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Review

Role of Ethylene in the Regulation 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. The presence of ethylene has been noted in different plant parts, including the stems, leaves, flowers, roots, seeds, and fruits. This review aims to provide a comprehensive overview of the regulatory impact of ethylene on pivotal plant developmental processes, such as cell division and elongation, senescence, abscission, fruit and flower development, root hair formation, chloroplast maturation, and photosynthesis. The review also encompasses ethylene biosynthesis and signaling: a snapshot of the regulatory mechanisms governing ethylene production. Understanding of the impact of ethylene's regulatory functions on plant developmental processes has significant implications for agriculture, biotechnology, and our fundamental comprehension of plant biology. This review underscores the potential of ethylene 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

Citation: Khan, S.; Alvi, A.F.; Khan, N.A. Role of Ethylene in the Regulation of Plant Developmental Processes. *Stresses* **2024**, *4*, 28–53. https://doi.org/10.3390/stresses4010003

Academic Editors: Magda Pál, Luigi Sanita' di Toppi and Mirza Hasanuzzaman

Received: 17 September 2023
Revised: 27 October 2023
Accepted: 30 October 2023
Published: 8 January 2024

1. Introduction

Plant development is influenced by several intrinsic and extrinsic factors that coordinate to regulate all processes in the life cycles of plants. Plant growth is one carefully regulated process that occurs throughout the vegetative phase. Plant growth regulators act as regulators of plant developmental processes and are crucial for the resilience of responses under stress. Ethylene (ET) is a versatile hormone involved in development, metabolism, and stress responses in plants. Researchers have shown manifold roles of this hormone in the development of plants, as a signaling agent, in leaf development, in senescence, in fruit ripening, in the promotion of germination, etc. ET is the second most fundamental unsaturated hydrocarbon. It exhibits peculiar dose-dependent actions 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]. Plants growing in compacted soil experience excessive accumulation and concentration of ET in root tissues, resulting in root growth inhibition [4]. Increasing evidence confirms that ET is crucial in plant architecture. In *Zea mays*, *ACS7* (*1-aminocyclopropane-1-carboxylic acid synthases 7*) mutation brought about a dwarf phenotype with a larger leaf angle on *Sdw3* (*semi-dwarf3*) due to increased ET synthesis [5].

ET plays a central role in the growth and development process, starting from seed germination to senescence. However, complex crosstalk between phytohormones like abscisic acid (ABA), gibberellin (GA), cytokinin, and auxin regulates the responses sometimes antagonistically or synergistically [6,7]. ET biosynthesis or signaling mutant showed differential responses to hormonal sensitivity and plant developmental processes. For

example, *ethylene overproduction 3* (*eto3*) and *constitutive triple response 1* (*ctr1*) mutants correspond to ABA insensitivity, whereas *ethylene receptor 1* (*etr1*), *ethylene-insensitive 2* (*ein2*), and *ethylene-insensitive 6* (*ein6*) show enhancement of ABA sensitivity [8]. The faulty hook formation in ET-insensitive mutant *ein2* signifies the prominence of ET-mediated auxin biosynthesis for hook development and regulation [9]. Moreover, EIN3 synchronizes the expression of chlorophyll biosynthesis genes *PORA/B* (*PROTOCHLOROPHYLLIDE OXIDOREDUCTASE A/B*) [10]: the pigment-binding proteins LHC which are essential for photosynthesis initiation. EIN3/EIL1 chiefly regulates ethylene signaling responses, thereby tuning the range of transcriptional regulation depending on spatiotemporal and environmental conditions [11]. Exogenous application of ET has been found to increase the number of lateral roots, root fresh weight, and mineral content in the root and shoot system, along with the upregulation of auxin biosynthesis and transportation genes [12]. In addition, ET has a significant effect on flower development and sex differentiation. *ACS* gene family has been widely studied and characterized for its potential function in sex determination [13] Fruit ripening is another ET-dependent process associated with multiple biological events like respiration, pigment accumulation, ET production, change in texture, and overall building up of fruit quality traits. ET activity participates in gene expression responsible for the aforementioned changes during ripening [14].

Importantly, ET is produced in response to various biotic and abiotic environmental stimuli, indicating that it connects environmental change and developmental adaptation [15–17]. Thus, under both normal and adverse conditions, ET confers plant growth and development. Moreover, ET's role in postharvest fruit and vegetable management, impacting quality and shelf life, has been extensively explored through biochemical, technological, molecular, and metabolomic investigations. Recent reviews reveal its diverse and crucial functions, tailored to specific fruits and vegetables, making it essential to understand and control ET effects for different postharvest products [18–20]. Considering ET's importance, we have tried to assemble the literature on recent advances and molecular insight into ET-mediated responses in regulating different phases of the plant life cycle. The research on ET's role in plant processes has increased in recent years and reviews have also been published [6,21–24]. The previously published reviews predominantly focused on individual developmental processes regulated by ET like root hair development, senescence, germination, abscission, and fruit ripening. However, this review presents a holistic and all-encompassing view of the diverse ET-regulated processes within a single comprehensive framework. This approach provides a unified perspective, consolidating insights from various specialized reviews, which can help researchers to gain a more thorough understanding of ET's effect on plant growth and development. With the overview of ET synthesis, signaling, and regulation of its biosynthesis, the details on ET-regulated processes are explained in the following areas: cell division and elongation, leaf and flower development, root hair development, fruit ripening, chloroplast development, photosynthesis, senescence, and abscission.

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) [25]. 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 [26]. Under normal basal ET production levels, ACS is believed to control the rate-limiting step in biosynthesis [25]. Nevertheless, specific circumstances can lead to ACO becoming the limiting factor [27]. Figure 1a illustrates the biosynthesis of ET.

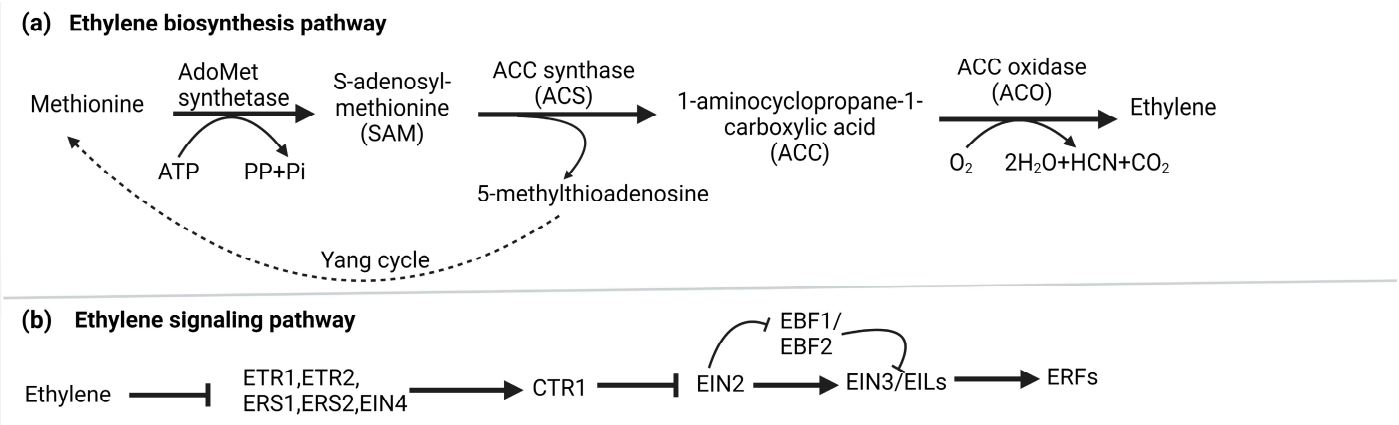

Figure 1. (**a**) Biosynthesis of ethylene: In higher plants, ethylene is produced through the Methionine/Yang cycle. This involves converting methionine into 1-aminocyclopropane-1-carboxylic acid (ACC) using ACC synthase (ACS), and then ACC is further converted into ethylene by ACC oxidase (ACO). The 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 EIN2s 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 EIN2s 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.

The canonical ethylene signaling pathway begins when ethylene binds to ER-localized receptor proteins, such as ETHYLENE RESPONSE 1 (ETR1), ETHYLENE RESPONSE 2 (ETR2), ETHYLENE-INSENSITIVE 4 (EIN4), ETHYLENE RESPONSE SENSOR 1 (ERS1), and ERS2 in Arabidopsis, organized into two subfamilies defined by their ET binding and histidine kinase domains. Without ET, these receptors activate CONSTITUTIVE TRIPLE RESPONSE (CTR1), a Ser-Thr protein kinase on the ER membrane, which phosphorylates ETHYLENE-INSENSITIVE 2 (EIN2) 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 [28]. Similarly, ETHYLENE-INSENSITIVE 3 (EIN3) is subject to ubiquitin-mediated proteasomal degradation, guided by F-box proteins EBF1 and EBF2, thereby inhibiting ET responses. ET binds to its receptor when it is present, facilitated by copper ions from RESPONSIVE-TO-ANTAGONIST (RAN1). This binding deactivates CTR1, leading to the dephosphorylation and cleavage of EIN2-CEND [29]. 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 or EIL (EIN3-LIKE) transcription factors, culminating in the transcription of ET-responsive genes [30]. Furthermore, an alternative non-canonical signaling pathway has been suggested, which encompasses the regulatory proteins AHP (histidine-containing phosphotransfer proteins) and ARR (response regulator proteins) [31]. Figure 1b represents the summary of the process.

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 pivotal enzymes' 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* genes, which exhibited distinct expression patterns in plants. Notably, four specific *ACS* genes in *S. lycopersicum* were pivotal in

orchestrating the shift from autoinhibitory to autocatalytic ET production during fruit ripening [32]. Leading the charge as the initial regulator of *ACS* expression was the MADS-box transcription factor SlRIN, which directly bolstered the expression of selected *S. lycopersicum ACS* genes [33]. Over the years, numerous other transcription factors have emerged as key players, promoters, and inhibitors of *ACS* gene expression, influencing diverse growth processes. However, there is also supporting information suggesting that ET itself can directly influence ACS transcription. For instance, the ET response factor SlERF2/TERF2 of *S. lycopersicum* interacts with the promoter of *NtACS3*, thereby stimulating its expression [34]. 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 [35]. Mutations in the phytochrome genes *PHYA* and *PHYB* have been found to affect ET biosynthesis, with *phyA* mutants displaying a more pronounced increase 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 [35].

Much like their ACS counterparts, *ACO* genes are subject to transcriptional regulation. Notably, the *S. lycopersicum* HD-ZIP transcription factor SlHB-1 and the ripening regulator RIN directly stimulate *ACO* gene expression. Across various species, different classes of transcription factors have also been shown to regulate *ACO*. Interestingly, ET can directly control *ACO* expression through intricate feedback mechanisms mediated by ERF (ethylene response factor) proteins [36]. 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 treatment of light-grown seedlings. During phases of ripening or stress, when ACS activity is maximum, 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 [35].

Transcriptional regulation of ET biosynthesis is complemented by posttranslational modifications of 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 (ACS7). 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 [36]. 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 [37]. Light-triggered posttranslational regulation of type-2 ACSs, especially ACS5, regulating hypocotyl elongation during the dark-to-light shift [29]. 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 [38]. PP2A, a regulatory component, plays a role in posttranslational ACS stability regulation. PP2A-mediated dephosphorylation negatively affects ACS6 protein stability in the dark [39]. 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 2a). Protein Phosphatase 2C family members (PP2C's) also play a role in stabilizing ACS7 [36].

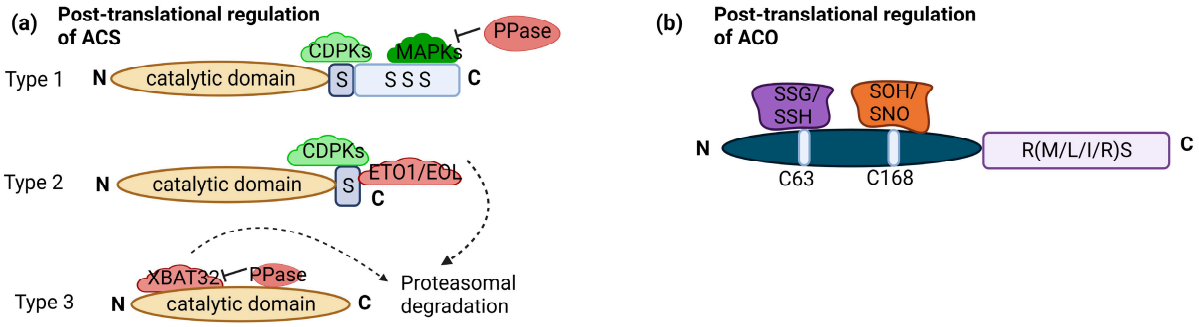

Figure 2. Posttranslational regulation of ACS and ACO: (**a**) ACS enzymes can be categorized into three groups based on their phosphorylation sites: type 1 with both CDPK (calcium-dependent protein kinase) and MAPK (Mitogen-activated protein kinase) sites, type 2 with only CDPK sites, and type 3 with 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. (**b**) 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-sulfhydration (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 figure is based on and modified from [36]. Dotted arrow—multistep pathway; solid arrow—promotion; flat-head arrow—inhibition.

While much is known about the posttranslational regulation of ACS, research on the posttranslational regulation of ACO has been comparatively limited. It is 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-sulfhydration (SSH) at cysteine (C63), S-sulfenylation (SOH), and S-nitrosylation (SNO) at C168. These modifications are recorded only in type 1 ACO (Figure 2b). Recent studies have highlighted the significance of these modifications in controlling ACO activity and structural stability [36].

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 [40,41].

4.1. Cell Division and Elongation

The role of ET in cell division is complex. Ethylene 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 and 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 the cell's expansion in the hooks convex side contributing to its curvature [42]. Additionally, ET has been found to control cell division rate in vascular tissue, promoting vascular cell differentiation. Mutants 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 stem [43]. 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 out that it does not directly affect mitotic activity in the root. However, it is important to note that ET modulates cell division within the quiescent center, developing additional columella layers in the root cap [44,45]. 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 [46]. 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 [47]. Ethylene regulates RAM size through the canonical pathway involving CTR1, EIN2, and EIN3/EIL, and an alternative pathway with ARR1. This highlights ET's complex role in controlling root apical meristem size and proliferation [48].

The impact of ET on leaf cell division is context-dependent. Under environmental stress, particularly when plants experience less than 10 h 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. Notably, this cell cycle arrest operates independently of the EIN3 transcriptional control [49]. Cell cycle inhibition by ET in leaves is multifaceted; ET accumulation activates BOLITA, an ERF, activating type II *TCP* (*TEOSINTE BRANCHED 1/CYCLOIDEA/PCF*) genes [50]. 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 [51]. 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 [51,52]. 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 the hyponastic phenomenon [53]. 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 (CMTs) perpendicular to the growth axis [54]. Ethylene rapidly alters CMT orientation in Arabidopsis roots and hypocotyls, inhibiting cell elongation and promoting radial swelling within 10 min [54]. Conversely, ET induces petiole elongation in well-lit conditions by reorienting CMT from longitudinal to transverse in abaxial cells [55], excluding adaxial cells. In ET-regulated cellular elongation, expansins (EXP) and xyloglucan endotransglycolases/hydrolases (XTH) play pivotal roles. ET induces *EXP* expression in Arabidopsis, influencing root hair formation and submergence–escape elongation [54]. However, in Arabidopsis leaf with elevated *EIN2* expression, *EXP3*, and *EXP5* expression was reduced, while in *ein2* knockout plants, these genes were upregulated. Additionally, the expression of *EXP1* and *EXP5* was significantly suppressed in dwarfed *BOLITA* (ERF) gain-of-function plants [50,56]. These findings demonstrated a tissue-specific linkage between ET and ex-

pansins in the regulation of cell elongation. Ethylene regulates *XTH* expression during root hair initiation and submergence-induced hyponastic responses [54]. A report showed that ET serves as a negative regulator of cell elongation in the primary root of Arabidopsis by impeding the uptake, accumulation, and distribution of gibberellic acid in the endodermis of the elongation zone [57]. 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 [47].

4.2. Leaf Growth and Flower Development

Ethylene overproduction in Arabidopsis resulted in dwarfed plants with reduced growth [58,59]. Accordingly, when positive regulators of the ET signaling pathway in plants were mutated, these plants exhibited rosette leaves compared to control plants. Mutation of the endoplasmic reticulum (ER)-anchored protein EIN2, for instance, has been linked to increased growth [56]. On the contrary, mutations in components that inhibited ET signaling, like the receptors ETR1 and ERS1, resulted in stunted growth. Furthermore, when the negative regulators *ARGOS* or *ARGOS-LIKE* (*ARL*) were excessively expressed, it promoted leaf growth in Arabidopsis [60,61]. Another relevant study states that certain rhizosphere bacteria enhance plant growth by expressing *ACC-DEAMINASE*, reducing ACC levels in stressed plants [62]. However, lower concentrations of ET have been reported to promote leaf growth. For instance, *Poa alpina* and *Poa compressa* showed increased leaf elongation rates [63], and the primary leaves of *Helianthus annuus* were enlarged following ET exposure [64]. However, the effect was altered by increasing ET concentration. Furthermore, studies also showed that the application of ethephon increased the leaf area [65,66]. Certain reports also observed no change in the leaf area of ET-insensitive Arabidopsis, *Nicotiana*, and *Petunia* relative to ET-sensitive plants [67]. Thus, it can be inferred that the effect of ET on leaf growth and development was influenced by the concentration of ET used and the specific plant species under investigation [7,41].

The regulatory mechanism of sex determination in plants represents a model experiment system in the case of unisexual plants [68]. Considerable focus has been directed towards identifying 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, ET emerged as a prominent regulator of unisexual flower development [69]. 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 [70]. *ACO2* has also been demonstrated to impact the formation of unisexual flowers by collaborating with *ACS11* to promote the selective production of ET in the floral region; dysfunctional *ACO2* results in the absence of female flowers [71]. Trebitsh et al. [72] discovered that the F (Female) locus contains an additional copy of *ACS1*, suggesting an initial connection between ET biosynthesis and female flower development. In *Cucumis sativus*, plants carrying the F locus duplication, *ACS1G* was 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 [70]. A study observed that in *Cucumis melo*, the WIP1, employed a corepressor TOPLESS to inhibit *CRC* (*CRABS CLAW*, carpel identity gene) expression through histone deacetylation, leading to male flower development. Disruption in the interaction between TOPLESS and WIP1 resulted in the expression of *CRC*, leading expression of the stamina inhibitor *CmACS7*, ultimately promoting female flower development [73]. Genome-wide analysis of the ET-responsive *ACS* gene family in *Cucumis melo* and *C. lanatus* revealed that *ACS1s* and *ACS6s* are mainly responsible for sex determination. Most of the genes are responsive to exogenous ethephon; however, *ACS1*, *9* and *10* show the opposite expression pattern [13]. Gene editing of *ACO2* in *Zea mays* leads to

decreased 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 [74]. Recent reports proposed that an 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 this level of ET insensitivity was a key factor in determining the ultimate sexual phenotype of the plant [75]. *CpACO1A*, *CpACS11A*, *CpACO2B*, and *CpACS271A* were found to be associated with female flowering transition and development as well as stamen arrest [76]. To understand how unisexual flowers develop in *Cucumis melo*, a mechanism was reported where ET originating from the carpel was sensed by ET receptors with distinct spatial expression in the stamen primordia. This leads to the activation of the CmEIN3/CmEIL1 ethylene signaling module within the stamen primordia. Consequently, this module triggers the expression of *CmHB40*, a transcription factor that downregulates genes essential for stamen development while upregulating genes associated with organ senescence [77]. Ethylene enhances petal maturation and flower opening through jasmonic acid biosynthesis but hinders ovary growth by reducing auxin production [76]. A recent study using the jasmonate-deficient mutant *lox3a 9* (*LIPOXYGENASE*, gene associated with jasmonate synthesis) confirmed the interplay between jasmonate and ET in regulating the opening of male and female flowers during their development [78]. A study in *Cucumis melo* identified a novel gene, *CmCPR5*, within locus b, regulating bisexual flower development. *CmCPR5* interacts with ET receptor CmETR1, impacting ET signaling. Malfunction of *CmCPR5* prevents stamen inhibition, leading to bisexual flower formation [79]. The description is illustrated in Figure 3.

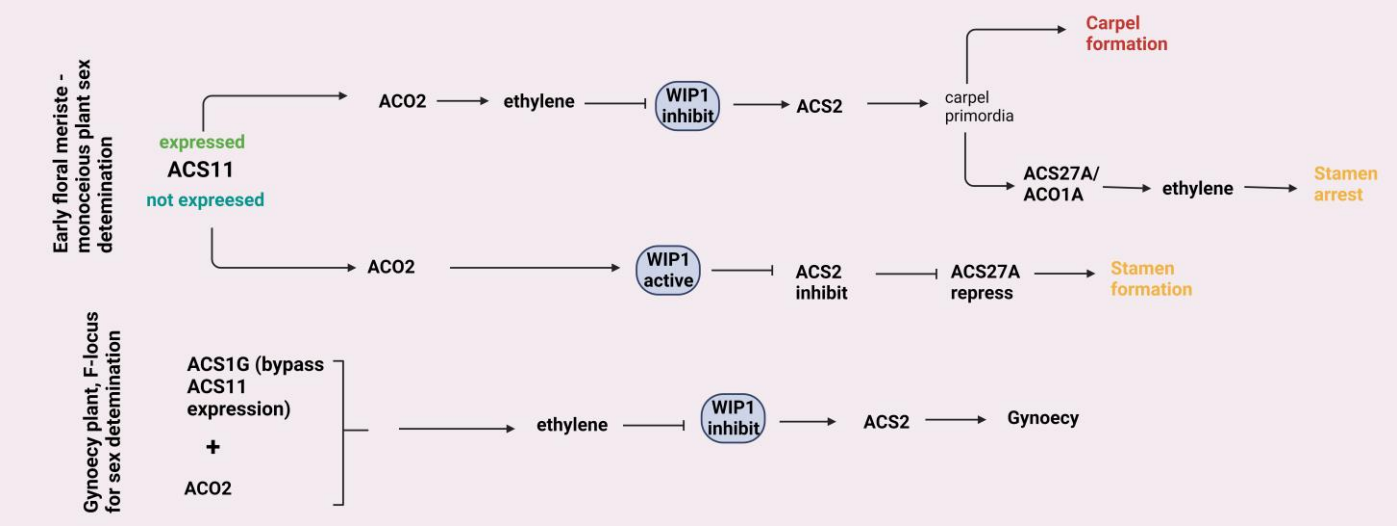

Figure 3. Flower development: In monoecious *Cucumis sativus* (cucumber) plants, the presence or absence of *ACS11* plays a crucial role in determining the sex of the flowers. When *ACS11* is expressed in the floral meristem, it produces ethylene, leading to the development of female flowers by suppressing 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. Solid arrow—promotion; flat-head arrow—inhibition.

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 ET 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 [21]. 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 [80]. 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's crucial role in controlling root hair length [80]. 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. A transcriptional cascade drives the core regulatory network. 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*) [81]. The WER-GL3/EGL3-TTG complex induces *GL2* and *CPC* expression in N-type cells, inhibiting root hair growth. CPC moves to adjacent H-type cells, competing with WER, inhibiting *GL2* expression, and promoting H-type cell differentiation [81]. 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 [82]. 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 [82]. 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 inducing the development of root hairs [83]. 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 the elongation of root hair [84]. A study centered on C2H2 family proteins specifically highlighted 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 [85]. The study aimed to understand ET's role in root hair initiation when the normal differentiation pattern of root epidermal cells is disrupted and 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 did not affect 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 [86]. 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 root hair elongation [87]. 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 [88]. Analysis of the transcriptome

showed that both auxin and ET could increase the expression of 90% of the 208 genes associated with root hair growth and development [89]. 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* exhibited inhibited root hair growth, which was ameliorated by applying exogenous naphthalene acetic acid. The ET overproducing mutant *eto1* displayed longer root hairs, while the loss of AUX1 in the *eto1* showed reduced root hair length [90–92]. 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. Studies 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 [93]. 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. In contrast, the elongation of root hairs necessitates a synergistic interaction between auxin and ethylene, utilizing their canonical signaling pathways [92]. Figure 4 illustrates ethylene-regulated root hair development.

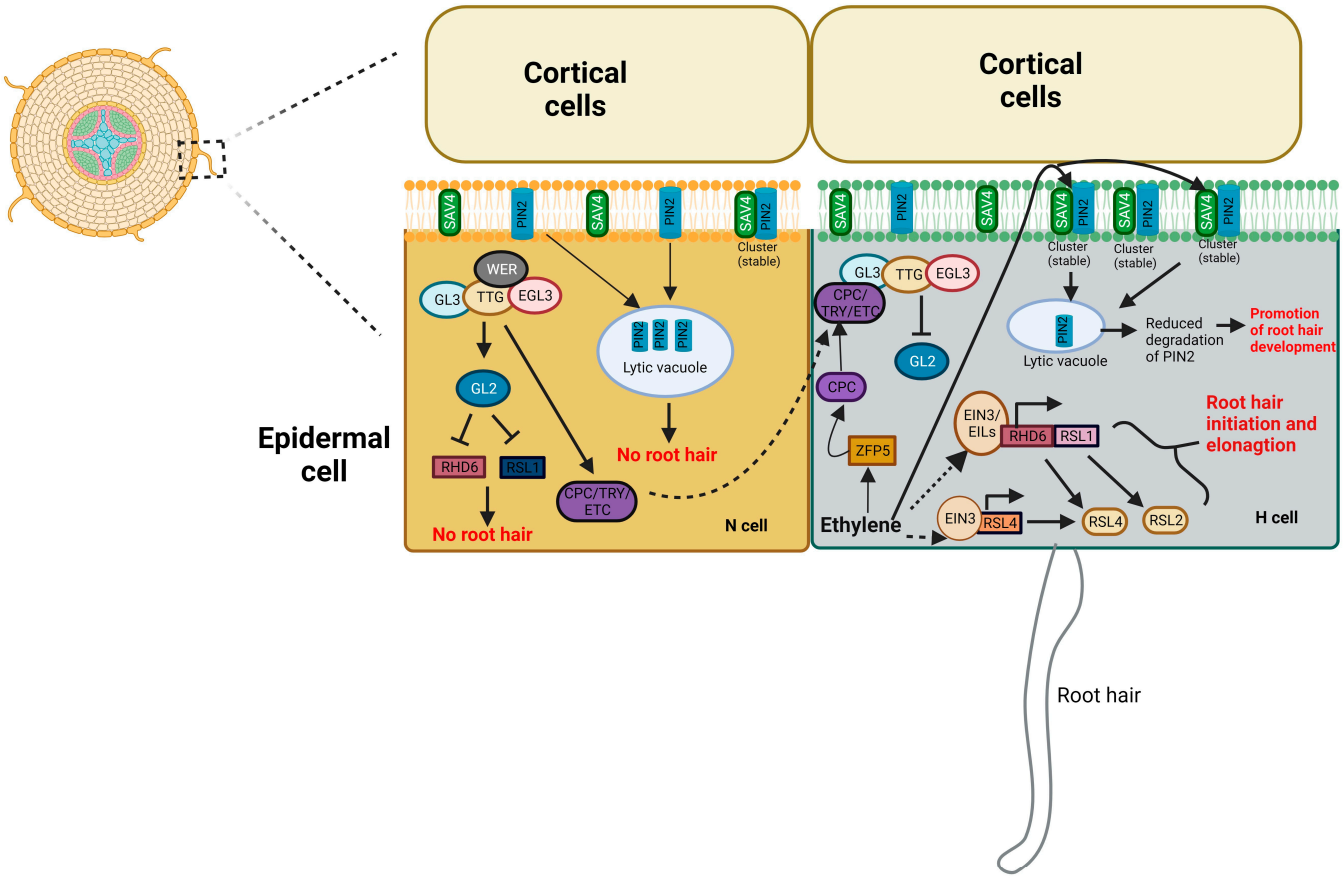

Figure 4. Role of ethylene in root hair development: In N-type cells (nonhair) of the epidermis of the root, a transcription complex consisting of WEREWOLF (WER), GLABRA3 (GL3), ENHANCER OF GLABRA3 (EGL3), and TRANSPARENT TESTA GLABRA (TTG) known as WER-GL3/EGL3-TTG induces the expression of GLABRA2 (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 PIN2 (PIN-FORMED2) protein levels 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 (PIN2 hydrophilic region), potentially promoting PIN2 protein clustering and stability on the membrane. This process encourages the downward movement of auxin, ultimately leading to the growth of root hairs. Figure is an updated illustration from [81]. Dotted arrow—multistep pathway; solid arrow—promotion; flat-head arrow—inhibition.

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 [14]. Excess ET production is chiefly associated with transcriptional upregulation of ET biosynthesis genes (*ACS* and *ACO*). Until now, 14 *ACS* genes have been identified in the *S. lycopersicum*, among these, *ACS2* and *ACS4* showed important fruit-ripening functions [94]. 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, *ACO1* and *ACO2* demonstrate high expression levels during the ripening process, while *ACO4* exhibits a gradual and slight increase in expression. Upon ripening, the undetectable transcript level of *ACO3*, *ACO5*, and *ACO6* suggests the least role in climacteric ET production [14]. During the climacteric stage, there is a well-known transition from system 1 to system 2, accompanied by a remarkable upregulation of *ACS2*, *ACS4*, *ACO1*, and *ACO4*. This upregulation leads to positive feedback regulation. In *S. lycopersicum*, the expressions of *ACS1A*, *ACS3*, *ACS6*, *ACO1*, and *ACO4* are associated with system 1 of ethylene production, while the expressions of *ACS2*, *ACS4*, *ACO1*, and *ACO4* are associated with system 2 [32,95].

Unlike climacteric fruits such as *Solanum lycopersicum*, non-climacteric fruits, such as *Fragaria x ananassa* (strawberry) do not rely on ET for the initiation and maintenance of the ripening process [96]. 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 to be achene-specific ripening-induced genes. Notably, certain *ACS* genes, including *FaACS27* and *FaACS29*, displayed strong expression during the developmental stages of achenes, ranging from the green achene to the white achene stage. These findings suggest a strong association between ET and the onset and progression of fruit ripening [97].

Shan et al. [98] discovered the mechanism for maintaining a balance of *MaNAC2*, *MaACS1*, and *MaACO1* levels in *Musa acuminata*. MaNAC1 and MaNAC2 suppress *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, facilitating its ubiquitination-mediated degradation. This process inhibits the transcrip-

tional repression mediated by MaNAC2. In addition, MaXB3 also targets proteasome degradation. Collectively, these findings unveil a regulatory cascade involving *MaXB3*, *MaNACs*, *MaERF11*, and *MaACS1/MaACO1* that controls ET biosynthesis during ripening in *Musa acuminata*. *MaNAC1* and *MaNAC2* repress *MaXB3*, creating a feedback mechanism in the cascade. The AP2/ERF superfamily, a substantial class of transcription factors, plays a pivotal role in regulating fruit ripening. It targets genes associated with various processes, such as softening (*POLYGALACTURONASE*, *PECTATE LYASE*, *EXPANSIN*, *XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE*), chlorophyll degradation (*CHLOROPHYLL-B-REDUCTASE*, *NON-YELLOW COLORING*, *PHEOPHORBIDEα OXYGENASE*, *RED CHLOROPHYLL CATABOLITE REDUCTASE RCCR*), anthocyanin accumulation (*CHALCONE SYNTHASE*, *DIHYDROFLAVONOL-4-REDUCTASE*), carotenoid accumulation (*LYCOPENEβ-CYCLASE*, *PHYTOENE DESATURASE*, *β-CAROTENE HYDROXYLASE*, *ZEAXANTHIN EPOXIDASE*, *9-CIS-EPOXYCAROTENOID DIOXYGENASE*, *CAROTENOID CLEAVAGE DIOXYGENASE*), and flavor development (*ALCOHOL DEHYDROGENASE*, *TERPENE SYNTHASE*, *ALCOHOL ACYLTRANSFERASE*) [99]. A finding demonstrated that ET response factor ERF D7 triggers the activation of SlARF2A/B (auxin response factor) controlling fruit ripening in *S. lycopersicum* [100]. Positive feedback regulation is observed in PpIAA1 and PpERF4 in promoting fruit ripening in *Prunus* by enhancing the expression of ripening regulator genes. PpERF4 activates transcription of *PpIAA1* and *PpACO1* and *PpIAA1* enhances transcription of *PpACS1* [101]. A recent study using genetic analysis on *S. lycopersicum* highlighted that ET promoted auxin production in seeds for cell division and fruit growth. Conversely, during fruit ripening, system-2 ET regulates the process through a complex network, including SlEIN2, SlEILs, and crucial developmental transcription factors NOR (NON-RIPENING), RIN (RIPENING INHIBITOR), and FUL1 (FRUITFULL1). This underscores the significance of ET and its regulatory network in shaping *S. lycopersicum* fruit development and ripening [24]. A recent study recorded that the trihelix transcription factor SlGT31 enhances the transcription of *ACS4* and *ACO1* and acts as a positive modulator of fruit ripening [102]. Studies have shown that posttranslational modifications also play a role in fruit ripening. For instance, a recent report observed SPINDLY (O-glycosylation enzymes) collaborated with EIN2 to enhance the process of ET signaling, which in turn promoted the ripening of fruits in *S. lycopersicum* plants [103]. Histone modifiers, like histone deacetylases, are enlisted by AP2/ERFs to regulate fruit ripening. In the case of *Malus*, MdHDA19 was brought into the MdERF4–MdTPL4 complex and hindered fruit ripening by decreasing *MdACSa* expression [104]. In *S. lycopersicum*, the protein complex SlERF.F12–TPL2–HDA1/HDA3 suppressed the expression of ripening-related genes, including *ACS2*, *ACS4* [105]. Figure 5 shows the summary of the fruit ripening process.

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 undergoes 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 the 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 [106]. 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 [106]. 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 [107]. 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 crucial role in maintaining skotomorphogenesis and inhibiting light-induced chloroplast development [108].

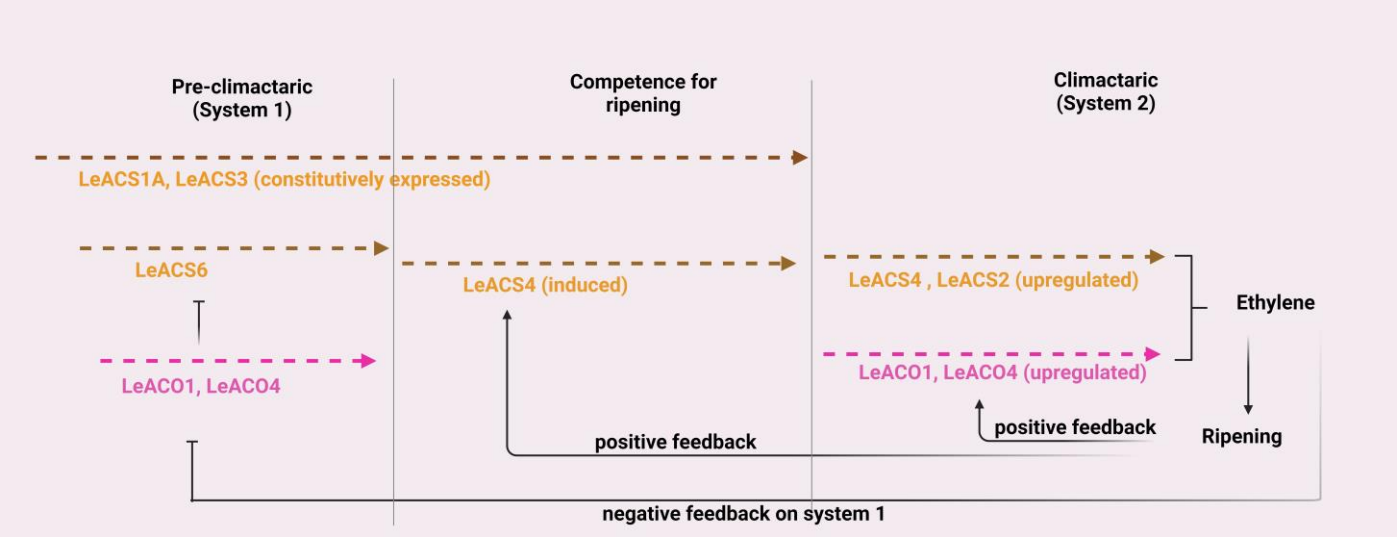

Figure 5. Fruit ripening: In *Solanum persicum* (tomato) fruit, the pre-climacteric phase involves system 1 ethylene response, which is likely controlled by continuously active genes, *LeACS1A* and *LeACS3*, along with negatively regulated LeACS6 genes, which interact with existing *Le ACO1* and *LeACO4* 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. The illustration is based on and modified from [32]. Dotted arrow—induction of specific gene and length of arrow defines the limit up to which gene expression occurs; solid arrow—promotion; flat-head arrow—inhibition.

Ethylene's regulatory functions hinge on two transcription factors, EIN3 and 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) [109–111]. 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) [111]. 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 [109]. 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 *PhANGs* [111]. EIN3/EILs inhibit protochlorophyllide (Pchlide) biosynthesis through PIF3 and EIN3/EILs directly trigger the expression of *PROTOCHLOROPHYLLIDE OXIDOREDUCTASE A* (*PORA*) and *PORB* in the cotyledon safeguarding against photooxidative damage during de-etiolation [10,112]. The EIN3-PIF3 module significantly suppresses *LIGHT-HARVESTING COMPLEX* (*LHC*) gene expression in darkness, preventing prema-

ture 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 [113]. 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 6 depicts the role of ethylene in chloroplast development.

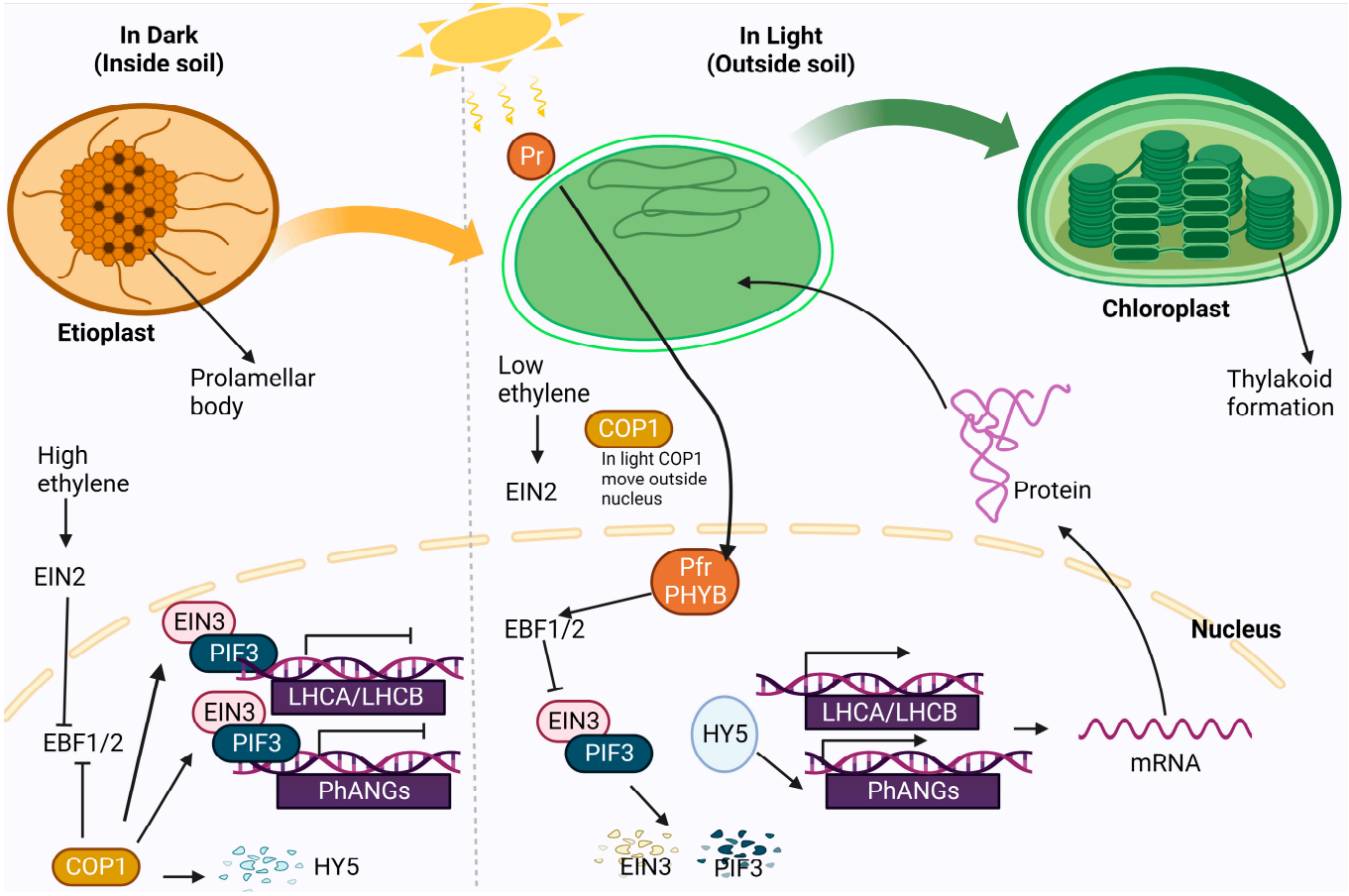

Figure 6. Role of ethylene in chloroplast development: During the early growth of seedlings in the dark underground, mechanical pressure triggers the production of a plant hormone called ethylene. This leads to an increase in the concentration of a protein called EIN3 in the nucleus of plant cells. EIN3 (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. The illustration is based on [111,113]. Solid arrow—promotion; flat-head arrow—inhibition

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.

4.6.1. Stomatal Regulation

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 CO_2 during photosynthesis, all while mitigating water loss through transpiration. ET's regulation of stomatal responses is characterized by its tendency to manifest dual and sometimes conflicting roles [62]. Ethylene induces stomatal closure in wild Arabidopsis by triggering H_2O_2 synthesis in guard cells, this process relies on NADPH oxidase AtrbohF. ETR1 mediates ethylene and H_2O_2 signaling in guard cells via EIN2 and ARR2-dependent pathway(s), identifying AtrbohF as a key mediator of stomatal responses to ET [114]. Ethylene-insensitive mutants (*etr1-1*) of Arabidopsis showed a smaller number of stomata and reduced stomatal conductance indicating ET influences the stomatal development process and negatively affects stomatal conductance [67,115]. 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 [116]. A recent study showed the effect of ET on stomatal movement. Elevated CO_2 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 CO_2. 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 CO_2 shifts. Conversely, ET receptor loss-of-function mutants (*etr2-3*; *ein4-4*; *ers2-3*, *etr1-6*; *etr2-3*; *etr1-6*) demonstrate notably accelerated stomatal reactions to CO_2 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*, or *ers2-3* mutants. These findings imply the crucial roles of ET production and signaling elements in fine tuning and expediting stomatal conductance responses to CO_2 and ABA [117]. 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. Ethephon 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 show that ET production and sensitivity play a role in high relative humidity-triggered stomatal opening in *S. lycopersicum* leaves [118]. Chen et al. [62] suggested that the 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.

4.6.2. Chlorophyll Content

According to Ceusters and Van de Poel [119], the impact of ET on photosynthesis is contingent upon the age of the leaves. ET directly regulates the photosynthetic process in younger, non-senescing leaves, while in mature leaves, its influence is more indirect, primarily driving leaf senescence. Studies on ethylene-insensitive mutants of Arabidopsis (*etr1-1*) and *Nicotiana* 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 [120–122]. Grbic and Bleecker [122] 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 *SAGs* (*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 [122,123]. 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 indicate 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 [119].

4.6.3. Light Reaction

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 in CO_2 in the 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 in photosystems. Chen and Gallie [124] demonstrated that ET controls energy-dependent non-photochemical quenching in Arabidopsis by inhibiting the xanthophyll cycle. In the above study, Arabidopsis *eto1-1* mutants (*ethylene overproducing*) exhibited reduced capacity 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. [125] 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. Notably, *etr1-1* mutant lines, which are 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. [125], 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 Wullschleger et al. [126] showed that ET exposure reduces electron transport capacity in *Glycine max* by over 30% within 4 h, leading to reduced CO_2 assimilation. This effect is not tied to Rubisco activity decrease. Measurements also showed lowered efficiency of excitation energy capture in PSII after ethylene

exposure. This impact was more substantial under higher light levels, indicating possible photoinhibition's role in ethylene-induced CO_2 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, and maximum rate of photosynthetic transport; however, the change in NPQ was less pronounced [127].

4.6.4. Dark Reaction

The available literature show that ET also controls the dark reaction of photosynthesis. Tholen et al. [120] demonstrated that as vegetative *Nicotiana* plants were cultivated under varying atmospheric CO_2 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 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 [127]. Nevertheless, ethephon treatment applied 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 [128]. Also, on evaluation of the influence of ethephon treatment on the photosynthesis of two *B. juncea* cultivars which have a contrast in their photosynthetic capacity, it became evident that alterations in net photosynthesis (Pn) in both cultivars 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 [129]. Ethylene affects Rubisco activases (RCAs), making carboxylation regulation more complex. RCAs are Rubisco chaperones. Recorded observations indicate that ethephon treatment increases carbonic anhydrase (CA) activity in *B. juncea* plants, helping maintain chloroplast pH and reducing photorespiration [66]. Nevertheless, reports observed that ET, at specific concentrations, increases photosynthesis and its related attributes, and beyond that concentration, it shows an inhibitory effect. Thus, it can be inferred that the effect of ET is concentration and sensitivity of species under study dependent [41,129]. In a study, *Never-ripe* (*Nr*) *S. lycopersicum*, which carries a loss-of-function mutation in the ET receptor SLETR3, exhibited a higher rate of carbon assimilation relative to their wild-type counterparts. Notably, 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 at midday, while ribose levels decreased in *Nr* plants. These findings suggest 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 [130]. 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 inhibit carbon fixation in most plant species.

4.7. Senescence

Leaf senescence is a highly programmed, regulated, and degenerative process. It is characterized by chlorophyll breakdown and degradation of macromolecules [131]. Studies reported increased ET production in senescent leaves with higher transcription rates of ET biosynthesis genes *ACS* and *ACO* [132]. On the other hand, the Octuple mutant of *ACS* genes showed a delayed senescence response [133]. Nevertheless, the recorded literature also reveal 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 [7,41].

A study revealed that EIN2 plays a role in regulating leaf senescence partially via microRNA164 (*miR164*) and *ORESARA1* (*ORE1*, also named *ANAC092* or *NAC2*) [134]. A recent study showed that EIN3 and ORE1 can directly regulate the expression of *CHLOROPHYLL CATABOLIC GENES* (*CCGs*), *NONYELLOWING1* (*NYE1*, also known as *STAYGREEN1*, *SGR1*), *NONYELLOW COLORING1* (*NYC1*), and *PHEOPHORBIDE A OXYGENASE* (*PAO*), thereby initiating chlorophyll breakdown during leaf senescence [135]. An *ETHYLENE-INSENSITIVE3-LIKE1* (*EIL1*) gene, *GhLY1* (*LINT YIELD INCREASING*), encodes a truncated protein that regulates senescence by directly targeting *SENESCENCE-ASSOCIATED GENE 20* (*SAG20*) in *Gossypium hirsutum* [136]. Yu et al. [137] demonstrated that WRKY71 can directly enhance the expression of ET signaling pathway genes EIN2 and ORE1. Additionally, it promotes ET synthesis by directly stimulating *ACS2*, thereby accelerating leaf senescence in Arabidopsis. However, a recent study found that transcription factor SbWRKY50 in *Sorghum bicolor* hinders chlorophyll degradation by binding to chlorophyll catabolic gene promoters, notably repressing *SbNYC1* (*NON-YELLOW COLORING 1*), thus suppressing leaf senescence [138]. Petal senescence is another phase in the flower developmental continuum accompanied by tissue differentiation, petal maturation, and finally, the growth and development of seeds coordinated by plant hormones [22]. Reports conducted so far indicate a close association of ET production with senescence in the *Dianthus* flower. In the *Dianthus* petal senescence induced by ET, the transcription factors DcHB30 and DcWRKY75 function antagonistically. They competitively modulate the expression of common target genes, specifically *DcACS1*, *DcACO1*, *DcSAG12*, and *DcSAG29*, resulting in a regulatory interplay that governs the process of petal senescence [139]. Another report observed that DcWRKY33 promotes petal senescence by activating genes involved in the biosynthesis of ET and ABA and the accumulation of ROS in *Dianthus* [140]. Ethylene-induced petal senescence in *Dianthus* is orchestrated by the transcription factor DcEIL3-1. Two genes, *DcEBF1* and *DcEBF2*, regulate the process by influencing downstream target genes of *DcEIL3-1*. *DcEBF1* and DcEBF2 also interact with DcEIL3-1 to promote its degradation through ubiquitination. This study uncovers the interplay between these factors, expanding our understanding of ET's role in *Dianthus* petal aging [141]. RNA-sequencing analysis showed that the protein kinase RhCIPK6 played an important role in the petal senescence of the *Rosa* flower [142]. During natural senescence, the early expression of *ACS* and *ACO* in gynoecium than in petals indicates that ET is first produced in gynoecium followed by petals [143]. Moreover, removing gynoecium prevents increased production of petal ET and significantly prolongs the flower's life [144,145]. Expression analyses of *ACS* and *ACO* in the floral organs of *Dianthus caryophyllus*, *Petunia*, *Solanum lycopersicum*, and *Rosa hybrida* have been performed [146–149]. Differential expression regulation has been observed for three cloned *ACS* genes, namely *DcACS1*, *DcACS2*, and *DcACS3*, in *Dianthus* flowers [150]. Okamoto et al. [151] 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 trigger the expression of *DcACS* and *DcACO* in the short-lived varieties but not in the long-lived varieties of *Dianthus* flowers [152]. A report in *Rosa hybrida* claimed that *RhACO1* was significantly correlated with vase life and ET sensitivity among 33 cultivars [153]. Although several transcription factors have been found to have favorable effects on ET biosynthesis, the regulation of *ACS* and *ACO* genes remains unclear. 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 and a dramatic increase in GA with reduced ET and ABA levels in petals [154]. Figure 7 summarizes the senescence process.

Figure 7. Senescence process: WRKY71 is a senescence-associated gene induced by ethylene. WRKY71 can 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

The shedding of plant organs such as seedpods, leaves, floral organs, and fruits by detaching them at the abscission zone is called abscission [155]. Developmental and environmental changes can trigger abscission in plants and are mainly subjected to the crosstalk between two plant hormones, ET and auxin [156]. Ethylene regulates the gene expression pattern of enzymes involved in cell separation, like cellulases and pectinases [157]. Before abscission occurs, auxin is transported to the abscission zone to inhibit ET sensitivity in the cells. When abscission occurs, the organs undergoing abscission release ET, which is then followed by the detachment of leaves [23]. Ethylene present in the abscission zone initiates a signal transduction pathway that activates transcription factors and genes responsive to ET [158] which in turn, 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 [159]. For uniform ripening, external ET application promotes 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 ethylene-induced AZ-C (calyx abscission zone) cells and adjacent FR (fruit rind) cells are responsible for citrus fruit abscission [160]. Hence, it appears that coordination between hydrolytic enzymes and ET production leads to plant organ abscission. 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-remodeling enzymes [161,162]. Pollination upregulated the *SlACS2* gene in *S. lycopersicum* [148]. In Petunia, pollination leads to a 20-fold increase in ET production autocatalytically from the stigmas contributing to wilting and eventually abscission [163]. 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* [164]. The transcription factor LcERF10 acts as a positive regulator in *Litchi* fruitlet abscission [165]. Nonetheless, clarifying the interaction between ET and other hormones like auxin and gibberellins is essential for obtaining 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 is 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 allow precise manipulation of these hormone profiles through molecular techniques to elicit desired plant responses.

In the years to come, ongoing research into ET's 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 still needs to be completed, 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 conflict of interest.

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