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Biosynthesis of Ascorbic Acid and Its Metabolism across Plant Growth Stages, Fruit Maturation, and Postharvest Physiology: A Review

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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ABSTRACT

Ascorbic acid (AsA), generally known as vitamin C, is essential for horticulture crops to grow, develop, and maintain themselves after harvest. It is essential for plant health, fruit quality, and human nutrition because of its role in enzymatic processes, hormone production, and antioxidant activity. Important plant hormones, including auxins and gibberellins, which control the growth and development of fruit, are involved in its production. The maintenance of optimal AsA levels in horticultural crops can help ensure their nutritional value and quality for consumers. This is done by utilizing suitable postharvest practices and by understanding the variables like temperature, light exposure, and oxygen that influence AsA content. To fully comprehend the function of ascorbic acid in horticulture crops throughout plant growth, fruit development and ripening, and postharvest physiology, more study is required. This information may be used to increase the ascorbic acid

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content of crops and improve their nutritional value. Key intermediates in the AsA biosynthesis pathway have been shown in a simplified schematic diagram. The control of plant AsA production and subsequent responses to horticulture crops throughout plant growth, fruit development and ripening, and postharvest physiology may now be better understood through future study.

Keywords: Ascorbic acid; biosynthesis; development; fruit; hormone; postharvest.

1. INTRODUCTION

The essential ingredient ascorbic acid (AsA), often known as vitamin C, plays a key role throughout the whole life cycle of horticultural crops [1]. AsA is essential for the development of plants, the ripening of fruits, and the physiology following harvest [2]. This crucial ingredient contributes to several physiological functions, antioxidant defense systems, and the general excellence of horticultural output [3]. AsA has various important roles in plant development, and takes part in photosynthesis, assisting in the production of chlorophyll and sugars [4,5]. It also functions as a cofactor for enzymes involved in biosynthetic pathways, including those that produce hormones, secondary metabolites, and parts of cell walls [6]. Ascorbic acid also helps plants tolerate stress, enabling them to resist challenging climatic circumstances, including high temperatures, drought, and disease attacks [7,8].

AsA is a vital element in determining fruit quality when it comes to the development and ripening of fruits [9]. It affects many activities, including fruit growth, color development, scent generation, and flavor [10]. Fruits acquire their brilliant hues due to ascorbic acid's role as a coenzyme for enzymes involved in pigment production. Additionally, AsA plays a role in the control of the hormone ethylene production, which ripens fruit [11]. The taste profile of horticultural crops is improved by ascorbic acid's role in the buildup of sugars, organic acids, and volatile chemicals [12].

Another stage of physiology where AsA is important is postharvest physiology. Horticultural crops go through physiological changes after harvest that may affect their shelf life and general quality [13]. Fruits and vegetables are shielded from oxidative stress by ascorbic acid, which also delays the aging process [9,14]. It aids in maintaining harvested produce's firmness, color, and nutritional value. In addition, AsA increases the activity of antioxidant enzymes, reducing oxidative damage-related postharvest losses [15,16]. Exogenously given AsA is best used to protect proteins and lipids from stress-induced oxidative damage [17-19]. AsA can boost a plant's resistance to abiotic stresses by speeding up transpiration, photosynthetic pigments, oxidative defense capacity, and photosynthesis rate. Exogenous applications of AsA (50 and 100 mg L^{-1}) enhanced the chlorophyll "a" concentrations of wheat seedlings during salt stress [20]. Similar to this, okra plants under drought stress exhibited reduced lipid peroxidation and ion leakage, as well as enhanced proline content and plant growth [21].

Uncertainty surrounds the precise mechanism and regulation of AsA production in horticultural crops, despite its critical role in the growth and development of plants. The AsA biosynthesis pathway's important enzymes and genes must be identified, as well as the elements that control how much ascorbic acid is produced in various plant tissues and various environmental settings. Numerous elements, including light intensity, temperature, water stress, and nutrient availability, can affect the amounts of AsA in horticultural crops. Furthermore, it is not well known how exactly these variables impact AsA content. Fruits can have varying amounts of AsA during different phases of their growth and ripening, and this can impact fruit quality and nutritional value. There is, however, little understanding of the variables that affect the AsA concentration during these phases as well as the mechanisms behind the transit and storage of AsA in various fruit tissues. Therefore, this current review focuses on the biosynthetic pathway of AsA in horticultural crops, the identification and role of key enzymes and genes in AsA biosynthesis in horticultural crops, and the regulatory factors and signaling pathways that control its production during different stages of plant growth, among others.

2. BIOSYNTHETIC PATHWAY OF ASCORBIC ACID IN HORTICULTURAL CROPS

The AsA biosynthetic pathway in horticultural crops, such as fruits and vegetables, is comparable to that in other plants and creatures. Through a series of enzymatic processes, these plants may produce ascorbic acid [22]. The conversion of different intermediates from the metabolism of glucose is a part of the pathway. The process by which glucose is transformed into D-glucose is the initial step in the production of ascorbic acid in horticultural crops. The enzyme glucose oxidase, sometimes referred to as D-glucose: oxygen 1-oxidoreductase, is responsible for catalyzing this reaction. D-galacton-1,4-lactone is created when glucose is oxidized by glucose oxidase [23,24].

The galactose oxidase enzyme then transforms D-galacton-1,4-lactone into L-galactose (Siddique, 2014). Conversion of D-galactose-1,4-lactone to L-galactose is catalyzed by this enzyme, also known as L-gulono-1,4-lactone oxidase [25,26]. L-galactose must then be changed into L-galactono-1,4-lactone in the next stage [27]. Galactose oxidase is also responsible for catalyzing this process, and an essential step in the production of ascorbic acid is L-galactono-1,4-lactone [27]. It is possible to further transform L-galacton-1,4-lactone into ascorbic acid (L-ascorbic acid) by a spontaneous reaction that does not call for any particular enzymes. It should be noted that environmental elements like temperature and pH might affect how easily L-gulono-1,4-lactone is converted to AsA [3].

The enzymatic processes that take place in the biosynthetic pathway are influenced by a number of variables, such as gene expression, substrate availability, and environmental circumstances [12]. Ascorbic acid production and accumulation in horticultural crops can be influenced by elements including light, temperature, nutrient availability, and stress. The AsA concentration of these crops can also be impacted by cultivation techniques, such as effective fertilization and irrigation [28].

It is significant to remember that the ability of various horticultural crops to produce ascorbic acid may vary. Oranges, lemons, strawberries, kiwis, and bell peppers are a few examples of crops with high AsA concentrations; other crops may have relatively lower amounts. Breeders and horticulturists frequently concentrate on creating cultivars with increased ascorbic acid content using methods from selective breeding or genetic engineering.

The enzymatic machinery required to generate ascorbic acid through a sequence of biochemical processes is present in horticultural crops, which means that this is true. In the biosynthetic process, glucose is converted to D-glucose, which is then converted to L-galactose and finally to L-gulono-1,4-lactone. Finally, L-gulono-1,4-lactone transforms into L-ascorbic acid on its own [29]. The AsA concentration of horticultural crops can be influenced by environmental conditions and growth techniques.

For ease of use, significant precursor chemicals and crucial routes have been clarified using a schematic diagram (Fig. 1).

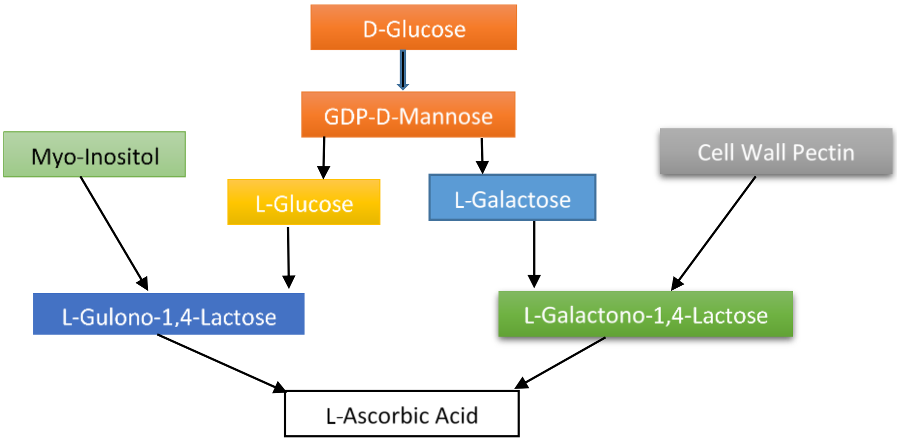

Fig. 1. Diagram showing various pathways and important precursor molecules involved in the biosynthesis of AsA in plants. The interconnectivity of these pathways reflects the intricacy involved in the production of ascorbic acid. Precursors are converted by enzymes into intermediate molecules, which are then converted into ascorbic acid. The way these pathways interact demonstrates how versatile and flexible plant metabolism is when it comes to generating ascorbic acid

3. IDENTIFICATION AND ROLE OF KEY ENZYMES AND GENES IN ASA BIOSYNTHESIS IN HORTICULTURAL CROPS

The biosynthesis of AsA in horticultural crops involves several key enzymes and genes [30]. Some of the major enzymes and genes associated with ascorbic acid biosynthesis in plants are discussed below:

Glucose oxidase (GOX) enzyme: This enzyme catalyzes the conversion of glucose to D-glucose, which is the initial step in the biosynthesis pathway of AsA. The gene encoding this enzyme is referred to as GOX [31].

Gluconolactone oxidase (GLO) enzyme: GLO is responsible for converting D-glucono-1,5-lactone to D-glucuronolactone and subsequently L-gulono-1,4-lactone, which is a key intermediate in AsA biosynthesis. The gene encoding this enzyme is known as GLO [31].

L-galactose-1-phosphate phosphatase (GPP) enzyme: GPP plays a role in the synthesis of L-galactose-1-phosphate, an intermediate in the AsA biosynthesis pathway. The gene encoding this enzyme is called GPP [12].

GDP-mannose pyrophosphorylase (GMP) enzyme: GMP is involved in the production of GDP-mannose, which serves as a precursor for the biosynthesis of L-galactose, another intermediate in AsA synthesis. The gene encoding this enzyme is referred to as GMP [32].

L-galactose dehydrogenase (GalDH) enzyme: GalDH converts L-galactose to L-galactono-1,4-lactone, which is an important intermediate in the final steps of AsA biosynthesis. The gene responsible for encoding GalDH is GalDH [33].

L-galactono-1,4-lactone dehydrogenase (GalLDH) enzyme: GalLDH plays a crucial role in the conversion of L-galactono-1,4-lactone to AsA (L-ascorbic acid). The gene encoding this enzyme is referred to as GalLDH [34].

These enzymes' transcriptional activity is controlled by a variety of transcription factors and signaling pathways. For instance, it is known that the ascorbate peroxidase (APX) enzyme and several other elements, including light, temperature, stress, and hormone signaling, control the ascorbic acid pathway [35]. In order to increase the ascorbic acid content of horticultural crops through breeding programs or genetic engineering approaches, breeders and researchers frequently concentrate on discovering and altering these important enzymes and genes. Understanding the control and operation of these enzymes and genes can help scientists create crop types with higher AsA levels, which would increase the nutritional quality and health advantages of those crops.

4. REGULATORY FACTORS AND SIGNALING PATHWAYS THAT CONTROL ASA PRODUCTION DURING DIFFERENT STAGES OF PLANT GROWTH

The complex synthesis of AsA involves many enzymatic steps and is tightly controlled by a variety of factors, including metabolic feedback mechanisms, environmental cues, and hormone signaling. The control of AsA synthesis in plants remains poorly understood, despite notable advances in recent times [36].

A key regulatory element in the AsA synthesis process is the enzyme GDP-D-mannose pyrophosphorylase (GMP), which converts GDP-D-mannose into L-galactose-1-P, the first committed step in ascorbic acid biosynthesis [37,38]. The activity of GMP is influenced by some factors, including light, temperature, and hormones including cytokinins and abscisic acid (ABA) [39].

Light is an essential environmental cue that regulates ascorbic acid synthesis. Studies show that light exposure promotes GMP activity, which in turn boosts AsA production in plants [40,41]. Although the precise mechanism by which light regulates GMP activity is unknown, it is believed to involve photoreceptors like phytochromes and cryptochromes.

Ascorbic acid production has been shown to increase at low temperatures by boosting GMP activity and AsA biosynthesis gene expression [42]. Although the precise process by which temperature regulates ascorbic acid synthesis is unclear, it is thought to include alterations in membrane fluidity and lipid composition.

Hormonal signaling pathways control the ascorbic acid cycle [43]. For instance, it has been proven that ABA boosts GMP activity in several plant species and induces the expression of genes involved in ascorbic acid synthesis [44]. Cytokinins have also been shown to regulate the production of AsA in plants, albeit the exact nature of this regulation is unknown.

In addition to these additional characteristics, the synthesis of ascorbic acid may also be regulated by metabolic feedback processes. For example, ascorbic acid may inhibit the activity of GMP and other enzymes required for its synthesis, reducing the quantity that may be created [45]. Similar to this, changes in the levels of other metabolites may also affect the production of ascorbic acid. The expression of certain genes controls the genetic regulation of AsA production. Specific genes are responsible for encoding important biosynthetic enzymes including GDP-L-galactose phosphorylase (GGP), L-galactose-1-phosphate phosphatase (GPP), and L-galactono-1,4-lactone dehydrogenase (GLDH) [32,33,46].

5. THE ROLE OF AsA IN PLANT GROWTH AND DEVELOPMENT

Most of the time, horticultural crops such as oranges, grapefruits, pineapple, papaya, tomatoes, etc., do not really "need" AsA, sometimes referred to as vitamin C, for growth and development. That being said, vitamin C is involved in several physiological functions in plants, such as antioxidant defense and oxidative stress resistance [47]. Plants produce it as part of their metabolic activities. The following are some critical facets of ascorbic acid's function in plants:

5.1 Photosynthesis

AsA is necessary for efficient photosynthesis, which is how plants convert light energy into chemical energy. AsA serves as an electron donor, preventing oxidative damage to the photosynthetic machinery. To maintain optimal photosynthetic activity, AsA also takes part in the regeneration of other antioxidants, such as glutathione [48].

5.2 Antioxidant Defense

Strong antioxidant AsA helps plants defend against oxidative stress caused by reactive oxygen species (ROS). High light intensity, dehydration, and pathogen infections are just a few of the stressful situations in which ROS can build up [49]. Ascorbic acid neutralizes ROS, limiting cellular deterioration and preserving plant health.

5.3 Enzymatic Reactions

A number of enzymes require AsA as a cofactor, including catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) [50]. AsA plays a role in the manufacture of vital substances such as lignin, collagen, and hormones. As an enzyme cofactor, AsA speeds up crucial biochemical processes necessary for plant growth and development.

5.4 Growth Regulation

The effects of AsA on cell division, extension, and differentiation affect plant development in general. It participates in the creation and alteration of cell walls, promoting cell growth and tissue formation. Ascorbic acid also plays a role in hormone signaling pathways, including auxin and gibberellin metabolism, which regulate plant growth processes [30].

5.5 Stress Tolerance

According to Godoy et al. [51], AsA improves plant resistance to a variety of abiotic stressors, including high temperatures, drought, salt, and heavy metal toxicity. By controlling antioxidant defense mechanisms, preserving cellular homeostasis, and influencing the expression of genes that respond to stress, it lessens the harmful consequences of stress [52].

5.6 Flowering and Reproduction

In horticultural crops, AsA affects flower growth and flowering time [53]. Gibberellins and ethylene, two phytohormones important in controlling flowering, are affected in their production and metabolism. Additionally, AsA affects pollen tube development and germination, which in turn affects fruit set and effective fertilization.

AsA is a vital chemical for the expansion and maturation of horticultural crops. Its diverse significance in plant physiology is highlighted by its involvement in photosynthesis, antioxidant defense, enzymatic reactions, growth control, stress tolerance, and reproduction. Understanding and maximizing ascorbic acid availability in horticulture crops can enhance plant health, production, and crop quality in general.

6. IMPACT OF AsA ON FRUIT DEVELOPMENT AND RIPENING

AsA plays a significant role in fruit development and ripening in horticultural crops. It affects several physiological and biochemical processes that are involved in fruit quality and ripening traits. Below are the effects of AsA on the growth and ripening of fruit:

6.1 Antioxidant Activity

Fruits are shielded by AsA, a powerful antioxidant, from the oxidative harm produced by reactive oxygen species (ROS) [54]. Due to the formation of ROS, oxidative stress increases throughout fruit growth and ripening. AsA aids in scavenging these ROS, lowering oxidative stress, and preserving fruit quality and shelf life [54].

6.2 Cell Wall Metabolism

AsA has an impact on how cell wall constituents are metabolized during fruit development and ripening [55]. It encourages the production of cellulose, hemicellulose, and other cell wall building blocks like pectin. Fruit firmness, texture, and post-harvest quality are influenced by this since they impact cell wall structure and texture.

6.3 Pigment Synthesis

AsA is involved in the production of pigments that give the fruit its color, such as anthocyanins, and carotenoids. The enzymes involved in the pathways for pigment production serve as a cofactor. The accumulation of these pigments, which results in the production of vivid and appealing fruit hues, depends on adequate AsA levels [56].

6.4 Flavor Development

The volatile molecules are responsible for fruit taste and fragrance and they are influenced by AsA during production. AsA contributes to the metabolism of the organic acids and sugars that are transformed into taste compounds when the fruit ripens. The balance of organic acids and sugars is influenced by AsA concentration, which also impacts the taste and sensory qualities of ripe fruits [57].

6.5 Hormonal Regulation

For instance, ethylene, a crucial regulator of fruit ripening, interacts with AsA in plants. AsA can alter the signaling and biosynthesis of ethylene, which affects the time and course of fruit ripening. AsA aids in preserving the harmony between fruit quality characteristics and ethylene-mediated ripening [23].

6.6 Stress Response

AsA helps plants respond to diverse environmental challenges by acting as a stress-responsive molecule [7,58]. Horticultural crops may experience biotic and abiotic challenges during fruit development and ripening, including infections, temperature changes, and light exposure. To reduce the detrimental effects of these stressors, maintain fruit quality, and improve stress tolerance, AsA is used [59].

It is significant to remember that AsA might have diverse effects on fruit growth and ripening in various horticultural crops and even within cultivars. AsA accumulation and its effects on fruit quality features can be influenced by factors including genetics, environmental circumstances, and cultural behaviors. To maximize fruit production and quality, it is crucial to understand the particular needs and interactions of AsA in various crop species.

7. ASCORBIC ACID AS AN ANTIOXIDANT IN POSTHARVEST PHYSIOLOGY OF HORTICULTURAL CROPS

In the postharvest physiology of horticultural crops, AsA performs as a strong antioxidant. Horticultural crops go through several metabolic processes after harvest that might result in the generation of ROS. AsA reduces oxidative stress and guards against cellular damage by acting as a scavenger of ROS such as superoxide anion, hydrogen peroxide, and hydroxyl radical [60]. Lipid peroxidation, which is brought on by ROS, can cause membrane lipids to break down and lose their integrity. AsA contributes to the suppression of lipid peroxidation, protecting cell membrane integrity and scavenging free radicals to prolong the shelf life and quality of postharvest crops [30].

The postharvest physiology of horticultural crops depends on AsA for the regeneration of other antioxidants including glutathione and alpha-tocopherol (vitamin E) [61]. These antioxidants may be recycled, enabling them to continue guarding against oxidative stress [62]. Enzymatic browning, a frequent physiological postharvest process that impairs the look and quality of fruits and vegetables, is prevented by ascorbic acid. To do this, it interferes with the polyphenol oxidase (PPO) enzyme's ability to catalyze the browning step [63].

AsA also aids in maintaining the nutritional value of postharvest horticulture crops by stopping the deterioration of oxidation-prone vitamins including folate and carotenoids. Ascorbic acid contributes to maintaining the nutritional content of harvested crops by safeguarding these vital components [36]. In horticultural crops, AsA improves the entire antioxidant defense system. It increases the activity of antioxidant enzymes like catalase and superoxide dismutase, which are essential for neutralizing ROS and preserving cellular homeostasis [21].

Ascorbic acid is a useful tool in the postharvest handling and storage of horticultural crops due to its antioxidant qualities. Its capacity to neutralize ROS, suppress lipid peroxidation, avoid enzymatic browning, and maintain nutritional quality helps to maintain crop quality overall and prolong the shelf life of harvested products [64-67].

8. PRESENT AND FUTURE PROSPECTS

Presently, AsA holds significant importance in horticultural crops throughout various stages of plant growth, fruit development/ripening, and postharvest physiology. Its role in these processes has both current and future prospects. AsA plays a crucial role in plant growth and development. It participates in numerous metabolic processes, including photosynthesis, hormone regulation, and enzymatic reactions. Adequate AsA levels are essential for optimal plant growth, chlorophyll synthesis, and overall plant health. Maintaining optimal AsA levels is vital for maximizing crop productivity. Future research may focus on understanding the genetic regulation of AsA biosynthesis and its impact on plant growth. This knowledge could lead to the development of crop varieties with enhanced AsA production, resulting in improved growth and yield potential.

AsA also influences fruit development and ripening processes in horticultural crops. It contributes to cell wall metabolism, pigmentation, flavor development, and antioxidative defense mechanisms. AsA content affects fruit quality attributes, such as texture, color, flavor, and nutritional value. Researchers may explore strategies to modulate ascorbic acid metabolism during fruit development and ripening to enhance desirable quality traits. This could involve targeted genetic modifications or agronomic practices to optimize ascorbic acid accumulation, leading to fruits with improved appearance, taste, and nutritional benefits.

AsA plays a significant role in postharvest physiology and storage of horticultural crops. It acts as an antioxidant, preventing oxidative damage during storage, thereby extending shelf life. Ascorbic acid treatment has been employed to maintain fruit quality, reduce decay, and preserve nutritional value during postharvest handling. Future studies may focus on developing innovative postharvest technologies to optimize ascorbic acid retention and minimize losses. This could involve the development of efficient storage techniques, novel packaging materials, and modified atmosphere conditions that maintain ascorbic acid levels, ensuring superior postharvest quality and longer shelf life.

The nutritional benefits of consuming fruits and vegetables rich in ascorbic acid include enhanced immunity, antioxidant protection, collagen synthesis, iron absorption, and overall well-being. With growing interest in nutrition and wellness, prospects for AsA in horticultural crops involve highlighting its nutritional benefits through education and awareness campaigns. There may be increased demand for crops with enhanced ascorbic acid content, leading to the development of new cultivars or production practices to meet consumer preferences.

In summary, the present and future prospects for ascorbic acid in horticultural crops encompass optimizing plant growth, enhancing fruit quality, improving postharvest storage techniques, and emphasizing the nutritional benefits of ascorbic acid-rich crops. Ongoing research and advancements in genetic engineering, breeding techniques, and postharvest technologies hold promise for harnessing the potential of ascorbic acid in horticulture to meet the evolving needs and demands of consumers.

9. CONCLUSION

In horticultural crops, AsA is a multifunctional chemical that affects postharvest physiology, development and ripening of fruit, and plant growth. In addition to influencing hormone production and transduction, AsA also affects fruit maturity. It plays a significant part in enhancing the general well-being, caliber, and market worth of horticulture crops due to its antioxidant qualities, signaling capabilities, and regulatory duties. The pursuit of AsA-related research and application presents encouraging opportunities for improving horticulture techniques and satisfying consumer needs for nutrient-dense, high-quality products.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

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 writing or editing of manuscripts.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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