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REVIEW ARTICLE

Lifecycle Transitions in Plant Development: Ripening, Senescence, & Cell Death

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Abstract: The process of fruit ripening is a pivotal and intriguing aspect of plant development, transitioning fruits from maturation to a state suitable for consumption. Unlike viewing it as a degenerative phase, it is considered a terminal stage in the developmental cycle. Fruits are broadly classified into two types: climacteric and non-climacteric. Climacteric fruits exhibit a ripening-associated respiratory burst, often accompanied by a surge in ethylene production. Remarkably, the ripening process in climacteric fruits can persist even after detachment from the parent plant, making post-harvest management a critical consideration. Ethylene exposure emerges as a key influencer, hastening the post-harvest ripening and influencing the overall quality of the produce. This classification and understanding of ethylene's impact provide valuable insights into the intricate dynamics of fruit maturation, aiding not only in agricultural practices but also in enhancing post-harvest preservation strategies.

Keywords: Climacteric; Fibrillins; Gerontoplasts; Lycopene; Metallothioneins; Non-climacteric.

1. Introduction

In the realm of plant development, understanding lifecycle transitions is essential to unraveling the mysteries of growth and adaptation. Key stages such as ripening, senescence, and cell death are pivotal moments that dictate the maturation and eventual decline of plants. This topic delves into the intricate processes that orchestrate these transitions, shedding light on the underlying molecular mechanisms and ecological significance. By exploring these phenomena, we gain profound insights into the dynamic journey of plant life, from the vibrant emergence of fruit to the graceful closure of a leaf's chapter [1].

Fruit ripening induces color changes in fruits like banana, pepper, tomato, and citrus, transitioning from green in their immature state to vibrant hues [1]. Chlorophyll catabolism during ripening exposes hydrophobic carotenoids in chromoplasts, forming structures associated with fibrillin proteins. Fibrillin genes show increased expression during fruit ripening, leaf senescence, floral organ development, and in response to abiotic stresses [2]. Carotenoids, such as lycopene in tomatoes and bell peppers, are synthesized through the isoprenoid pathway, with enzymes becoming more active during capsicum ripening [3]. Fruit color can also be attributed to colored water-soluble substances produced through phenylpropanoid metabolism, which gather in the central vacuole [4].

Phenylpropanoid pathways, derived from phenylalanine, are responsible for creating various phytochemicals such as phenolics, tannins, and flavonoids. Examples of fruits rich in anthocyanins include red grapes, cherries, red apples, black currants, and strawberries [5]. Anthocyanin coloration in fruits results from coordinated gene expression for flavonoid biosynthesis controlled by specific MYB transcription factors [6]. The vibrant pigments in maple tree foliage, with red and purple anthocyanins and yellow flavonoids, also stem from these genetic processes.

Lifecycle transitions in plant development, encompassing ripening, senescence, and cell death, is of paramount importance across agricultural, ecological, and evolutionary domains. These processes are not mere biological phenomena; they profoundly influence

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plant fitness, productivity, and ecological interactions. Ripening dictates the flavor, nutritional content, and market value of fruits, making it crucial for optimizing harvest timing and reducing post-harvest losses. Senescence, despite signaling decline, plays a vital role in nutrient recycling and stress tolerance, impacting plant longevity and reproductive success. Programmed cell death (PCD) shapes organ formation, regulates defense responses, and influences ecosystem dynamics by driving nutrient cycling and species interactions, these lifecycle transitions reveal how plants have evolved to adapt to diverse environmental challenges, offering insights for crop improvement, sustainable agriculture, and conservation efforts. In essence, studying these processes illuminates the intricate web of relationships between plants and their environment, paving the way for more effective strategies in agriculture, ecology, and evolutionary biology [7]. The introduction sets the stage for a comprehensive exploration of the lifecycle transitions in plant development, offering a deeper appreciation of nature's cyclical rhythms and evolutionary strategies. [3, 4]

2. Morphological changes during ripening

2.1. Change in fruit texture

A change in fruit texture during ripening is a fundamental aspect of fruit development that significantly impacts consumer appeal, nutritional quality, and post-harvest handling. As fruits ripen, they undergo biochemical and structural transformations that lead to alterations in texture, such as softening and changes in juiciness. Understanding these changes is essential for farmers, food processors, and consumers alike [8]. One of the key transformations during ripening is the breakdown of complex carbohydrates like pectin, cellulose, and hemicellulose in the fruit cell walls. This enzymatic breakdown, facilitated by enzymes like pectinases and cellulases, results in the softening of fruit tissues. For example, firm, crunchy apples become softer and juicier as they ripen due to the degradation of cell wall components, changes in water content and the accumulation of sugars and organic acids contribute to alterations in fruit texture. Ripening fruits often experience an increase in sugar content, leading to a sweeter taste and a softer, more succulent texture. Meanwhile, acidity levels decrease, which can affect the perceived tartness and overall flavor profile [9]. From a practical standpoint, understanding fruit texture changes is crucial for determining the optimal harvesting time and post-harvest storage conditions. Harvesting fruits at the right stage of ripeness ensures optimal flavor, texture, and shelf life. For instance, fruits harvested too early may lack sweetness and desirable texture, while overripe fruits can be mushy and prone to spoilage.

Changes in fruit texture as they ripen occur due to chemical alterations in cell walls, leading to a decrease in firmness. Enzymes like pectin methylesterase (PME) and polygalacturonase (PG) play roles in breaking down cell wall carbohydrates. This process involves de-esterification and depolymerization of complex polysaccharides, particularly pectins, which modify the physical characteristics of the wall structure, loosening cell-cell adhesion in soft fruits such as tomato and peach. Pectins, making up over 50% of unripe fruit walls, consist mainly of homogalacturonan (HG) and rhamnogalacturonan (RG). Despite the increased activity of enzymes during ripening, they are not the sole determinant of tissue softening. PME and PG work together with other wall-modifying enzymes like xyloglucan endotransglycosylase, endo-1,4-β-glucanases, and expansins to facilitate the softening process [6].

2.2. Changes in fruit flavor and fragrance

Changes in fruit flavors and fragrances during ripening are attributed to a complex interplay of biochemical processes involving the synthesis and breakdown of various compounds. As fruits ripen, there is a significant increase in the production of sugars, particularly fructose and glucose, due to the enzymatic conversion of starches. This rise in sugar content contributes to the sweetness perceived in ripe fruits. Concurrently, acids like citric acid and malic acid may decrease, leading to a reduction in tartness. Another crucial aspect of flavor development is the accumulation of volatile compounds, such as esters, aldehydes, alcohols, and terpenoids, which impart characteristic aromas to fruits [9]. These volatile compounds are often synthesized from precursor molecules during ripening and are responsible for the fruity, floral, or spicy notes associated with ripe fruits. For example, esters contribute to fruity aromas (e.g., isoamyl acetate in bananas), while aldehydes and alcohols may add floral or green notes (e.g., benzaldehyde in cherries). The balance and proportion of these volatile compounds evolve throughout ripening, influencing the overall flavor profile. Hormonal changes, particularly ethylene, play a crucial role in regulating the expression of genes involved in flavor compound biosynthesis, further influencing the development of desirable fruit flavors and fragrances. Understanding these dynamic changes is essential for optimizing fruit quality and enhancing consumer satisfaction [10].

Fruit ripening involves sugar transformation and starch hydrolysis, regulated by enzymes such as apoplastic invertase. Transgenic tomatoes affirm invertase's role in sugar composition and fruit size, impacting sweetness. Starch accumulation includes enzymes like sucrose synthase, fructokinase, and ADP-glucose pyrophosphorylase. Banana pulp ripening sees an increase in starch degradation enzymes. Sourness is attributed to organic acids and amino acids, while astringency is influenced by phenolic compounds. Phenolics and pigments (anthocyanins) coordinate taste and color during ripening. Enhanced fragrance results from elevated volatile organic compounds via diverse pathways, affected by ethylene suppression. Ripe fruits are vital sources of antioxidants and vitamins, containing carotenoids, vitamin A, and folic acid [11]

2.3. Fruit ripening through genetic and hormonal regulation

Fruit ripening is a multifaceted process intricately regulated by both genetic and hormonal mechanisms. Genetically, ripening is orchestrated by precise transcriptional changes in the expression of ripening-related genes. Specific genes involved in fruit ripening encode enzymes responsible for key biochemical transformations, such as the conversion of starches into sugars, the degradation of cell wall components leading to softening, and the synthesis of volatile compounds contributing to aroma and flavor development [8]. The coordinated activation and repression of these genes are controlled by transcription factors and epigenetic regulators that respond to developmental cues and environmental signals. Hormonal regulation, particularly by ethylene, plays a central role in coordinating and accelerating the ripening process [12]. Ethylene is a gaseous plant hormone synthesized in ripening fruits, triggering a series of downstream events that promote ripening-associated changes. Ethylene-responsive genes are activated, leading to further production of ethylene and amplifying the ripening cascade. There are, other hormones such as auxins, abscisic acid, and gibberellins also modulate ripening processes by interacting with ethylene signaling pathways or regulating specific aspects of fruit physiology. The interplay between genetic and hormonal regulators during fruit ripening is fundamental for advancing agricultural practices aimed at optimizing fruit quality, shelf life, and postharvest handling strategies [13].

Mutations within tomato genes, such as NOR, RIN, and CNR, provide valuable insights into the ripening process, contributing to the development of a comprehensive model. These genes serve as overarching regulators independently of ethylene, indicating the involvement of transcription factors in an ethylene-independent pathway.[13] RIN, identified as a MADS-box factor, exerts influence over the expression of ethylene biosynthesis genes both before and after the climacteric phase. Ethylene production continues through autocatalysis. Receptor proteins like NR and GR, along with ETRs, play pivotal roles in initiating and sustaining ripening by activating genes. Light, under the regulation of HP proteins and UV light via the HP gene, affects the accumulation of carotenoids [14, 15]

3. Plant senescence

Senescence, a process reliant on energy, involves self-digestion and is subject to the influence of environmental factors as well as genetically regulated programs. Abscission, the separation of cellular layers in leaves, flowers, and fruits, occurs through the abscission zone, a predetermined site where cell adhesion weakens. Ethylene stimulates abscission, while auxin inhibits it. The development of the abscission zone is impacted by various factors including stress, abscisic acid, and the level of senescence. [16] Enzymes such as cellulase, polygalacturonase, peroxidase, and expansin in the abscission zone are controlled by activated transcription factors and protein kinases encoded by genes. Stress-responsive elements like metallothioneins and pathogenesis-related proteins act to protect against pathogens and environmental stressors [17, 18]. Necrosis indicates tissue death from physical damage, poisons (e.g., herbicides), or external agents. Three types of plant senescence exist

3.1. Programmed cell death

Programmed cell death (PCD) in plants is a sophisticated and regulated process critical for plant development, stress responses, and defense mechanisms. Unlike necrosis, which is accidental cell death due to injury or stress, PCD is a genetically controlled process that occurs under normal physiological conditions. In plant development, PCD shapes organ and tissue structures by eliminating specific cells to form essential structures like xylem vessels and tracheids. Additionally, PCD plays a vital role in leaf senescence, facilitating nutrient remobilization from aging leaves to support seed development and storage organ growth. In response to environmental stresses such as pathogen attacks or adverse conditions, plants activate PCD pathways to contain and eliminate damaged cells, thereby preventing the spread of disease or further injury. Hormones like ethylene and salicylic acid regulate PCD processes, particularly during fruit ripening and senescence. Studying PCD in plants not only provides insights into fundamental cellular mechanisms but also offers opportunities for developing stress-tolerant crops and enhancing agricultural sustainability by optimizing nutrient use efficiency and disease resistance strategies [20].

(PCD) is a vital aspect of normal plant development, denoting an energy-dependent, genetically programmed phase with orderly metabolic processes. Typically autolytic, PCD involves the removal of cell contents through autodigestion, catalyzed by enzymes like proteases and nucleases [19]. PCD contributes significantly to xylogenesis, the formation of secretory structures, the differentiation of surface defenses (spines, thorns), the creation of perforations and indentations, and aerenchyma formation in aquatic plant stems and roots, as well as the development of unisexual flowers [21].

3.2. Development and survival of plants

The development and survival of plants are governed by a complex interplay of genetic, physiological, and environmental factors that influence various aspects of plant growth and adaptation. Plant development encompasses the entire life cycle of a plant, from seed germination to flowering, fruiting, and eventually seed production [22]. Throughout this process, plants undergo morphological, physiological, and biochemical changes that are finely orchestrated by genetic regulation [17]. The plant life cycle begins with seed germination, triggered by favorable environmental conditions such as moisture, temperature, and light. During germination, the seed absorbs water, activating metabolic processes that break dormancy and initiate root and shoot growth. As the seedling emerges, primary growth processes including cell division, elongation, and differentiation occur. The plant develops roots for anchorage and nutrient uptake, and shoots for photosynthesis and reproductive structures. Hormones like auxins, cytokinins, gibberellins, and ethylene regulate these growth processes. During vegetative growth, the plant continues to develop leaves, stems, and branches. This phase is characterized by increased biomass accumulation and the establishment of a robust root system. Photosynthesis plays a critical role in providing energy and building blocks for growth. When conditions are favorable, plants transition to reproductive development, marked by the formation of flowers and subsequent pollination. This stage involves intricate genetic control to ensure the production of viable gametes and successful fertilization, pollination and fertilization, fruits develop from fertilized ovaries, fruits protect and nourish developing seeds. Once mature, fruits facilitate seed dispersal, ensuring the survival and propagation of plant species [43]. Throughout their life cycle, plants must adapt to diverse environmental factors, including light intensity, temperature, water availability, and nutrient availability. Plants have evolved various mechanisms to cope with stress, such as altering leaf orientation, closing stomata to reduce water loss, and synthesizing protective compounds [12]. Plants establish complex interactions with soil microbes, mycorrhizal fungi, and symbiotic bacteria, which enhance nutrient uptake, improve tolerance to stress, and promote overall plant health. Plants have evolved diverse survival strategies, including drought tolerance, salt tolerance, and resistance to pests and diseases. These traits are often mediated by specific genes and biochemical pathways.

Normal PCD is a generic term for plant protoplasm or cell wall elimination through genetically determined actions. Throughout a plant's life cycle, from germination to seed generation, PCD influences various phases. Responses to abiotic (water, temperature, nutrient deficiency) and biotic stresses (pathogens, pests, pollinators) often involve programmed cell death. While apoptosis is extensively studied in animal PCD, plant PCD appears distinct, involving different genes and pathways [23, 24]

3.3. Cell death during growth and morphogenesis

Cell death during growth and morphogenesis in plants is a tightly regulated process essential for shaping plant structure, optimizing resource allocation, and fine-tuning developmental programs. Unlike cell death resulting from stress or damage, programmed cell death (PCD) during growth and morphogenesis is a natural and controlled mechanism orchestrated by genetic and hormonal signals, cell death during plant development is its role in sculpting organs and tissues, PCD occurs at specific locations to create spaces between leaf veins, optimizing nutrient and water transport. Similarly, in root development, PCD helps establish root cap structures and define root architecture, cell death during growth and morphogenesis ensures proper spacing between cells and eliminates excess cells to achieve optimal organ size and shape. This process is crucial for maintaining structural integrity and functional efficiency in plants, PCD is involved in the formation of specialized structures such as tracheary elements in xylem and root hairs, which are essential for water and nutrient uptake [9].

The regulation of cell death during growth and morphogenesis involves complex signaling networks. Plant hormones like auxin, cytokinin, and ethylene play critical roles in modulating PCD pathways to coordinate growth and development processes. Environmental cues and stress signals can also influence PCD dynamics, enabling plants to adapt and respond to changing conditions, the mechanisms and significance of cell death during growth and morphogenesis is fundamental for agricultural and biotechnological applications. Manipulating PCD pathways can potentially enhance crop yield, improve stress tolerance, and optimize plant architecture for increased productivity, elucidating the molecular and cellular basis of PCD in developmental processes contributes to our broader understanding of plant biology and evolution, highlighting the remarkable adaptability and resilience of plants in diverse ecological settings [22]

3.3.1. Formation of vascular and mechanical tissues

The formation of vascular and mechanical tissues in plants involves intricate developmental processes that give rise to specialized tissues essential for structural support and nutrient transport. Vascular tissues, namely xylem and phloem, are crucial components of the plant's vascular system. Xylem tissue is responsible for conducting water and minerals from the roots to the rest of the plant. It consists of tracheids, vessel elements, fibers, and parenchyma cells [30]. Xylem cells undergo differentiation from meristematic cells, where they develop thick secondary cell walls impregnated with lignin, providing strength and durability to the tissue. Phloem, on the other hand, transports organic compounds such as sugars, amino acids, and hormones throughout the plant. It comprises sieve tube elements, companion cells, fibers, and parenchyma cells [25]. Phloem cells differentiate from meristematic tissues and form specialized sieve elements that facilitate the movement of nutrients through pores called sieve plates. Besides vascular tissues, plants also develop mechanical tissues like collenchyma, sclerenchyma, and fibers that provide structural support and rigidity [31]. Collenchyma cells have unevenly thickened primary cell walls and are found in young stems and leaves, offering flexible support during growth. Sclerenchyma cells, including sclereids and fibers, have thick secondary cell walls strengthened with lignin, providing mechanical strength and protection [27]. Together, these tissues enable plants to withstand mechanical stress, grow upright, and efficiently transport water, nutrients, and signaling molecules throughout the plant body. The development of vascular and mechanical tissues is critical for studying plant physiology, adaptation, and agricultural practices aimed at improving crop yield and resilience [29].

Programmed cell death (PCD) plays a crucial role in the development of tracheary elements (TE). Xylogenesis, the process of forming these elements, initiates during embryonic growth and persists throughout the plant's life cycle. [26] As differentiation nears completion, tracheary tissues undergo secondary cell wall thickening, followed by tonoplast rupture and organelle breakdown through autolysis. [28] Ultimately, only the cell wall remains, characterized by its secondary thickenings, forming the continuous network of water-conducting vascular tissue. The Zinnia system has emerged as a valuable model for studying xylogenesis in Arabidopsis and wood formation in Populus trees [32]

3.3.2. Formation of ducts, glands, and channels in plant tissues

The formation and development of these ducts, glands, and channels are genetically regulated processes involving the differentiation and specialization of specific cell types. These features are often essential for plant adaptation, defense, and reproduction.

Ducts and channels in plant tissues are specialized structures that facilitate the movement and storage of fluids and substances within the plant. They can be classified based on their origin, structure, and function. Laticifers are specialized cells or ducts that produce and transport latex, a milky fluid containing various secondary metabolites such as alkaloids, terpenoids, and proteins. Laticifers are found in diverse plant families and play roles in defense against herbivores and pathogens, as well as wound healing. Resin ducts are channels or cavities within plant tissues that produce and store resin, a viscous mixture of terpenes and other compounds. Resin ducts are often associated with coniferous trees and are involved in defense against pests and pathogens, as well as wound sealing. Aerenchyma is a specialized tissue composed of large air spaces that facilitate oxygen transport within the roots, stems, and leaves of aquatic and marshland plants. Aerenchyma helps plants adapt to waterlogged conditions by enhancing oxygen diffusion to submerged tissues [33].

Glands in plant tissues are specialized structures that produce and secrete substances important for plant function and interactions with the environment. Glandular trichomes are hair-like structures found on the surface of leaves, stems, and other plant parts. They secrete various substances, such as oils, resins, and mucilage that deter herbivores, trap insects, or provide protection against environmental stresses. Nectaries are specialized glands that produce nectar, a sugary fluid used to attract pollinators. Nectar production is crucial for successful pollination and seed production in flowering plants. Hydathodes are specialized structures at the margins of leaves that secrete water in the form of droplets, a process known as guttation. Hydathodes help regulate water balance in plants and remove excess water from the vascular system [34].

Programmed cell death and shedding contribute to diverse plant shapes and adaptations. In citrus peel, oil glands form through lysigeny and schizogeny. Mucilaginous canals in Tilia cordata bud scales result exclusively from lysigenous cell death. Resinous secretory ducts in Anacardiaceae phloem tissues develop schizogenously. Cell separation events, like abscission of leaves and flowers, anther dehiscence, and dry fruit opening, occur due to middle lamellae degradation under the regulation of ethylene and auxin [35].

3.3.3. Selective death of cells and tissues

Selective death of cells and tissues, also known as programmed cell death (PCD) or apoptosis, is a crucial process in plant development and stress responses. Unlike necrosis, which is uncontrolled cell death due to external factors like injury or infection, PCD is a highly regulated process orchestrated by specific genetic and molecular mechanisms. PCD plays important roles in shaping plant morphology, eliminating unwanted or damaged cells, and maintaining overall plant health. For example, during leaf senescence, PCD helps dismantle chloroplasts and remobilize nutrients from senescing tissues to developing organs or storage tissues. PCD is also involved in the formation of developmental structures such as root cap sloughing, xylem vessel formation, and seed coat formation. PCD acts as a defense mechanism against pathogens by confining infections to localized regions through hypersensitive response (HR), preventing further spread of disease, the regulation and function of selective cell death in plants is essential for improving crop resilience, enhancing stress tolerance, and optimizing agricultural practices [36].

Selective cell death plays a pivotal role in various aspects of plant vegetative development. It is responsible for localized programmed cell death during the formation of prickles and thorns, as well as the creation of perforations in the leaves of plants like the Swiss cheese plant (Monstera) and the aquatic lace plant (Aponogeton). Throughout reproductive development, programmed cell death processes are integral. They facilitate the selective demise of reproductive structures during the maturation of unisexual flowers, while also governing the senescence of petals and sepals. Furthermore, specific cells undergo senescence and death as part of the process of gamete and embryo formation [37]

4. Whole plant and organ senescence

Whole-plant senescence refers to the complete death of the entire plant. Typically, annuals and biennials reproduce only once before undergoing senescence, whereas perennials have the capacity to reproduce multiple times before senescing. This process represents an expedited form of aging in which tissues are programmed to deteriorate rapidly once specific thresholds are surpassed. In monocarpic plants, the redistribution of nutrients or hormones from vegetative parts to reproductive organs may initiate whole-plant senescence [38].

Organ senescence refers to the aging and degradation of specific plant organs, such as leaves, flowers, and fruits. Each organ undergoes a programmed senescence process characterized by changes in morphology, physiology, and biochemical composition. For example, leaf senescence involves chlorophyll degradation, breakdown of cellular structures, and remobilization of nutrients from senescent leaves to other parts of the plant. Flower senescence is marked by wilting, petal abscission, and fruit development following successful pollination and fertilization. Fruit senescence encompasses ripening processes and changes in texture, color, flavor, and aroma as the fruit matures and becomes ready for seed dispersal, the mechanisms and regulation of organ senescence is important for crop management, postharvest physiology, and extending the shelf life of harvested produce [39]

5. Leaf senescence

Leaf senescence, a critical phase in plant life, reallocates food resources for grain filling or tuber development, potentially attracting pathogens. Defense mechanisms are upregulated during senescence, mediated by hormones like jasmonates and salicylates [40]. All leaves, including evergreens, undergo senescence due to age-dependent factors, environmental signals, and stresses. This active process retrieves nutrients (C and N) at a leaf's end-of-life, occurring sequentially, seasonally, or stress-induced. Developmental leaf senescence includes initiation, reorganization (degenerative), and terminal phases. Initiation signals a decline in photosynthesis and a shift from a nitrogen sink to a source [41]. The reorganization phase involves organelle autolysis, remobilizing nutrients to growing sinks via phloem [42, 43]

5.1. Change in leaf color, cell structure, and metabolism

In the process of leaf senescence, the initial noticeable change is in coloration. The green hue fades, succeeded by the emergence of red pigmentation, which correlates directly with the regulation of nutrient extraction from leaf cells. Consequently, the breakdown of chlorophyll and the synthesis of anthocyanins are pivotal aspects of senescence. The initial phase involves the liberation of chlorophyll from chlorophyll-protein complexes within the thylakoid membrane, facilitated by SGR, a factor encoded by the senescence-upregulated gene STAY-GREEN. This dissociation of the complex enables the recycling of protein nitrogen [44].

During catabolism, chloroplasts undergo a transformation into gerontoplasts, which involves the breakdown of grana lamellae, disappearance of the thylakoid membrane, and significant accumulation of plastoglobuli. Consequently, there is a decrease in photochemical reactions and enzyme activities associated with the Calvin cycle, including Rubisco. Other organelles such as protein storage vacuoles in senescing storage cotyledons and aleurone layers experience both structural and functional alterations. Peroxisome function shifts towards lipid breakdown or gluconeogenesis. Senescent cells activate pathways related to hydrolytic, oxidative, and secondary metabolism. Additionally, in certain plants, there is synthesis or modification of secondary metabolites, which can influence interactions with other organisms [46]

5.2. Degradation of macromolecules

Senescence is essential for recycling macromolecules (proteins, lipids, and nucleic acids) in plants. This process recovers nitrogen (N) and phosphorus (P) from mature tissues, transferring them to growing plant parts or storage tissues. Hydrolytic enzymes, such as proteases, nucleases, and phosphatases, are crucial during senescence. Proteases release amino acids like glutamine and asparagine, serving as the primary form of recycled nitrogen [47]. Nucleases break down nucleic acids into nucleotides, and phosphatases release phosphate, leading to the catabolism of nucleosides into ammonia and carbon dioxide [48]

5.3. Modification of energy and oxidative metabolism

Senescence shifts energy metabolism in plastids, peroxisomes, and mitochondria, impacting redox reactions. Signals like H2O2, regulated by antioxidant metabolites and enzymes (catalase, ascorbate peroxidase), play a role [49]. Over 50 senescence-associated genes include catabolic enzymes (ubiquitin, proteolytic enzymes, and metallothioneins) and stay-green mutants for delayed leaf senescence [50]. Stay-green traits benefit agriculture but may hinder nutrient remobilization. The SGR and NAM genes regulate senescence and nutrient remobilization. Cytokinin rejuvenates leaves, and mutations in ethylene metabolism delay senescence. Genomic analyses reveal numerous differentially expressed SAGs linked to remobilization, stress response, and transcription factors [51, 52].

6. Effect of environmental conditions on senescence and death

Similar to various other physiological processes, senescence, and specifically programmed cell death (PCD), also react to extreme environmental circumstances. Seasonal changes or other foreseeable environmental factors can trigger senescence as a component of an adaptive response [53].

6.1. Effect of seasons on leaf senescence

Photoperiods govern senescence in non-equatorial ecosystems, serving as crucial cues for plants facing abiotic stress [54]. In temperate regions, leaf senescence is vital for carbon-nitrogen balance [54]. Autumnal senescence in deciduous forests, exemplified by coordinated fall senescence in Aspen trees, responds to decreasing day length independent of temperature [55]. Events like chloroplast-to-gerontoplast conversion and color display are temperature-dependent. MADS-box transcription factors and phytochrome integrate senescence with growth, flowering, and dormancy. Chilling temperatures induce foliar senescence in apple, pear, and some Rosaceae species, deviating from photoperiod influence [56]. High sugar concentrations signal senescence, accelerated by sugar depletion and darkness. Cytokinins delay senescence, while auxins and gibberellins suppress it; senescence-promoting regulators include ethylene, ABA, jasmonic acid, salicylic acid, and brassinosteroids [57].

6.2. Complex relationships between programmed senescence, death, and aging

Aging in plants encompasses diverse longevities, from weeks in ephemeral weeds like Arabidopsis to millennia in trees [58]. Monocarpic plants, like semelparous animals, face reproductive exhaustion and senescence after flowering. Monocarpic senescence sacrifices the entire vegetative body for seed production and the next generation's propagation. Long-lived plants prioritize individual maintenance and survival, potentially facing susceptibility to genetic errors and declining physiological integrity [59, 60].

6.3. Programmed senescence and death are common responses to abiotic stresses

Flooding induces aerenchyma development in plant roots, enhancing air flow. Ethylene-signaling pathways regulate programmed cell death (PCD) in specific root cells, forming air spaces through schizogenous or lysigenous processes [61]. Aerenchyma differentiation involves DNA fragmentation and activation of genes related to respiratory, carbohydrate, nitrogen, and secondary metabolism [62]. Regulatory systems, including calcium signaling, protein phosphorylation, dephosphorylation, and ethylene biosynthesis, lead to cell wall breakdown and increased cellulase activity. Research in Arabidopsis aims to understand the genetic basis of aerenchyma development. Crop plants like rice and maize, susceptible to reduced yield due to flooding, are extensively studied for aerenchyma development [63, 64].

6.4. Senescence and cell death: adaptive and pathological responses to biotic interactions

Senescence and cell death represent intricate and dynamic responses in plants to various biotic interactions, encompassing both adaptive and pathological aspects. In adaptive scenarios, these processes serve crucial roles in plant defense mechanisms against pathogens, herbivores, and competing organisms. For example, induced senescence and cell death at the site of pathogen invasion or herbivore feeding can limit the spread of infection or deter further damage by sacrificing affected tissues. This localized response helps contain the threat and protect vital plant organs, contributing to overall plant health and survival [65].

Conversely, senescence and cell death can also be exploited or manipulated by pathogens for their own benefit, leading to pathological outcomes for the plant. Some pathogens can trigger premature senescence or accelerate cell death in host tissues as part of their infection strategy, facilitating nutrient acquisition or providing a niche for pathogen proliferation. This exploitation of plant physiological processes underscores the intricate co-evolutionary dynamics between plants and pathogens, where each party employs sophisticated strategies to gain an advantage in the ongoing arms race of biotic interactions [69].

The dual nature of senescence and cell death in biotic interactions is crucial for developing effective strategies for crop protection and disease management. By deciphering the underlying molecular mechanisms and signaling pathways involved in these processes, researchers can identify potential targets for enhancing plant resistance to pathogens or modulating defense responses to achieve sustainable agricultural practices. Harnessing natural variation in senescence and cell death pathways through breeding or biotechnological approaches can lead to the development of novel crop varieties with improved resilience and reduced susceptibility to biotic stresses. Ultimately, integrating this knowledge into agricultural systems can help mitigate the impact of plant diseases and pests, ensuring global food security and environmental sustainability [70].

PCD is crucial in biotic interactions, both beneficial (pollinator attraction, dispersal) and harmful (pests, pathogens). Pathogens are necrotrophs (kill and feed on dead tissues) or biotrophs (require live host tissues). The hypersensitive response (HR) induces PCD to neutralize infection, resembling autophagy in vacuolar lytic activities. ROS and reactive nitrogen species induce HR [65]. Gene interactions in the resistance-avirulence system trigger PCD. Defense genes are prominent among senescent tissues' vulnerability to pathogen attack, as reflected in senescence-associated genes [67, 67].

7. Discussion

Lifecycle transitions in plant development, including ripening, senescence, and cell death, are essential processes that contribute to plant growth, reproduction, and adaptation to the environment. Ripening is a critical stage where fruits undergo biochemical and physiological changes, becoming attractive to seed dispersers and consumers. Senescence, or aging, involves the programmed deterioration of plant tissues, allowing for nutrient remobilization and seed production. Cell death, including programmed cell death (PCD), regulates developmental processes and responses to stress. These lifecycle transitions is crucial for various applications in agriculture and horticulture. For example, controlling ripening processes can optimize fruit quality and shelf life, reduce postharvest losses, and improve marketability. Managing senescence can enhance crop yield by optimizing nutrient use efficiency and prolonging reproductive phases. Exploring cell death mechanisms can lead to strategies for enhancing stress tolerance and disease resistance in plants. A comparative overview of ripening, senescence, and cell death in plant development have been provided in the Table 1

Table 1. A comparative overview of ripening, senescence, and cell death in plant development

Aspect	**Ripening**	**Senescence**	**Cell Death**	**Ref.**
Definition	Terminal phase of development	Aging and maturation process	Programmed elimination of cells	[68]
Nature	Not considered degenerative	Natural aging and deterioration	Part of developmental processes	[69]
Trigger	Ethylene-induced processes	Genetic and environmental factors	Various internal and external cues	[70]
Respiratory Burst	Common in climacteric fruits	Associated with aging tissues	May accompany specific cell death	[71]
Detachment Impact	Climacteric fruits can ripen post-harvest	Accelerated aging upon detachment	Detachment often triggers cell death	[72]
Physiological Changes	Enhanced metabolic activity	Gradual decline in physiological functions	Controlled breakdown of cellular components	[73]

8. Recommendations

8.1. Optimizing fruit ripening

Research on ripening processes can lead to the development of methods for controlling ripening timing and quality. For example, understanding the role of hormones like ethylene can guide the use of inhibitors or enhancers to modulate ripening in fruits.

8.2. Improving post-harvest management

Implementing technologies that slow down senescence and cell death processes can extend the shelf life of fruits and vegetables. This includes using controlled-atmosphere storage, temperature management, and postharvest treatments.

8.3. Enhancing stress tolerance

Investigating the molecular mechanisms of cell death can help identify genes and pathways associated with stress responses. Utilizing this knowledge, breeders can develop stress-tolerant crop varieties through genetic engineering or traditional breeding approaches.

8.4. Conservation and ecosystem

Understanding plant lifecycle transitions contributes to conservation efforts by preserving biodiversity and ecosystem functioning. Conservation strategies can focus on maintaining genetic diversity in wild plant populations to ensure their resilience to environmental changes.

9. Conclusion

Fruit ripening is the climax of development and maturity, marked by complex biological processes. This phenomena is divided into two types: climacteric and non-climacteric, based on their sensitivity to ethylene. Climacteric fruits can continue to mature even after they have been detached from the parent plant, which is assisted by ethylene exposure. Non-climacteric fruits, on the other hand, have a smaller ripening window and are less impacted by ethylene after harvest. This difference is critical in agricultural techniques, since it influences harvest time and management. Furthermore, careful regulation of ethylene exposure in climacteric fruits is critical in managing the ripening process, ensuring that customers obtain fruits at their best flavor and nutritional value.

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