

Review

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Posted Date: 19 September 2023

doi: 10.20944/preprints202309.1166.v1

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Review

The Fascinating Role of Ethylene in the Control of Plant Developmental Processes

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Abstract: Ethylene, a gaseous phytohormone, is emerging as a central player in the intricate web of plant developmental processes from germination to senescence under optimal and stressed conditions. It is present in different plant parts, encompassing the stems, leaves, flowers, roots, seeds, and fruits. This review aims to provide a comprehensive overview of ethylene's fascinating roles in shaping various plant growth and adaptation aspects. It intricately examines the multifaceted impact of ethylene on pivotal aspects of plant development, including but not limited to cell division and elongation, senescence, abscission, fruit and flower development, root hair formation, chloroplast maturation, and photosynthesis. This comprehensive assessment encompasses the intricate pathways of ethylene biosynthesis and signaling, providing a snapshot of the regulatory mechanisms governing ethylene production. Understanding ethylene's multifaceted functions has significant implications for agriculture, biotechnology, and our fundamental comprehension of plant biology. This review underscores the need for continued investigation into ethylene's intricate mechanisms and its potential to revolutionize plant development and crop management.

Keywords: ethylene biosynthesis and regulation; cell division and elongation; flower and fruit development; chloroplast development; photosynthesis; senescence and abscission

1. Introduction

The sessility of plants, which mean that their survival may be challenged by environmental perturbations, is without a doubt their most unfavorable aspect when compared to other living species. Nevertheless, plants have created intriguing mechanisms that quickly recognize changing environmental conditions and extremely sophisticated biochemical reactions, leading to amazing phenotypic flexibility. Plant growth is one carefully regulated process throughout the vegetative growth stage. To permit ongoing food intake and production of energy via photosynthesis, respectively, root and shoot growth is essential under favourable conditions. Plant growth regulators synthesised all over the plant, are crucial for supporting the resilience responses. However, apical and young tissues are a rich source of these compounds. Ethylene (ET) is a versatile hormone regulating plant development, stress responses, and secondary metabolism. Researchers have been captivated by the manifold roles of this hormone as a signaling agent, leading to the elucidation of its synthesis, signaling pathways, and the discovery of its diverse functions, which encompass the regulation of leaf development, senescence, fruit ripening, and the promotion of germination, etc. ET is the second most fundamental unsaturated hydrocarbon. It exhibits peculiar dose-dependent action under ideal and external disruptions for all its suppression or promotion responses like germination, ripening, growth and senescence. For instance, a low concentration of ET facilitates the activation of defense signaling in plants, its high concentration seems to inhibit development in *Triticum aestivum* and *Cucumis sativus* [1–3]. Importantly, ET is produced in response to various biotic and abiotic environmental stimuli, indicating that it links environmental change and developmental adaptation. The sole subject of the review is ET regulation in plant development, We will try to sum up the relatable information in detail.

2. Ethylene biosynthesis and signaling

Ethylene biosynthesis involves a two-step enzymatic pathway starting with methionine, which is converted into S-adenosyl-L-methionine (SAM or S-AdoMet) by S-AdoMet synthetase. This transformation utilizes one ATP molecule. Subsequently, S-AdoMet is enzymatically converted into 1-aminocyclopropane-1-carboxylic acid (ACC) and 5'-methylthioadenosine (MTA) by ACC synthase (ACS) [4]. Lastly, ET is generated through the oxidation of ACC, facilitated by ACC oxidase (ACO). In parallel, the Yang cycle operates to convert MTA, a byproduct of the second stage, back into methionine, ensuring an optimal methionine pool [5]. Typically, under normal basal ET production levels, ACS is believed to control the rate-limiting step in biosynthesis [4]. Nevertheless, specific circumstances can lead to ACO becoming the limiting factor [6]. Figure 1a shows the illustration.

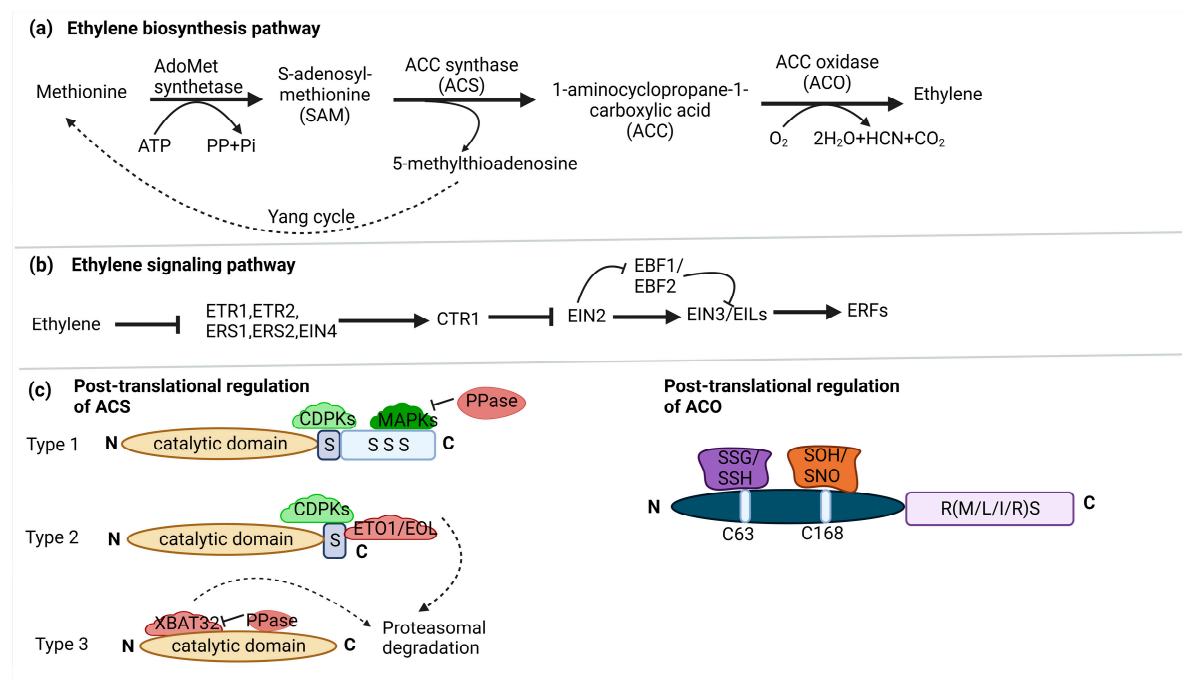


Figure 1. (a) Biosynthesis of ethylene: In higher plants, ethylene is produced through the Methionine/Yang cycle. This involves converting methionine into 1-aminocyclopropane-1-carboxylic acid (ACC) using ACC synthase (ACS), and then ACC is further converted into ethylene by ACC oxidase (ACO). The Yang cycle recycles 5-methylthioadenosine to regenerate methionine, which is crucial for this process. **(b) Signaling pathway of ethylene:** Ethylene receptors (ETR1, ERS1, EIN4, ETR2, and ERS2) on the endoplasmic reticulum (ER) activate CTR1 kinase, which phosphorylates and degrades EIN2's C-terminal part, preventing its nucleus entry. Simultaneously, EBF1/2 transcripts produce F-box proteins that target EIN3/EIL transcription factors for degradation, blocking ethylene response. Ethylene binding, deactivates CTR1, leading to EIN2 dephosphorylation. A protease cleaves EIN2's C-terminal part (EIN2-CEND) in the nucleus and cytoplasm. EIN2-CEND then enters the nucleus and binds to EIN3/EIL transcription factors, initiating gene expression for ethylene response. **(c) Post-translational regulation of ACS and ACO:** ACS enzymes can be categorized into three groups based on their phosphorylation sites: type 1 with both CDPK (calcium dependent protein kinase) and MAPK (Mitogen activated protein kinase) sites, type 2 with only CDPK sites, and type 3 with no C-terminal regulatory sites. Type 1 ACS is positively regulated by MAPKs and CDPKs, significantly boosting its activity and ethylene production. Phosphatases (PPase) are involved in dephosphorylation, negatively impacting protein stability. Type 2 ACSs are regulated by the ETO1-containing E3 ligase, recognizing the TOE (Target of ETO1) domain in their C-termini. CDPK phosphorylation likely plays a role in regulating this ubiquitination process and thus the stability of Type 2 ACS protein. XBAT32 directly binds to type 3 ACS, leading to protein degradation, while PPase plays a role in stabilizing. ACO enzymes, fall into three related groups based on amino acids in the RXS motif: type 1 with RMS intermediate residue, type 2 with R-L/I-S intermediate residue, and

type 3 with RRS intermediate residue. Type 1 ACOs can undergo modifications at C63, including S-glutathionylation (SSG) and S-sulphydration (SSH), as well as at C168, including S-sulfenylation (SOH) and S-nitrosylation (SNO). No such modifications have been observed in type 2 and type 3 ACOs.

The ethylene signaling pathway begins when ethylene binds to ER-localized receptor proteins, such as ETR1, ETR2, EIN4, ERS1, and ERS2 in Arabidopsis, organized into two subfamilies defined by their ethylene binding and histidine kinase domains. Without ET, these receptors activate CTR1, a Ser-Thr protein kinase on the ER membrane, which phosphorylates EIN2's C-terminal end (EIN2-CEND). F-box proteins ETP1 and ETP2 target phosphorylated EIN2 for degradation by the 26 S proteasome, preventing its nuclear translocation [7]. Similarly, EIN3 is subject to ubiquitin-mediated proteasomal degradation, guided by F-box proteins EBF1 and EBF2, thereby inhibiting ET responses. When ET is present, it binds to its receptor, facilitated by copper ions from RAN1. This binding deactivates CTR1, leading to the dephosphorylation and cleavage of EIN2-CEND [8]. EIN2-CEND subsequently obstructs the translation of EBF1 and EBF2 mRNA by transporting them to cytoplasmic P-bodies responsible for mRNA degradation. Furthermore, EIN2-CEND moves into the nucleus, activating EIN3/EIL transcription factors, culminating in the transcription of ET-responsive genes [9]. Figure 1b represents the summary.

3. Snapshot of regulation of ethylene biosynthesis

Since ACS and ACO are the exclusive enzymes involved in ET biosynthesis, most regulation concerning overall ET production revolves around modulating these two pivotal enzyme's transcription, translation, and protein stability. However, these enzymes are also affected by phytohormones and other stimuli like light and stress. In the early stages of research on the transcriptional regulation of ET biosynthesis, scientists uncovered the presence of a multigene family known as ACS (1-Aminocyclopropane-1-carboxylic acid synthase) genes, which exhibited distinct expression patterns in plants. Notably, four specific ACS genes in tomatoes held pivotal roles in orchestrating the shift from autoinhibitory to autocatalytic ET production during fruit ripening [10]. Leading the charge as the initial regulator of ACS expression was the MADS-box transcription factor SIRIN, which directly bolstered the expression of selected *S. lycopersicum* ACS genes [11]. Over the years, numerous other transcription factors have emerged as key players, promoters, and inhibitors of ACS gene expression, influencing diverse growth processes. Intriguingly, there is also supporting information suggesting that ET itself can exert a direct influence on ACS transcription. For instance, the ET response factor SIERF2/TERF2 of *S. lycopersicum* interacts with the promoter of NtACS3, thereby stimulating its expression [12]. The regulation of ET synthesis is further complicated by its interaction with light, phytohormones, and various biotic or abiotic stresses. The impact of light on ACS gene expression varies, contingent on developmental stages and light conditions. Notably, different ACS isozymes seem to have specific functions, with ACS5, 6, 8, and 9 primarily influencing ET production in dark-grown seedlings, while ACS2 and ACS4 assume control over ET production in well-lit conditions [13]. Mutations in the phytochrome genes PHYA and PHYB have been found to affect ET biosynthesis, with phyA mutants displaying more pronounced increases in ET production. Furthermore, transgenic lines engineered to overexpress Arabidopsis PHYTOCHROME-INTERACTING FACTOR5 (PIF5) have exhibited enhanced ET production, underscoring the role of PIFs in the regulation of ET biosynthesis, which appears to be stage-dependent [13].

Much like their ACS counterparts, ACO genes are subject to transcriptional regulation. Notably, the *S. lycopersicum* HD-ZIP transcription factor SIHB-1 and the ripening regulator RIN directly stimulate ACO gene expression. Across various species, different classes of transcription factors have also been implicated in regulating ACO. Interestingly, ET can directly control ACO expression through intricate feedback mechanisms mediated by ERF (ethylene response factor) proteins [14]. In *S. lycopersicum*, ACO1 experiences upregulation in response to white light pulses. This phenomenon propels ET production and serves as a reporting mechanism for ET responses, thus establishing a positive feedback loop. Additionally, ACO transcript levels surge after ACC (1-aminocyclopropane-

1-carboxylic acid) treatment of light-grown seedlings. During phases of ripening or stress, when ACS activity is heightened, ACO activity becomes rate-limiting, prompting an upswing in ACO expression. This orchestrated feed-forward mechanism is pivotal in eliminating excess ACC when ACO activity imposes restrictions on ET production [13].

Transcriptional regulation of ET biosynthesis is complemented by posttranslational modifications of ACC synthase (ACS) proteins. ACS proteins share a conserved N terminus and catalytic core, there's notable variability in the C terminus among different ACS isoforms. This variability leads to the classification of ACS proteins into three major groups in Arabidopsis: type 1 (ACS1,2 and 6), type 2 (ACS4,5,8,9 and 11), and type 3 (ACS 7). Type 1 has a phosphorylation site for mitogen-activated protein kinases (MAPKs) and calcium-dependent protein kinases (CDPKs). Type 2 has a site for CDPKs and ETO1 (Ethylene Overproducer1) /ETO1-LIKE1 (EOL), an E3 ligase leading to degradation. Type 3 has no target site. Phosphorylation stabilizes type 1 ACS, promoting ET production. Conversely, dephosphorylation can lead to ACS degradation, although this effect depends on the type of ACS [14]. Moreover, phosphorylation can destabilize type 2 ACS, as exemplified by the phosphorylation of ACS5 (type 2) by Casein Kinase 1.8 (CK1.8), resulting in E3 ubiquitin ligases mediated degradation [15]. Light-triggered post-translational regulation of type-2 ACSs, especially ACS5, regulating hypocotyl elongation during the dark-to-light shift [16]. PIF3 plays a key role, with ET stabilizing PIF3 in light. This light-stimulated stabilization of ACS enzymes increases ET production, potentially contributing to PIF3 stability and the subsequent promotion of ET-driven hypocotyl elongation under light exposure [16]. PP2A, a regulatory component, plays a role in post-translational ACS stability regulation. PP2A-mediated dephosphorylation negatively affects ACS6 protein stability in the dark [17]. Posttranslational regulation of ACS also involves ubiquitination, with type 3 ACS7 being targeted for degradation through ubiquitination mediated by XBAT32 (XB3 orthologue 2 in Arabidopsis, Figure 1c). Protein Phosphatase 2C family members (PP2C's) also play a role in stabilizing ACS7 [14].

While much is known about the posttranslational regulation of ACS, research into the posttranslational regulation of ACC oxidase (ACO) has been comparatively limited. It's worth mentioning that the three categories of ACO can be distinguished based on the specific intermediate amino acid present within the conserved RXS motif. Type 1 ACOs contain an RMS intermediate residue, type 2 ACOs possess an R-L/I-S intermediate residue, and type 3 ACOs feature an RRS intermediate residue. ACO proteins undergo redox-specific posttranslational modifications. These modifications involve cysteine residues and include S-glutathionylation (SSG), S-sulphydration (SSH) at cysteine (C63) and S-sulfenylation (SOH), S-nitrosylation (SNO) at C168. These modifications are recorded only in type 1 ACO (Figure 1c). Recent studies have highlighted the significance of these modifications in controlling ACO activity and structural stability [14].

4. Involvement of ethylene in plant developmental processes

Ethylene plays various roles in regulating cellular, molecular, and whole-plant metabolism. It influences the performance of plants under optimal and stressful environments by interacting with other signaling molecules. The impact of ET is contingent on its concentration within the cell and the plant's sensitivity to this hormone. Ethylene has garnered attention due to its dual influence on controlling plant processes at both physiological and molecular levels [18,19]. In Table 1 we listed the effect of the exogenous application of ET in different concentrations on plant development in different species. Here are some of the processes regulated by ET:

Table 1. Effect of exogenously applied ethylene on plant development in various plants.

Plant species	Ethylene concentration	Response	Reference
<i>Arabidopsis thaliana</i>	1-5 µL L ⁻¹ ethylene	Strong hyponastic response of leaf	[20]
<i>Brassica juncea</i>	400 µL L ⁻¹ ethephon	Net photosynthesis and stomatal conductance decreases	[21]

<i>Brassica juncea</i>	200 µL L ⁻¹ ethephon	Net photosynthesis and stomatal conductance increases	[22]
<i>Triticum aestivum</i>	50mM ethephon	No effect on photosynthesis and stomatal conductance increases	[23]
<i>Solanum tuberosum</i>	199.3 µL L ⁻¹ ethylene	inhibited the sprouting of potato tubers by influencing their carbohydrate metabolism.	[24]
<i>Solanum lycopersicum</i>	1 mM ethephon	Reduced growth due to alteration in cell wall composition (accumulation of cellulose and lignin) and reduction in photosynthesis	[25]
<i>Pyrus bretschneideri</i>	5 µL L ⁻¹ ethylene	Ethylene effectively inhibited postharvest peel browning by enhancing the activity of antioxidant enzymes such as CAT, APX, and SOD, while reducing Polyphenol oxidase activity. Additionally, it led to lower rates of electrolyte leakage and respiration in the peel.	[26]
<i>Camellia sinensis</i>	3000mg L ⁻¹ ethephon	Induced abscission of flower and flower bud, enhances shoot length and caffeine content	[27]
<i>Cucumis sativus</i>	0.5 Mm ethrel	Adventitious root formation	[28]
<i>Solanum lycopersicum</i>	0,0.2, 1 and 2mM ACC	Ethylene suppresses the process of fruit set by affecting the metabolism of gibberellin	[29]

4.1. Cell division and elongation

The role of ET in cell division is a complex and context-dependent phenomenon. Ethylene, a plant hormone, affects cell division depending on the specific tissue type and the internal and external signals at play. In certain situations, ET acts as a stimulator of cell division. For example, during the development of the apical hook, during the early stages of apical hook development, ethylene appears to play a synergistic role with auxins in stimulating cell division within the subepidermal layers. This collaborative effect is crucial for the bending of the apical hook. Specifically, ET is believed to facilitate cell's expansion in the hook's convex side contributing to its curvature [30]. Additionally, ET has been found to control cell division rate in vascular tissue, promoting vascular cell differentiation. Mutations like *eto1* and *eto2* (ETHYLENE OVERPRODUCER) enhance vascular cell division. Emphasizing the necessity of ET signaling transcription factors ERF018 and ERF109 further boost cell division during vasculature development in Arabidopsis stems [31]. In this specific context, ET has a positive impact on cell division.

However, the role of ET in cell division is not uniform across all plant tissues. Ethylene's effects on cell division in the root system are somewhat contradictory. Studies have shown that ET does not significantly alter the expression pattern of *CYCLIN-DEPENDENT PROTEIN KINASE B1;1* (*CYCB1;1*), pointing that it does not directly affect mitotic activity in the root. However, it's important to note that ET modulates cell division within the quiescent center, developing additional columella layers in the root cap [32,33]. Moreover, ET control over the root apical meristem (RAM) size and cell number depends on CULLIN3-type E3 ligases, demonstrating an ET-dependent regulatory mechanism [34]. In addition, loss of function mutant *ctr1-2*, results in a reduced meristematic zone. Conversely, ethylene-insensitive mutant *etr1-1*, exhibits an extended meristematic zone relative to wild-type plants [35]. Ethylene regulates RAM size through the canonical pathway involving CTR1, EIN2, and EIN3/EIL, and an alternative pathway with ARR1. This highlights ET complex role in controlling root apical meristem size and proliferation [36].

The impact of ET on leaf cell division is context-dependent. Under environmental stress, particularly when plants experience less than 10 hours of osmotic stress, ET mediates transient and reversible cell cycle cessation. This effect is thought to involve the phosphorylation-mediated inactivation of CYCLIN-DEPENDENT KINASE A (CDKA), possibly via the MPK3/6 pathway. Intriguingly, this cell cycle arrest operates independently of the EIN3 transcriptional control [37].

Cell cycle inhibition by ethylene in leaves is multifaceted, ET accumulation activates BOLITA, an ERF, activating type II TCP (*TEOSINTE BRANCHED 1/CYCLOIDEA/PCF*) genes [38]. These TCP proteins then bind to the promoter of *RBR1* (*RETINOBLASTOMA RELATED 1*), phosphorylating E2Fa and repressing E2F target gene transcription, thereby impeding progression into the S-phase and cell division [39]. Furthermore, ET induces the expression of *ERF5* and *ERF6* in stressed leaves. *ERF6*, in turn, prompts the expression of *GA2-OX6* (*GA2-OXIDASE6*) reducing active GA levels and accumulating DELLA proteins, which repress *DEL1* and *UVI4* (Regulates the transition from the mitotic cell cycle to endoreduplication) gene expression, resulting in an early exit from the cell cycle [39,40]. Furthermore, ET restricts the mitotic cell cycle within the leaf petiole's abaxial cells. This inhibition is achieved by suppressing the expression of *CYCLIN2A;1*, thereby partially playing a role in hyponastic phenomenon [41]. These findings provide comprehensive insights into ET's intricate control of cell division.

Cellular growth relies on key processes like: the rearrangement of the cytoskeleton, the modification of the cell wall facilitated by cell wall-remodeling enzymes, and water uptake via aquaporins. Cell elongation involves rearranging cortical microtubules (CMT) perpendicular to the growth axis [42]. Ethylene rapidly alters CMT orientation in Arabidopsis roots and hypocotyls, inhibiting cell elongation and promoting radial swelling within 10 minutes [42]. Conversely, ET induces petiole elongation in well-lit conditions by reorienting CMT from longitudinal to transverse in abaxial cells [43], excluding adaxial cells. In ET-regulated cellular elongation, expansins (EXP) and xyloglucan endotransglycosylases/hydrolases (XTH) play pivotal roles. ET induces *EXP* expression in Arabidopsis, influencing root hair formation and submergence-escape elongation, leading to localized, tissue-specific elongation responses. Ethylene regulates *XTH* expression during root hair initiation and submergence-induced hyponastic responses [42]. It was documented that ET serves as a negative regulator by impeding the uptake, accumulation, and distribution of gibberellic acid in the endodermis of the elongation zone of the primary root of Arabidopsis. Additionally, cytokinin influences cell elongation, partly through an ET-dependent pathway, as evidenced by the reduced cell elongation response to cytokinins in the ethylene-insensitive *ein2* mutant compared to the wild type [35]. Furthermore, it was also observed in Arabidopsis that with elevated *EIN2* expression, *EXP3* and *EXP5* exhibit reduced levels, while in *ein2* knockout plants, these genes are upregulated. Additionally, the expression of *EXP1* and *EXP5* is significantly suppressed in dwarfed *BOLITA* gain-of-function plants [39].

4.2. Leaf growth and flower development

Ethylene overproduction in Arabidopsis resulted in dwarfed plant with reduced growth [44,45]. Accordingly, when positive regulators of the ethylene signaling pathway in plants are mutated, it is typically observed that these plants exhibit larger rosettes and leaves compared to control plants. Mutation of the endoplasmic reticulum (ER)-anchored protein *EIN2*, for instance, has been linked to increased growth [46]. On the contrary, mutations in components that inhibit ethylene signaling, like the receptors *ETR1* and *ERS1*, result in stunted growth. Furthermore, when the negative regulators *ARGOS* or *ARGOS-LIKE* (*ARL*) are excessively expressed, it promotes leaf growth in Arabidopsis [47,48]. Another relevant study states that certain rhizosphere bacteria enhance plant growth by expressing *ACC-DEAMINASE*, reducing the levels of 1- aminocyclopropane-1-carboxylic acid (ACC) in stressed plants [49]. However, lower concentration of ET has reported to promote leaf growth. For instance, *Poa alpina* and *Poa compressa* showed increased leaf elongation rates [50] and the primary leaves of *Helianthus annuus* were enlarged on ET exposure [51]. However, the effect was altered on increasing ethylene concentration. Furthermore, studies also showed that application ethephon increases the leaf area [21,52]. Certain reports also observed no change in leaf area of ET insensitive Arabidopsis, *Nicotiana* and *Petunia* relative to ET-sensitive plants [53]. Thus, it can be inferred that the effect of ethylene on leaf growth and development is influenced by the concentration of ET used and the specific plant species under investigation [19,54].

Regulatory mechanism of sex determination in plant represents a model experiment system in case of unisexual plants [55]. Considerable focus has been directed towards the identification of genes

responsible for regulating the development of male and female flowers. Although various plant hormones were investigated for their impact on the proportion of unisexual flowers, ethylene emerged as a prominent regulator of unisexual flower development [56]. The primary genes determining flower sex type encode crucial enzymes engaged in ethylene production, with Wiskott-Aldrich syndrome protein-interacting protein (WIP1), which encodes a C2H2 zinc finger transcription factor of the WIP family. The M (Monoecious) gene encodes *ACS2*, expressed in the carpel region of the female flower; its inactivation (*m*) leads to the development of a bisexual flower [57]. *ACO2* has also been demonstrated to impact the formation of unisexual flowers by collaborating with *ACS11* to promote the selective production of ethylene in the floral region; dysfunctional *ACO2* results in the absence of female flowers [58]. Trebitsh et al., [59] discovered that the F (Female) locus contains an additional copy of *ACS1* suggesting initial connection between ET biosynthesis and female flower development. In *Cucumis sativus*, plants carrying the F locus duplication, *ACS1G* is expressed early in floral bud development, triggering ET burst when functioning with *ACS2*. Following the initiation of gynoecy, ET engages in the repression of WIP1 and activation of *ACS2*. This leads to the early expression of *ACS1G*, bypassing the requirement for *ACS11* in ET production and establishing a dominant pathway for female floral development [57]. Gene editing of *ACO2* in maize leads to a decrease in ET production during ear development. This alteration facilitates the enhancement of meristem and flower development, resulting in a significant boost of approximately 13.4% in grain yield per ear in hybrid lines [60]. Recent reports proposed that integrated genetic network of both ET biosynthesis and receptor genes regulates sex determination. In *C. pepo*, the extent of ethylene insensitivity is influenced by both the potency and quantity of mutant alleles in at least three collaborating *ETHYLENE RESPONSE (ETR)* genes, and that this level of ET insensitivity is a key factor in determining the ultimate sexual phenotype of the plant. The female flowering transition and development was found to be associated with upregulation of *CpACS11*, *CpACO2* and *CpACS27* [61]. The description is illustrated in Figure 2.

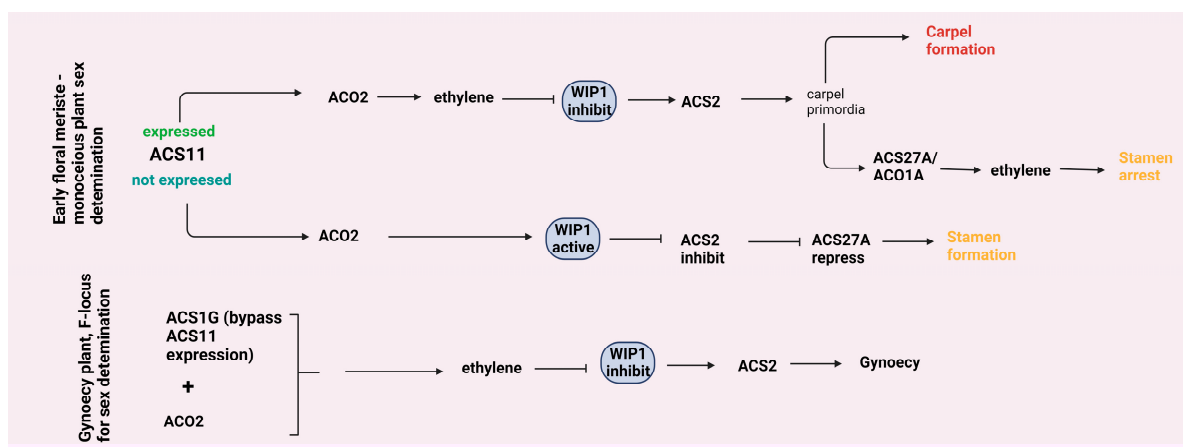


Figure 2: Flower development: In monoecious *Cucumis sativus* (cucumber) plants, the presence or absence of *ACS11* plays a crucial role in determining the sex of the flowers. When *ACS11* is expressed in the floral meristem, it produces ethylene, leading to the development of female flowers by suppressing WIP1 (Wiskott-Aldrich syndrome protein-interacting protein, encodes a C2H2 zinc finger transcription factor) and activating *ACS2*. Later, *ACO1A* and *ACS27A* produce ethylene, causing stamen arrest. In buds without *ACS11* expression, the male development program takes over. However, the presence of the *F-gene* (*ACS1G*) ensures the production of female flowers, conferring gynoecy, regardless of *ACS11*, by directly upregulating *ACS2* through its interaction with *ACO2* and promoting carpel development.

4.3. Root hair development

Root hairs represent an extensive network of epidermal cells within the root system, playing a vital role in nutrient uptake, anchoring the plant in the soil, and facilitating interactions with the environment in stationary plants. The plant hormone ethylene not only fosters the growth of these

root hairs but also acts as a mediator for various signals that trigger the development of hair cells [62]. Ethylene's role in Arabidopsis root hair formation is elucidated through ET biosynthesis mutants. Root hairs of *eto1*, *eto2*, and *eto4* mutants develop longer hairs than wild-type ones on trichoblasts cells. Interestingly, the *eto3* mutant stands out as it produces higher levels of ET than other *eto* alleles. Remarkably, it also triggers the development of hairs on atrichoblasts, which are typically hairless cells [63]. Mutations in genes involved in ET signaling confirm ET necessity for root hair elongation, for example, *etr1* and *ein2* receptor mutations yield shorter root hairs (50-70% of wild type), while *ctr1* loss-of-function mutations produce longer root hairs. This underscores ET crucial role in controlling root hair length [63]. In Arabidopsis, root epidermal cell fate depends on their position relative to cortical cells. Hair (H) cells form over the junction of two cortical cells, while nonhair (N) cells develop over a single cortical cell. The core regulatory network is driven by a transcriptional cascade. The genes involved in root hair cell fate determination in root epidermal cells of Arabidopsis include *TRANSPARENT TESTA GLABRA* (*TTG*), *GLABRA3* (*GL3*), *ENHANCER OF GLABRA3* (*EGL3*), *WEREWOLF* (*WER*), *GLABRA2* (*GL2*) and *CAPRICE* (*CPC*), and its homologs *TRIPTYCHON* (*TRY*) and *ENHANCER OF TRY AND CPCs* (*ETC*) [64]. In N-type cells, WER-GL3/EGL3-TTG complex induces *GL2* and *CPC* expression, inhibiting root hair growth. *CPC* moves to adjacent H-type cells, competing with *WER*, inhibit *GL2* expression, and promoting H-type cell differentiation [64]. *GLABRA 2* (*GL2*), a crucial transcription factor, maintains N cell fate by repressing a group of basic helix-loop-helix (bHLH) factors that promote root hair development in H cells. *ROOT HAIR DEFECTIVE 6* (*RHD6*) and its homolog *RHD6-LIKE 1* (*RSL1*) are key players in this process, positively regulating other bHLH factors (*RSL2-5*) that enhance root hair growth, with *RSL4* being directly regulated by *RHD6* [65]. The ET-activated transcription factors *EIN3/EIL1* interact with *ROOT HAIR DEFECTIVE 6* (*RHD6*)/*RHD6-LIKE 1*, leading to the direct coactivation of the *RSL4* (*ROOT HAIR DEFECTIVE 6-LIKE 4*) gene, thereby enhancing the growth of root hairs [65]. A recent study showed that *EIN3* influences the WER-GL3-TTG1 complex formation by competing with *GL3* for *TTG1* binding, consequently reducing *GL2* transcription via diminished WER-GL3-TTG1 complex formation and induces the development of root hairs [66]. Furthermore, *MYB30*, belonging to the MYB protein family, functions as a plant transcription factor with a negative role in root hair elongation. *MYB30* directly interacts with the *RSL4* promoter region, suppressing its transcription and inhibiting root hair elongation. Ethylene promotes the formation of a complex between *EIN3* and *MYB30* by decreasing the interaction between *MYB30* and the *RSL4* promoter. The activation of *RSL4* transcription ultimately stimulates elongation of root hair [67]. A study centered on C2H2 family proteins, specifically highlighting the role of ZINC FINGER PROTEIN 5/6 (*ZFP5/6*) within this family. They confirmed that *ZFP5/6* serves a dual function, acting as a downstream component of gibberellins, ethylene, and cytokinins, while also operating as an upstream regulator of the *CAPRICE* (*CPC*)/*GLABRA3*/*ENHANCER OF GLABRA3* (*GL3/EGL3*)/*TRANSPARENT TESTA GLABRA1* (*TTG1*) complex in the control of root hair development [68]. The study aimed to understand ET role in root hair initiation when the normal differentiation pattern of root epidermal cells is disrupted showed that *CPC* and *TRY* are crucial for root hair formation. Interestingly, exogenous ET triggered root hair formation in the *cpc* mutant at certain positions but had no effect in the *cpc try* mutant. This suggests that ET-induced root hair initiation depends on the functionality of the *CPC-TRY* complex, even if it is partially functional [69]. Applying phytohormones like auxin and cytokinin induces root hair growth in a dependent manner. Ethylene's influence on root hair development could be, at least partially, linked to the auxin pathway. *RSL4* was pivotal in bridging the ET and auxin pathways during root hair development. Multiple *AUXIN SIGNALING F-BOX* genes induced by auxin directly bind to the promoter of *RSL4*, activating its expression and facilitating the root hair elongation [70]. Additionally, the initiation of root hairs induced by low-pH (acidification), which involves cortical microtubule randomization, was associated with elevated auxin synthesis and its subsequent effects [71]. Analysis of the transcriptome showed that both auxin and ET had the capacity to increase the expression of 90% of the 208 genes associated with root hair growth and development [72]. In comparison to the wild type, the auxin-insensitive mutant *axr1* had shorter root hairs, which could be restored with exogenous ACC. The ET-insensitive mutant *ein2-1*

showed restrained root hair growth, which was alleviated by exogenous naphthalene acetic acid treatment. The ET overproducing mutant *eto1* displayed longer root hairs, while the loss of AUX1 in the *eto1* showed reduction in root hair length [73–75]. An auxin efflux carrier PIN2 (PIN-FORMED2) plays a crucial role in creating the right auxin gradient in root tips, which is essential for root hair growth. A recent study introduces *SAV4* (*SHADE AVOIDANCE 4*), a novel regulator that influences PIN2 abundance membrane clustering, and stability through direct interactions and regulates polar auxin transport. Study showed that ET treatment increases the *SAV4* protein level, which leads to a decrease in the breakdown of PIN2. The higher levels of PIN2 on the cell membrane of the epidermis enhance the transport of auxin towards the base of the root, consequently stimulating root hair development [76]. Often, ET and auxin appear to be closely interconnected, resulting in cooperative and complementary impacts on root hair development. Ethylene-induced auxin activity plays a substantial role in promoting root hair initiation (Figure 3), while the elongation of root hairs necessitates a synergistic interaction between auxin and ethylene, utilizing their canonical signaling pathways [75].

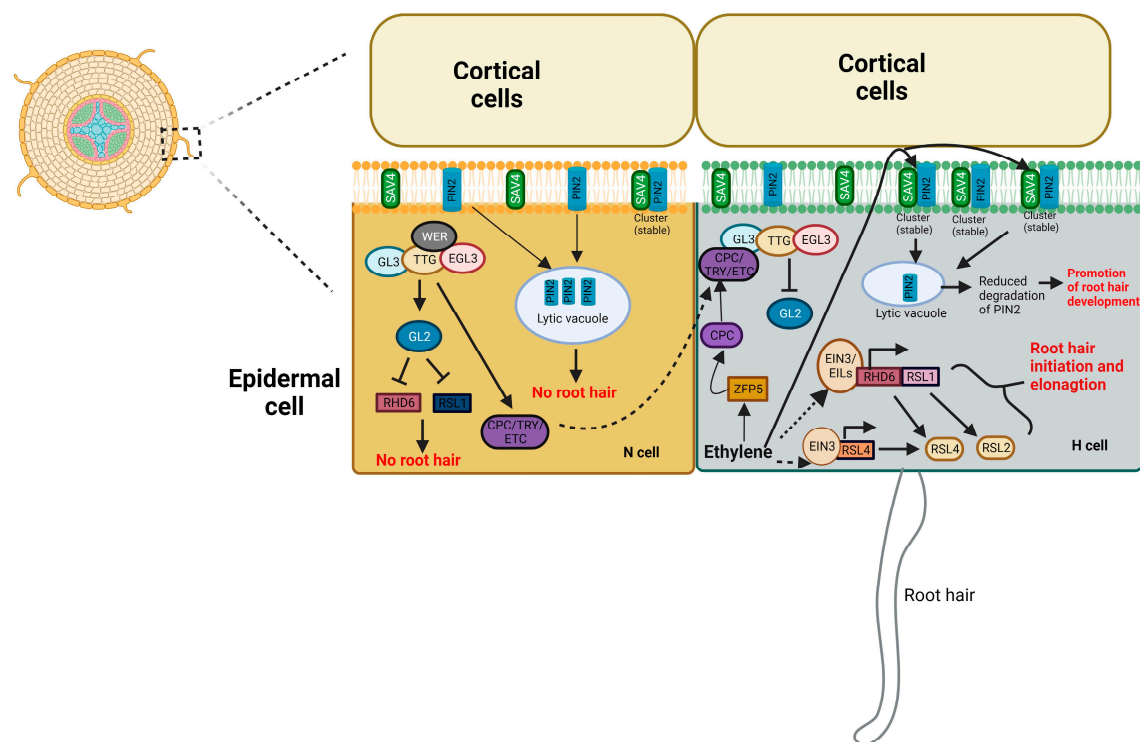


Figure 3. Role of ethylene in root hair development: In N-type cells ((Non-hair), of the epidermis of the root, a transcription complex consisting of WEREWOLF (WER), GLABRA3 (GL3), ENHANCER OF GLABRA3 (EGL3), and TRANSPARENT TESTA GLABRA (TTG) known as WER-GL3/EGL3-TTG induces the expression of GLABRA2 (GL2) and CAPRICE (CPC). GL2 is responsible for determining the differentiation of N-type cells, and the hormone ethylene inhibits the transcription of GL2 in these cells. GL2, in turn, suppresses the expression of ROOT HAIR DEFECTIVE 6 (RHD6) and RHD6 LIKE1 (RSL1), which are positive regulators of root hair initiation and elongation. RHD6 and RSL1 promote the expression of RSL2 and RSL4, which further stimulate root hair elongation by upregulating genes responsible for elongation. CPC can move laterally from N-type cells to neighboring H-type (Hair cell) cells of the root's epidermis. CPC competes with WER for binding to the GL3/EGL3-TTG complex in H-type cells. Additionally, CPC, along with functionally redundant homologs TRIPTYCHON (TRY) and ENHANCER OF TRY AND CPCs (ETC1), inhibits the expression of GL2, which regulates the differentiation of H-type cells. ETH promotes the transcription of CPC by involving the transcription factor ZINC FINGER PROTEIN 5 (ZFP5). CPC, TRY, ETC1, TTG, GL3, and EGL3 collectively work to suppress the expression of GL2 in H-type cells. Furthermore, EIN3/EIL1 can form a complex with RHD6/RSL1, promoting root hair initiation. EIN3 also binds to the promoter region of RSL4, enhancing its transcription and promoting both root hair initiation and

elongation. In addition, ethylene has a regulatory role in root hair development by affecting SAV4 (SHADE AVOIDANCE 4, regulator of auxin transport). SAV4 is responsible for managing the levels of PIN2 (PIN-FORMED2) proteins on the cell membrane, ensuring their stability and preventing degradation in the vacuole. Ethylene treatment boosts SAV4 levels, resulting in an increase in PIN2 proteins on the cell membrane. SAV4 interacts with PIN2 through PIN2HL, potentially promoting these proteins' clustering and maintaining their stability on the membrane. This process encourages the downward movement of auxin, ultimately leading to the growth of root hairs.

4.4. Fruit ripening

Ethylene plays a crucial role in the regulation of fruit ripening by orchestrating the expression of genes involved in various biological processes. These processes encompass pigment accumulation, respiration, ET production, texture change, and the overall enhancement of fruit quality traits [77]. Excess ET production is chiefly associated with transcriptional upregulation of ET biosynthesis genes (*ACS* and *ACO*). Until now, 14 *ACS* genes were identified in the *S. lycopersicum*, among these, *ACS2* and *ACS4* showed important fruit ripening functions [78]. Through genome-wide identification, six *ACO* genes have been identified in *S. lycopersicum*. Interestingly, during the pre-ripening stages, the expression levels of all *ACO* genes remain undetectable. However, during the ripening process, *ACO1* and *ACO2* demonstrate high expression levels, while *ACO4* exhibits a gradual and slight increase in expression. The undetectable transcript level of *ACO3*, *ACO5*, and *ACO6* at ripening suggests the least role in climacteric ET production [77]. During the climacteric stage, there is a well-known transition from system 1 to system 2, which is accompanied by a remarkable upregulation of *ACS2*, *ACS4*, *ACO1*, and *ACO4*. This upregulation leads to positive feedback regulation. In *S. lycopersicum*, the expression of *ACS1A*, *ACS3*, *ACS6*, *ACO1*, and *ACO4* is associated with system 1 of ethylene production, while the expression of *ACS2*, *ACS4*, *ACO1*, and *ACO4* is associated with system 2 [10,79].

In contrast to climacteric fruits, such as *Solanum lycopersicum*, *Fragaria x ananassa* (strawberry), being non-climacteric, do not rely on ET for the initiation and maintenance of the ripening program [80]. However, the measurement of ACC revealed that it is present in large quantities as strawberries progress towards the stages of fruit ripening. ACC accumulation in strawberry directly indicates higher expression of *ACS* genes. According to the expression analysis, the genes *FaACS1* and *FaACS26* exhibited ripening-specific expression in the receptacle tissues of strawberries. On the other hand, the genes *FaACS17*, *FaACS21*, *FaACS19*, and *FaACS23* were considered as ripening-induced genes specific to the achenes. It is worth noting that certain *ACS* genes, including *FaACS27* and *FaACS29*, displayed strong expression during the developmental stages of achenes, ranging from the green achene stage to the white achene stage suggesting strong association of ET with fruit ripening [81].

Shan et al., [82] discovered the mechanism that maintains a balance of *MaNAC2*, *MaACS1*, and *MaACO1* levels in *Musa acuminata*. *MaNAC1* and *MaNAC2* act as suppressors of *MaERF* expression, which is recognized for its inhibitory effect on the genes involved in ET biosynthesis, namely *MaACS1* and *MaACO1*. A RING E3 ligase *MaXB3* interacts with *MaNAC2* and facilitates its ubiquitination mediated degradation. This process inhibits the transcriptional repression mediated by *MaNAC2*. In addition, *MaXB3* also targets for proteasome degradation. Collectively, these findings unveil a regulatory cascade involving *MaXB3*, *MaNACs*, *MaERF11*, and *MaACS1/MaACO1* that controls ET biosynthesis during ripening in bananas. *MaNAC1* and *MaNAC2* repress *MaXB3*, creating a feedback mechanism in the cascade. Figure 4 shows the summary of the fruit ripening process.

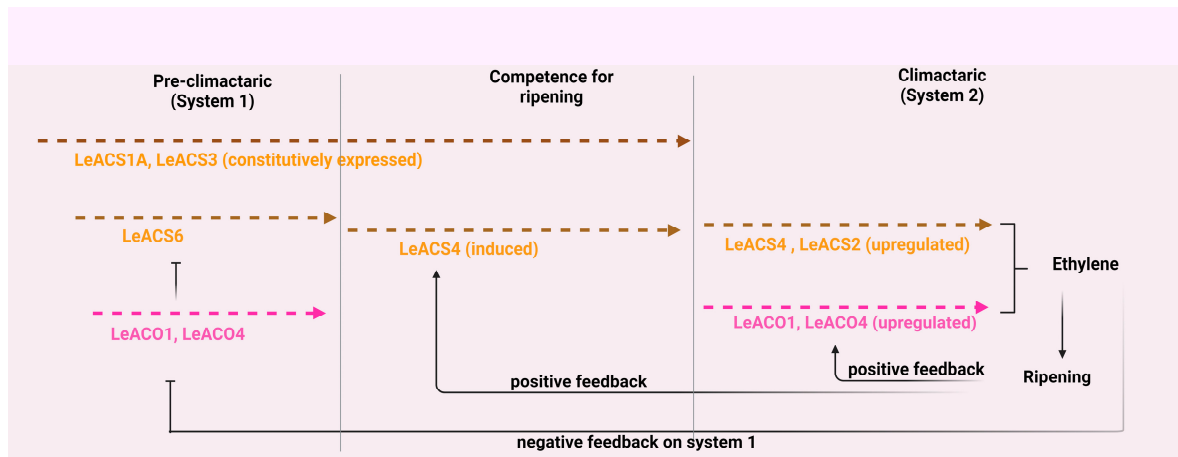


Figure 4. Fruit ripening: In *Solanum persicum* (tomato) fruit, the pre-climacteric phase involves system 1 ethylene response, which is likely controlled by continuously active genes, *LeACS1A* and *LeACS3*, along with negatively regulated *LeACS6* genes, which interact with existing *LeACO1* and *LeACO4* mRNAs. As the fruit reaches competence, the expression of *LeACS1A* and *LeACS6* is delayed, while *LeACS4* expression is induced. Upon entering the climacteric stage, there is a transition to system 2, characterized by a significant increase in *LeACS2*, *LeACS4*, *LeACO1*, and *LeACO4* mRNA levels due to positive feedback regulation. This surge in ethylene production leads to negative feedback on system 1, resulting in balanced ethylene production during the climacteric stage.

4.5. Chloroplast development

When seeds start to sprout in conditions lacking light, they activate a specific developmental program called skotomorphogenesis. In the case of plants like *Arabidopsis*, which undergo hypogeal germination (germination below the soil surface), an enhancement in the length of the hypocotyl (the embryonic stem) occurs due to cell elongation. This elongation helps push the cotyledons against the mechanical pressure of the soil, allowing them to reach the light source. In the course of process, proplastids, the precursors to all plastids, undergo both proliferation and differentiation. This transformation leads them to become etioplasts within the cotyledon cells, thus preparing plants for photosynthetic apparatus during the dark-to-light transition [83]. Etioplasts have a semi-crystalline membrane cluster called the prolamellar body (PLB). This structure contains essential components for photosynthesis, including prothylakoid membranes, protochlorophyllide, and protochlorophyllide oxidoreductase, a light-dependent enzyme that transforms protochlorophyllide into chlorophyllide [83]. In *Arabidopsis*, phytochromes (phyA and phyB) influence seedling photomorphogenesis. Etiolated seedlings produce phytochromes in their inactive Pr form in the cytoplasm. When exposed to light, Pr converts to the active Pfr form and moves to the nucleus [84]. This light-induced transformation triggers the photoactivated phytochromes' degradation of certain bHLH transcription factors, known as PHYTOCHROME INTERACTING FACTORS (PIFs). PIF3 and its homologs PIF1, PIF4, and PIF5 play a key role in maintaining skotomorphogenesis and inhibiting light-induced chloroplast development [85].

Ethylene's regulatory functions hinge on two transcription factors, ETHYLENE-INSENSITIVE3 (EIN3) and ETHYLENE-INSENSITIVE3-LIKE1 (EIL1). During seedling emergence, the photomorphogenic regulator CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1) senses light fluctuations, while ET processes mechanical stress cues, collaboratively influencing EIN3 protein levels. In the nucleus transcription of *PhANGs* (*PHOTOSYNTHESIS ASSOCIATED NUCLEAR GENE*) is suppressed by PIFs in coordination with other protein EIN3. COP1, an E3 ligase, targets EBF1/2 for degradation, stabilizes PIF/EIN3 and degrades photomorphogenesis stimulating transcription factors like HY5 (ELONGATED HYPOCOTYL5) [86–88]. The perception of light by photoreceptors initiates chloroplast biogenesis and the shift toward photoautotrophic growth. Light causes a transformation in the structure of phytochrome (phy), converting it from an inactive state to an active nuclear form. This active form then initiates the degradation of the PIFs (PHYTOCHROME INTERACTING

FACTORS) [88]. Crucially, the photoreceptor phyB has directly influenced EIN3 in a light-dependent manner, promoting EIN3 degradation through enhanced interactions with EBF1/2 upon exposure to light [86]. When exposed to light, COP1 is prevented from entering the nucleus, and transcription factors like HY5 become more stable. Consequently, this leads to an upsurge in the expression of Photosynthesis-Associated Nuclear Genes (*PhANGs*) [88]. EIN3/EILs inhibits protochlorophyllide (Pchlde) biosynthesis through PIF3 and EIN3/EILs directly triggers the expression of *PROTOCHLOROPHYLLIDE OXIDOREDUCTASE A (PORA)* and *PORB* in the cotyledon safeguarding against photooxidative damage during de-etiolation [89,90]. The EIN3-PIF3 module significantly suppresses *LIGHT HARVESTING COMPLEX (LHC)* gene expression in darkness, preventing premature thylakoid membrane development. Overexpressing *LHC* genes in dark conditions leads to partially formed thylakoid membranes. This strict repression maintains the prolamellar body and safeguards against photooxidation upon exposure to light [91]. Thus, EIN3-PIF3 interdependence ensures proper etioplast-to-chloroplast development, enabling seedlings to adapt to changing environmental conditions during emergence. Thus, ethylene signaling oversees chloroplast development by preserving the correct levels of protochlorophyllide and PORA/PORB enzymes, thus preventing harmful photooxidative damage during de-etiolation. Figure 5 depicts the role of ethylene in chloroplast development.

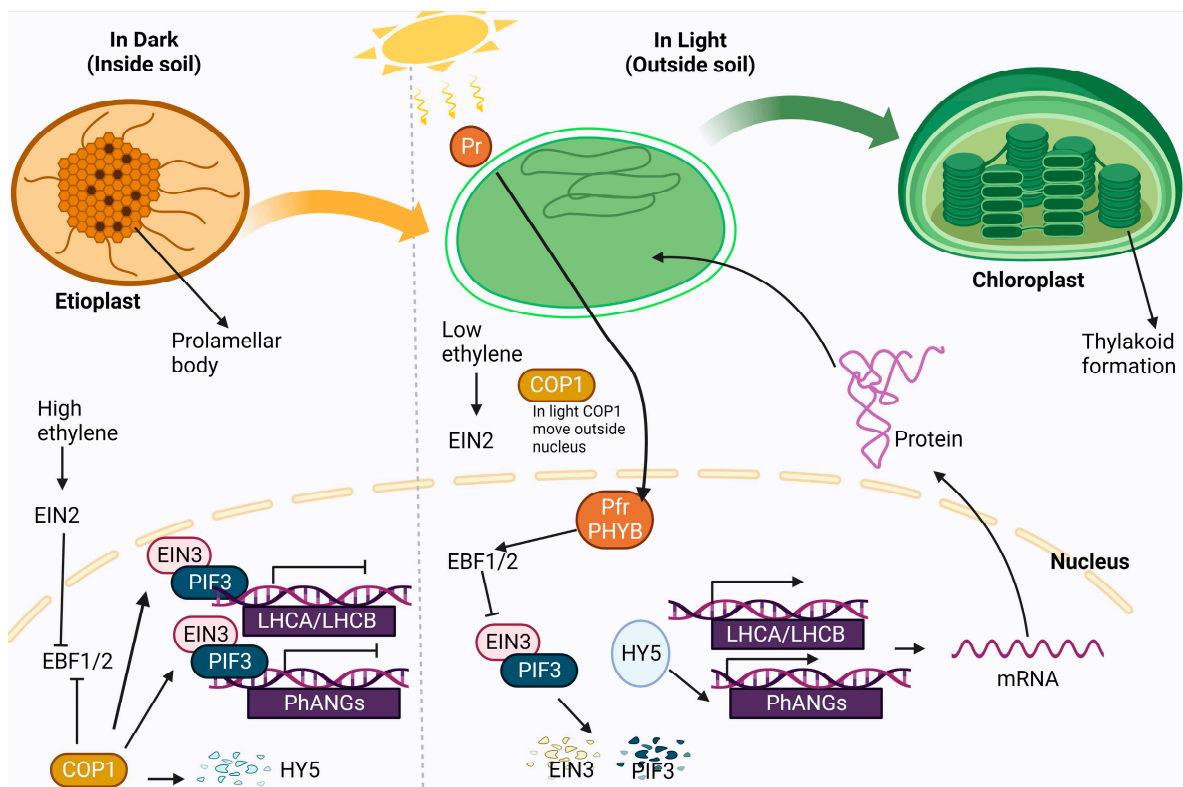


Figure 5. Role of ethylene in chloroplast development: During the early growth of seedlings in the dark underground, mechanical pressure triggers the production of a plant hormone called ethylene. This leads to an increase in the concentration of a protein called EIN3 in the nucleus of plant cells. EIN3 (ETHYLENE-INSENSITIVE3) and another protein called PIF3 (PHYTOCHROME INTERACTING FACTORS), which is stabilized in the dark, directly interact and bind to the promoters of *PhANGs* (PHOTOSYNTHESIS ASSOCIATED NUCLEAR GENE) and *LHC* (LIGHT HARVESTING COMPLEX) genes. This interaction strongly suppresses the expression of these genes and helps maintain prolamellar bodies in etioplasts. In the absence of light, a key photoreceptor called PHYB Pr remains inactive, and a regulatory protein called COP1 (CONSTITUTIVE PHOTOMORPHOGENIC1) becomes active. COP1 controls the levels of various proteins involved in plant development, including EBF1/2 (F-box protein), and it stabilizes PIFs and EIN3 while degrading transcription factors that promote photomorphogenesis, such as HY5 (ELONGATED HYPOCOTYL5).

When the etiolated seedlings emerge into the light, removing mechanical pressure reduces ethylene production and EIN3 levels. At the same time, light activates PHYB Pfr, which prevents COP1 from entering the nucleus. This, in turn, leads to the rapid degradation of PIFs and EIN3, promoting the transition of prolamellar bodies to thylakoid membranes and stabilizing transcription factors like HY5. Consequently, there is an increase in the expression of *LHC* and *PhANGs* genes involved in chloroplast maturation, facilitating the development of chloroplasts for photosynthesis.

4.6. Photosynthesis

Photosynthesis is the foundational production mechanism for life to thrive on our planet. This mechanism not only boosts carbon acquisition but also leads to the enhancement of both crop yield and overall quality. The intricate regulation of this process involves a diverse range of signals, from environmental stressors to the influential role played by phytohormones. These phytohormones are pivotal in governing photosynthesis across biochemical and physiological contexts, operating through varied molecular mechanisms. As a result, photosynthesis remains a highly dynamic and finely tuned process, shaped by many factors. Many factors affect photosynthesis like stomatal movement. Stomata play a pivotal role in managing the exchange of gases between the leaf's interior and the atmosphere by regulating turgor pressure in guard cells. These dynamic stomatal adjustments facilitate the precise assimilation of CO₂ during photosynthesis, all while mitigating water loss through transpiration. The regulation of stomatal responses by ET is characterized by its tendency to manifest dual and sometimes conflicting roles [49]. Ethylene induces stomatal closure in wild *Arabidopsis* by triggering H₂O₂ synthesis in guard cells, this process relies on NADPH oxidase AtrbohF. ETR1 mediates ethylene and H₂O₂ signaling in guard cells via EIN2 and ARR2-dependent pathway(s), identifying AtrbohF as a key mediator of stomatal responses to ET [92]. Ethylene-insensitive mutants (*etr1-1*) of *Arabidopsis* showed a smaller number smaller stomata as well as reduced stomatal conductance indicating ET influences the stomatal development process and also negatively affects stomatal conductance [53,93]. Also, another study showed that the application of exogenous ET enhances stomatal conductance, photosynthesis, and growth in *Brassica juncea* plants under optimal and deficient nitrogen fertilization [22]. A recent study showed the effect of ET on stomatal movement. Elevated CO₂ levels were observed to induce higher ET production in *Arabidopsis* rosettes. ACC-synthase octuple mutant, resulting in reduced ethylene biosynthesis, experiences disrupted stomatal responses triggered by elevated CO₂. Ethylene-insensitive gain-of-function receptor mutants (*etr1-1* and *etr2-1*) and signaling mutants (*ein2-5* and *ein2-1*) retain unaltered stomatal responses to CO₂ shifts. Conversely, ET receptor loss-of-function mutants (*etr2-3*; *ein4-4*; *ers2-3*, *etr1-6*; *etr2-3*, and *etr1-6*) demonstrate notably accelerated stomatal reactions to CO₂ changes. Further examination shows compromised stomatal closure in the ACC-synthase octuple mutant and hastened stomatal responses in *etr1-6*; *etr2-3* and *etr1-6* mutants, but not in *etr2-3*; *ein4-4*; *ers2-3* mutants. These findings imply the crucial roles of ET production and signaling elements in fine-tuning and expediting stomatal conductance responses to CO₂ and ABA [94]. A study explored the role of abscisic acid and ET in high relative air humidity triggers stomatal opening in *S. lycopersicum* leaves. Elevated relative humidity led to a slight decrease in ABA levels during darkness but significantly increased ET evolution. Ethepon enhanced conductance and stomatal aperture under moderate relative humidity, while amino-ethoxyvinylglycine (AVG) and ET receptor inhibition blocked stomatal opening during a shift to high relative humidity. Ethylene-insensitive mutant responses were reduced in high relative humidity conditions. Exogenous ABA spray countered conductance increase upon transferring to high relative humidity. These findings manifest that ET production and sensitivity play a role in high relative humidity-triggered stomatal opening in *S. lycopersicum* leaves [95]. Chen et al., [49] suggested that decreased responsiveness of older leaves to ABA and soil drying in terms of stomatal closure is probably attributed to the modified sensitivity of stomata to ET, as opposed to ET production.

According to Ceusters and Van de Poel [96], the impact of ET on photosynthesis is contingent upon the age of the leaves. In younger, non-senescent leaves, ET directly regulates the photosynthetic process, while in mature leaves, its influence is more indirect, primarily driving leaf senescence.

Studies on ethylene-insensitive mutant of Arabidopsis (*etr1-1*) and tobacco showed a decline in the overall photosynthetic capacity of young non-senescing leaves of the plant due to a reduction in the expression of crucial photosynthesis-associated genes like *CAB* (chlorophyll a/b-binding protein) and the small subunit of rubisco [97–99]. Grbic and Bleeker [99] found that in *etr1-1* mutants, there was a delay in the initiation of leaf senescence, which correlated with a postponement in the activation of senescence-associated genes. Furthermore, they observed elevated expression levels in genes associated with photosynthesis. When non-senescing leaves were treated with external ET, it reduced the expression of *CAB* and a subsequent decrease in chlorophyll content. These findings suggest that ET negatively regulates photosynthesis in non-senescing leaves, implying that a basal level of ET production and perception is necessary for normal photosynthetic function. In contrast, elevated levels of ET inhibit photosynthesis. In mature leaves prone to senescence, ethylene-insensitive mutants (*etr1-1* and *ein2-1*) and *S. lycopersicum* typically display increased chlorophyll content [99,100]. This implies that ET contributes to establishing appropriate chlorophyll levels in non-senescing leaves while promoting chlorosis by inducing chlorophyll degradation in mature leaves. These observations strongly imply ET participation in governing photosynthesis specifically in leaves that have not yet begun the senescence process. Also, when combining data from various surveys conducted on different species, it becomes evident that a species-specific regulation of photosynthesis is influenced by ET [96].

The process of photosynthesis transforms light energy into chemical energy. For this absorption of light energy by PSII and PSI is essential to facilitate electron transport and reduction of CO₂ in chloroplast. But sometimes excessive absorption can lead to photochemical damage due to excessive ROS generation. Plants employ protective mechanisms like non-photochemical quenching (NPQ) to prevent over-reduction of photosystems. Chen and Gallie [101], demonstrated that ET controls energy-dependent non-photochemical quenching in Arabidopsis by inhibiting the xanthophyll cycle. In the study it was observed that Arabidopsis *eto1-1* mutants, producing enhanced ET, exhibit reduced ability to convert violaxanthin to zeaxanthin due to impaired violaxanthin de-epoxidase activity. This leads to elevated reactive oxygen species production and increased photosensitivity in response to high light in these plants. Analyzing the intricacies of chlorophyll fluorescence through pulse-amplitude modulation fluorimetry, Kim et al., [102] have shed light on the impact of ET signaling mutations on photosystem II (PSII) activity in Arabidopsis. Specifically, their study uncovers that ET-insensitive mutants (*etr1-1*) exhibit diminished PSII activity in comparison to their wild-type counterparts. It is noteworthy to mention that *etr1-1* mutant lines, often used for ET-related investigations, can carry a consequential secondary mutation in *ACCUMULATION AND REPLICATION3* (a second mutation in *etr1-1* mutant of Arabidopsis responsible for producing premature stop codon in *ARC3*), prompting the need for supplementary corroborative lines of evidence, particularly in photosynthesis research. Ethylene signaling mutants derived from the *arc3* secondary mutation (*etr1-1sg*) also demonstrate reduced maximum quantum efficiency, prolonged chlorophyll fluorescence lifetime of PSII, and decreased quantum yield of PSII. According to Kim et al., [102], these findings underline the necessity of regular ET sensitivity for optimal photochemical efficiency of PSII, irrespective of any modifications in chloroplast structure resulting from the secondary *arc3* mutation. A study by Wulschleger et al., [103], showed that ET exposure reduces electron transport capacity in *Glycine max* by over 30% within 4 hours, leading to reduced CO₂ assimilation. This effect isn't tied to Rubisco activity decrease. Measurements also showed lowered efficiency of excitation energy capture in PSII after ethylene exposure. This impact was stronger under higher light levels, indicating possible photoinhibition's role in ethylene-induced CO₂ assimilation reduction. In addition, another study showed that overexpression of *CitERF13* in *Nicotiana* leaves, leads to a substantial decline in Fv/Fm, effective quantum efficiency of both PSI and PSII, apparent quantum yield, maximum rate of photosynthetic transport, however change in NPQ was less pronounced [104].

Available literature showed that ET also controls the dark reaction of photosynthesis. Tholen et al., [97], demonstrated that as vegetative plants of tobacco were cultivated under varying atmospheric CO₂ concentrations, an inverse relationship was observed between glucose concentration within

leaves and the expression of the rubisco gene. This repression of gene expression was distinctly amplified by heightened glucose levels in plants insensitive to ethylene. The insensitivity to ET led to equivalent nitrogen allocations in light harvesting while experiencing diminished levels in electron transport and Rubisco. This, in turn, resulted in a noticeably diminished photosynthetic capacity in ethylene-insensitive transgenic *Nicotiana* plants compared to the wild type. These findings imply that the lack of ET perception enhanced the plants' vulnerability to glucose, potentially due to escalated ABA concentrations. Ultimately, this increased susceptibility to endogenous glucose detrimentally affected rubisco content and affected these plants' carboxylation process and overall photosynthetic capacity. A similar decrease in the photosynthesis of *Arabidopsis etr1* mutant was observed due to a decline in the content of rubisco protein and expression level. Another study observed that overexpression of *CitERF13* in tobacco leaves decreases the maximum rate of rubisco carboxylase activity [104]. However, it was recorded that ethephon (ethylene releaser) treatment to ET-sensitive *Brassica juncea* plants increases rubisco activity, stomatal conductance, and net photosynthesis compared to ET-insensitive plants. These results showed that ET sensitivity influences the photosynthesis of *B. juncea* plants [105]. Also, on evaluation of the influence of ethephon treatment on photosynthesis of two *B. juncea* cultivars that contrast in their photosynthetic capacity, it was recorded that in both cultivars, alterations in net photosynthesis (Pn) resulted from effects on stomata and mesophyll. Ethephon-induced Pn was linked to ET emission. The high-capacity cultivar Varuna displayed a weaker ethephon response than the low-capacity RH30. RH30's low Pn was attributed to minimal ET. Enhancing RH30's ethylene levels could boost its lower photosynthetic capacity and increase Pn [106]. Ethylene affects Rubisco activases (RCAs), making carboxylation regulation more complex. RCAs are Rubisco chaperones. Also, it was recorded that ethephon treatment increases carbonic anhydrase (CA) activity in *B. juncea* plants, helping maintain chloroplast pH and reducing photorespiration [52]. Nevertheless, reports observed that ET at specific concentration increases photosynthesis and its related attributes, beyond that concentration it shows inhibitory effect. Thus, can be inferred that effect of ET is concentration and sensitivity of species under study dependent [19,106]. In a study, *Never ripe (Nr)* *S. lycopersicum*, which carry a loss-of-function mutation in the ET receptor SLETR3, exhibited a higher rate of carbon assimilation relative to their wild-type counterparts. Importantly, there were no significant differences in stomatal conductance or chlorophyll parameters between *Nr* and wild-type plants. The heightened photosynthetic rates in *Nr* plants resulted in increased levels of glucose, fructose, idose, mannose, and myo-inositol during midday, while ribose levels decreased in *Nr* plants. These findings proposed that the enhanced carbon assimilation, elevated sugar levels, and overall growth improvement in *Nr* plants are most likely due to increased enzymatic activity in the Calvin cycle [25]. In summary, it can be deduced that maintaining basal levels of ET synthesis and signaling is essential for the normal regulation of rubisco levels. However, elevated ethylene levels tend to inhibit carbon fixation in most plant species.

4.7. Senescence

Leaf senescence is highly programmed, regulated, and also a degenerative process. It is characterized by chlorophyll breakdown and degradation of macromolecules [107]. Studies reported increased ET production in senescent leaves with higher transcription rates of ET biosynthesis genes ACS and ACO [108]. On the stark, Octuple mutant of ACS genes showed a delayed senescence response [109]. Nevertheless, recorded literature also showed that its impact on growth and senescence processes varies depending on factors such as its concentration, timing of application, and the specific plant species involved [19,54].

Study revealed that EIN2 plays a role in regulating leaf senescence partially via microRNA164 (*miR164*) and *ORESARA1* (*ORE1*, also named *ANAC092* or *NAC2*)[110]. A recent study showed that EIN3 and ORE1 are able to directly regulate the expression of *CHLOROPHYLL CATABOLIC GENES*(CCGs), *NONYELLOWING1* (*NYE1*, also known as *STAY-GREEN1*, *SGR1*), *NONYELLOW COLORING1* (*NYC1*) and *PHEOPHORBIDE A OXYGENASE* (*PAO*), thereby initiating chlorophyll breakdown during leaf senescence [111]. Yu et al., [112], it was demonstrated that WRKY71 has the ability to directly enhance the expression of ethylene signaling pathway genes EIN2 and ORE1.

Additionally, it promotes ethylene synthesis by directly stimulating ACS2, thereby accelerating leaf senescence in Arabidopsis. Petal senescence is another phase in flower developmental continuum accompanied with tissue differentiation, petal maturation, and finally the growth and development of seeds coordinated by plant hormones [113]. Reports conducted so far indicate close association of ET production with senescence in the carnation flower. During natural senescence early expression of ACS and ACO in gynoecium than in petals clearly indicates that ET is firstly produced in gynoecium followed by petals [114]. Moreover, removing gynoecium prevents increased production of petal ET and significantly prolongs the flower's life [115,116]. Expression analyses of ACS and ACO in the floral organs of *Dianthus caryophyllus*, *Petunia*, *Solanum lycopersicum*, and *Rosa hybrida* have been performed [117–120]. Differential regulation of expression has been observed for three cloned ACS genes, namely *DcACS1*, *DcACS2*, and *DcACS3*, in *Dianthus* flowers [121]. Okamoto et al., [112] revealed the differential expression of ACS and ACO genes in *Delphinium grandiflorum*. In this study, ET generation in the receptacle showed a significant increase during natural senescence, while the gynoecium exhibited only a slight enhancement in ET production. Ethylene application at low concentrations could triggers the expression of *DcACS* and *DcACO* in the short-lived varieties but not in the long-lived varieties of *Dianthus* flowers [123]. The report in *Rosa hybrida*, claimed that *RhACO1* was significantly correlated with vase life and ET sensitivity among 33 cultivars [124]. Although several transcription factors have been found to have favorable effects on ET biosynthesis, it is still unclear how the ACS and ACO genes are regulated. A study reported that upregulation of *PLMYB308* (MYB transcription factor gene) is associated with ET application in herbaceous ponies. The gene silencing approach of *PLMYB308* revealed delayed flower senescence as well as a dramatic increase in GA with reduced ET and ABA levels in petals [125]. Figure 6 summarizes the senescence process.



Figure 6. Senescence process: WRKY71 is a senescence-associated gene induced by ethylene. WRKY71 is able to activate ethylene synthesis by directly upregulating ACS2, thus WRKY71 and ACS2 form a positive feedback loop and promote senescence by activating downstream genes.

4.8. Abscission

Shedding plant organs such as seedpods, leaves, floral organs, and fruits by detaching them at the abscission zone is called as abscission [126]. Developmental and environmental changes can trigger abscission in plant and is mainly subjected to the crosstalk between two plant hormones, ET and auxin [127]. Ethylene regulate the gene expression pattern of enzymes involved in cell separation like cellulases and pectinases [128]. Before abscission occurs, auxin is transported to the abscission zone to inhibit ET sensitivity in the cells. When abscission takes place, the organs undergoing abscission release ET, which is then followed by the detachment of leaves [129]. Ethylene present in the abscission zone initiates a signal transduction pathway that results in the activation of transcription factors and genes responsive to ET [130] which inture regulate abscission. In addition, the induction of ethylene production by methyl jasmonate was identified as the cause of fruit abscission in 'Hamlin' and 'Valencia' orange varieties [131]. For uniform ripening external ET application is practiced for promoting abscission in fruit crops. On the other hand, 2-aminoethoxyvinyl glycine (AVG), ET biosynthesis inhibitors are used to reduce abscission before harvest. Vesicle transport pathways genes in of ethylene-induced AZ-C (calyx abscission zone) cells and adjacent FR (fruit rind) cells are responsible for citrus fruit abscission [132]. Hence, it appears that coordination between hydrolytic enzymes and ET production consequently leads to organ abscission in plants. The key ET biosynthetic enzymes ACS and ACO are found to be highly expressed during organ abscission which facilitates ET production followed by activation of genes

encoding cell wall remodelling enzymes [133,134]. Pollination upregulated *SlACS2* gene in *S. lycopersicum* [119]. In *Petunia*, pollination leads to 20-fold increase in ET production autocatalytically from the stigmas contributing to wilting and eventually abscission [54,135]. Few studies have analyzed ACS and ACO expression in flowers displaying petal abscission. The expression of ACS and ACO genes in *Pelargonium* flowers has been partially assessed using RNA gel blot analysis. It has been observed that in ET-sensitive flowers, the application of exogenous ET and pollination can expedite sepal abscission in *D. grandiflorum*. cKNAT1, a KNOTTED-LIKE FROM ARABIDOPSIS THALIANA1 (KNAT1)-like protein from *Litchi chinensis*, controlling abscission by influencing production of ethylene. In vitro and in vivo assays showed that LcKNAT1 hinders the expression of *LcACS/ACO* genes by directly binding to their promoters and delaying abscission in *Litchi chinensis* [136]. Nonetheless, it is essential to comprehensively clarify the interaction between ethylene and other hormones like auxin and gibberellins (GAs) to gain a better understanding of abscission.

5. Conclusions

In summary, ET is a remarkable and versatile plant hormone, wielding significant influence across a spectrum of plant developmental and physiological processes. It plays a pivotal role in a plant's life cycle, including cell division, elongation, leaf growth, senescence, abscission, flower and fruit development, chloroplast maturation, and photosynthesis regulation. As our comprehension of ET involvement in plant development deepens, the potential for leveraging its properties to enhance crop performance and stress resilience becomes increasingly evident.

Ethylene's capacity to finely regulate growth and development, modulate responses to environmental challenges, and control the maturation of fruits and flowers holds substantial promise for agriculture and food security, particularly in the face of a changing global climate. Nevertheless, it's worth noting that the specific mechanisms underlying ET regulation of photosynthesis, a fundamental process, remain largely unexplored. Investigating the downstream ET-responsive transcription factors governing photosynthesis-related gene expression is essential. Additionally, understanding the intricate interplay between ET and other plant hormones in orchestrating growth and development is crucial. Deciphering the cross-talk between ET and other phytohormones and their synergistic or antagonistic effects could offer valuable insights and open up opportunities for precise manipulation of these hormone profiles through molecular techniques to elicit desired plant responses.

In the years to come, ongoing research into ET multifaceted role is likely to unveil novel avenues for steering plant growth and development, ultimately contributing to the advancement of sustainable agriculture and addressing the challenges posed by a rapidly changing climate. The captivating narrative of ethylene in the realm of plant biology remains far from complete, offering a wealth of prospects for scientific discovery and practical application.

Author Contributions: Conceptualization, S.K. and N.A.K.; validation, N.A.K.; writing—original draft preparation, S.K. and A.F.A.; writing—review and editing, N.A.K.; visualization, S.K.; supervision, N.A.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflicts of interest.

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