strawberry. *Proc Natl Acad Sci USA* 115: E11542–E11550
- [44] Liu M, Chen Y, Chen Y, Shin J-H, Mila I, Audran C, Zouine M, Pirrello J, Bouzayen M. 2018. The tomato Ethylene Response Factor Sl-ERF.B3 integrates ethylene and auxin signaling via direct regulation of Sl-Aux/IAA27. *New Phytologist* 219: 631–64.
- [45] Mazzoni-Putman, S. M., Brumos, J., Zhao, C., Alonso, J. M., and Stepanova, N. A. (2021). Auxin interactions with other hormones in plant development. *Cold Spring Harb. Perspect. Biol.* 13:a039990. doi: 10.1101/cshperspect.a039990
- [46] Miura, K., Lee, J., Miura, T., and Hasegawa, P. M. (2010). SlZ1 controls cell growth and plant development in Arabidopsis through salicylic acid. *Plant Cell Physiol.* 51, 103–113. doi: 10.1093/pcp/pcp171
- [47] Mok DW, Mok MC 2001. Cytokinin metabolism and action. *Annu Rev Plant Physiol Plant Mol Biol* 52:89-118.
- [48] Muday GK, Rahman A, Binder B 2012. Auxin and ethylene: collaborators or competitors *Trends Plant Sci*, in press.
- [49] Nemhauser JL, Hong FX, Chory J 2006. Different plant hormones regulate similar processes through largely nonoverlapping transcriptional responses. *Cell* 126: 467–475.
- [50] Ogawa M, Hanada A, Yamauchi Y, Kuwahara A, Kamiya Y, Yamaguchi S (2003) Gibberellin biosynthesis and response during Arabidopsis seed germination. *Plant Cell* 15: 1591–1604.
- [51] Pacifici, E., Polverari, L., and Sabatini, S. 2015. Plant hormone cross-talk: the pivot of root growth. *J. Exp. Bot.* 66:1113–1121.
- [52] Pasternak, T., Groot, E. P., Kazantsev, F. V., Teale, W., Omelyanchuk, N., Kovrizhnykh, V., et al. (2019). Salicylic acid affects root meristem patterning via auxin distribution in a concentration-dependent manner. *Plant Physiol.* 180, 1725–1739. doi: 10.1104/pp.19.00130.
- [53] Perilli S, Moubayidin L, Sabatini S. 2010. The molecular basis of cytokinin function. *Current Opinion in Plant Biology* 13, 21–26.
- [54] Perrot-Rechenmann, C. (2010). Cellular responses to auxin: division versus expansion. *Cold Spring Harb. Perspect. Biol.* 2:a001446. doi: 10.1101/cshperspect.a001446.
- [55] Pokotylo, I., Hodges, M., Kravets, V., and Ruelland, E. (2021). A ménage à trois: salicylic acid, growth inhibition, and immunity. *Trends Plant Sci.* doi: 10.1016/j.tplants.2021.11.008 [Epub ahead of Print].

- [56] POSPÍŠILOVÁ J 2003. Interaction of cytokinins and abscisic acid during regulation of stomatal opening in bean leaves. *Photosynthetica* 41: 49.
- [57] Qiao, H., Chang, K. N., Yazaki, J., Ecker, J. R. (2009). Interplay between ethylene, ETP1/ETP2 F-box proteins, and degradation of EIN2 triggers ethylene responses in Arabidopsis. *Genes & Development*, 23(4), 512-521.
- [58] Rashotte, A. M., Carson, S. D., To, J. P., & Kieber, J. J. (2003). Expression profiling of cytokinin action in Arabidopsis. *Plant Physiology*, 132(4), 1998-2011.
- [59] Rate, D., Cuenca, J., Bowman, G., Guttman, D., and Greenberg, J. (1999). The gain-of-function Arabidopsis *acd6* mutant reveals novel regulation and function of the salicylic acid signaling pathway in controlling cell death, defenses, and cell growth. *Plant Cell* 11, 1695–1708. doi: 10.1105/tpc.11.9.1695.
- [60] Reid JB (1990) Phytohormone mutants in plant research. *J Plant Growth Regul* 9: 97.
- [61] Rivas-San Vicente, M., and Plasencia, J. (2011). Salicylic acid beyond defence: its role in plant growth and development. *J. Exp. Bot.* 62, 3321–3338. doi: 10.1093/jxb/err031.
- [62] Sanders MJ, Grondin PO, Hegarty BD, Snowden MA, Carling D (2007) Investigating the mechanism for AMP activation of the AMP-activated protein kinase cascade. *Biochem J* 403: 139–148
- [63] Sedeer El-Showk, Raili Ruonala and Ykä Helariutta 2013 . cytokinin signalling and crosstalk The Company of Biologists Ltd Crossing paths: *Development* 140, 1373-1383.
- [64] Seo, D. H., Jeong, H., Choi, Y. D., and Jang, G. (2021). Auxin controls the division of root endodermal cells. *Plant Physiol.* 187, 1577–1586. doi: 10.1093/plphys/kiab341
- [65] Serino, L., Reimann, C., Baur, H., Beyeler, M., Visca, P., and Haas, D. (1995). Structural genes for salicylate biosynthesis from chorismate in *Pseudomonas aeruginosa*. *Mol. Gen. Genet.* 249, 217–228. doi: 10.1007/bf00290369.
- [66] Shkolnik-Inbar D, Bar-Zvi D 2010. ABI4 mediates abscisic acid and cytokinin inhibition of lateral root formation by reducing polar auxin transport in Arabidopsis. *Plant Cell* 22: 3560–3573.
- [67] Silverstone AL, Chang C, Krol E, Sun TP 1997 .Developmental regulation of the gibberellin biosynthetic gene GA1 in Arabidopsis thaliana . *Plant J* 12: 9–19.
- [68] Skoog, F. and Miller, C.O. 1957. Chemical regulation of growth and organ formation in plant Tissues cultured in vitro. *Symp.Soc. Exp. Biol.* 11: 118–131.
- [69] Solano, R., Stepanova, A., Chao, Q., & Ecker, J. R. (1998). Nuclear events in ethylene signaling: A transcriptional cascade mediated by ETHYLENE-INSENSITIVE3 and ETHYLENE-RESPONSE-FACTOR1. *Genes & Development*, 12(23), 3703-3714.
- [70] Stephen Depuydt and Christian S. Hardtke 2011. Hormone Signalling Crosstalk in Plant Growth Regulation *Current Biology* 21, R365–R373.
- [71] Sun TP, Gubler F 2004 .Molecular mechanism of gibberellin signaling in plants. *Annu Rev Plant Biol* 55: 197–223
- [72] Swarup R, Parry G, Graham N, Allen T, Bennett M 2002. Auxin cross-talk: integration of signalling pathways to control plant development. *Plant Mol Biol* 49: 411–426.
- [73] Tyler L, Thomas SG, Hu J, Dill A, Alonso JM, Ecker JR, Sun TP. 2004. DELLA proteins and gibberellin regulated seed germination and floral development in Arabidopsis. *Plant Physiology* 135, 1008–1019.
- [74] Vanacker, H., Lu, H., Rate, D. N., and Greenberg, J. T. (2001). A role for salicylic acid and NPR1 in regulating cell growth in Arabidopsis. *Plant J.* 28, 209–216. doi: 10.1046/j.1365-3113.2001.01158.
- [75] Vlot, A. C., Dempsey, D. A., and Klessig, D. F. (2009). Salicylic acid, a multifaceted hormone to combat disease. *Annu. Rev. Phytopathol.* 47, 177–206. doi: 10.1146/annurev.phyto.050908.135202.
- [76] Wang, X., Chory, J. (2006). Brassinosteroids regulate dissociation of BKI1, a negative regulator of BRI1 signaling, from the plasma membrane. *Science*, 313(5790), 1118-1122.
- [77] Wang, Z., Rong, D., Chen, D., Xiao, Y., Liu, R., Wu, S., et al. (2021). Salicylic acid promotes quiescent center cell division through ROS accumulation and down-regulation of PLT1, PLT2, and WOX5. *J. Integr. Plant Biol.* 63, 583–596. doi: 10.1111/jipb.13020
- [78] Wei Z. and Li J. 2016. Brassinosteroids Regulate Root Growth, Development, and Symbiosis. *Mol. Plant.* 86–100.
- [79] Weng JK, Ye M, Li B, Noel JP (2016) Co-evolution of hormone metabolism and signaling networks expands plant adaptive plasticity. *Cell* 166: 881–893.
- [80] WILLEM ABTS , BERT VANDENBUSSCHE , MAURICE P. DE PROFT AND BRAM VAN DE POEL 2017 . The Role of Auxin-Ethylene Crosstalk in Orchestrating Primary Root Elongation in Sugar Beet doi: 10.3389/fpls.2017.00444.
- [81] Wilkinson S, Davies WJ (1997) Xylem sap pH increase: A drought signal received at the apoplastic face of the guard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. *Plant Physiol* 113: 559–573
- [82] Xu, L., Zhao, H. Y., Ruan, W. Y., Deng, M. J., Wang, F., Peng, J. R., et al. (2017). ABNORMAL INFLORESCENCE MERISTEM1 functions in salicylic acid biosynthesis to maintain proper reactive oxygen species levels for root MERISTEM activity in rice. *Plant Cell* 29, 560–574. doi: 10.1105/tpc.16.00665.
- [83] Yang, S. F., & Hoffman, N. E. (1984). Ethylene biosynthesis and its regulation in higher plants. *Annual Review of Plant Physiology*, 35(1), 155-189.

- [84] Yang Y, Guo Y (2018) Elucidating the molecular mechanisms mediating plant salt-stress responses. *New Phytol* 217: 523–539.
- [85] Yeshitila, M., & Gobena, A. (2020). Review on phytohormones signaling cross-talk: To control plant growth and development. *International Journal of Advanced Research in Biological Sciences*, 7(3), 54-57.
- [86] Yin, Y., Wang, Z. Y. (2002). Molecules in brassinosteroid signaling. *In Vitro Cellular & Developmental Biology - Plant*, 38(2), 117-124.
- [87] Zhang, W., To, J. P. C., Cheng, C.-Y., Eric Schaller, G. and Kieber, J. J. 2011. Type-A response regulators are required for proper root apical meristem function through post-transcriptional regulation of PIN auxin efflux carriers. *Plant J.* 68, 1-10.
- [88] Zhang, Y. L., and Li, X. (2019). Salicylic acid: biosynthesis, perception, and contributions to plant immunity. *Curr. Opin. Plant Biol.* 50, 29–36. doi: 10.1016/j.pbi.2019.02.004.
- [89] Zhao Y, Zhang Z, Gao J, Wang P, Hu T, Wang Z, Hou YJ, Wan Y, Liu W, Xie S, Lu T, Xue L, Liu Y, Macho AP, Tao WA, Bressan RA, Zhu JK (2018) Arabidopsis duodecuple mutant of PYL ABA receptors reveals PYL repression of ABA-independent SnRK2 activity. *Cell Rep* 23: 3340–3351.
- [90] Zhu JK (2016) Abiotic stress signaling and responses in plants. *Cell* 167: 313–324.

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