Coordinated Regulation: Interplay between Ethylene and ABA in Fruit Ripening and Development

Abstract

Ripening is crucial for seed dispersal and the survival of plants. Both climacteric and non-climacteric fruits exhibit fleshy characteristics. Ethylene and abscisic acid (ABA) enhance respiration in climacteric fruits such as apples and pears during ripening. Non-climacteric fruits, such as strawberries, primarily ripen in response to abscisic acid (ABA). Recent studies indicate that ethylene and ABA interact in complex ways to regulate fruit ripening. Research on climacteric fruits, such as tomatoes, has identified ethylene biosynthesis genes, including *LeACS1*, *LeACS2*, and *LeACO1*. These genes are crucial for ethylene synthesis and exhibit increased expression in response to ABA supplementation. Abscisic acid (ABA) stimulates the expression of ethylene biosynthetic genes in bananas and berries, thereby facilitating the ripening process. In berries, endogenous ethylene activates the *VvNCED1* gene, leading to the production of ABA, thereby illustrating their reciprocal relationship. Ethylene and ABA exhibit either synergistic or antagonistic interactions depending on the specific context, representing a significant finding in this area of study. Ethylene has the capacity to inhibit ABA signaling pathways, thereby delaying stomatal closure, as demonstrated in studies utilizing ethylene signaling mutants such as *eto-1* (an ethylene over-producing mutant) and *etr1-1* or *ein3-1* (ethylene-insensitive mutants). Ethylene and ABA potentially influence physiological processes through a complex hormonal interplay. Ripening is regulated by hormones and environmental factors such as temperature, humidity, and light. The aforementioned factors substantially influence the biosynthesis and activity of ripening hormones, enzymes, and pigments. Advancements in agricultural technology facilitate precise post-harvest management of these factors, thereby optimizing fruit quality and extending shelf life. Research into the genetic and molecular mechanisms of ripening has led to an expansion of innovation. Utilizing CRISPR-Cas9 to target ripening-related genes allows researchers to improve fruit characteristics, extend shelf life, and minimize post-harvest losses. Modifications in ethylene and ABA biosynthesis or signaling pathways can yield fruits with customized ripening timelines for international food markets. Examining the evolutionary significance of ripening reveals the adaptations of plants' reproductive strategies to various ecological niches. Ripening enhances seed dispersal and viability in optimal conditions. The investigation of these processes is essential because of their ecological and agricultural implications. Fruit ripening research demonstrates the interaction between ethylene and ABA, elucidating a complex hormonal network that integrates genetic, biochemical, and environmental signals. This research has the potential to transform fruit cultivation and storage, thereby enhancing global food security and sustainability initiatives. Future research will employ advanced technologies to enhance the understanding of plant development and adaptation.

Keywords: Ethylene, Abscisic acid (ABA), Fruit ripening, Climacteric fruits ,Hormonal interplay

Introduction:

The plant life cycle is a complex system, with seed development and dispersal being crucial for the survival of the next generation. Seed dispersal involves various mechanisms, and its rate is influenced by physical, biological, external, and internal conditions surrounding the plant. To ensure effective seed dispersal and protection under unfavorable conditions, plants have evolved diverse strategies. These strategies not only facilitate dispersal but also safeguard seeds from predation and physical damage. Initially, seeds are encased within the fleshy ovary wall, forming what is known as a fleshy fruit. During dormancy, seeds remain within a dry fruit. The ripening process, which is critical for seed dispersal, involves the coordinated formation and degradation of genes, RNA, and proteins. Watada *et al*. (1984) defined ripening as "the changes that occur from the latter stages of growth and development through the early stages of senescence, resulting in characteristic aesthetic and/or food quality changes." Ripening is a highly intricate process, primarily governed by ethylene in climacteric fruits and abscisic acid (ABA) in non-climacteric fruits (Giovannoni, 2001; Klee & Giovannoni, 2011). Both hormones are interconnected and play essential roles in regulating the ripening process. Ripening encompasses numerous physiological and biochemical changes, including gene expression, enzyme activity, and hormone signaling, resulting in the fruit's final characteristics, such as color, texture, flavor, and aroma. These changes are vital for effective seed dispersal and survival. Ethylene serves as a signaling molecule that initiates a cascade of events in climacteric fruits, including increased respiration, enzyme activity, and the synthesis of ripening-related proteins (Alexander & Grierson, 2002). In non-climacteric fruits, ABA regulates stress tolerance and dormancy in seeds and fruits (Leng *et al*., 2014). Both hormones interact with other signaling pathways, highlighting their multifaceted roles in ripening. Enzymes play a pivotal role in fruit ripening. Cellulases and pectinases degrade cell wall components, leading to fruit softening, while amylases hydrolyze starch into sugars, contributing to flavor development (Brummell & Harpster, 2001). These enzymatic changes enhance the palatability of fruits, attracting dispersal agents. A hallmark of ripening is the change in color due to chlorophyll breakdown and the synthesis of carotenoids and anthocyanins. These pigments act as visual cues to dispersal agents, signaling fruit ripeness (Rodríguez-Concepción *et al*., 2010). Ripening involves the production of volatile compounds, such as esters, sugars, and organic acids, which give fruits their distinctive aroma and flavor. These traits attract animals, facilitating seed dispersal (Baldwin *et al*., 2000). The softening of fruit results from the degradation of pectin and cellulose in the cell walls. This change makes fruits easier for animals to consume, aiding in seed dispersal (Brummell & Harpster, 2001). ABA often induces seed dormancy during ripening, ensuring germination occurs under favorable conditions. As ABA levels decrease, gibberellins and other hormones promote seed germination, highlighting the balance of hormonal regulation (Seo *et al*., 2006). Temperature, humidity, and light significantly impact fruit ripening. For instance, temperature affects enzyme activation rates, while light influences pigment and volatile compound synthesis (Giovannoni, 2004). Extreme temperatures can delay ripening or cause premature senescence. During ripening, plants develop mechanisms to protect seeds, such as hardening seed coats and producing chemical defenses like tannins and alkaloids. Secondary metabolites act as deterrents to herbivores, ensuring seed viability (Seymour *et al*., 2013). Seed dispersal strategies include both biotic and abiotic mechanisms. Animals play a major role in biotic dispersal by consuming fruits and excreting seeds in new locations. Abiotic dispersal involves wind, water, or gravity, aided by structural modifications such as wings or hooks on fruits (Howe & Smallwood, 1982). In agricultural crops, ripening often continues post-harvest, especially in climacteric fruits that produce ethylene even after being picked. Controlled conditions, such as temperature and humidity, optimize post-harvest ripening, enhancing fruit quality for consumption or sale (Saltveit, 1999). At the molecular level, ripening is controlled by a network of genes regulating enzymes, transport proteins, and hormones. Key genes, such as those encoding ethylene biosynthesis enzymes (e.g., *LeACS1*, *LeACS2*) and ABA signaling components, have been identified (Giovannoni, 2007). Advances in genetic research enable the manipulation of ripening processes, improving fruit quality and shelf life. Ripening has evolved as a critical mechanism to ensure reproductive success. By optimizing seed dispersal timing and enhancing seed viability under favorable conditions, ripening supports the continuation of plant species. The diversity of ripening strategies reflects the ecological niches plants occupy and the evolutionary pressures shaping their reproductive adaptations (Janzen, 1971).

Role of Ethylene and Abscisic Acid from Fruit Set to Maturation

Fruit set

Fruit set, the initial phase following pollination, is a critical process regulated by various plant hormones. Recent studies highlight the complex interplay between abscisic acid (ABA) and ethylene in this stage. Following pollination, ABA levels typically decline, as genes responsible for its degradation are upregulated, facilitating fruit set. This reduction in ABA is often accompanied by a decrease in ethylene expression, as these hormones exhibit antagonistic effects during fruit set. Ethylene's inhibitory action on ABA signaling has been observed in several species, further reinforcing this antagonism (Wu *et al*., 2023; Mou *et al*., 2016).Recent work has expanded on this by showing how ABA's role in fruit set and subsequent stages of ripening is influenced by both ethylene and other hormonal pathways. For instance, in tomato, changes in ABA levels affect ethylene production, which in turn modulates the response of ABA. This suggests a coordinated regulation between these two hormones, where ABA may promote the initial stages of fruit development while ethylene becomes more involved later in ripening (Mou *et al*., 2016; Tipu & Sherif, 2024). Furthermore, ongoing research into ethylene signaling mutants like *eto-1* and *ein3-1*, and ABA signaling mutants like *nced1*, provides insights into how hormone antagonism governs fruit set and ripening (Zou *et al*., 2022). These findings underscore the significance of hormone balance in fruit development, highlighting the necessity of precise regulation for successful fruit set and growth.

Fruit Growth:

The growth of fruit and the development of seeds are strongly influenced by plant hormones, particularly abscisic acid (ABA) and ethylene. Both hormones play essential roles in regulating fruit growth, including cell expansion, seed formation, and overall fruit size. Recent research on ABA-deficient mutants has shown that these plants produce smaller fruits, indicating that ABA is crucial for cell expansion and fruit development. For instance, in a study on Arabidopsis and tomato mutants lacking ABA biosynthesis, it was observed that the fruits were smaller and had impaired growth, demonstrating ABA's role in promoting cell division and expansion during early fruit development (Nitsch *et al*., 2012; Finkelstein *et al*., 2016).

Ethylene, on the other hand, has a well-established role in fruit growth and ripening, especially in climacteric fruits. Chromatographic studies have shown that ethylene is present at various stages of fruit development, from the early stages of growth to the final stages of ripening. It is particularly noted for its stimulatory effects on cell expansion and fruit swelling during the later stages of development. Ethylene promotes the enlargement of fruit cells, which contributes to the overall increase in fruit size, particularly in climacteric fruits such as tomatoes, apples, and bananas (Burg, 1965; Rodríguez *et al*., 2017). In addition, ethylene regulates the synthesis of enzymes that break down cell wall components, such as pectin and cellulose, which also leads to fruit softening and expansion during ripening.

In recent studies, the interaction between ABA and ethylene during fruit growth has been investigated in more detail. While ABA is crucial for early fruit development, regulating processes such as seed development and initial cell expansion, ethylene's role becomes more pronounced as the fruit matures, particularly during the final stages of growth and ripening. The balance between these two hormones is essential for the proper development of fruit size and seed formation, and disruptions in this balance can result in abnormal fruit development. Recent work on fruit growth in genetically modified plants, such as those overexpressing or silencing specific ethylene and ABA-related genes, has shed light on how these hormones work together to ensure proper fruit growth (Liu *et al*., 2018; Klee, 2020).

Fruit Maturation:

Fruit maturation represents a critical phase in fruit development, where significant biochemical, physiological, and morphological changes occur. During this stage, both ethylene and abscisic acid (ABA) play essential roles, with ABA being particularly crucial for continued cell expansion and flesh growth. ABA influences various processes, including the regulation of stress responses, seed dormancy, and fruit ripening. It is involved in the regulation of genes responsible for cell wall modification, which is essential for tissue expansion and growth in many fruit species, particularly non-climacteric fruits (Xie *et al*., 2020). Studies have shown that during fruit maturation, ABA levels increase, facilitating the transition from rapid cell division to cell expansion, leading to fruit enlargement. In many fruit species, ABA is necessary for the accumulation of reserves, such as sugars and starches, in the fruit flesh, which contribute to fruit growth and the development of texture and flavor (Finkelstein *et al*., 2008; Zhang *et al*., 2019). In contrast, while ethylene also plays a role in maturation, especially in climacteric fruits, its involvement is primarily linked to the regulation of fruit ripening processes, such as softening and color change, rather than in the expansion of fruit cells during maturation (Burg and Burg 1965). ABA's role in cell expansion during maturation is supported by its ability to modulate the expression of genes involved in the synthesis of pectin and other cell wall components. This leads to cell wall loosening, allowing for fruit enlargement without compromising cell structure (Yoshida *et al*., 2020). Furthermore, ABA interacts with other hormones, such as gibberellins and cytokinins, to fine-tune the balance between cell division, expansion, and differentiation during maturation (García *et al*., 2015). In addition to cell expansion, ABA also influences water balance and fruit firmness, two key factors in fruit maturation. By regulating water uptake and maintaining cellular turgor pressure, ABA helps ensure that fruits grow to their optimal size and maintain texture until they are fully matured (Zhang *et al*., 2019). This is particularly important in fleshy fruits, where water content and cellular integrity are critical for both the quality of the fruit and its ability to withstand external stresses.

Fruit Ripening:

Fruit ripening is a crucial phase of plant development that involves a series of complex physiological, biochemical, and molecular changes. This process results in significant modifications in fruit color, aroma, texture, and nutritional content. These transformations are orchestrated by various plant hormones, with abscisic acid (ABA) and ethylene being the most prominent regulators. Ethylene, in particular, has been extensively studied due to its central role in initiating and promoting the ripening process, especially in climacteric fruits. Climacteric fruits such as apples, bananas, mangoes, and tomatoes undergo a characteristic increase in respiration and ethylene production during ripening, often referred to as the "climacteric rise. Ethylene acts as a signal that triggers the activation of genes involved in color change, softening, and the breakdown of cell wall components like pectin, which is crucial for fruit softening. In tomatoes, for instance, ethylene regulates the expression of genes responsible for carotenoid biosynthesis, leading to the characteristic color change from green to red (Klee and Giovannoni, 2011; Bapat *et al*., 2010). The role of ethylene in fruit ripening has been widely studied in several species, and its effect is well understood in climacteric fruits. In these fruits, ethylene triggers a cascade of reactions that lead to changes in fruit texture, aroma, and taste. For example, in mangoes and bananas, ethylene-induced changes are responsible for the softening of fruit flesh, which is essential for the sensory qualities of ripened fruit (Giovannoni, 2004; Paul *et al*., 2012). Ethylene also interacts with other hormones, including auxins and gibberellins, to fine-tune the ripening process (Fedoroff, 2002). In contrast, non-climacteric fruits like strawberries and peaches have been less studied in terms of ethylene's role in ripening. Initially, it was believed that ethylene did not play a significant role in the ripening of non-climacteric fruits. However, recent research has revealed that ethylene does indeed influence the ripening process in these fruits, although the mechanism and extent of its involvement are less pronounced compared to climacteric fruits. In strawberries, for example, ethylene has been shown to modulate fruit softening, and its interaction with ABA has become a key focus in understanding how ripening occurs in these species (Setha, 2012). Similarly, in peaches, the interaction between ethylene and ABA has been identified as essential for regulating ripening, including fruit firmness and sugar accumulation (Fedoroff, 2002; Giovannoni, 2004). ABA, in addition to ethylene, plays a pivotal role in fruit ripening. ABA regulates several processes associated with maturation, such as the accumulation of sugars, ripening-related gene expression, and fruit senescence. In particular, ABA's role in regulating cell wall modification and maintaining fruit firmness is well established. ABA is also involved in the regulation of stress responses, ensuring that the fruit ripens under optimal conditions (Setha, 2012).

Ethylene biosynthesis

Ethylene biosynthesis was first elucidated long before its role in plant physiology was fully understood (Yang and Hoffmann, 1984). In plants, ethylene is synthesized through a well-defined pathway that begins with the amino acid methionine. The process occurs predominantly in the cytoplasm, where methionine is first converted into S-adenosyl-L-methionine (SAM) by the enzyme SAM synthase. This is the first critical step in ethylene production. Next, 1-aminocyclopropane-1-carboxylic acid (ACC) is formed from SAM via the action of the enzyme ACC synthase. Finally, ACC is converted to ethylene by ACC oxidase, which requires oxygen and copper ions as cofactors for the oxidation process. Recent research has continued to shed light on the nuances of this biosynthetic pathway. In particular, new studies have further characterized the enzymes involved, particularly ACC synthase and ACC oxidase, emphasizing their regulation in different plant tissues and under various environmental conditions (Zhou *et al*., 2020; O'Brien *et al*., 2021). For instance, recent work has revealed that the ACC oxidase gene family in plants shows considerable diversity, and its expression can be tightly regulated depending on developmental and stress-related signals (Wang *et al*., 2022). Additionally, more recent studies suggest that the feedback mechanisms regulating this pathway, including the involvement of transcription factors such as EIN3 and ERF1, are more intricate than previously thought (Liu *et al*., 2023).

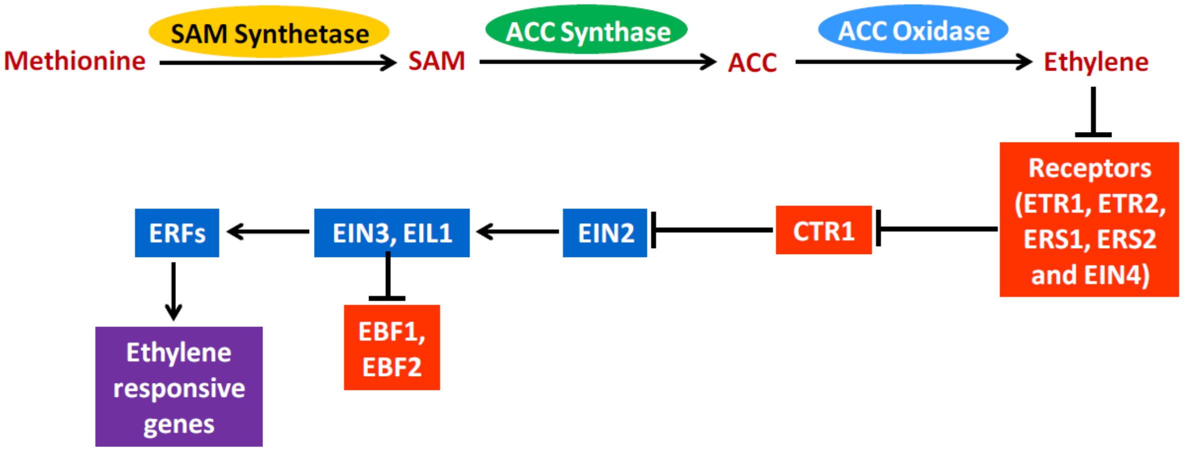

Figure 1: The ethylene biosynthesis and signaling pathway in plants in general in Arabidopsis: Arrows indicate positive regulation, and perpendicular lines indicate inhibitory effects (Song and Liu, 2015).

Furthermore, research has expanded on the role of methionine as a precursor not only for ethylene biosynthesis but also in various other metabolic processes, highlighting its broader influence on plant growth and response to abiotic stresses (Bari and Jones, 2022). Thus, ethylene synthesis remains a central process in plant physiology, influencing a wide range of developmental processes, from fruit ripening to response to stress. The ethylene signaling pathway in plants has been refined in recent research, highlighting its critical role in regulating growth, development, and stress responses. Ethylene perception begins with its binding to receptors like ETR1, ERS1, EIN4, ETR2, and ERS2, located on the endoplasmic reticulum (ER). In the absence of ethylene, these receptors activate the CTR1 kinase, which phosphorylates and inhibits the EIN2 protein. This process prevents EIN2 from releasing its C-terminal domain (CEND), thereby blocking the activation of downstream transcription factors like EIN3 and EILs. When ethylene binds to its receptors, CTR1 is inactivated, allowing dephosphorylation and cleavage of EIN2-CEND. The cleaved fragment translocates into the nucleus, where it interacts with EIN3/EIL transcription factors to regulate gene expression. These transcriptional changes trigger a cascade of ethylene-mediated responses, such as fruit ripening, stress tolerance, and development (Li *et al.*, 2020; Zhao *et al.*, 2023). Recent studies also emphasize the complexity of ethylene signaling in stress conditions. For instance, ethylene aids in managing abiotic stresses like heavy metal toxicity by modulating antioxidant pathways and interacting with other hormonal signaling pathways such as ABA. This interaction fine-tunes plant responses to environmental challenges, providing resilience and enhancing productivity (Sehar *et al.*, 2023).These advancements underline the interconnected nature of ethylene signaling with other regulatory networks, offering opportunities for crop improvement and stress management. Beyond its classical signaling mechanisms, recent advancements highlight the complex interplay between ethylene and other regulatory networks, which influence its functionality in diverse contexts. Ethylene's interaction with hormonal pathways such as jasmonic acid (JA) and salicylic acid (SA) contributes to a coordinated defense response during biotic stress. For instance, ethylene can modulate pathogen resistance by synergizing with JA to regulate the expression of pathogenesis-related genes, thereby enhancing immunity in plants under pathogen attack (Chen *et al.*, 2022).

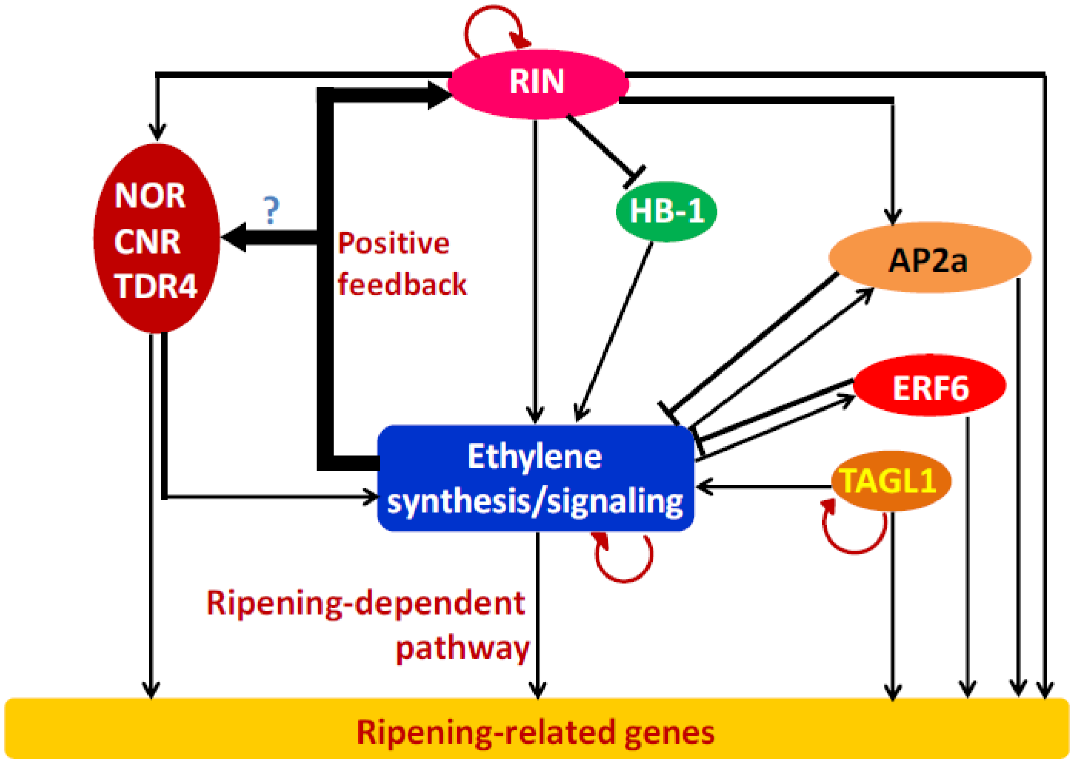

Figure 2 : A diagrammatic illustration of the Model for ethylene signaling network: This was proposed by Fujisawa *et al.* (2013) for regulatory network of tomato fruit ripening. This network is regulated by ethylene along with RIN and Other Factors.

Moreover, ethylene's role extends to developmental processes like fruit ripening and abscission. Its influence on cell wall-modifying enzymes and regulatory transcription factors such as ERFs (Ethylene Response Factors) ensures the timely onset of ripening and separation of mature fruits. This understanding has implications for agriculture, where manipulating ethylene levels could enhance fruit shelf-life and quality (He *et al*., 2023). Ethylene’s impact on abiotic stress tolerance has also been studied extensively. Under conditions such as drought, salinity, or metal toxicity, ethylene interacts with key signaling components to regulate ion homeostasis, water transport, and antioxidant enzyme activity. These adaptations involve the upregulation of genes linked to osmoprotection and reactive oxygen species (ROS) detoxification, as observed in crops like mustard and rice under arsenic and salinity stress (Sehar *et al*., 2023; Zhao *et al*., 2023). Advances in genomic and transcriptomic technologies have further unraveled ethylene's regulatory networks. Gene editing tools like CRISPR-Cas9 offer prospects for modifying ethylene-related genes to enhance plant resilience and productivity. For example, targeting ethylene biosynthesis genes (e.g., ACS or ACO) or components of the receptor pathway (e.g., ETR1 and CTR1) can fine-tune ethylene responses to meet agricultural demands while minimizing stress susceptibility (Angulo *et al*., 2021; Binder, 2020). This growing body of research underscores the potential of ethylene signaling as a target for genetic engineering, paving the way for innovations in crop management and sustainable agriculture. These findings also reinforce the importance of integrating molecular biology with applied agricultural practices to harness the full potential of ethylene in improving plant performance.

ABA biosynthesis

Abscisic acid (ABA) plays a crucial role not only in abiotic stress responses but also in non-climacteric fruit ripening, highlighting its broader biological significance. ABA biosynthesis occurs primarily through the carotenoid pathway, beginning in the plastids. The key precursor, zeaxanthin, is converted into violaxanthin and then into neoxanthin by enzymes like zeaxanthin epoxidase (ZEP) and neoxanthin synthase (NSY). These enzymes are essential for ABA production and have been identified through mutant analyses in species like *Arabidopsis* and maize. Mutations in ZEP result in reduced ABA levels, underscoring its significance in the pathway.

The crucial cleavage of 9-cis-epoxycarotenoids into xanthoxin is catalyzed by 9-cis-epoxycarotenoid dioxygenase (NCED). NCED genes, such as VP14 in maize and its homologs in *Arabidopsis* and tomato, are pivotal for ABA biosynthesis, as they influence stress and developmental responses. The xanthoxin is then transported to the cytosol, where it is converted to abscisic aldehyde by xanthoxin dehydrogenase (XD). Finally, abscisic aldehyde is oxidized to ABA by abscisic aldehyde oxidase (AAO3), which requires molybdenum as a cofactor. Mutations in molybdenum cofactor biosynthesis genes lead to ABA deficiencies, affecting various physiological processes. Recent advances emphasize the complex regulatory network governing ABA biosynthesis and signaling. For instance, E3 ubiquitin ligases regulate ABA levels by modulating the stability of key enzymes like NCED and AAO3. Additionally, ABA biosynthesis interacts with other pathways, such as strigolactones, sharing common precursors like carotenoids. These interactions underline the hormone's multifunctional role in stress adaptation and developmental regulation (Kou *et al*., 2024; Korek *et al*., 2023).

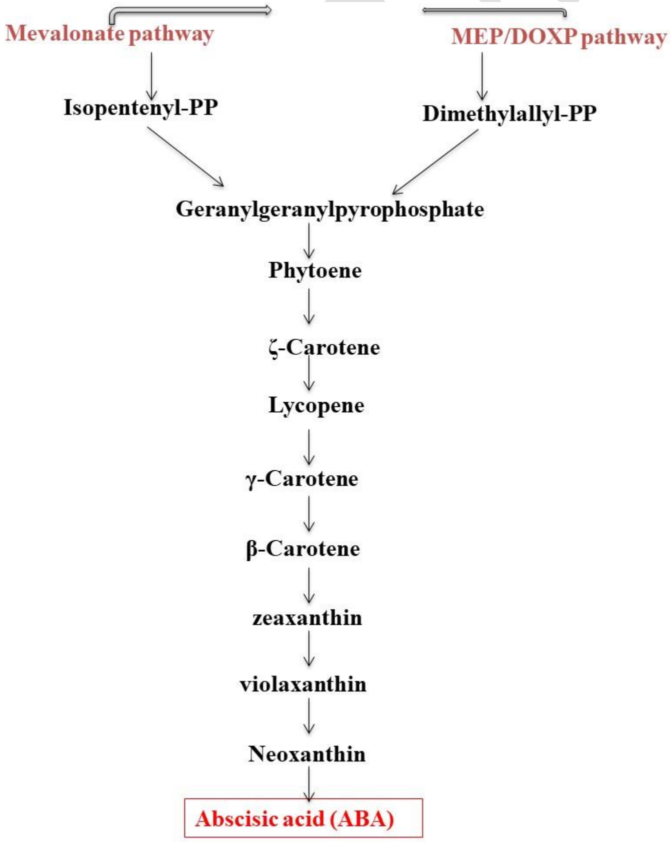

Figure 3: ABA biosynthesis pathway in plants.

The regulation of ABA biosynthesis and signaling is increasingly recognized as a dynamic process influenced by internal and external cues. Key transcription factors, such as ABI3 and ABI5, modulate ABA-responsive gene expression during seed maturation and stress responses. Furthermore, epigenetic regulation, including DNA methylation and histone modifications, has been implicated in the control of ABA biosynthesis genes like NCED3, allowing plants to fine-tune ABA levels in response to changing environmental conditions (Zhang *et al*., 2023; Sharma *et al*., 2022). Interactions with other signaling pathways highlight ABA's versatility in plant physiology. For example, crosstalk between ABA and ethylene pathways can synergistically regulate stress responses, while its interaction with strigolactones influences developmental processes such as shoot branching and root architecture. This integration enables plants to optimize growth and survival strategies under varying environmental conditions (Chai *et al*., 2022; Korek *et al*., 2023). Advances in CRISPR-Cas9 technology have opened new avenues for manipulating ABA biosynthetic and signaling genes. Targeted editing of NCED, ZEP, or AAO3 genes has shown potential to enhance drought tolerance and crop productivity without adversely affecting growth. Such innovations aim to balance ABA-mediated stress tolerance with normal developmental processes, ensuring sustainable agricultural outputs (Lee *et al*., 2023; Wu *et al*., 2023).

ABA Signaling Mechanisms

Significant breakthroughs in ABA signaling have elucidated its molecular framework, particularly through receptor identification and functional analysis in various plant species. In *Arabidopsis thaliana*, the discovery of ABA receptors like PYR/PYL/RCAR highlighted the START-domain structure essential for ABA binding and signaling. These receptors inhibit type 2C protein phosphatases (PP2Cs) upon ABA binding, activating sucrose non-fermenting 1-related kinase 2 (SnRK2), which phosphorylates downstream targets involved in stress responses and growth regulation (Finkelstein *et al*., 2002; Hirayama *et al*., 2007).

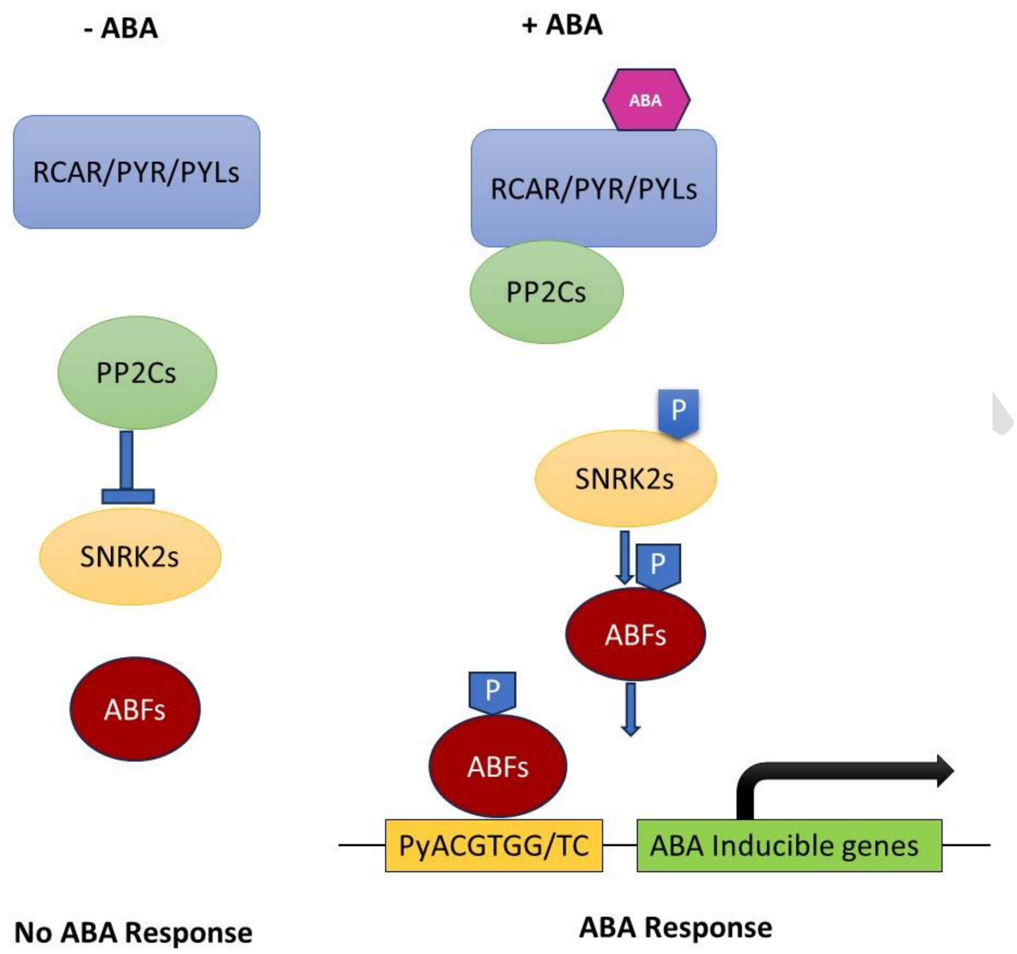

Figure 4: ABA signaling Pathway in Plants.

The Mg-chelatase H subunit (*CHLH*, also known as ABAR) emerged as another receptor with a dual role in ABA perception and chloroplast-related functions. However, its involvement in ABA signaling, particularly in crops and non-climacteric fruits like strawberries, demonstrates species-specific adaptations (Jia *et al*., 2011; Shang *et al*., 2010). In strawberries, gene silencing approaches such as tobacco rattle virus (TRV)-induced gene silencing (VIGS) revealed the critical roles of receptors like FaPYR1 and FaCHLH/ABAR. Silencing these genes demonstrated their importance as positive regulators of ABA signaling, with downstream effects on the expression of ABA-responsive genes like *ABI1*, *ABI3*, *ABI4*, and *ABI5*, as well as sugar metabolism-related genes including *SigE*, *AMY*, and *CHS*. Furthermore, the strawberry genome was found to harbor 11 members of the FaPYR receptor family, along with a single member of FaCHLH/ABAR, emphasizing the diversification of ABA signaling components (Jia *et al*., 2011; Chai *et al*., 2011; Zhang *et al*., 2009).

In climacteric fruits like grapes, ABA accumulation has been linked to the modulation of fruit ripening via soluble sugars, particularly sucrose. The action of 9-cis-epoxycarotenoid dioxygenase 1 (NCED1), which catalyzes a key step in ABA biosynthesis, is upregulated by sugar signaling, establishing a feedback loop that integrates ABA and sugar pathways for ripening control (Gambetta *et al*., 2010; Seo *et al*., 2009).

Transcriptional and Metabolic Regulation by ABA

ABA signaling intricately regulates sugar metabolism and transcriptional networks during plant growth and development. In *Arabidopsis*, proteins such as ABI3, ABI4, and ABI5 serve as critical regulators in sugar and ABA signaling. ABI3 represses amylase activity during seed development, while SnRK2 proteins mediate sugar metabolism during vegetative growth (Zheng *et al*., 2010; Hoecker *et al*., 1995). Similarly, FaCHLH/ABAR in strawberries interacts with SigE, a negative regulator of sugar metabolism, inhibiting its activity during ABA-mediated processes (Chai *et al*., 2011; Zhang *et al*., 1999). Recent studies highlight the role of WRKY transcription factors, which act as repressors of ABA signaling under low-ABA conditions but are deactivated upon ABA binding. This mechanism allows the activation of ABA-responsive genes crucial for stress adaptation and fruit ripening. Notably, WRKY proteins are also involved in regulating secondary messengers like reactive oxygen species (ROS), linking ABA signaling to broader stress response networks (Osanai *et al*., 2009; Shang *et al*., 2010).

Crosstalk with Sugars and Hormonal Pathways

ABA and sugar signaling are tightly interconnected, particularly in regulating fruit ripening and stress responses. Soluble sugars like sucrose enhance ABA biosynthesis through enzymes such as NCED1, which contributes to ABA accumulation during ripening. In addition, ABA interacts with other hormones, including ethylene and auxins, coordinating the transcriptional regulation of ripening-related genes. In grapes, for instance, ABA and sugar interactions modulate transcription factors such as AP1, promoting ripening processes (Seo *et al*., 2009; Audran *et al*., 1998).

Advancements in genome editing and transcriptomics continue to shed light on ABA signaling networks. Tools like CRISPR-Cas9 have enabled targeted manipulation of ABA-related genes, offering opportunities to enhance stress tolerance and optimize crop ripening. Furthermore, integrating omics approaches can provide a comprehensive understanding of how ABA signaling interacts with environmental and metabolic cues to fine-tune plant development and resilience (Al-Babili *et al*., 2000; Seo *et al*., 2009).

Ethylene and ABA crosstalk Ethylene and abscisic acid (ABA) are two key hormones involved in the regulation of fruit ripening, and their interaction plays a significant role in both climacteric and non-climacteric fruits. While ethylene has been traditionally recognized as the dominant hormone in the ripening process of climacteric fruits, recent studies suggest that ABA also plays a pivotal role, influencing the rate of ripening in both fruit types.

Ethylene and ABA in Fruit Ripening

Ethylene has long been considered the key hormone involved in ripening of climacteric fruits, such as bananas, tomatoes, and apples, which produce large amounts of ethylene during ripening. Ethylene triggers a cascade of biochemical events, including the activation of ethylene biosynthesis genes such as *ACS* (1-aminocyclopropane-1-carboxylate synthase) and *ACO* (1-aminocyclopropane-1-carboxylate oxidase), and the induction of enzymes responsible for cell wall degradation, such as polygalacturonases, which are critical for fruit softening (Bowers *et al*., 2000; Lurueña *et al*., 2004). On the other hand, ABA has a more indirect role in fruit ripening. It is involved in regulating the early stages of ripening, particularly by controlling the accumulation of sugars and pigments. ABA levels tend to rise in the early phases of ripening and can promote ripening by enhancing the sensitivity of fruits to ethylene (Gambetta *et al*., 2010). The interplay between ABA and ethylene during fruit ripening is complex, as ABA acts as an upstream signal that can modulate ethylene production. In bananas, for example, ABA promotes the production of ethylene biosynthesis genes, which in turn accelerates ripening (Lohani *et al*., 2004). This suggests that ABA enhances ethylene sensitivity, thus contributing to fruit softening and color changes during ripening (Trainotti *et al*., 2007). In non-climacteric fruits such as strawberries and grapes, ABA plays a dominant role in the regulation of ripening, while ethylene contributes to specific processes. For instance, in strawberry, ABA regulates fruit color, softness, and sugar accumulation by modulating the expression of genes such as *FaNCED1* (ABA biosynthesis) and *FaACS* (ethylene biosynthesis) (Sun *et al*., 2010). In grapes, both ABA and ethylene interact to regulate the expression of *VvNCED1* and other key genes involved in fruit ripening (Zhang *et al*., 2009).

Figure 5 : The overview of ripening in climacteric and non-climacteric fruits: All fruit virtually respond to phytohormones, ABA and ethylene. In climacteric fruits, ABA regulates ripening indirectly through activating the biosynthesis of ethylene. While in case of nonclimacteric fruits, ABA has more dominant role to play but ethylene-dependent ripening characters are still there.

Ethylene and ABA in Climacteric Fruits

Climacteric fruits, such as bananas, tomatoes, and grapes, typically experience a burst of ethylene production during the ripening process, which is crucial for the progression of ripening. Traditionally, ethylene has been considered the primary regulator of this process. However, recent research has highlighted a significant interaction between ethylene and ABA in these fruits. In particular, ABA has been found to enhance the rate of ripening in certain climacteric fruits. For instance, in bananas, ABA has been shown to increase the rate of ripening by promoting ethylene production (Vendrell, 1985). Similarly, in grapes and tomatoes, ABA contributes to ripening by modulating ethylene biosynthesis (Zhang *et al*., 2009; Ohta *et al*., 1992). In tomato, ABA has been found to increase the expression of ethylene biosynthesis genes, such as *LeACS1*, *LeACS2*, and *LeACO1* (Child *et al*., 1998; Kou *et al*., 2012), further supporting the notion that ABA plays an important regulatory role in ripening. Guo *et al*. (2024) investigated the impact of four phytohormone treatments—gibberellin (GA), indole-3-acetic acid (IAA), abscisic acid (ABA), and ethylene (ETH)—on pear (Pyrus pyrifolia) fruit at various stages, specifically at 30, 45, 60, 75, and 90 days after flower blooming (DAFB). Consequently, exogenous GA application may enhance fruit enlargement, diminish fruit firmness, and suppress the accumulation of titratable acid in ripening fruit (110DAFB). Both exogenous IAA and ABA applications can facilitate fruit enlargement. Furthermore, both exogenous ABA and ETH treatments facilitated the accumulation of soluble solids at 110 DAFB, suggesting the participation of ABA and ETH in the fruit ripening process. Quantitative real-time PCR (qRT-PCR) analysis indicated that *PbZEP1*, *PbNCED.B*, *PbSDR4*, and *PbAO3* are essential genes for ABA biosynthesis, while *PbACS1b* and *PbACO1* are vital genes for ethylene biosynthesis in pear fruit. EMSA and Dual-luciferase assays indicated that PbABF.B and PbABF.C.2 directly interact with the promoter of *PbACS1b*, whereas PbABF.E.1 and PbABF.E.2 directly associate with the promoter of *PbACO1* to augment their activities. The results suggest that the four ABF proteins may play a role in ethylene biosynthesis during fruit ripening. Their research delineates the functions of GA, IAA, ABA, and ethylene in pear fruit and identifies the interaction between ABA and ethylene during fruit ripening. In tomatoes, ABA activates calcium-dependent protein kinases (CPK4 and CPK11), leading to the phosphorylation and stabilization of 1-aminocyclopropane-1-carboxylate synthase 6 (ACS6). This stabilization enhances ethylene production, thus expediting fruit ripening (Gupta *et al*., 2022)

These findings suggest that while ethylene remains a major driver of ripening, ABA's role should not be underestimated, as it modulates ethylene production and sensitivity, thereby accelerating the ripening process.

Ethylene and ABA in Non-Climacteric Fruits

Non-climacteric fruits, such as apples and pears, do not undergo a significant ethylene-induced climacteric rise during ripening. Instead, ABA is considered the primary hormone regulating ripening. However, recent studies have shown that ethylene and ABA interact in these fruits as well. In apples and pears, the crosstalk between ABA and ethylene has been reported to influence various aspects of the ripening process (Frenkel and Dyck, 1973; Yuan and Carbaugh, 2007). This interaction suggests that ABA and ethylene together coordinate the ripening process, even in non-climacteric fruits. For example, in non-climacteric fruits like strawberries, the interplay between ethylene and ABA has been observed to regulate the timing and progression of ripening. Exogenous application of ABA in strawberries has been shown to enhance the production of ethylene biosynthesis genes and accelerate ripening (Sun *et al*., 2010). This demonstrates that ABA can influence ethylene-mediated ripening even in fruits that do not exhibit a climacteric ethylene burst.

The Role of ABA in Modulating Ethylene Production

ABA not only influences ethylene biosynthesis in climacteric fruits but also plays a role in modulating ethylene sensitivity in non-climacteric fruits. In bananas, ABA has been shown to enhance ethylene sensitivity, promoting the ripening process (Yuemingjiang *et al*., 2000). Similarly, in mangoes, ABA affects ethylene production and modulates the response to ethylene-mediated processes such as fruit softening and color change (Trainotti *et al*., 2007). These findings underscore the critical role of ABA in regulating ethylene sensitivity, which in turn influences ripening. In strawberries, a fruit that requires little ethylene for ripening, ABA plays a crucial role in regulating the ripening process by enhancing ethylene sensitivity. ABA influences various aspects of fruit ripening, including color change, firmness, and sugar content. Exogenous application of ABA has been shown to increase the production of ethylene biosynthesis genes, leading to accelerated ripening (Setha, 2012).

Feedback Regulation between ABA and Ethylene

The interaction between ABA and ethylene during ripening is not a one-way process. Feedback regulation between these two hormones has been observed in several fruit species. In tomato, for example, ABA-induced ethylene biosynthetic genes can enhance the production of ethylene, which in turn accelerates the ripening process (Jones *et al*., 2002; Trainotti *et al*., 2007). Conversely, in the absence of exogenous ABA, ripening is delayed, suggesting that ABA is essential for the timely initiation of the ripening process (Sun *et al*., 2012a). Moreover, in berries, the production of endogenous ethylene promotes the transcription of *VvNCED1*, a gene involved in ABA biosynthesis, further illustrating the interplay between these two hormones during ripening (Liang Sun, 2010). As ABA levels rise, some of it is stored as ABA-glucose ester (ABA-GE), and upon harvesting, ABA levels increase again, stimulating the transcription of *VvNCED1* and promoting ripening.

Impact on Metabolic and Physiological Changes

During the ripening process, both ethylene and ABA influence key metabolic and physiological changes in fruits, such as color change, softening, sugar metabolism, and the accumulation of secondary metabolites. In strawberry fruits, exogenous ABA application has been shown to increase ethylene production and enhance the activity of enzymes such as phenylalanine ammonia-lyase

(PAL), which is involved in anthocyanin and phenolic compound biosynthesis (Yueming Jiang *et al.*, 2002). Similarly, in banana, ethylene and ABA work synergistically to promote fruit softening (Lohani *et al.*, 2004). Additionally, the interaction between ethylene and ABA influences color changes during ripening. In grapes and strawberries, ABA has been reported to regulate color change during ripening, and the application of 1-methylcyclopropene (1-MCP), an ethylene inhibitor, delays this process (Chervin *et al.*, 2004; Deytieux *et al.*, 2005; Jia *et al.*, 2011). This suggests that both ABA and ethylene contribute to the regulation of fruit pigmentation, a key characteristic of ripening.

Seed Development and Dormancy

ABA and ethylene also interact during seed development and dormancy. Ethylene has been shown to influence ABA signaling in seed dormancy, while ABA acts as a negative regulator of ethylene signaling during seed germination (Cheng *et al.*, 2013). In tomato, for example, blocking ethylene signaling in certain mutants restores ABA sensitivity, further supporting the notion that ABA and ethylene interact during seed development and dormancy (Abel Rosado, 2006). In conclusion, the crosstalk between ABA and ethylene plays a crucial role not only in fruit ripening but also in other physiological processes such as seed development, germination, and stress responses. Both hormones work together to coordinate various aspects of plant growth and development, and their interaction can have significant implications for agricultural practices, particularly in the regulation of fruit ripening and postharvest quality.

Conclusion

In conclusion, the intricate interplay between abscisic acid (ABA) and ethylene in fruit ripening. ABA has been found to act as an upstream regulator, modulating ethylene biosynthesis by influencing key genes in the ethylene pathway. For instance, in tomatoes, ABA activates calcium-dependent protein kinases (CPK4 and CPK11), which phosphorylate and stabilize 1-aminocyclopropane-1-carboxylate synthase 6 (ACS6), thereby promoting ethylene production and accelerating ripening. In mangoes, transcriptomic analyses have revealed that ABA plays a pivotal role in triggering fruit ripening. The application of exogenous ABA accelerates ripening, while inhibitors of ABA biosynthesis delay the process. This effect is associated with the upregulation of ABA biosynthesis genes and a corresponding increase in ABA levels during ripening stages.

Furthermore, the crosstalk between ABA and ethylene is not unidirectional. Ethylene can also influence ABA biosynthesis. In peach fruits, ethylene response factors (ERFs) have been shown to directly activate or suppress the expression of ABA biosynthetic genes, indicating a reciprocal relationship between these hormones during fruit ripening. These findings underscore the complexity of hormonal interactions in fruit ripening, highlighting that ABA and ethylene function both synergistically and antagonistically, depending on the specific physiological process and fruit type. Continued research into these interactions is essential for developing strategies to manipulate fruit ripening and improve post-harvest quality.

Conflicts of Interest: The authors declare no conflicts of interest regarding the content of this chapter. The research and analysis presented herein are based on publicly available scientific literature and previous studies, and no personal, financial, or professional relationships have influenced the findings or interpretations. All the information provided is intended solely to advance the understanding of the crosstalk between ethylene and ABA in fruit ripening.

Disclaimer (Artificial intelligence)

Option 1:

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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