Print ISSN 2710-0200 *Full text available online at* *Ethiop J Nat Comp Sci.*
Electronic ISSN 2710-0219 *http://journal.uog.edu.et/index.php/EJNCS* *Vol. 5 (1) 672-702*
***https://doi.org/**10.20372/ejncs/Ag.2025.03*

REVIEW ARTICLE

Delaying Floral Senescence: Molecular Mechanisms and Ethylene Regulation

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Received: 09 November 2024; Accepted: 18 December 2024; Published: 08 January 2025

Abstract

Floral senescence, the aging process through which flowers deteriorate and die, is a critical determinant of flower longevity and quality, particularly in the floriculture industry where flower preservation is economically significant. This review synthesizes recent advancements in understanding the molecular and hormonal mechanisms that govern floral senescence, with a particular emphasis on ethylene's role. Ethylene, a key phytohormone, plays a crucial regulatory role in floral aging by orchestrating complex genetic and signaling networks. This hormone impacts various transcription factors, including Ethylene Response Factors *(ERFs),* and regulates senescence-associated genes *(SAGs)*, driving the aging process in ethylene-sensitive flowers. This review provides a detailed examination of the physiological and molecular changes occurring during floral senescence, focusing on ethylene's effects on gene regulation, transcription factors such as *RhWRKY33*, and other key components of senescence pathways. The review further explores the genetic regulation of floral senescence, highlighting ethylene's interaction with other plant hormones like auxin, cytokinins, polyamines, and abscisic acid. Recent research on gene regulation mechanisms and signaling pathways is discussed, alongside technological advancements like ethylene inhibitors and genetic engineering approaches aimed at mitigating floral senescence. The implications of ethylene's role in gene regulation and its interaction with other phytohormones are examined in depth. We also analyze the feasibility of applying ethylene-related technologies from both an economic and practical perspective, including a comparison of hormone treatment costs and their impact on flower pricing and longevity in the floriculture market. Despite the focus on ethylene, other environmental and hormonal factors such as climate conditions, macronutrients, and ecosystem influences are also considered in relation to their simultaneous impact on floral senescence. This review concludes by offering future research directions to address existing gaps in our understanding and provide potential solutions for enhancing flower quality, longevity, and productivity.

Keywords: *floral senescence, ethylene regulation, gene expression, RhWRKY33, transcription factors, genetic engineering*

1. Introduction

The global floriculture industry has experienced significant growth, driven by increasing consumer demand for ornamental plants and flowers. Valued at over *USD* 50 billion and continuing to grow annually, this sector is a crucial contributor to many economies, offering employment and supporting related industries such as packaging, logistics, and retail (International Trade Centre, 2023; United Nations, 2023). Cut flowers are highly prized for their beauty, diversity, and fragrance, serving vital roles in celebrations ranging from weddings to festivals, which further drives market demand (Jones *et al*., 2024). Major exporters like the Netherlands, Colombia, and Kenya, along with key importers such as the United States and Japan, dominate global trade (European Union, 2023; *USDA*, 2023). Notably, Colombia's flower industry is a vital export sector and a major source of employment, contributing significantly to its economy (Gómez *et al*., 2023).

However, floral senescence—the aging process of flowers—remains a considerable challenge for the industry. This process, marked by physiological and biochemical changes that degrade flower quality, involves programmed cell death *(PCD)*, which affects critical attributes such as color, texture, and fragrance (Van Doorn & Woltering, 2022). The rate of senescence is influenced by environmental factors, handling practices, and genetic predispositions, all of which affect post-harvest life and contribute to issues like petal wilting and color fading (Morris et al., 2023). The economic consequences of floral senescence are substantial, with shorter vase life leading to reduced sales and increased waste management costs (Lee et al., 2022).

To tackle these challenges, significant research has been devoted to developing post-harvest technologies and treatments aimed at extending flower longevity. A thorough understanding of the molecular mechanisms underlying floral senescence is crucial for devising effective strategies to maintain flower quality (Pérez et al., 2023; Davis et al., 2023). Ethylene, a key phytohormone, plays a central role in regulating floral senescence. Recent studies have advanced our understanding of ethylene's biosynthesis, signaling pathways, and its impact on flower longevity. Ethylene influences gene regulation and activates senescence-associated genes *(SAGs)* that govern the aging process in ethylene-sensitive flowers (Khan et al., 2017; Liu *et al*., 2024). Furthermore, recent breakthroughs in ethylene inhibitors and genetic engineering approaches, such as silencing key transcription factors like RhWRKY33, hold promise for improving flower preservation and extending post-harvest life (Zhang *et al*., 2023).

This review aims to provide a comprehensive overview of floral senescence, emphasizing the molecular and physiological mechanisms that drive the aging process, with a particular focus on the role of ethylene in gene regulation and transcription factor activation. It also highlights recent advancements in ethylene-related technologies, including genetic engineering and post-harvest treatments. By examining the biological processes underlying floral senescence and the technological innovations in flower preservation, this review seeks to identify opportunities for improving flower longevity and quality. Finally, it emphasizes the importance of collaboration between researchers and industry stakeholders to address the challenges of floral senescence and foster future breakthroughs in the field..

2. Methodology

This review aims to synthesize recent advancements in the molecular mechanisms of floral senescence, focusing on the regulatory role of ethylene, key molecular pathways, regulatory genes, and hormonal interactions. A comprehensive search strategy was employed using reputable databases, including PubMed, Web of Science, Scopus, and Google Scholar. Relevant studies were identified based on their use of genetic analysis, transcriptomic profiling, and hormone assays.

The search was conducted with the following keywords: "floral senescence," "molecular mechanisms," "ethylene regulation," "gene expression," and "floriculture," focusing on studies published in the last fifteen years. The inclusion criteria encompassed peer-reviewed journal articles, original research, and comprehensive reviews that addressed the molecular mechanisms, gene regulation, and the role of ethylene in floral senescence. Articles not directly related to the topic and non-English publications were excluded from the review. The search process, including the terms and databases used, was systematically documented.

The results were organized thematically, with a focus on ethylene-sensitive versus ethylene-insensitive flowers, gene regulation, key transcription factors like *RhWRKY33***,** and the effects of ethylene on flower senescence. Comparative analysis was employed to summarize findings, identify common themes, and highlight any discrepancies or gaps in current research. Finally, the review provides recommendations for future research directions to enhance our understanding of floral senescence and its regulation.

3. Effects of Ethylene on post-harvest quality Flowers

Ethylene, a naturally occurring plant hormone, plays a pivotal role in regulating the senescence of flowers, significantly impacting their quality and longevity. When flowers are cut from the plant, they initiate ethylene production as part of their natural life cycle. This internal ethylene production is further amplified by external sources such as tobacco smoke, exhaust fumes, fruits, and microorganisms, which contaminate the surrounding atmosphere. These external sources of ethylene, when absorbed by flowers, accelerate their senescence and reduce their resistance to environmental stress (Felix Instruments, 2024; Lee et al., 2022).

The effects of ethylene on flowers are detrimental, leading to a range of undesirable physical changes. These include bent necks, abnormal opening, petal wilting, petal shattering, discoloration, and flower popping, and yellowing or shedding of foliage (Liu et al., 2023). Such changes not only diminish the aesthetic quality of the flowers but also reduce their market value by affecting flower development, color, and consistency. As a result, ethylene exposure can lead to dissatisfaction among consumers, who expect fresh, vibrant flowers with long vase lives For the floriculture industry, managing ethylene levels throughout the distribution chain—from storage to sale—is crucial for ensuring flowers reach consumers in optimal condition (Pérez et al., 2023; Smith et al., 2024). Without effective control of ethylene exposure, the flower industry faces financial losses, decreased shelf life, and challenges to sustainability efforts.

Although ethylene is a naturally occurring hormone, its effects on cut flowers are particularly pronounced. Ethylene is colorless, odorless, and gaseous, making it difficult to detect without specialized equipment. All plants produce ethylene, and while some species or varieties are more sensitive to its effects (Table 1), the damage often goes unnoticed until the flowers are removed from cold storage, reach the point of sale, or are in the consumer's home (Morris et al., 2023). The combined impact of internally produced ethylene and external sources accelerates the flower's life cycle, leading to premature senescence and reduced flower quality (Fig. 1). Ethylene's detrimental effects on flowers underscore the importance of monitoring and managing its presence to preserve flower quality, extend their vase life, and meet consumer expectations. Effective mitigation strategies, including the use of ethylene inhibitors and optimal handling conditions, are essential for minimizing the adverse effects of this hormone on cut flowers (Lee et al., 2023).

Table 1: How cut flower species are affected by ethylene damage (Felix Instruments,2024).

Scientific Name	Common Names	Symptoms of Ethylene Damage
Alstroemeria spp.	Alstroemeria Peruvian Lily	Leaf-yellowing; petal transparency
Anemone spp.	Anemone	Bloom abscission; shattering
Antirrhinum majus	Snapdragon	Bloom abscission; petal transparency
Bouvardia spp.	Bouvardia	Bloom shattering; wilting
Campanula spp.	Bellflower	Premature flower; wilting
Chamelaucium uncinatum	Wax Flower	Bloom abscission; leaf abscission
Consolida spp.	Larkspur	Bloom abscission; shattering
Delphinium spp.	Delphinium	Bloom abscission; shattering
Dianthus spp.	Carnation	In-rolling of petals; "sleepiness"
Euphorbia pulcherrima	Poinsettia	Leaf and bract epinasty (downward curl)
Eustoma grandiflorum	Lisianthus	Flower wilting and reduced vase life
Freesia spp.	Freesia	Young buds fail to open; flower wilting
Gypsophila paniculata	Baby's Breath	Excessive brown flowers
Hlelianthus annuus	Sunflower	Abscission of floret
IIex	Holly, Ilex	Berry and leaf abscission
Iris X hollandica	Iris	Shorter flower life; forced flower unfolding
Lathyrus odoratus	Sweet Pea	Flower wilting
Jliurn spp.	Lily, Asiatic, Oriental	Leaf-yellowing; petal transparency; bud abscission
Jmonium spp.	Statice, German Statice	Flower wilting
Phlox paniculata	Phlox	Bloom abscission
Ranunculus asiaticus	Persian Buttercup	Bloom shattering
Rosa spp. and hybrids	Rose	Bent neck; improper opening
Tulipa spp.	Tulip	Flower bud abortion

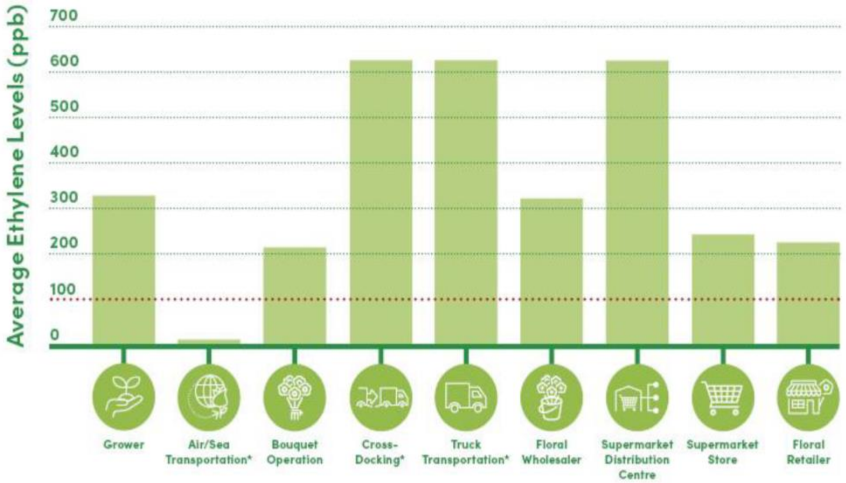

Figure 1: Sources of ethylene in the supply chain (Felix Instruments, 2024). The graph shows the average amount of ethylene exposure encountered at each stage of the supply chain. Ethylene damage starts at 100 ppb.

As indicated in Figure 1, the negative effects of ethylene on the flower industry include several critical challenges that can result in significant financial losses. Flowers may not withstand longer shipment periods, such as sea freight, leading to products that do not reach retailers in sellable condition (Fig. 1). This quality reduction extends to retail displays, where flowers exhibit a shorter shelf life, and to consumers, who experience a diminished vase life in their homes, leading to dissatisfaction. These issues also negatively impact sustainability efforts, culminating in financial losses, customer dissatisfaction, and damage to brand reputation (Felix Instruments, 2024; van Doorn et al., 2011). To mitigate these detrimental effects, several preventative measures can be implemented. While the developmental stages of flowers are irreversible, ethylene production can be managed effectively. Since ethylene is always present, often undetectable, it is recommended to treat flowers with action inhibitors such as EthylBloc™ or FloraLife® EthylGuard (Felix Instruments, 2024). These inhibitors work by binding to the ethylene receptors in plant cells and blocking ethylene action. The chemicals remain active, continuing to bind to the flowers even after unpacking, with effects lasting 10–14 days post-treatment. It is essential to use these products throughout the distribution chain to minimize ethylene's impact and protect the flowers from the farm to the consumer's home (Felix Instruments, 2024; Wang et al., 2018). Additional recommendations include maintaining temperature control and following proper care and handling procedures throughout the distribution chain. These practices will enhance vase life, increase resilience to external conditions, reduce waste, and positively impact sustainability efforts, ultimately boosting profits (Felix Instruments, 2024; Schlereth et al., 2010).

4. Floral Senescence: Impact on Consumer Preferences and Industry Challenges

Floral senescence, the aging process of cut flowers after harvest, involves a series of physiological and biochemical changes that lead to visible signs of deterioration, including wilting, petal drop, and color fading. These changes are driven by enzymatic degradation of cell walls, loss of turgor pressure, and alterations in pigment composition (Lee et al., 2023). Senescence significantly affects the commercial value of cut flowers, reducing their aesthetic appeal and marketability. For the floriculture industry, flowers with reduced longevity require more frequent replacements, increasing costs for growers, wholesalers, and retailers. Additionally, flowers that age quickly often lead to higher waste levels, as they may not meet quality standards upon reaching consumers (Zhao et al., 2022). Therefore, effectively managing floral senescence is essential for maximizing profitability and maintaining a competitive edge in the market (Smith & Reynolds, 2023).

Consumer preferences are directly influenced by the freshness and longevity of flowers, with consumers favoring those that remain vibrant and attractive for extended periods. Flowers with better post-harvest performance often drive higher customer satisfaction, repeat business, and increased demand (Liu et al., 2023). However, the industry faces significant challenges in managing senescence, including optimizing post-harvest handling practices, developing effective preservative treatments, and understanding the underlying biological mechanisms driving flower aging. Addressing these challenges requires a multifaceted approach that integrates advances in molecular biology, genetics, and environmental management to improve flower longevity and reduce losses (Dai et al., 2021).

To meet consumer demands for long-lasting flowers, the industry has focused on technological innovations aimed at extending flower freshness. Post-harvest treatments, such as new preservatives and hormonal treatments, are being developed to slow down the senescence process (Seymour et al., 2019). Innovations in storage solutions, including controlled atmosphere storage and advanced refrigeration technologies, are also being implemented to preserve flower quality during transport and sale (Zhang et al., 2021). Additionally, managing ethylene levels, a critical regulator of floral aging, is a central focus, with the use of ethylene inhibitors being explored as a way to extend flower life (Zhao et al., 2022). These advancements are essential for aligning with consumer expectations and addressing industry challenges, ultimately contributing to improved floral products and market success.

Floral senescence progresses through several stages: early senescence marked by initial signs of aging such as slight wilting and color fading; mid-senescence, during which more pronounced symptoms, such as petal drop and increased ethylene production, occur; and late senescence, which involves extensive deterioration, including complete wilting and color loss, rendering the flower unfit for commercial use (Seymour et al., 2019). Ethylene plays a crucial role in accelerating this process by regulating various physiological changes, such as protein and lipid breakdown, cell wall degradation, and water loss, leading to wilting and drooping of flowers (Zhang et al., 2020). Additionally, changes in pigment composition, particularly the degradation of anthocyanins and carotenoids, contribute to the fading of flower color (Kumar et al., 2023).

From an economic perspective, floral senescence has profound implications on the longevity and quality of cut flowers. Flowers with extended freshness and aesthetic appeal are highly valued, leading to higher prices and reduced waste, while flowers that deteriorate quickly have lower market value and contribute to increased waste, affecting profitability for growers and retailers (Dai et al., 2019). The cost implications are evident throughout the distribution chain. Rapid senescence may require more frequent harvesting and processing, which increases labor and operational costs (Wang et al., 2021). Furthermore, flowers that age quickly may need specialized transport conditions, such as controlled temperatures and humidity levels, which add to logistical costs (Smith & Reynolds, 2019). At the retail level, flowers with short shelf lives lead to higher unsold inventory and waste, further reducing profitability (Williams & Morgan, 2022).

5. Advances in Delaying Flower Aging: Strategies, Regulatory Pathways, and Ethylene's Role

Floral senescence is controlled by intricate regulatory networks that involve hormones, transcription factors, and signaling molecules (Fig. 2). Ethylene is a primary regulator of this aging process, significantly accelerating the decline in flower quality. Other hormones, such as abscisic acid *(ABA)* and jasmonic acid *(JA)*, also contribute to modulating senescence through various pathways (Zhao et al., 2022). Transcription factors, including *WRKY*, *MYB*, and *NAC*, are key players in regulating the expression of genes associated with senescence. These transcription factors coordinate the gene expression programs required to drive the senescence process (Havaux et al., 2019). In addition to hormones and transcription factors, various signaling pathways, such as Mitogen-Activated Protein Kinase *(MAPK)* and cyclic Guanosine Monophosphate *(cGMP)* pathways, integrate signals from hormones, environmental factors, and developmental cues to regulate the senescence process (Wang et al., 2021).

The coordination of metabolic activities during floral senescence involves significant changes at the cellular and metabolic levels. Cell wall remodeling, driven by enzymes like cellulases and pectinases, is upregulated to facilitate cell death and tissue collapse, contributing to wilting and flower degradation (Zhang et al., 2020). Furthermore, a shift from anabolic to catabolic metabolism provides the energy needed for the senescence process. This includes increased respiration rates and alterations in carbohydrate metabolism (Li et al., 2021). Furthermore, changes in secondary metabolites, including the accumulation of antioxidants and flavonoids, play protective roles against oxidative stress during the senescence process.

Ethylene, synthesized via the methionine pathway, plays a crucial role in floral senescence by accelerating aging in flowers. Ethylene production begins with the conversion of methionine into S-adenosylmethionine *(SAM)* by *SAM* synthetase. *SAM* is then converted into 1-aminocyclopropane-1-carboxylic acid *(ACC)* by *ACC* synthase *(ACS)*, which is subsequently converted into ethylene by *ACC* oxidase (Wang et al., 2019; Yoshida et al., 2023). Ethylene regulates processes such as cell wall degradation and pigment breakdown, leading to reduced vase life and faster wilting in flowers (Bleecker & Kende, 2023).

The ethylene signaling pathway involves several key components (Fig. 2), including membranebound ethylene receptors such as *ETR1*, *ERS1*, and *ETR2*, which initiate the signaling cascade upon ethylene binding (Schaller & Bleecker, 1995). These receptors act as negative regulators of ethylene signaling. In the absence of ethylene, the *CTR1* protein kinase inhibits the signaling pathway by phosphorylating and inactivating *EIN2*. Upon ethylene binding, *EIN2* is dephosphorylated, translocates to the nucleus, and activates transcription factors like EIN3 and *EIN3*-Like *(EIL)*, which drive the expression of ethylene-responsive genes (Alonso et al., 1999; Chao et al., 1997). *ERF1*, a member of the Ethylene Response Factor *(ERF)* family, plays a key role in regulating genes associated with senescence and stress responses.

Ethylene's impact on flower longevity is particularly evident in flowers such as roses and lilies, where the hormone accelerates senescence by influencing the expression of genes involved in cell wall degradation and pigment breakdown, which ultimately reduces vase life (Li et al., 2011; Zhang et al., 2012). Ethylene synthesis involves the action of two key enzymes: ACC synthase, which converts *SAM* into *ACC*, and *ACC* oxidase, which converts *ACC* into ethylene (Yang & Hoffman, 2022). The ethylene signaling pathway, mediated by receptors and transcription factors like *EIN3*, regulates the expression of genes associated with senescence (Bleecker & Kende, 2023). To counteract ethylene's negative effects and extend flower lifespan, strategies such as ethylene inhibitors, controlled atmosphere storage, and gene editing are essential (Yoon et al., 2023; Yang & Hoffman, 2022).

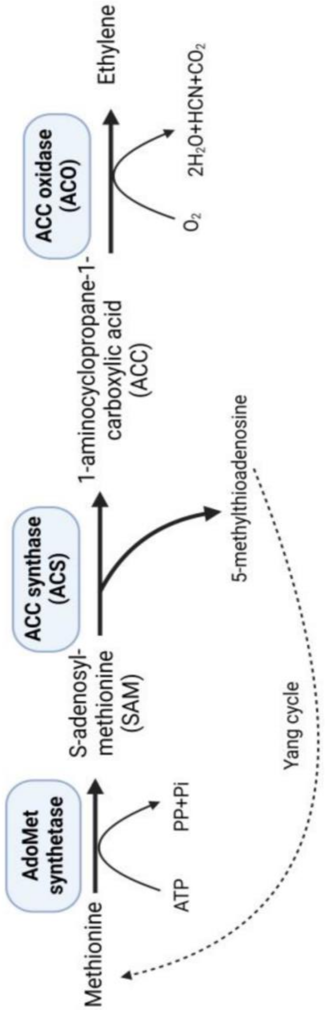

Figure 2: Ethylene biosynthetic pathway, illustrating the key steps and enzymes involved (Yang, & Hoffman, 2022).

Description of the Pathway

1. Methionine to S-Adenosylmethionine (SAM)
   - Enzyme: SAM Synthetase
   - Reaction: Methionine is converted to SAM using ATP.
2. SAM to 1-Aminocyclopropane-1-Carboxylic Acid (ACC)
   - Enzyme: ACC Synthase
   - Reaction: SAM is converted to ACC through a series of intermediate steps involving decarboxylation.
3. ACC to Ethylene
   - Enzyme: ACC Oxidase

  - Reaction: ACC is converted to ethylene via oxidation, producing ethylene and CO_2.

Further Explanation for the pathway

- Methionine is the starting substrate for ethylene biosynthesis.
- SAM Synthetase converts methionine to S-Adenosylmethionine (SAM).
- ACC Synthase then converts SAM into 1-Aminocyclopropane-1-Carboxylic Acid (ACC).
- ACC Oxidase converts ACC into Ethylene, along with by-products CO_2 and H_2O.

After extensive research to date, the ethylene biosynthesis pathway has become more apparent (Fig. 2) (Yang & Hoffman, 2022). The precursors for ethylene synthesis in plants include S-adenosyl-l-methionine *(SAM)* and 1-amino-1-carboxycyclopropane *(ACC)* (Bleecker & Kende, 2023). The ethylene biosynthesis pathway consists of three enzyme-catalyzed reactions: methionine *(Met)* is catalyzed by methionine adenylyl transferase to form *SAM; SAM* is catalyzed by *ACC* synthase *(ACS)* to form *ACC,* which simultaneously forms 5′-methylthioadenosine *(MTA)*, and then passes through the Yang cycle (a specific regulatory loop in the context of ethylene signaling in plants) to synthesize new methionine *(Met)* (Schaller & Bleecker, 1995). Finally, *ACC* is catalyzed by *ACC* oxidase *(ACO)* to synthesize ethylene (Figures 2&3) (Li et al., 2021). *ACS* and *ACO* are two important rate-limiting enzymes involved in ethylene synthesis (Bleecker & Kende, 2023).

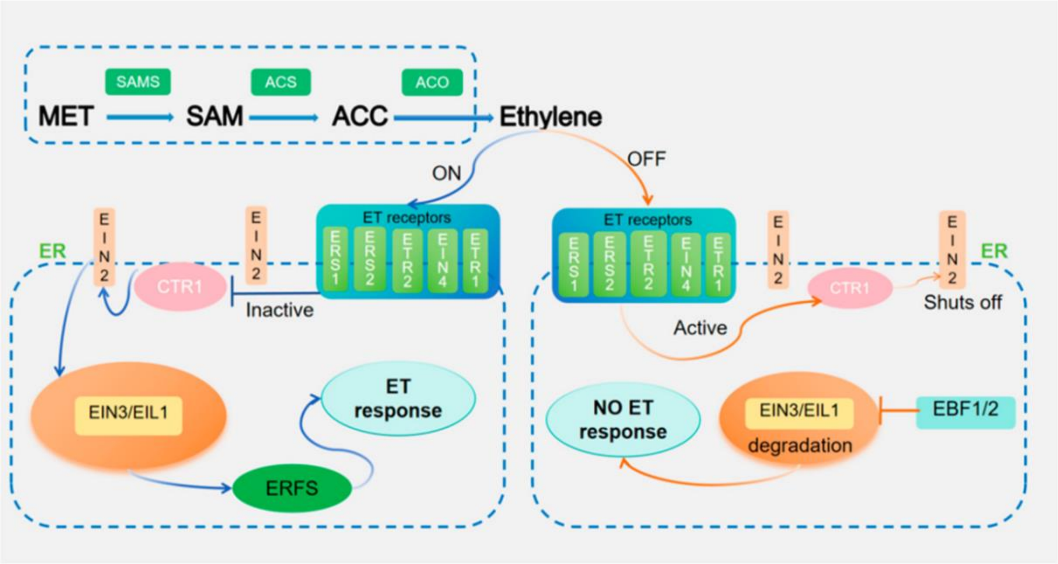

Figure 3: Ethylene Biosynthesis and Signal Transduction Pathways in Plants (Yang & Hoffman, 2022)

In the absence of ethylene, its receptor activates *CTR1*, which phosphorylates and inhibits *EIN2*, a membrane protein on the endoplasmic reticulum (ER). This inhibition leads to the degradation of *EIN3* and *EIL1*, blocking transcription. When ethylene is present, it binds to the receptor, inactivating *CTR1*, which enhances *EIN3/EIL1* activity. Ethylene stabilizes *EIN3/EIL1*, enabling the transcription of ethylene-responsive factors (ERFs). **Key Terms:** *MET* (Methionine), *SAM* (S-adenosyl-L-methionine), ACC (1-amino-1-carboxycyclopropane), ACS (ACC synthase), *ACO (ACC* oxidase), *EIN* (Ethylene insensitive), *ETR1/2 (EIN2*-Targeting protein 1/2), *ERS1/2* (Ethylene response sensor 1/2), *CTR1* (Constitutive triple response 1), *ERFs* (Ethylene-responsive factors), *EBF1/2* (*EIN3*-Binding *F-BOX* Protein 1 and 2).

Ethylene is detected by a group of receptors located on the membrane of the endoplasmic reticulum (ER). In Arabidopsis, for example, these receptors include *ETHYLENE RESPONSE1/2 (ETR1/2), ETHYLENE RESPONSE SENSOR1/2 (ERS1/2), and ETHYLENE INSENSITIVE4 (EIN4)*, which play a suppressive role in ethylene signaling (Fig. 4) (Schaller & Bleecker, 1995). These receptors are associated with two-component histidine kinase receptors. In the absence of ethylene, the receptor family recruits the Raf-like kinase Constitutive Triple Response 1 (CTR1) to phosphorylate the C-terminal domain of EIN2 (Alonso et al., 1999). Subsequently, the F-box proteins EIN2-Targeting Protein 1 and 2 (ETP1 and ETP2) degrade the phosphorylated EIN2, preventing the downstream transmission of ethylene signaling (Chao et al., 1997). This process is further regulated by EIN3-Binding F-BOX Proteins 1 and 2 (EBF1 and EBF2), which interact with EIN3/EIL1 and promote their degradation via the 26S proteasome, shutting down the ethylene signaling pathway (Bleecker & Kende, 2023).

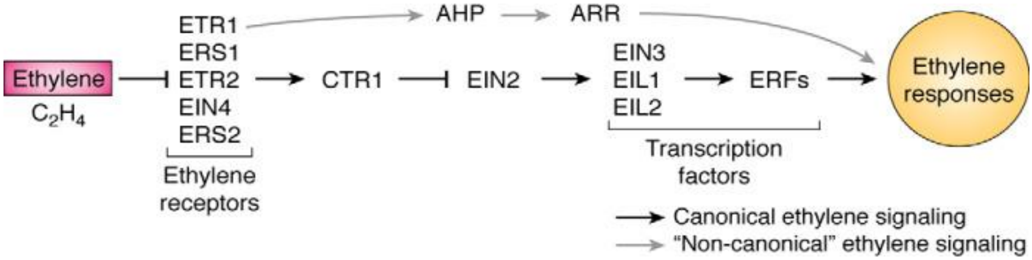

Figure 4: Simplified Ethylene Signaling Model (Bleecker & Kende, 2023).

This model, based on Arabidopsis genetic experiments, shows ethylene signaling involving receptors *(ETR1, ERSI, ETR2, EIN4, ERS2), CTR1* protein kinase, and *EIN2*, which activates transcription factors (EIN3, EIL1, EIL2). These factors then trigger other transcription factors, like *ERFs*, leading to ethylene responses. *CTR1* acts as a negative regulator. Ethylene inhibits receptors, reducing *CTR1* activity and releasing downstream components from inhibition. Additionally, an alternative "non-canonical" pathway (in gray) has been identified, where *ETR1* signals through AHPs to ARRs, modulating ethylene responses.

Notes:

- Ethylene Receptors: Detect ethylene and modify downstream signaling.
- *CTR1:* A negative regulator of the ethylene response.
- *EIN2*: Central component in transducing ethylene signals.
- *EIN3/EIL1*: Key transcription factors activated by EIN2.
- *ERFs:* Transcription factor that regulates stress and developmental responses.
- Interactions: Arrows indicate the interaction between ethylene and other hormonal pathways, showing either synergistic or antagonistic effects.

When ethylene is present, it binds to the receptors and inactivates both the receptor and *CTR1*, which inhibits the phosphorylation of *EIN2* (Schaller & Bleecker, 1995). Without phosphorylation, *EIN2* is not degraded by *ETP1/2* but instead undergoes cleavage. The cleaved *EIN2-C*-terminus then moves to the nucleus, where it activates the downstream *EIN3/EIL1* transcription cascade, opening the ethylene signaling pathway (Alonso et al., 1999). *EIN3* directly binds to the promoter regions of Ethylene Response Factors *(ERFs)*, which modulate gene expression in response to environmental stresses (Bleecker & Kende, 2023). ERFs are plant-specific transcription factors that regulate ethylene and stress-related responses. Ethylene biosynthesis, the upstream process, and ethylene signaling, the downstream pathway, together govern the biological effects of ethylene. A relatively complete signaling pathway has been established in the model crop Arabidopsis, from ethylene detection by the receptor family to gene expression via ERFs (Chao et al., 1997).

5.1. Epigenetic Modifications in Ethylene Signal Transduction and DNA Methylation

Epigenetic modifications regulate gene expression without altering the *DNA* sequence and can affect various aspects of gene transcription, such as splicing, stability, translation, nucleosome assembly, and chromatin structure (Zhang et al., 2020). These modifications influence both the physiological and pathological processes within cells and can impact the phenotype of offspring (Li & Zhang, 2021). Ethylene signaling is also subject to epigenetic regulation, and *DNA* methylation, as a key epigenetic modification, plays a crucial role in this process (Yang et al., 2019). The regulation of genes involved in ethylene biosynthesis and signal transduction can be influenced by changes in *DNA* methylation. For instance, environmental factors like stress can induce changes in the *DNA* methylation status, which in turn modulates ethylene signaling pathways (Liu et al., 2022).

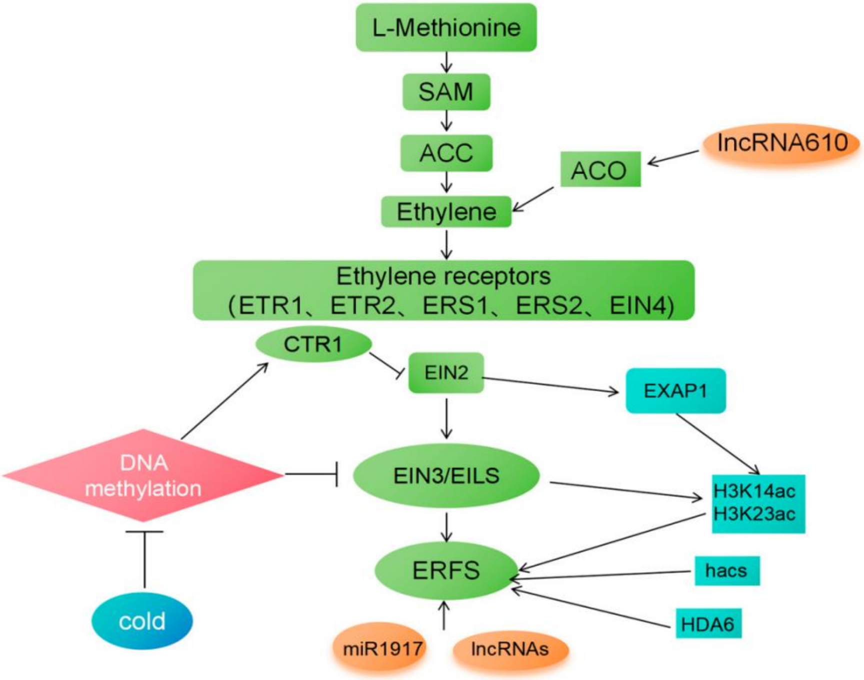

Figure 5: Overview of crosstalk between ethylene and epigenetic modifications in ethylene signal transduction (Liu et al., 2022).

DNA methylation, the most common form of epigenetic modification, plays an essential role in regulating plant growth and development (Liu et al., 2020). It can activate or inhibit the expression of genes associated with ethylene synthesis and signaling. Hypermethylation in the promoter regions of specific genes can reduce gene expression and affect ethylene signaling (Zhang et al., 2021). For example, research in tomatoes has shown that low-temperature stress leads to changes in *DNA* methylation in the promoter regions of ethylene-related genes, such as *SlEIN3, SlERF-A1, and SlERT10* (Chen et al., 2022). Methylation changes in these regions resulted in lower expression levels of these genes, while the expression of *SlCTR1* increased. This altered gene expression inhibited the ripening process in tomato fruit, demonstrating that changes in *DNA* methylation and gene expression regulate ethylene signaling and help plants adapt to environmental conditions (Wang et al., 2021).

5.2. Ethylene Signaling Pathways and Hormonal Interactions in Flower/Petal Senescence

Flower senescence is a complex process regulated by various plant hormones, with ethylene being a key player. Ethylene, a gas naturally produced by plants, accelerates senescence in flowers by triggering changes following pollination. In many flowers, a rise in ethylene production after pollination initiates petal senescence. For example, in Petunia, the increase in ethylene production after pollination is linked to the expression of the *ACO1* gene, specifically in senescing corollas (Wang et al., 2021). The role of ethylene receptors and downstream signaling genes, such as *DC-ERS2* and *DC-ETR1* in carnation, is also critical in regulating flower senescence (Chen et al., 2020). Studies have shown that ethylene receptor genes, such as ETR3 in roses and *ERS1* and *CTR1* in Delphinium, are expressed during senescence, indicating the importance of ethylene perception in the process (Li et al., 2022). Furthermore, transgenic flowers with mutations in ethylene-related genes, like *ACO* and *etr1-1*, exhibit delayed senescence, enhancing vase life (Yang et al., 2019).

Flower senescence involves nutrient transfer from petals to other tissues, like developing ovaries or young leaves, as the flower ages (Rogers, 2013; Rogers and Munné-Bosch, 2016). Several plant hormones, including ethylene, jasmonic acid, salicylic acid *(SA)*, abscisic acid *(ABA)*, and brassinosteroids, act as inducers of senescence, while cytokinins, gibberellins *(GA)*, and auxin are inhibitors (Reid and Chen, 2008). Ethylene is particularly significant in flowers, as it triggers the aging process and accelerates senescence after pollination, coordinating cellular events such as wilting and abscission (Woltering and Van Doorn, 1988). Studies have shown that exogenous application of ethylene or its precursor *ACC* accelerates corolla senescence, whereas inhibitors of ethylene biosynthesis, such as *AOA* and *1-MCP*, delay senescence (Trivellini et al., 2011a; Ferrante et al., 2015). Besides ethylene, other hormones such as abscisic acid *(ABA)*, cytokinins, and gibberellic acids *(GA)* also play roles in flower senescence. ABA is known to accelerate senescence in ethylene-insensitive flowers like daylilies, where it acts as the primary hormonal regulator (Rogers, 2013). In ethylene-sensitive flowers, such as carnation, *ABA* can hasten senescence by increasing endogenous ethylene production (Reid & Chen, 2008). In contrast, cytokinins tend to delay senescence by reducing ethylene sensitivity. Studies have shown that transgenic plants with overexpressed IPT genes, which increase cytokinin levels, exhibit delayed senescence and reduced ethylene sensitivity (Woltering & Van Doorn, 1988). On the other hand, the effects of auxins and gibberellic acids *(GA)* on senescence are less understood, but GA has been shown to delay senescence in certain flowers by antagonizing ethylene (Trivellini et al., 2011). Moreover, jasmonic acid has been observed to promote flower senescence by stimulating ethylene production, although its role in some species, like orchids, remains unclear.

Furthermore, Ethylene interacts with various other plant hormones, significantly influencing growth and developmental processes. Ethylene and auxins often work together to regulate processes such as root development and fruit ripening. Ethylene can modify auxin distribution, and in some contexts, ethylene enhances auxin-induced responses (Vanneste & Friml, 2009). Conversely, ethylene and gibberellins *(GAs)* typically exhibit antagonistic effects. While gibberellins promote stem elongation, ethylene can inhibit this process. The interaction between these hormones is context-dependent, varying with developmental stages and environmental factors (Achard *et al.*, 2003).

Ethylene also interacts with Abscisic Acid *(ABA)* in mediating plant stress responses. ABA is primarily involved in stress responses such as drought tolerance, while ethylene modulates these responses in a synergistic or antagonistic manner, depending on the specific stress condition (Zhang et al., 2006). Ethylene has generally antagonistic effects on cytokinin signaling, where it can inhibit cytokinin-induced cell division and differentiation. This balance between ethylene and cytokinins is essential for processes such as leaf senescence and root development (Moubayidin et al., 2009). Furthermore, ethylene and jasmonic acid *(JA)* often interact during responses to wounding and pathogen attacks. Both hormones enhance defense-related gene expression, and their interaction can vary, with each hormone modulating the signaling pathways of the other (Schilmiller et al., 2007).

Hormonal interaction plays a significant role in flower and petal senescence, with specific hormones influencing the process in complex and species-specific ways. Ethylene is a key hormone that triggers petal senescence in most flowers following pollination. In many species, ethylene production rises after pollination, leading to changes in petals associated with senescence, such as in Petunia and carnations (Shibuya et al., 2002). The expression of ethylene biosynthetic genes, including *ACC* oxidase *(ACO)* genes, has been linked to the senescence process in flowers like Petunia, Geranium, and orchids (Stead and van Doorn, 1994). Ethylene receptors and signaling pathways also play an active role in this process, with genes such as *DC-ERS2, DC-ETR1*, and *ETR3* influencing senescence in carnations, roses, and other species (Shibuya et al., 2002). Mutant studies in carnations, Petunia, and tomato have shown that reducing ethylene sensitivity can delay flower senescence, thereby extending vase life (Hunter et al., 2004).

In contrast to ethylene, other hormones like abscisic acid *(ABA)* and cytokinins regulate senescence in different ways. ABA, particularly in ethylene-insensitive species like daylilies, accelerates senescence by increasing ion leakage, lipid peroxidation, and expression of proteases and nucleases (Hunter et al., 2004). In ethylene-sensitive flowers, ABA enhances senescence by promoting ethylene production. Cytokinins, on the other hand, delay senescence by maintaining floral tissue health and reducing ethylene sensitivity. Transgenic plants overexpressing IPT genes, which increase cytokinin content, show delayed senescence and reduced ethylene responsiveness (Chang et al., 2003). Auxins and gibberellic acid *(GA)* also influence flower senescence, though their effects are less understood. While auxins can stimulate senescence in some ethylene-sensitive flowers, *GA* has been shown to delay senescence in some species by antagonizing ethylene (Saks et al., 1992). Jasmonic acid is another hormone that can promote senescence by increasing *ACC* levels and stimulating ethylene production, although its role in specific flowers remains varied (Setyadjit et al., 2006).

5.3. Enzymatic Pathways and programmed Cell Death in Floral Senescence

Floral senescence involves programmed cell death *(PCD)***,** critical enzymatic activities, and structural modifications in floral tissues. PCD in floral tissues encompasses processes similar to apoptosis and autophagy, where the cell undergoes controlled dismantling (Fig. 6). Key enzymes, such as proteases**,** lipoxygenases**,** and cell wall-degrading enzymes**,** are essential in the breakdown of cellular components during senescence (Zhu et al., 2016; Li et al., 2021). These enzymes facilitate the degradation of proteins, lipids, and polysaccharides, which are vital in the progression of senescence. Structural changes associated with floral senescence include cell wall degradation**,** chlorophyll breakdown**,** and cell collapse**,** leading to visible signs of aging, such as petal wilting and color loss (Yuan et al., 2020; Li et al., 2023). Understanding these molecular and structural mechanisms is crucial for developing strategies to manage and extend flower longevity by delaying senescence and enhancing post-harvest quality (Kim et al., 2022).

Programmed cell death *(PCD)* is a hallmark of floral senescence and involves chromatin condensation, cellular shrinkage, and cell collapse (Fig. 6). This process is orchestrated by senescence-associated proteins and enzymes that contribute to the ultimate death of cells in the senescing tissue (Moulin et al., 2013). The precise regulation of *PCD* during senescence ensures that cellular resources are efficiently dismantled, which is crucial for the overall plant's response to aging and stress.

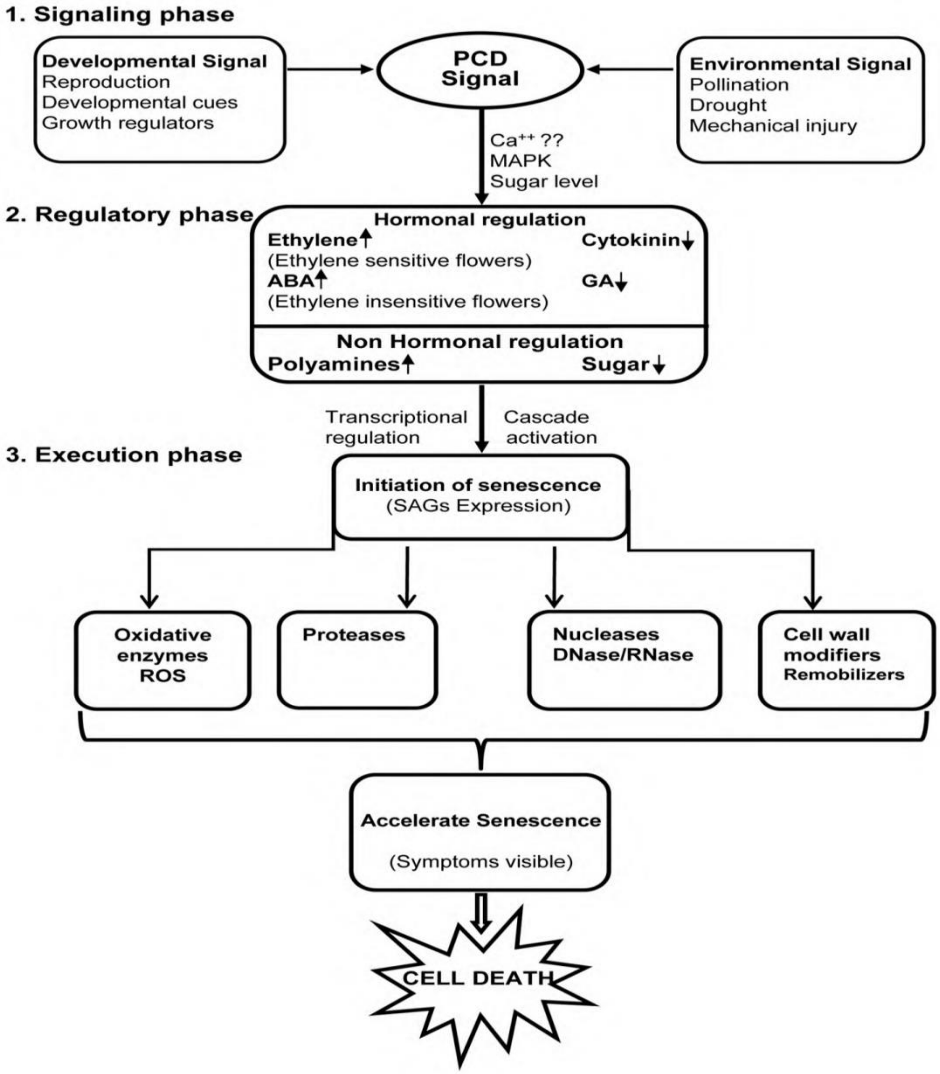

Figure 6: A model for regulatory pathways in flower senescence (Li et al., 2023). The *PCD* signal is generated by both external and internal stimuli and transduced by some signals resulting hormonal imbalance in the cell. This altered level of hormones further activates several cascade and transcriptional regulation. The initiation of senescence starts with expression of several *SAGs* like proteases, nucleases, wall degrading and oxidative enzymes. Now the collective actions of all these enzymes accelerate the senescence process and it became irreversible. At the later stage of senescence symptoms become visible and ultimately lead to cell death of flowers.

Senescence in plants involves physiological and biochemical changes, such as water loss from tissues, ion leakage, and transport of metabolites, along with the generation of reactive oxygen species *(ROS)*, increased membrane fluidity, and lipid, protein, nucleic acid, and carbohydrate hydrolysis. Membrane degradation is a characteristic early event in senescence, leading to structural changes like vacuolar vesiculation and loss of membrane permeability, as observed in carnations and daylilies (Stead and van Doorn, 1994). This process is associated with a decrease in membrane phospholipids and an increase in neutral lipids, largely due to the activation of phospholipases and acyl hydrolases (Hempel et al., 2001). Lipid peroxidation, mediated by lipoxygenases, plays a key role in membrane damage in flowers like carnations (Hong et al., 2000), daylilies (Kende and Zeevaart, 1982), and roses (Lennon et al., 1994). In ethylene-sensitive plants, lipoxygenase activity contributes to oxidative damage, accelerating senescence (Pichersky et al., 1983). However, in ethylene-insensitive flowers like Alstroemeria, lipoxygenase does not appear to be involved in senescence (Leverentz et al., 2002). Interestingly, in plants like Phalaenopsis, lipoxygenase seems to have no significant role in the senescence process (Lennon et al., 1994). These findings highlight the complex nature of senescence and its dependence on species-specific responses to ethylene and lipid peroxidation.

The exploration of transcription factors and their influence on senescence pathways has revealed their essential roles in regulating aging. For instance, the *ORE1* transcription factor integrates ethylene signaling with the expression of senescence-related genes in *Arabidopsis* (Balazadeh et al., 2010). NAC transcription factors, such as *ANAC092*, have been shown to influence cell death and stress responses, further connecting ethylene signaling with plant aging (Wu et al., 2009). Furthermore, *WRKY53* and *MYB* transcription factors interact with other signaling pathways to regulate senescence (Miao et al., 2004; Sablowski & Meyerowitz, 1998). Ethylene Response Factors *(ERFs)*, particularly ERF1, also play a crucial role in mediating the effects of ethylene on stress responses and senescence (Solano et al., 1998). These insights into transcriptional regulation are vital for developing strategies to manage floral senescence and improve plant longevity.

5.4. Advances in Ethylene Signaling and Senescence Research: Inhibitors, Genes, Markers, and Transcription Factors

Recent research into ethylene's role in plant senescence has significantly advanced the understanding of its impact on longevity through complex signaling mechanisms (Fig. 7). Ethylene receptors, such as *ETR1* and *ERS1*, are central to ethylene perception and signal transduction. Ongoing studies continue to explore their interactions and regulatory mechanisms, particularly in relation to how these receptors influence downstream signaling components and senescence progression (Schaller et al., 2015; Zhang et al., 2023). Key components like *EIN2* and *EIN3/EIL1* have been identified as central regulators of ethylene signaling. EIN2 integrates ethylene signals with other stress and developmental cues through various post-translational modifications, highlighting its critical role in regulating flower aging (Qiao et al., 2012; Liu et al., 2020). This understanding is crucial for developing specific inhibitors targeting these pathways to manage flower aging effectively. Advances in ethylene biosynthesis research have led to the development of inhibitors that selectively block ethylene production, offering significant potential for extending the shelf life of fruits and flowers. Compounds like amino-ethoxyvinyl-glycine *(AVG)* and *CoA* inhibitors target enzymes such as *ACC* synthase and *ACC* oxidase to reduce ethylene production, thereby slowing the aging process in flowers (Liu et al., 2019). Moreover, selective antagonists like 1-methylcyclopropene *(1-MCP)* bind to ethylene receptors, preventing ethylene from triggering the senescence process (Sisler & Serek, 1997).

Recent studies also focus on modulators that target signaling components like *EIN3* and *ERF1*, offering opportunities to fine-tune ethylene responses to enhance crop management and stress resilience (Huang et al., 2016; Klee & Tieman, 2020). Also, recent research highlights that transcription factors such as *WRKY53* and *ERF1* have been identified as critical regulators of leaf senescence due to their role in modulating gene expression linked to aging processes (Miao et al., 2004; Fujimoto et al., 2000).

5.4.1. Regulation of Leaf Senescence by Ethylene and Transcription Factors

Ethylene plays a crucial role in regulating leaf senescence, with its signaling pathway linked to both the promotion and inhibition of this process (Fig. 7). Studies have shown that ethylene production is associated with leaf senescence, with the ethylene receptor *ETHYLENE RESISTANT1 (ETR1)* serving a repressive role in this pathway. Mutations in ethylene receptors, such as the etr1 mutation in Arabidopsis and petunia, delay leaf senescence (Grbić and Bleecker, 1995; Wang et al., 2013). Conversely, Arabidopsis mutants lacking ethylene receptor genes exhibit accelerated senescence, indicating a constitutive ethylene response (Qu et al., 2007). The key protein *EIN2* positively regulates leaf senescence, as evidenced by mutations in *EIN3* that delay senescence and overexpression that accelerates it (Li et al., 2013; Kim et al., 2014). However, the role of *CTR1* in this process remains unclear, as mutants show no precocious leaf senescence (Jing et al., 2005).

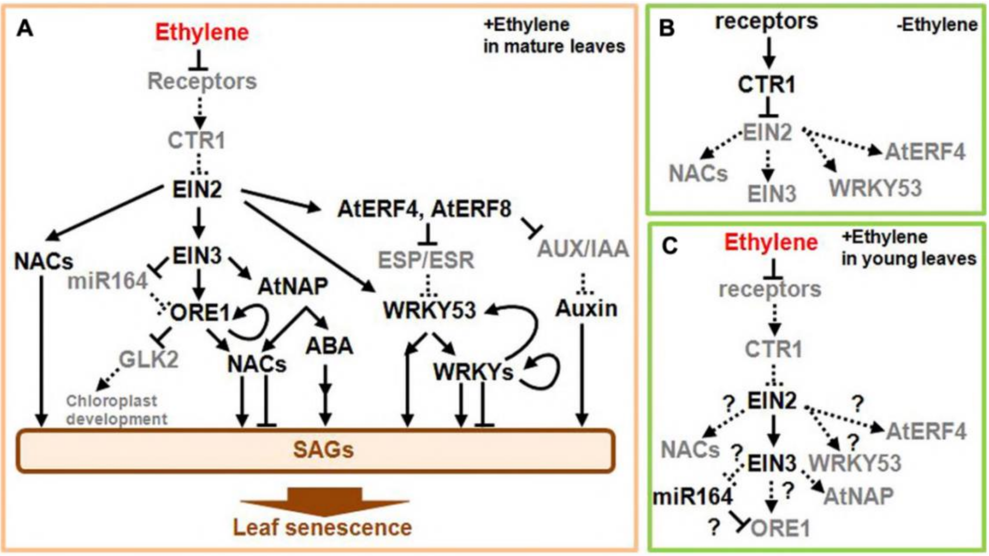

Figure 7: Scheme of the ethylene signaling pathway leading to the onset of leaf senescence (Zhang et al., 2014). **(A)** In mature leaves, the detection of ethylene activates the downstream signaling pathway leading to *SAG* induction and leaf senescence; **(B)** In young and mature leaves, the receptors constitutively repress the downstream signaling in the absence of ethylene; **(C)** In young leaves, the detection of ethylene activates the downstream signaling pathway, but doesn't itself induce leaf senescence.

Note that *EIN2* and *EIN3* are active and induce some ethylene responses, but not leaf senescence by an uncharacterized mechanism, in which some regulators of leaf development are likely involved. Arrows and bars at the end of each line show positive and negative regulations, respectively. Solid lines and black gene names designate the active form, while dotted lines and gray gene names indicate the inactive form. Several transcription factors *(TFs)* and signals such as jasmonic acid *(JA)* are not drawn in this scheme owing to space limitations.

Transcription factors *(TFs)*, particularly *NAC* proteins, play a significant role in ethylene-mediated leaf senescence. Several *NAC* genes, including *ORESARA1 (ORE1)* and *ANAC019*, are activated by ethylene through the *EIN2* pathway (Kim et al., 2009, 2014). *ORE1*, in particular, is crucial for the onset of senescence, as it activates its own expression and other genes involved in the senescence process (Kim et al., 2009). *ORE1* activity is regulated by microRNA miR164, whose levels decrease with leaf aging, facilitating *ORE1* accumulation (Kim et al., 2009). Additionally, *EIN3* directly activates *ORE1* expression, reinforcing the involvement of ethylene signaling in regulating leaf senescence (Li et al., 2013). Other *NAC* genes, such as *AtNAP*, play roles in the ABA signaling pathway, promoting both leaf senescence and stress responses (Guo and Gan, 2006). Some NAC genes act downstream of *ORE1* and *AtNAP*, influencing leaf senescence through various mechanisms, including stress responses and hormone signaling (Kim et al., 2014).

Ethylene-responsive transcription factors *(ERFs)* are also central to the regulation of leaf senescence. A subgroup of ERF proteins, including *AtERF4* and *AtERF8*, act as positive regulators of senescence, promoting the repression of negative regulators like the *EPITHIOSPECIFIER PROTEIN (ESP/ESR),* which inhibits senescence (Miao and Zentgraf, 2007). The expression of ERFs is modulated by age and ethylene, with increased accumulation in older leaves (Koyama et al., 2013). In contrast, other *ERFs,* such as *RAV1,* negatively regulate leaf senescence, with overexpression delaying the process (Woo et al., 2010). Additionally, interactions between WRKY TFs and ethylene signaling suggest a complex network that integrates ethylene and jasmonic acid *(JA)* signals during leaf senescence. WRKY53, for instance, is modulated by both ethylene and JA, influencing leaf senescence (Miao and Zentgraf, 2007; Breeze et al., 2011). The cooperation of these *TFs,* along with environmental and developmental factors, determines the timing of leaf senescence, ensuring a regulated and context-dependent response to ethylene signaling.

5.4.2. Ethylene-Mediated Gene Regulation and Senescence: Signaling, Hormonal Interactions, and Mechanisms

Ethylene is a pivotal plant hormone that regulates a range of physiological processes, including fruit ripening, leaf and flower senescence, and stress responses, through intricate signaling pathways (Jiang et al., 2023). Ethylene perception begins when the hormone binds to its receptors, such as *ETR1*, *ETR2*, *EIN4*, and *ERS1*, located in the endoplasmic reticulum (Schaller et al., 2015). This binding triggers a signaling cascade involving the *CTR1* kinase, which inhibits ethylene signaling until *EIN2* accumulates and translocates to the nucleus. In the nucleus, *EIN3* and *EIL1* transcription factors are activated, driving the expression of ethylene-responsive genes by binding to ethylene response elements *(EREs*) (Alon et al., 2003; Chao et al., 1997). During floral senescence, ethylene accelerates aging by upregulating senescence-associated genes *(SAGs)* such as *SAG12,* which encodes a cysteine protease involved in protein degradation (Gepstein et al., 2003), and by regulating programmed cell death (Buchanan et al., 2000). Ethylene also coordinates the regulation of Ethylene Response Factors *(ERFs),* which mediate stress responses and developmental processes (Solano et al., 1998). In fruit ripening, ethylene enhances softening and regulates genes associated with cell wall degradation and flavor (Brummell, 2020; Klee and Giovannoni, 2021).

As mentioned earlier, Ethylene interacts with other plant hormones to regulate stress responses and defense mechanisms. For example, ethylene collaborates with abscisic acid *(ABA)* and jasmonic acid *(JA)* to modulate stress responses and pathogen defense pathways (Fujita et al., 2023; Sakuma et al., 2022). This cross-talk between hormones is essential for coordinating plant responses to environmental stressors. Furthermore, ethylene's influence on gene regulation involves activation, repression, and post-transcriptional modifications. Ethylene promotes gene activation by facilitating the binding of transcription factors such as *EIN3* and *ERFs* to specific *DNA* sequences in gene promoters (Alon et al., 2003). In contrast, ethylene can repress genes associated with Jasmonate ZIM-Domain *(JAZ)* proteins, which play a role in modulating defense responses (Chini et al., 2007). Additionally, ethylene affects the regulation of microRNAs *(miRNAs)*, which control mRNA stability and translation, as well as alternative splicing, producing different protein isoforms involved in stress responses and senescence (Zhao et al., 2022; Morris and Kramer, 1998).

Post-Translational Modifications and WRKY Transcription Factors and enzymes play a critical role in the regulation of gene expression. WRKY transcription factors, which are involved in regulating both defense and senescence-related genes, are also modulated by ethylene (Rushton et al., 2010). These modifications impact their stability and activity, further enhancing the fine-tuning of senescence and stress responses at the molecular level (Zhao et al., 2022). Transcription factors such as *NAC* and *MYB* play significant roles in regulating genes involved in cell death and stress responses, further driving the senescence process (Kim et al., 2009; Solfanelli et al., 2006). These transcription factors are involved in activating the expression of genes that regulate programmed cell death *(PCD)* and tissue degradation, essential for the progression of senescence. Their actions contribute to the dismantling of cellular structures and the overall decline in cell function during senescence.

Transgenic plants with suppressed *ACS* or *ACO* genes show delayed senescence and longer floral display life, as seen in carnations and other ornamental species (Savin et al., 1995; Kiss et al., 2000; Huang et al., 2007). The upregulation of ethylene-related genes in senescing flowers is often accompanied by increased ethylene production and activation of transcription factors such as *ETHYLENE RESPONSE FACTORS (ERFs)*, which regulate the expression of senescence-associated genes (Liu et al., 2011). Studies in petunia and Arabidopsis show that modifying the expression of ethylene receptors and signaling pathways can delay flower senescence and enhance flower longevity (Gubrium et al., 2000; Shibuya et al., 2004).

Ethylene Inhibitors in Floral Senescence Management indicates that inhibitors are critical tools for managing floral senescence and improving flower quality. Ethylene receptor antagonists, such as 1-Methylcyclopropene *(1-MCP)*, block ethylene binding and signaling, thereby extending the vase life of flowers (Sisler and Serek, 2021). Biosynthesis inhibitors like Silver Thiosulfate *(STS)* prevent ethylene production by inhibiting *ACC* oxidase (Lester and Dunlap, 1985). Other inhibitors, including cyclohexylamine and natural extracts from ginger and garlic, disrupt ethylene signaling pathways (Buchanan et al., 2000; Bai et al., 2015).

Technological advancements, such as controlled atmosphere storage and slow-release formulations, have enhanced the efficiency of ethylene inhibitors in large-scale applications (Paull, 2022; Serek et al., 2023). These inhibitors are widely employed in floriculture to extend vase life, manage flowering schedules, and reduce waste, ultimately benefiting post-harvest management and improving commercial flower production (De Meyer et al., 2012; Serek et al., 2023). By manipulating key components of the ethylene signaling network, such as transcription factors and receptor antagonists, the floriculture industry can mitigate the aging process of cut flowers and improve their shelf life. Moreover, the development of novel inhibitors and technological applications will continue to play a significant role in managing senescence and enhancing flower quality in commercial settings.

5.4.3. Dynamics of DNA Methylation in Leaf Senescence

DNA methylation plays a critical role in regulating plant leaf senescence, with significant changes in methylation patterns occurring as leaves age (Fig. 8). In Arabidopsis, there is a global decline in DNA methylation during senescence, associated with the downregulation of DNA methyltransferases like *CMT3* and *MET1*, and an upregulation of demethylase genes such as *ROS1*, *DME*, *DML2*, and *DML3* (Ogneva et al., 2016). This shift in *DNA* methylation levels affects the expression of genes linked to aging. For instance, in Gossypium hirsutum, DNA methylation decreases at specific regions, including promoters and *CpG* islands in senescent tissues, which correlates with metabolic changes (Dou et al., 2017). Studies on bamboo and rice also highlight the dynamic nature of *DNA* methylation during senescence, with changes in methylation contexts, such as *CG, CHH,* and *CHG,* influencing the expression of genes involved in senescence and stress responses (Zhang et al., 2021; Moritoh et al., 2012).

The regulation of *DNA* methylation during senescence is largely governed by the balance between *DNA* methyltransferases and demethylases. In Arabidopsis, mutations in methyltransferases like *MET1* or the loss of the demethylase *DML3* result in abnormal senescence progression, underlining the critical role of *DNA* methylation in regulating senescence-associated genes (Kim et al., 2008; Yuan et al., 2020). For example, the loss of *DML3* leads to increased *DNA* methylation at promoters of senescence-related genes, which delays their expression and slows the senescence process (Yuan et al., 2020). Conversely, the demethylase *ROS1* accelerates senescence by modulating the methylation status of specific regions, further influencing the timing of senescence. Studies on tomato and pak choi reinforce the idea that *DNA* methylation, particularly in the promoter regions of senescence-related genes, plays a vital role in regulating the onset of senescence (Zhu et al., 2015; Li et al., 2022). The intricate interplay between *DNA* methyltransferases and demethylases in controlling *DNA* methylation during senescence highlights the complexity of epigenetic regulation of leaf aging in plants.

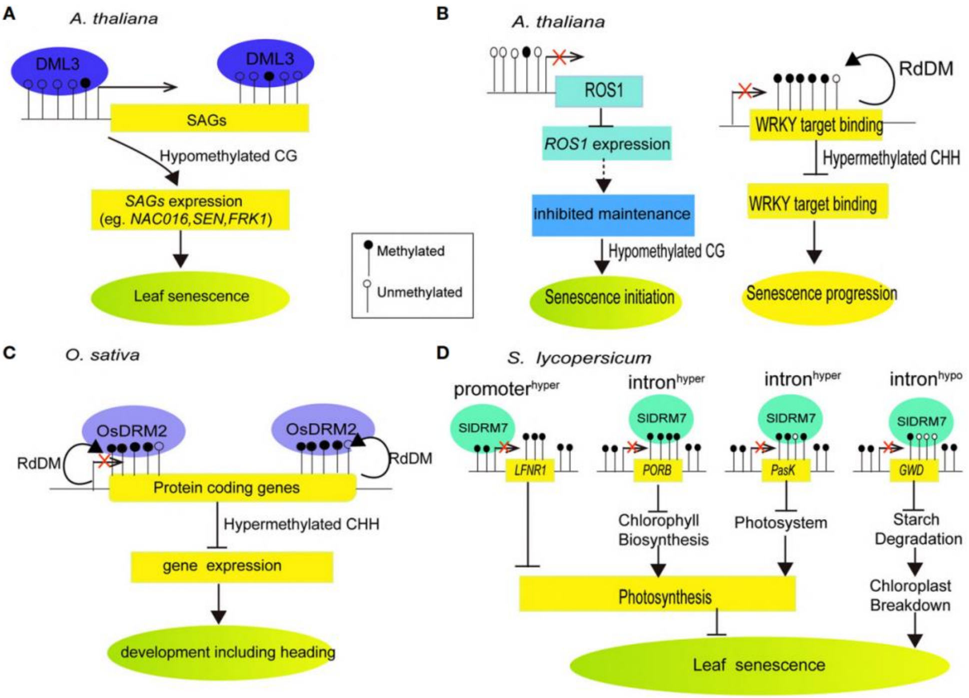

Figure 8: Senescence Research Advances indicating Summarized models of Gene regulation through targeted gene transcription and metabolism-related aging in different plant species. (A) In Arabidopsis, *DNA* demethylase *DML3* reduces *CG* methylation in gene regions, activating senescence-associated genes and promoting leaf senescence (Yuan et al., 2020); (B) *ROS1*, a *DNA* demethylase, is involved in leaf senescence in Arabidopsis. Reduced *ROS1* expression during senescence indicates decreased demethylation activity, with *CG* hypomethylation attributed to inhibited maintenance (Vatov et al., 2022); (C) In rice, *DNA* methylase *OsDRM2* regulates development and heading by controlling CHH methylation, particularly in small TEs near protein-coding genes (Moritoh et al., 2012; Tan et al., 2016); (D) In tomato, *DNA* methylase *SlDRM7* influences leaf chlorosis and senescence. Silencing *SlDRM7* disrupts *DNA* methylation and gene expression related to chlorophyll synthesis, photosynthesis, and starch degradation, leading to senescence and chlorosis (Wen et al., 2022).

Isolating and characterizing senescence-related genes involves various advanced techniques to understand plant aging at the molecular level (Fig. 8). For instance, Gene expression profiling, including microarrays and RNA sequencing (RNA-Seq), identifies critical genes involved in senescence, such as *SAG12* and *SAG21* (Gepstein et al., 2003; Ding et al., 2012). These methods help elucidate the molecular networks underlying aging by quantifying gene expression levels across various developmental stages. Functional analyses, including gene knockout and overexpression studies using *CRISPR/Cas9*, *RNA* interference *(RNAi)*, and transgenic approaches, help determine the roles of these genes in the aging process (He et al., 2004; Liu et al., 2023). These techniques allow for the precise manipulation of candidate genes to understand their contributions to plant senescence at both molecular and phenotypic levels.

Complementary methods, such as yeast two-hybrid screening and co-immunoprecipitation, investigate protein–protein interactions and regulatory mechanisms that govern senescence-related gene expression (Choi et al., 2008; Gregersen et al., 2008). These techniques enable the identification of key regulatory proteins and complexes involved in the senescence process. Furthermore, integrating transcriptomic, proteomic, and metabolomic approaches provides a comprehensive view of how these genes influence cellular functions and metabolic pathways during senescence (Miller et al., 2007; Munne-Bosch and Pallas, 2007). Combining these multi-omics data enhances our understanding of the complex network of gene expression, protein activities, and metabolic shifts that occur as plants undergo senescence.

Key genes such as *SAG12*, a cysteine protease, and *ORE1*, a transcription factor, are pivotal for understanding and potentially enhancing crop longevity and quality through genetic and agricultural innovations (Gepstein et al., 2003; He et al., 2004). Techniques like *RT-PCR*, high-throughput sequencing, and bioinformatics tools have significantly advanced the practical application of these findings in plant breeding and crop improvement (Saha et al., 2017; Zhao et al., 2017).

5.4.4. Role of Ethylene in Fruit Ripening

Ethylene plays a crucial role in the ripening of climacteric fruits, where it regulates key processes such as color, texture, and the production of volatile organic compounds *(VOCs)* (Fig. 9). Ethylene promotes the breakdown of chlorophyll, enhances the synthesis of carotenoids and anthocyanins, and triggers the biosynthesis of *VOCs*, which contribute to the characteristic aroma of ripe fruits (Barry & Giovannoni, 2007). Inhibiting ethylene biosynthesis or its signaling pathways has been shown to reduce *VOC* production, as seen in transgenic apples and melons expressing antisense genes for ethylene biosynthesis enzymes like *ACS* and *ACO* (Dandekar et al., 2004; Bauchot et al., 1998). Ethylene's regulation of *VOCs* is also influenced by inhibitors like *AVG* and *1-MCP*, which either block ethylene biosynthesis or its action, respectively, and can reverse or enhance the synthesis of *VOCs* depending on the context (Valdes et al., 2009).

The ripening process of fruits is closely linked to their ethylene production and respiration patterns, classifying fruits into climacteric and non-climacteric types. In climacteric fruits, such as tomatoes, ethylene production increases and reaches a peak during ripening, promoting autocatalytic ethylene biosynthesis (Lelièvre et al., 1998). This system is characterized by two stages: a low ethylene production phase where the fruit is unripe and insensitive to external ethylene (System 1), followed by a stage of high ethylene production where the fruit becomes responsive to exogenous ethylene (System 2). The regulation of this ethylene production is controlled by genes like *ACS6* and *ACS1*, which play pivotal roles in the synthesis of ethylene (Alexander & Grierson, 2002). The inhibition of ethylene action is a common post-harvest technique to extend the shelf life of climacteric fruits, delaying ripening and senescence.

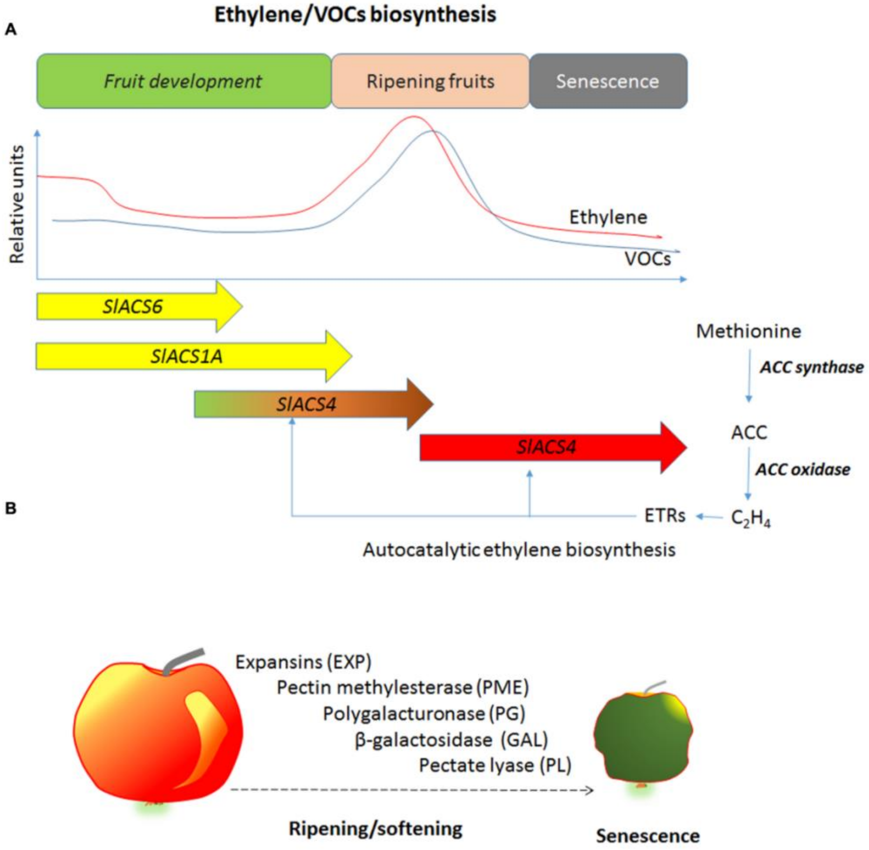

Figure 9: (A) Schematic and simplified ethylene and *VOCs* biosynthesis during fruit development (Kevany & Klee, 2007). SlACS (Solanum lycopersicum *ACC* synthase) families are differentially expressed during fruit development. *VOCs* biosynthesis derives from different pathways such as phenylpropanoids, fatty acid, and carotenoids degradation. **(B)** The main enzymes involved in cell wall degradation during fruit ripening and senescence. The action of these enzymes induces loss of firmness and softening.

Ethylene also regulates the expression of several genes that influence fruit ripening. In tomatoes, ethylene affects genes like polygalacturonase *(PG)*, pectin methylesterase *(PME)*, and phytoene synthase, all of which are involved in cell wall degradation and fruit pigmentation (Smith et al., 1988; Fray & Grierson, 1993). Studies on the ethylene receptor in tomatoes, including the *LeETR4* and *LeETR6* genes, have shown their involvement in both flowering and ripening processes (Tieman et al., 2000; Kevany et al., 2007). In the mutant Never-ripe tomato, which exhibits reduced ethylene sensitivity, alterations in gene expression, fruit morphology, and carotenoid biosynthesis further highlight ethylene's central role in regulating fruit development and ripening (Alba et al., 2005). Moreover, the E8 gene in tomato is involved in regulating ethylene biosynthesis and signaling during ripening, with its expression increasing as the fruit matures (Penarrubia et al., 1992).

Fruit softening, a critical quality indicator, is primarily driven by cell wall degradation, which is regulated by various enzymes, including pectin methylesterases *(PMEs)*, polygalacturonase *(PG)*, cellulase, galactosidases, pectate lyase *(PL)*, and expansins. These enzymes, encoded by multi-gene families, are spatially and temporally regulated and activated during fruit ripening and senescence. Ethylene plays a pivotal role in modulating the expression of these enzymes, with its action facilitating cell wall degradation, leading to fruit softening. Expansins, in particular, assist in cell matrix enlargement during ripening, and their activity is regulated by pH and ethylene levels. For example, during tomato ripening, ethylene induces the *EXP1* gene, while inhibition of ethylene biosynthesis reduces its expression (Rose et al., 1997). This pattern of enzyme regulation by ethylene is observed in other climacteric fruits like banana (Trivedi and Nath, 2004).

PME is an essential enzyme activated prior to ripening that de-esterifies pectin, making it susceptible to degradation by *PG.* This enzyme is stimulated by ethylene and plays a critical role in the softening of fruit during senescence (El-Sharkawy et al., 2016). Similarly, *PG,* which hydrolyzes the bonds in galacturonic acid, is activated by ethylene and is involved in the breakdown of the cell wall (Sitrit and Bennett, 1998). β-galactosidase also contributes to fruit softening by breaking down β-(1,4)-galactans in the cell wall (Eda et al., 2016). Transgenic tomatoes with antisense β-galactosidase show higher firmness during ripening, and ethylene exposure in avocado increases its activity (Jeong and Huber, 2004; Karakurt and Huber, 2002). PL, another key enzyme in cell wall breakdown, also shows increased activity in the presence of ethylene, as seen in bananas and mangoes (Lohani et al., 2004; Chourasia et al., 2006).

The regulation of fruit senescence by ethylene is intricately linked with other plant hormones (Liu et al., 2023). These hormones interact to regulate growth, senescence, and fruit ripening, influencing traits such as yield, appearance, and shelf life (Zhang et al., 2022). The understanding of how ethylene interacts with other phytohormones, especially in regulating post-translational processes, offers potential strategies for enhancing crop quality and longevity (Wu et al., 2021). Ethylene's impact on plant performance, particularly under stress conditions, depends on the balance between its biosynthesis and perception, which is influenced by other hormones (Chen et al., 2023). Further studies on these hormonal interactions at different developmental stages and plant organs could help optimize agricultural practices, particularly in extending the shelf life of climacteric fruits (Liu et al., 2023).

6. Advances and Gaps in Ethylene Inhibitors and Technological Interventions for Enhancing Floral Quality and Longevity

Advances in gene expression profiling, functional analyses, and multi-omics approaches have revealed key genes and transcription factors involved in the senescence process, while ethylene and other hormones modulate the aging process at both the molecular and physiological levels. Furthermore, the understanding of enzymatic activities during senescence enhances our ability to manipulate and improve the longevity and quality of crops. The combination of these approaches offers promising avenues for enhancing agricultural practices and developing crops with extended shelf life and improved resilience. Ethylene inhibitors, such as 1-Methylcyclopropene *(1-MCP),* have become essential tools in extending the vase life of cut flowers. By blocking ethylene receptors, *1-MCP* prevents ethylene from exerting its effects, delaying senescence, and preserving flower quality (Blankenship & Dole, 2023). Other inhibitors, including silver compounds (such as Silver Thiosulfate) and Amino-ethoxyvinyl-glycine *(AVG)*, either inhibit ethylene biosynthesis or act as receptor antagonists to reduce ethylene's impact on floral aging. In addition to these chemical interventions, recent advances in genetic engineering have contributed significantly to extending floral longevity. By creating transgenic plants with reduced ethylene production or modified ethylene receptor activity, researchers have developed innovative approaches to enhance flower preservation (Zhao et al., 2021). These breakthroughs provide long-term solutions for improving the preservation of cut flowers.

In parallel with chemical inhibitors, technological interventions have played a crucial role in enhancing floral quality and longevity. Controlled

Atmosphere Storage *(CAS)* and Modified Atmosphere Packaging *(MAP)* are commonly employed to regulate environmental conditions and gas composition, suppressing ethylene production and enhancing the freshness of flowers (Lafuente et al., 2011; Ning et al., 2020). Another effective strategy is the use of ethylene scrubbers, which remove ethylene from the air, often utilizing materials like potassium permanganate (Wiley & Roupas, 1991). The combination of these chemical and technological methods provides a holistic approach to managing ethylene-related senescence and maintaining the quality of flowers post-harvest.

Recent research has significantly deepened our understanding of the molecular mechanisms driving floral senescence. Studies have highlighted the roles of key transcription factors, such as *WRKY* and *MYB,* which regulate genes involved in cell wall degradation, chlorophyll breakdown, and pigment loss during senescence (Li et al., 2020). In orchids, ethylene signaling has been shown to accelerate the expression of stress response genes, contributing to aging processes (Liu et al., 2021). By understanding these intricate molecular processes, researchers are able to identify targets for new strategies aimed at improving flower longevity and managing senescence.

Looking ahead, future advancements in floral senescence research will focus on optimizing both ethylene inhibitors and genetic modification techniques. CRISPR/Cas9 technology offers the potential for precise genetic modifications that could enhance flower longevity by directly influencing ethylene biosynthesis and signaling pathways (Gepstein *et al*., 2021). Additionally, innovations in smart packaging and controlled atmosphere storage will further enhance flower preservation by better regulating the internal environment of floral products (Zhao *et al*., 2021). Continued collaboration between researchers and the floriculture industry will be critical for translating these advancements into practical applications, ultimately improving the quality and longevity of flowers in commercial and consumer markets (Kader, 2002; Lafuente et al., 2011).

7. Conclusion, Recommendations, and Future Research Directions

Advances in understanding floral senescence and ethylene regulation have significantly impacted the floriculture industry, revealing complex molecular mechanisms and offering new strategies to enhance flower longevity and quality. Key insights include the role of ethylene as a major regulator, the identification of senescence-related genes such as *SAG12* and *SAG13,* and the development of technologies like ethylene inhibitors and controlled atmosphere storage. These findings suggest that targeted genetic modifications and advanced postharvest technologies can substantially extend flower vase life and improve overall quality.

Recommendations include the continued exploration of molecular pathways and ethylene regulation to discover new targets for intervention. Investment in advanced genomic tools, synthetic biology, and microbiome studies can further enhance our ability to manage floral senescence. Developing and applying these technologies will require interdisciplinary collaboration and strong industry partnerships to translate research into practical applications.

Future research directions should focus on bridging knowledge gaps in regulatory networks and post-translational modifications, and on leveraging synthetic biology to design precise genetic circuits for senescence control. Investing in these areas, along with fostering industry-academic collaborations, will drive innovation and improve the sustainability and profitability of the floriculture sector. Enhanced flower preservation not only benefits growers and distributors through reduced waste and improved quality but also offers consumers longer-lasting, more appealing flowers. Focused areas will include:

1. Integration of advanced techniques such as *CRISPR/Cas9* gene editing, which allows for precise modifications of specific genes associated with flower quality and longevity.
2. Development of cultivars with tailored traits, such as enhanced resistance to ethylene and improved postharvest characteristics.

3. Integrating real-time monitoring and control systems into postharvest practices could provide more effective management of flower quality throughout the supply chain
4. Integrating consumer insights with advanced technologies, such as artificial intelligence and machine learning, to predict and respond to consumer preferences more effectively.
5. Enhanced data collection methods and predictive analytics can offer deeper insights into evolving consumer trends, enabling the industry to adapt quickly and maintain high standards of flower quality and longevity.

Data availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflict of interest

The author has no conflict of interest with anyone regarding the review paper.

Ethical Clearance

The author follows all ethical guidelines necessary to produce the review paper.

Acknowledgment

The author would like to acknowledge all the resources used in review paper are properly addressed.

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