



Review

Ascorbate, as a versatile regulator of plant development: practical implications for enhancing crop productivity, quality, and postharvest storage

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ABSTRACT

Ascorbate (Asc), commonly known as vitamin C, is a vital molecule for plant growth, development, and stress resilience. It is also known to play a crucial role in various physiological processes, including photosynthesis, cell division, and differentiation. This article thoroughly explores the processes governing the metabolism of Asc in plants and its roles in physiological functions. It lays down a robust theoretical groundwork for delving into Asc production, transportation, functions, and its potential applications in stress alleviation and horticulture. Furthermore, recent studies indicate that Asc plays a role in regulating fruit development and affecting postharvest storage characteristics, thereby influencing fruit ripening and resilience to stress. Hence, there is a growing importance in studying the synthesis and utilization of Asc in plants. Although the critical role of Asc in controlling plant redox signals has been extensively studied, the precise mechanisms by which it manages cellular redox homeostasis to maintain the equilibrium between reactive oxygen scavenging and cell redox signaling remain elusive. This gap in knowledge presents fresh opportunities to explore how the production of Asc in plants is regulated and how plants react to environmental stressors. Furthermore, this article delves into the potential for a comprehensive investigation into the essential function of Asc in fruits, the development of Asc-rich fruits, and the enhancement of postharvest storage properties.

Keywords: Ascorbate; Environmental factors; Fruit; Metabolism; Oxidative stress; Postharvest technology; Ripening; Softening

1. Introduction

Ascorbate (Asc) or vitamin C is a crucial compound present in plants, with significant implications for human health. While Asc is vital for preventing scurvy and potentially reducing the risk of diseases and slowing down ageing in humans (Kietzmann, 2023), humans lack the ability to synthesize Asc due to the absence of the enzyme L-gulonolactone oxidase, which is typically found in most animals (Chatterjee, 1973).

Consequently, humans depend on fruits and vegetables as their primary source of Asc.

The Asc content of fruits and vegetables varies depending on the plant species, variety, and environmental conditions (Kandel et al., 2025). Fruits usually have higher Asc levels than leaves, but they tend to decrease during ripening and postharvest storage. Asc plays a significant role in fruit development and quality by participating in diverse physiological processes, including cell wall formation, hormone synthesis, and

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stress response. The biosynthesis of Asc involves several enzymes. For instance, enzymes like L-galactono-1,4-lactone dehydrogenase become active during fruit ripening, as demonstrated in tomato (Alhagdow et al., 2007). The balance between Asc biosynthesis, degradation, and recycling determines the relative accumulation of Asc in plant tissues. Modifying Asc levels in fruits is of high interest, as it can improve their nutritional and organoleptic properties (Aguilar et al., 2023; Su et al., 2025).

As one of the most abundant compounds in plants, Asc is present in millimolar concentrations in leaves and storage organs. Within the leaf, Asc concentrations are highest in the cytoplasm (approximately $22 \text{ mmol} \cdot \text{L}^{-1}$), peroxisomes ($23 \text{ mmol} \cdot \text{L}^{-1}$), nuclei ($16 \text{ mmol} \cdot \text{L}^{-1}$), and lower in chloroplasts ($11 \text{ mmol} \cdot \text{L}^{-1}$), mitochondria ($10 \text{ mmol} \cdot \text{L}^{-1}$), and vacuoles ($2 \text{ mmol} \cdot \text{L}^{-1}$). Notably, Asc was not detected in the lumen of thylakoids or cristae but rather in the matrix and stroma of non-stressed cells' mitochondria and chloroplasts (Zechmann, 2018).

Asc plays a crucial role in protecting enzymes from oxidative damage and recycling the lipid-soluble α -tocopherol by reducing its oxidized form (Munné-Bosch and Alegre, 2002). Additionally, Asc modulates various physiological processes in plants, including photoprotection, photosynthesis, root elongation, cell expansion, cell division, and ethylene production (Celi et al., 2023). Furthermore, Asc is indispensable for preserving fruits at low temperatures after harvest, enhancing their cold tolerance (Lo'Ay and El-Khateeb, 2018).

In horticultural crops, Asc significantly influences fruit ripening and development. Treatment with exogenous Asc can enhance the quality and shelf life of banana and strawberry fruits stored at low temperatures (Lo'Ay and El-Khateeb, 2018; Saleem et al., 2021). Moreover, Asc content can impact fruit size and color, as observed in tomatoes, where both low and high levels of Asc result in smaller fruits (Alhagdow et al., 2007; Bulley et al., 2012). Understanding the metabolism and regulation of Asc in fruits is crucial for improving fruit quality and post-harvest preservation.

This review paper summarizes the recent research on Asc biosynthesis, degradation, recycling, and transport in fruits, as well as the physiological and molecular mechanisms of Asc-mediated fruit development and ripening.

2. Biosynthesis, metabolism and transport of Asc in plants

2.1. Biosynthesis and metabolism of Asc in plants

Asc is mainly synthesized by the Smirnoff–Wheeler pathway in vascular plants, which involves a series of enzymatic reactions in the cytosol. In *Arabidopsis thaliana*, the enzyme GDP-mannose pyrophosphorylase (GMP, also called VITAMIN C DEFECTIVE1, VTC1) plays a crucial role in Asc biosynthesis by catalyzing the formation of GDP-D-mannose from mannose 1-P. Its contribution to Asc synthesis was initially established by identifying VTC1 as GMP in *Arabidopsis* (Conklin et al., 1999), and further validated through experiments involving the suppression of its activity using antisense techniques in potato (Keller et al., 1999; Smirnoff

and Wheeler, 2024). Subsequently, GDP-D-mannose is converted to GDP-L-galactose by GDP-D-mannose 3',5' epimerase (GME), followed by the formation of L-galactose-1-phosphate by GDP-L-galactose phosphorylase (GGP, encoded by VTC2 and VTC5). Then, L-galactose-1-phosphate is hydrolyzed to L-galactose by L-galactose-1-P phosphatase (GPP, encoded by VTC4), which is then oxidized to L-galactono-1,4-lactone by L-galactose dehydrogenase (GDH) (Wheeler et al., 1998; Smirnoff, 2018). In the last stage of the process, within the mitochondria, L-galactono-1,4-lactone is converted into Asc by L-galactono-1,4-lactone dehydrogenase (GLDH) at Complex I (Millar et al., 2003).

The Smirnoff–Wheeler pathway serves as the primary route for Asc biosynthesis in both leaves and fruits (Smirnoff and Wheeler, 2024). Despite this, three alternative Asc biosynthesis pathways have been proposed: the L-gulose, myo-inositol, and galacturonate pathways (Ntagkas et al., 2018; Liao et al., 2023; Quinones et al., 2024). However, experimental findings suggest that the L-gulose pathway is unlikely to make a significant contribution to Asc biosynthesis in leaves or fruits (Broad et al., 2020; Liao et al., 2023). Similarly, the myo-inositol pathway appears to be non-functional in leaves (Kavkova et al., 2019). However, it may indirectly affect Asc content in fruits. A key gene in this pathway, myo-inositol oxygenase (MIOX, EC 1.13.99.1), is involved in regulating cell wall formation (Arner et al., 2002). Overexpression of MIOX leads to increased cell wall thickness and fruit firmness, along with an improved Asc content (Cronje et al., 2012; Zheng et al., 2022a) (Fig. 1).

The galacturonate pathway is likely to be functional in ripening fruits, such as strawberry (Agius et al., 2003), grape (Cruz-Rus et al., 2010), kiwifruit (Li et al., 2011), as well as chestnut rose (Huang et al., 2014). Increased expression of the D-galacturonate reductase gene in plants has been associated with enhanced stress tolerance as well (Broad et al., 2020).

Reactive oxygen species (ROS) are generated during various cellular processes, including photosynthesis and photorespiration. These ROS, such as superoxide (O_2^-), singlet oxygen ($^1\text{O}_2$), and hydrogen peroxide (H_2O_2), can directly oxidize Asc to monodehydroascorbate (MDA). In addition to this, stromal and thylakoid-bound superoxide dismutases (SODs) and Asc peroxidases (APXs) (Asada, 2006) catalyze the scavenging of superoxide and H_2O_2 generated in the chloroplast, respectively. The oxidized forms of Asc can undergo recycling back to Asc through various enzymes and pathways. MDA can be reduced either by MDA reductases (MDARs) or by reduced ferredoxin at the acceptor side of photosystem I (PSI) (Asada, 2000; Foyer et al., 2020). Alongside this series of processes, known as the Mehler peroxidase reaction (Asada, 2006), a secondary enzymatic cascade, commonly referred to as the Asc-glutathione cycle, is responsible for regenerating reduced Asc from DHA (Foyer and Kunert, 2024). While this cycle operates in multiple cellular compartments, the Mehler-peroxidase sequence is specific to the chloroplast (Foyer and Halliwell, 1976; Horemans et al., 2000).

The recycling of MDA and DHA to Asc is critical for maintaining sufficient Asc levels within the cell. Under normal physiological conditions, the recycling system exhibits high efficiency, predominantly maintaining the Asc pool in its reduced state. However, an exception occurs in the apoplast, where Asc is

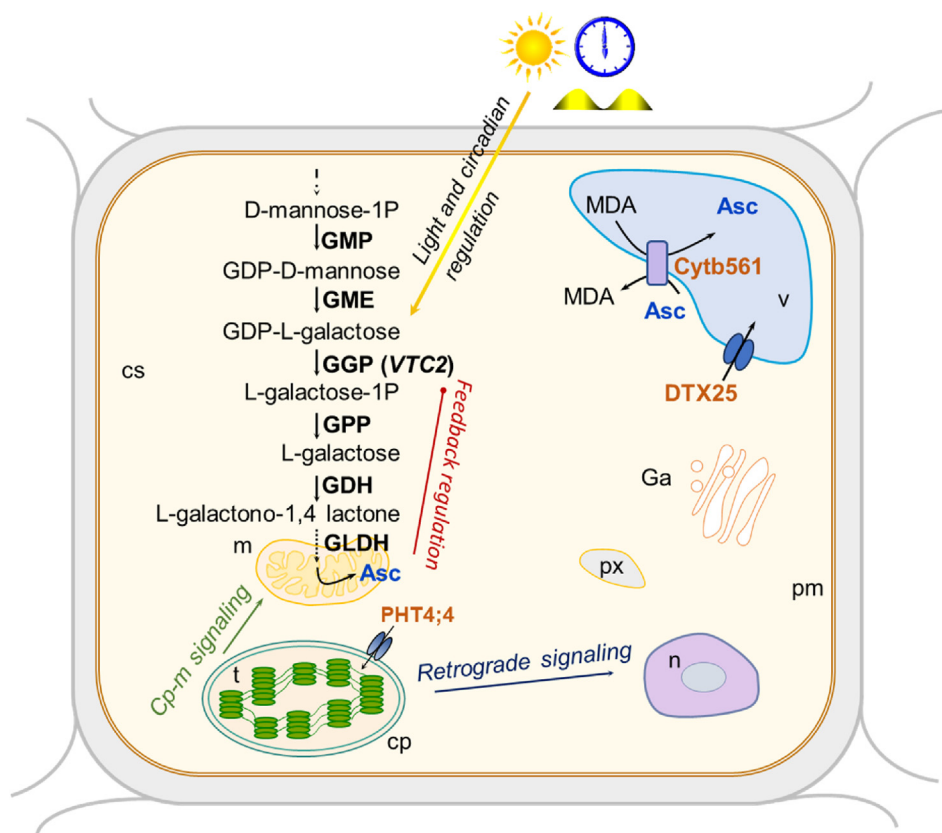


Fig. 1 Ascorbate biosynthesis and its regulation in vascular plants

In vascular plants, Asc is synthesized via the Smirnoff–Wheeler pathway with the majority of the steps taking place in the cytosol and the last step in the mitochondria at Complex I. Asc biosynthesis is regulated by light, the circadian clock, the photosynthetic electron transport, and feedback regulatory mechanisms. From the mitochondria, Asc is transported to all cell compartments. The Asc transporters characterized at a molecular level include PHT4; 4, belonging to the family of phosphate transporters found in the chloroplast envelope membrane, and DTX25, a multidrug and toxic compound extrusion family transporter located in the tonoplast of *Arabidopsis* seedlings. The tonoplast cytochrome b561 is a transmembrane Asc-dependent MDA reductase. Asc, ascorbate; cp, chloroplast; cs, cytosol; DTX25, vacuolar Asc transporter; Ga, Golgi apparatus; GDH, L-galactose dehydrogenase; GGP, GDP-L-galactose phosphorylase (encoded by VTC2); GLDH, L-galactono-1,4 lactone dehydrogenase; GME, GDP-D-mannose 3',5'-epimerase; GMP, GDP-D-mannose pyrophosphorylase; GPP, L-galactose-1-P phosphatase; m, mitochondrion; n, nucleus; PHT4; 4, chloroplastic Asc transporter; pm, plasma membrane; px, peroxisome; t, thylakoids; v, vacuole.

primarily oxidized by Asc oxidase and lacks the recycling system (Fry, 1998; Green and Fry, 2005; Mellidou and Kanellis, 2024).

Failure to recycle DHA can result in its degradation into oxalate, L-threonate, or tartaric acid, depending on the plant species (Green and Fry, 2005; Truffault et al., 2017; Ford et al., 2024). The degradation of Asc may be associated with processes such as cell wall loosening, growth, and fruit ripening.

The concentration of Asc in *Arabidopsis* leaves varies depending on the time of day and growth conditions. Under normal circumstances, Asc levels range from 2 to 5 $\mu\text{mol} \cdot \text{g}^{-1}$ fresh weight (FW), but can increase to 10 $\mu\text{mol} \cdot \text{g}^{-1}$ FW under stress conditions such as high light, ozone exposure, nitrogen starvation, drought, and salt stress (Broad et al., 2020; Terzaghi and De Tullio, 2022). Additionally, Asc levels fluctuate throughout the day, with lower levels at night and higher levels in the afternoon, as its biosynthesis is regulated by the circadian rhythm (Kiyota et al., 2006; Dowdle et al., 2007; Maruta et al.,

2008). Application of L-galactono-1,4-lactone, a precursor of Asc biosynthesis, can further increase Asc content by 50% (Yabuta et al., 2008; Bulley et al., 2021). However, excessively high Asc concentrations can have adverse effects on plant metabolism, including photosynthesis (Castro et al., 2018). Thus, Asc in plants is regulated within an optimal concentration range by multiple mechanisms, emphasizing the importance of understanding Asc biosynthesis regulation to potentially control Asc levels in plants.

Soluble carbohydrates can influence the rate of Asc biosynthesis (Yabuta et al., 2007), and plants grown in darkness are unable to produce Asc (Yoshimura et al., 2014). The final step of Asc biosynthesis, the conversion of L-galactono-1,4-lactone to Asc at Complex I in the mitochondria, is influenced by light and photosynthesis (Yabuta et al., 2008). H_2O_2 generated under stress conditions can deactivate GLDH, but this inhibition can be prevented by L-galactono-1,4-lactone and Asc (Leferink et al., 2009). Thus, the levels of H_2O_2 , L-galactono-1,4-lactone, and Asc may

regulate Asc biosynthesis in vascular plants. Chloroplastic signals may regulate Asc biosynthesis, although the molecular mechanisms remain unknown. It is plausible that ROS generated during photosynthesis could impact the expression of Asc biosynthesis genes, although this hypothesis has not been experimentally validated.

The synthesis of Asc is also influenced by phytohormones. Studies have demonstrated that jasmonic acid and methyl jasmonate can elevate Asc concentration and enhance the expression of Asc biosynthesis genes in liquid-cultured seedlings and cell suspension cultures of *Arabidopsis* (Sasaki-Sekimoto et al., 2005; Wolucka et al., 2005). In fruits, Asc levels are influenced by other hormones such as abscisic acid, gibberellin, ethylene, and salicylic acid (Li et al., 2015; Miret and Munné-Bosch, 2016; Yu et al., 2019; Zheng et al., 2022a). However, the mechanisms by which plant hormones affect Asc biosynthesis remain poorly understood.

The expression of several genes involved in Asc biosynthesis depends on the photosynthetic electron transport chain, including GMP, VTC2, GPP, and GLDH (Yabuta et al., 2007). Light also directly affects the Asc content of plants by regulating various steps of Asc biosynthesis. As a case in point, light can control GMP activity through the photomorphogenic factor CSN5B (Chen et al., 2010; Nezames and Deng, 2012; Wang et al., 2013). Ascorbic acid mannose pathway regulator 1 (AMR1) is another factor that influences the expression of several Asc biosynthesis genes, such as GMP, GME, GGP, GPP, L-GalDH, and GLDH, in a light-dependent manner (Zhang et al., 2009). In tomato, an HD-Zip I family transcription factor, SLH24, positively regulates the accumulation of Asc by binding to the promoter of *SlGMP3*, also affecting the expression of *GME* and *GGP* (Hu et al., 2016).

GGP, encoded by *VTC2* and *VTC5* in vascular plants, catalyzes the first committed step of Asc biosynthesis, and plays a vital role in its regulation (Conklin et al., 1996; Fenech et al., 2021). The *vtc2* *Arabidopsis* mutants have an approximately 80% reduction in Asc level (Conklin et al., 1996; Lim et al., 2016), while the *vtc5* mutants do not exhibit a significant decline in Asc content. The double *vtc2 vtc5* mutants are unable to survive in soil (Dowdle et al., 2007). These results demonstrate not only the essentiality of GGP in Asc biosynthesis but also the greater importance of *VTC2* than *VTC5* in determining the Asc level in *Arabidopsis* leaves.

Asc regulates GGP translation through a feedback mechanism (Laing et al., 2015; Bulley and Laing, 2016; Deslous et al., 2021; Terzaghi and De Tullio, 2022). This process is mediated by a conserved upstream open reading frame (uORF) in the 5'-UTR of *VTC2* (Laing et al., 2015). Genome editing to remove the uORF region increased Asc concentration in *Arabidopsis*, lettuce, and tomato (Laing et al., 2015; Li et al., 2018; Zhang et al., 2018). However, the remarkable increase of Asc concentration in fruits was accompanied by impaired flower and pollen development in tomato (Deslous et al., 2021).

GGP (*VTC2*) expression is also affected by light intensity, given that it possesses a light-responsive cis-element in its promoter, namely a G-box motif (Li et al., 2013). Recent findings have demonstrated that PAS/LOV PROTEIN (PLP) A and B interact with *VTC2* in a light-dependent manner and regulate its activity. PLPB

knockout mutants exhibited approximately 1.6-fold elevations in their Asc levels, suggesting that PLP plays a critical role in elevating Asc levels during high light acclimation (Aarabi et al., 2023).

2.2. Asc transport in plants

The final step of Asc biosynthesis, involving the conversion of L-galactono-1,4-lactone to Asc, occurs in the mitochondria. To transport Asc to other cellular compartments, specific transporters are necessary, as Asc and its oxidized form, DHA, cannot pass through lipid bilayers due to their negative charge and relatively large size. Currently, only two Asc transporters have been molecularly characterized in plants, although there is biochemical evidence suggesting the existence of several others (Tóth, 2023).

One of these transporters is AtDTX25, which belongs to the multidrug and toxic compound extrusion family in *A. thaliana*. AtDTX25 serves as a vacuolar Asc transporter that regulates intracellular iron cycling during seedling development (Hoang et al., 2021). Additionally, AtDTX25 expression has been detected in flowers, but not in leaves (Hoang et al., 2021).

The AtPHT4;4 transporter is a member of the phosphate transporter 4 family of *A. thaliana* that is located in the chloroplast envelope membrane (Guo et al., 2008; Fernie and Tóth, 2015; Miyaji et al., 2015). AtPHT4;4 knockout mutants exhibit only a 30% decrease in chloroplastic Asc content, as well as a slight impairment of the xanthophyll cycle and a decrease in non-photochemical quenching (NPQ) at high light (Miyaji et al., 2015). The mild phenotype of the AtPHT4;4 knockout mutant is suggestive of the fact that there are other Asc transporters in the chloroplast envelope membrane. Moreover, it is possible that the thylakoid membrane contains transporters for Asc (and potentially DHA) to support photosynthetic functions.

Interestingly, maintaining the appropriate Asc concentration within a specific cell compartment may also involve transmembrane Asc-dependent MDA reductases, such as cytochrome b561. Recently, it was demonstrated that cytochrome b561 isoform A (CYB561A) functions as a tonoplast redox protein in *Arabidopsis* vacuoles, potentially mediating Asc-dependent electron transport that connects the redox states of different Asc pools (Gradogna et al., 2023).

3. The physiological roles of Asc in the plant cell

3.1. Asc in controlling oxidative metabolism

The predominant focus of research on the function of Asc in plant cells has been its role in mitigating oxidative stress under various stress conditions, such as cold, salt, and drought stress (Bybordi, 2012; Raza et al., 2013; Shafiq et al., 2014; Li et al., 2021). There are excellent recent reviews available on this topic (Foyer et al., 2020; Krieger-Liszka and Shimakawa, 2022; Mittler et al., 2022; Foyer and Kunert, 2024; Yoshimura and Ishikawa, 2024).

In response to stress, plants typically synthesize ROS-neutralizing compounds, including both non-enzymatic and enzymatic antioxidants, and Asc plays a crucial role in both

processes. The substantial intracellular concentration of Asc indicates its fundamental role in scavenging ROS as part of the essential housekeeping duties for the aerobic existence of eukaryotic cells (Liao et al., 2023). Ascorbate is indispensable for the enzymatic scavenging of ROS in processes such as the Mehler reaction or water–water cycle (Ivanov et al., 2022; Foyer and Kunert, 2024). This reaction becomes particularly pertinent under intense illumination and when the Calvin–Benson cycle slows down, as occurs during drought, salt, or cold stress. The slow outflow of electrons at the PSI acceptor side leads to overreduction of the electron transport chain and superoxide (O_2^-) is produced, via the reduction of O_2 by ferredoxin. In the subsequent step, it is reduced to H_2O_2 by superoxide dismutase (SOD), and H_2O_2 is reduced by Asc peroxidase (APX) to water.

MDA can be directly reduced back to Asc by ferredoxin at the acceptor side of photosystem I, or in the Asc-glutathione cycle (Asada, 2006; Foyer and Kunert, 2024). In this cycle, MDA reductase (MDAR) and dehydroascorbate reductase (DHAR) regenerate MDA to Asc. MDAR utilizes NAD(P)H to convert MDA to Asc directly, while DHAR catalyzes the conversion of glutathione (GSH) to glutathione disulfide (GSSG), which is then reduced back to GSH with the concomitant utilization of NAD(P)H by glutathione reductase.

Ascorbate and glutathione work together in the mitigation of ROS. However, ROS also function as crucial signaling molecules that enable cells to rapidly adapt to stress conditions and integrate various environmental signals to activate defense mechanisms (Mittler et al., 2022). Consequently, Asc plays a pivotal role in redox signaling, regulating plant responses to biotic stress, and indirectly influencing plant growth, development (Pastori et al., 2003; Pignocchi and Foyer, 2003; Foyer et al., 2020), and possibly metabolism (Tóth et al., 2024).

The regeneration of Asc is highly efficient, as most of the Asc pool remains in the reduced state under normal conditions, except during severe stress. An exception is the apoplast, where Asc is more oxidized due to the activity of Asc oxidase (Smirnoff and Wheeler, 2000; Szarka et al., 2004; De Tullio et al., 2013; Mellidou and Kanellis, 2024). Dehydroascorbate in the apoplast is transported into the cytosol, where it is exchanged for Asc to maintain a steady redox balance in the apoplast (Horemans et al., 2000; De Tullio et al., 2013; Anjum et al., 2014). Asc present in the extracellular space serves as the first line of defense against oxidants (Plöchl et al., 2000; Anjum et al., 2014; Kangasjärvi and Kangasjärvi, 2014). Conversely, the high activity of Asc oxidase is also associated with cell wall loosening and growth (Fry, 1998; Green and Fry, 2005).

3.2. Asc-dependent redox reactions in the chloroplast distinct from ROS scavenging

Non-photochemical quenching (NPQ) of excitation energy represents a mechanism by which plants alleviate photooxidative stress (Bassi and Dall'Osto, 2021; Krieger-Liszak and Shimakawa, 2022). NPQ comprises several components with distinct underlying mechanisms, including energy-dependent (qE), zeaxanthin-related (qZ), state-transition-related (qT), and potentially other components associated with photoinhibition

(Pinnola and Bassi, 2018; Kaiser et al., 2019). In vascular plants, Asc primarily modulates the qZ component, which involves the conversion of violaxanthin to zeaxanthin by violaxanthin de-epoxidase (VDE), located in the thylakoid membrane (Dall'Osto et al., 2005; Nilkens et al., 2010). Activation of VDE is induced by high light levels in a pH-dependent manner (Arnoux et al., 2009; Hallin et al., 2016). Ascorbate serves as a co-substrate, supplying the reducing power required for the de-epoxidation reaction (Bratt et al., 1995). Apart from its role in NPQ, zeaxanthin may contribute to photoprotection by acting as an antioxidant (Havaux et al., 2007).

Heat stress can disrupt the oxygen-evolving complex (OEC), resulting in the release of extrinsic proteins, Ca- and Mn-ions from their binding sites (Yamane et al., 1998; Barra et al., 2005). Consequently, electron flow from water to photosystem II (PSII) is impeded, leading to the accumulation of various oxidizing species that deactivate the reaction centers in the light (Jegerschöld and Styring, 1996; Spetea et al., 1997). This phenomenon, known as donor-side induced photoinhibition, is partly mitigated by Asc, which acts as an alternative electron donor and sustains a steady electron flow (Tóth et al., 2009). Moreover, Asc facilitates the recovery from the photoinactivated state. These findings underscore the vital role of Asc in enhancing plant tolerance to heat stress (Tóth et al., 2011).

In C4 plants like maize and sorghum, Asc can function as an alternative electron donor to PSII in bundle sheath chloroplasts (Ivanov et al., 2005, 2007). These chloroplasts exhibit reduced levels of PSII activity, supported by electron donation from Asc to PSII. This moderate photosynthetic electron transport rate adequately maintains cyclic electron flow around PSI to energize the thylakoid membrane and produce ATP for the Calvin–Benson cycle (Ivanov et al., 2005, 2007).

While Asc generally supports PSII activity, it can also have inhibitory effects under specific conditions. Podmaniczki et al. (2021) observed that in *Arabidopsis*, Asc may deactivate the OEC following prolonged darkness, possibly facilitated by dark-induced dissociation of extrinsic OEC proteins, which would otherwise hinder Asc access to the Mn-cluster. The data suggest that OEC inactivation by Asc could represent an early step in dark-induced senescence. These findings underscore the importance of tightly regulating Asc concentration and localization, especially when manipulating Asc levels in crops.

3.3. Asc and mitochondrial electron transport

The final oxidation step of Asc biosynthesis is physically linked to the mitochondrial respiratory chain through complexes I, III, and cytochrome c. During the oxidation of L-galactono-1,4-lactone to Asc by GLDH, electrons are transferred into the mitochondrial electron transport chain via cytochrome c, located between Complexes III and IV (Bartoli et al., 2000; Millar et al., 2003; Gordon et al., 2007). This connection between L-galactono-1,4-lactone oxidation and mitochondrial electron transport chain activity via cytochrome c may facilitate the coordination of Asc biosynthesis and respiration (Welchen and Gonzalez, 2016). Moreover, it has been demonstrated that the conversion of L-galactono-1,4-lactone itself relies on the activity of the photosynthetic electron transport chain (Yabuta et al., 2008), indicating

a cross-talk between photosynthetic and respiratory electron transport chains.

3.4. Asc, as a chaperone for 2-oxoglutarate-dependent dioxygenases (2-ODDs)

By maintaining Fe in the reduced form at their active sites, the enzymes belonging to the large superfamily of 2-oxoglutarate-dependent dioxygenases (2-ODDs) utilize Asc as a chaperone to support their catalytic activity. In plants, 2-ODDs catalyze a wide range of reactions, including hydroxylation, epoxidation, and desaturation of specific substrates involved in the biosynthesis and catabolism of plant hormones (abscisic acid, auxin, ethylene, gibberellins, salicylic acid), hydroxyproline, along with myriad other secondary metabolites (Smirnov, 2018; De Tullio, 2020).

Moreover, 2-ODDs play a crucial role in epigenetic gene expression regulation by modulating cytosine and histone methylation. This includes TET (ten-eleven translocation) hydroxylases, which catalyze the conversion of methylcytosine (5mC) to hydroxymethylcytosine (5hmC), and the Jumonji family of histone demethylases. TET hydroxylases have been thoroughly characterized and studied in animal cells, and there is emerging interest in exploring their potential functions in plants (Xue et al., 2019; Lucibelli et al., 2022). Histone demethylation mediated by specific 2-ODDs occurs during various plant developmental processes and in response to stress conditions (Chen et al., 2021). However, the precise extent to which the availability of Asc influences epigenetic regulation in plants remains an open question.

4. Application of Asc in horticulture

4.1. Asc priming: enhancing seed germination, growth, and stress tolerance

Seeds play a pivotal role in shielding the embryo from mechanical damage and desiccation while storing essential reserves crucial for embryo development until favorable germination conditions arise. The initiation of the developmental program toward seedling establishment necessitates extensive epigenetic and hormonal reprogramming. Growing evidence suggests that Asc serves as a pivotal player in the diverse stages of seed development, desiccation, after-ripening, and germination.

During seed development, Asc content increases but significantly decreases during dehydration, virtually becoming undetectable in dry seeds. This decline may be associated with seed quiescence and longevity (Arrigoni et al., 1992; De Gara et al., 2003; Ye et al., 2012). Apart from the downregulation of Asc biosynthesis, Asc catabolism might also be activated during dehydration. The exact cause for the substantial decrease in Asc content during seed dehydration remains elusive; however, Terzaghi and De Tullio (2023) recently suggested that during early seed germination stages, Asc recycling and biosynthesis experience a notable increase, emphasizing their significance for germination (Barba-Espin et al., 2012). Notably, seed development is regulated by the coordinated action of gibberellins and abscisic acid, and the biosynthesis of these plant growth regulators is regulated by Asc-dependent 2-ODDs (see section 3.4) (Dilley et al., 2013).

Ensuring high seed quality is paramount in agriculture. Achieving rapid and synchronized seedling emergence is crucial for crop productivity, as delayed germination exposes young plants to harsh environmental conditions and soil-borne diseases. Priming, a well-established technique for enhancing germination rates, results in increased resistance to biotic and abiotic stresses, ultimately enhancing crop yields.

When seeds are primed with suitable biologically active substances, they can elicit metabolic responses both before and during germination. During the initial stages of germination, amylase and protease catalyze the oxidative breakdown of starch and protein to produce nutrients and energy. During priming, the hydration level of seeds is carefully regulated to prevent endosperm rupture and suppress pre-germination metabolism production (Corbineau et al., 2023). Increasing evidence indicates that seed priming with Asc can interact with various metabolic pathways, including ROS management and signaling, leading to the modulation of genes, enzymes, and ultimately, plant development.

Multiple studies have explored the impacts of seed priming with Asc in different crops (such as tomato, mung bean, and cauliflower) under various abiotic stress conditions. For example, Ghoohestani et al. (2012) demonstrated that treating tomato seeds with $150 \text{ mg} \cdot \text{L}^{-1}$ Asc during priming resulted in enhanced seed vigor, root length, and shoot length, thus mitigating the negative effects of salinity. Similarly, Latif et al. (2016) found that Asc priming effectively alleviated drought stress in cauliflower seeds by reducing H_2O_2 accumulation and enhancing relative water content and modulating the levels of various beneficial compounds and enzyme activities, including phenolic compounds, proline, glycine betaine, endogenous Asc concentrations, superoxide dismutase, and catalase. Another study by Kumar et al. (2011) demonstrated that Asc in mung bean mitigated oxidative stress and modulated antioxidant enzyme activities, resulting in heightened heat tolerance and productivity under challenging environmental conditions. Furthermore, exogenous Asc application in durum wheat was observed to support ROS homeostasis, particularly during seed germination and seedling growth and alleviated the effects of salinity (Fercha et al., 2014).

In addition to seed priming, there are also reports on the foliar and soil application of Asc being beneficial to plants. For instance, according to Hassan et al. (2021), foliar application of Asc has been shown to improve salinity stress tolerance in barley by regulating photosynthesis and the oxidative stress response (Fig. 2).

4.2. The role of Asc in fruit development and enhancing fruit Asc content

The distribution of Asc varies within plants, with the highest concentrations typically found in leaves and flowers. Conversely, tissues with lower photosynthetic activity, such as roots and stems, tend to exhibit lower levels of Asc (Smirnov, 2011). Asc plays a diverse role in fruit development and ripening, with accumulation patterns varying among different fruit crops, categorized based on the timing of Asc accumulation. For instance, kiwifruits and apples represent the first group, accumulating Asc primarily during fruit growth and development. In contrast, jujubes exhibit peak Asc accumulation during fruit expansion, forming the second category. In the third group,

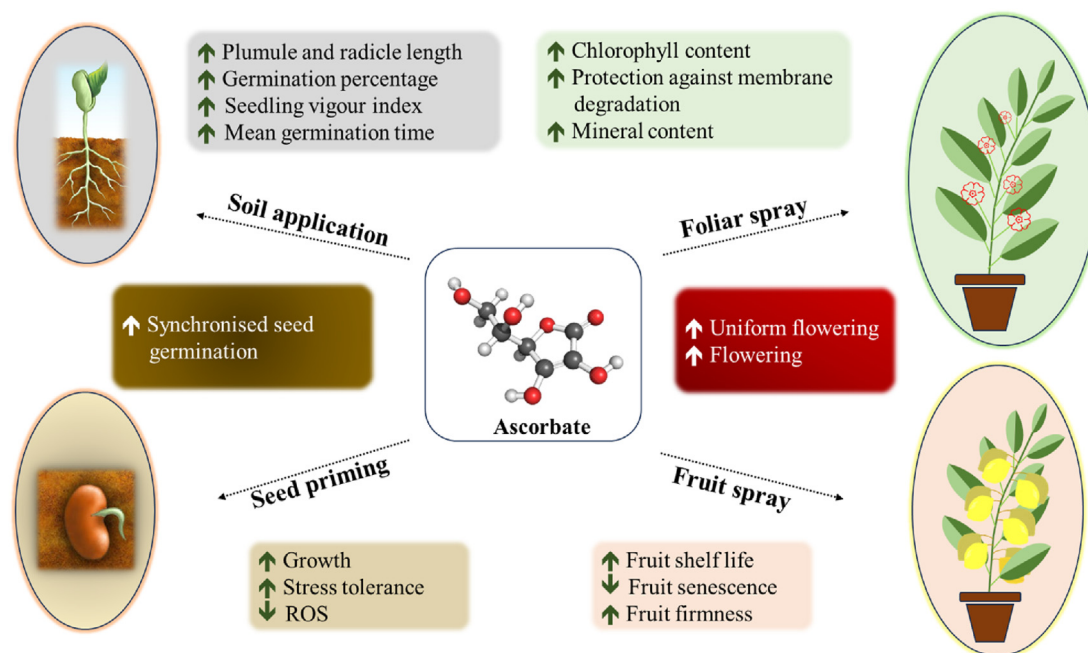


Fig. 2 Physiological effects of Asc applications in different stages of plant growth

Asc regulates plant growth and development and improves plant stress tolerance. Arrows indicate upregulation (↑) or downregulation (↓) of physiological parameters.

exemplified by chestnut rose, strawberries, and tomatoes, Asc accumulation predominantly occurs during fruit maturation (Cruz-Rus et al., 2010; Li et al., 2010, 2011; Huang et al., 2014; Do et al., 2022; Wang et al., 2022).

The Smirnov-Wheeler pathway presents a promising target for manipulating Asc levels in plants, as the expression levels of its enzymes have been shown to influence Asc levels in leaves and various fruits, including apples, kiwifruits, and jujubes (Bulley et al., 2009; Liao et al., 2021; Lu et al., 2022). Expressing kiwifruit GGP in tomato, strawberry, and potato also resulted in a two to threefold increase in Asc content (Bulley et al., 2012). Rodríguez-Ruiz et al. (2017) suggested that GLDH is a crucial player in the physiology of pepper plants, potentially influencing Asc distribution among different organs.

Yeast-derived arabinono-1,4-lactone oxidase (ALO), GMPase, and MIOX2 from *A. thaliana*, presumably involved in Asc biosynthesis have been independently expressed in tomato. Expression of ALO and GMPase led to significant (25%–70%) increase in Asc levels in leaves and fruits. Conversely, fluctuations in Asc concentration were not consistent in plants expressing the MIOX2 gene. Rather, it seemed that MIOX may serve as a useful means to alter cell wall composition instead of solely increasing Asc levels in fruits (Cronje et al., 2012).

Moreover, high Asc content in jujube fruits has been shown to be related to the L-galactose pathway, as several biosynthesis genes (GMP1, GME1, GGP, and GPP) were upregulated in a jujube variety with high Asc content. As indicated by a higher expression level of MDHAR, Asc recycling was also enhanced. On the other hand, and the expression level of MIOX1 was also increased in the variety with high Asc content. Therefore, it appears that multiple factors are responsible for establishing high Asc concentration in jujube fruits (Wang et al., 2022) (Table 1).

Asc undergoes long-distance transport in the phloem from photosynthetically active leaves to sink tissues such as roots. It is found in sink organs of various plants, including tomatoes, kiwis, chestnut flowers, and apples (Li et al., 2010; Huang et al., 2014). Studies on apple and chestnut rose fruit suggest that Asc stored in fruits may originate from Asc synthesized in other tissues and transported as DHA (Li et al., 2010; Huang et al., 2014). Additionally, Asc plays a regulatory role in cell growth and division, influencing overall fruit development and growth.

The balance between Asc and DHA is tightly regulated by ascorbate oxidase (AO) and APX, not only in leaves but also in fruits. APX plays a particularly crucial role in modulating Asc levels during fruit ripening, storage, and in response to injuries, while AO appears to be associated with tissue growth (Gomez and Lajolo, 2008). Moreover, Asc serves as a substrate for the formation of essential organic acids such as L-glyceric, L-oxalic, L-tartaric, and L-threonic acids, which play significant roles in fruit ripening in tomato and strawberry (Truffault et al., 2017; Liu et al., 2022).

Illumination conditions bear a strong impact on Asc. Kang et al. (2020) showed that exposing Chinese cabbage seedlings to blue LED light stimulated the expression of APX, MDAR, DHAR, and GR genes involved in Asc metabolism. D-galacturonic acid reductase gene expression and protein levels in grape berries were up-regulated in tandem with an increase in Asc concentration during fruit ripening and intense light exposure (Cruz-Rus et al., 2010).

4.3. Harvest to table: Asc's influence on post-harvest technology for horticultural products

Fruit ripening, characterized by a series of intricate physiological and biochemical changes, profoundly impacts the color, flavor, aroma, and texture of mature fruits (Giovannoni et al.,

Table 1 Relationship between genes regulating Asc metabolism and Asc accumulation in fruits

Name of the gene	Gene source	Plant transformed	Plant responses	Reference
<i>D</i> -galacturonic acid reductase (<i>GalUR</i>)	<i>Fragaria</i> × <i>ananassa</i>	<i>Solanum lycopersicum</i>	Lines of overexpressing <i>FaGalUR</i> gene resulted in 2-fold and 1.6-fold increase in Asc level in fruit and leaf. <i>FaGalUR</i> overexpressing plants showed enhanced tolerance to abiotic stresses as compared to the wild-type plants.	Cai et al. (2015)
		<i>Solanum tuberosum</i>	The over-expression of <i>GalUR</i> resulted in 1.6–2-fold increase in Asc in transgenic potato and the levels of Asc were positively correlated with increased <i>GalUR</i> activity. The transgenic lines with enhanced vitamin C content showed enhanced tolerance to abiotic stresses.	Upadhyaya et al. (2009)
<i>L</i> -galactono-1,4-lactone dehydrogenase (<i>GalLDH</i>)	<i>Fragaria</i> × <i>ananassa</i>	<i>Arabidopsis thaliana</i> <i>Arabidopsis thaliana</i>	Overexpression of <i>GalUR</i> enhanced vitamin C content two to three-fold. Transient over-expression and ectopic expression of <i>FaGalLDH</i> increased Asc production, while transient RNAi targeting <i>FaGalLDH</i> resulted in decreased Asc content.	Agius et al. (2003) Dun et al. (2023)
	<i>Nicotiana tabacum</i>	<i>Nicotiana tabacum</i>	Overexpression of <i>GalLDH</i> can increase Asc content in tobacco.	Tokunaga et al. (2005)
<i>L</i> -Galactose dehydrogenase (<i>GalDH</i>)	<i>Pisum sativum</i>	<i>Nicotiana tabacum</i> & <i>Arabidopsis thaliana</i>	In tobacco lines over-expressing <i>GalDH</i> had a 3.5-fold increase in extractable activity. <i>Arabidopsis thaliana</i> , transformed with antisense <i>l-GalDH</i> construct, produced lines with only 30% of wild-type activity.	Gatzek et al. (2002)
<i>L</i> -gulono- γ -lactone oxidase (<i>GLOase</i>)	Rat	<i>Nicotiana tabacum</i> & <i>Lactuca sativa</i>	Transgenic lettuce and tobacco and plants expressing rat cDNA encoding <i>L-gulono-γ-lactone oxidase</i> produced up to seven times more ascorbic acid than wild type.	Jain and Nessler (2000)
<i>GDP-L</i> -galactose phosphorylase (<i>GGP</i>)	<i>Actinidia chinensis</i> <i>Arabidopsis thaliana</i> <i>Solanum tuberosum</i>	<i>Solanum lycopersicum</i> <i>Fragaria</i> × <i>ananassa</i> <i>Solanum tuberosum</i>	Over-expression of <i>GGP</i> showed three to six-fold increase in fruit ascorbate content in three lines of tomato, two-fold increase in all lines of strawberry and up to three-fold in all but one line of each potato tuber.	Bulley et al. (2012)
<i>GDP-D</i> -mannose epimerase (<i>GME</i>)	<i>Solanum lycopersicum</i>	<i>Solanum lycopersicum</i>	<i>SIGME1</i> and <i>SIGME2</i> allowed normal ascorbate accumulation in the leaf and fruits. Repression of either of these genes did not change Asc content in the plant. Specific silencing of these genes showed that both were involved in ascorbate biosynthesis and their actions were functionally complementary in their transgenic lines.	Mounet-Gilbert et al. (2016)
Asc Mannose pathway Regulator 1 Like 1 (<i>MdAMR1L1</i>)	<i>Malus</i> × <i>domestica</i>	<i>Malus</i> × <i>domestica</i>	Overexpression of <i>MdAMR1L1</i> caused a decrease in the Asc level, while silencing the gene increased the Asc level, which indicated that <i>MdAMR1L1</i> negatively impacted Asc levels in apple. Furthermore, the <i>MdAMR1L1</i> protein interacts with <i>MdGMP1</i> to promote its degradation via the ubiquitination pathway.	Ma et al. (2022)
Myoinositol monophosphatase 3 (<i>IMP3</i>)	<i>Solanum lycopersicum</i>	<i>Solanum lycopersicum</i>	Overexpression of <i>SLIMP3</i> improved Asc and myoinositol content. It also improved fruit firmness, increased cell wall thickness, decreased water loss, delayed fruit softening, and extended shelf-life. Overexpression of <i>SLIMP3</i> also increased uronic acid, rhamnose, xylose, mannose, and galactose content in cell wall of fruit.	Zheng et al. (2022b)
Phosphomannomutase (<i>PMM</i>)	<i>Nicotiana benthamiana</i> & <i>Arabidopsis thaliana</i>	<i>Nicotiana benthamiana</i> & <i>Arabidopsis thaliana</i>	Reducing <i>PMM</i> expression level through virus-induced gene silencing resulted in substantial decrease in the Asc content. In addition, enhancing the <i>PMM</i> expression level using vector-mediated ectopic expression resulted in 20%–50% increase in Asc content.	Qian et al. (2007)

2017). It involves a meticulously orchestrated sequence of events that culminate in the distinctive chemical properties of ripe fruits (Giovannoni et al., 2017).

The role of Asc in fruit ripening carries significant implications for fruit development and postharvest storage (Zheng et al., 2022b). Asc and its derivatives have been effectively utilized to postpone postharvest ripening in various fruits. However, during postharvest ripening, fruits often encounter stress factors that trigger the generation of ROS within the fruits, consequently leading to a decline in fruit quality (Zheng et al., 2022b).

A study by Sogvar et al. (2016) demonstrated the combined benefits of a 5% Asc solution and aloe vera gel on strawberries. This treatment delayed ripening while also reducing microbial presence, leading to enhanced fruit quality during storage. These findings are congruent with consistent research documenting Asc's antimicrobial effects on various fresh-cut fruits, including apples (Perez-Gago et al., 2006; Qi et al., 2011), papayas (Tapia et al., 2008), and jackfruits (Acedo et al., 2012). These investigations suggest that Asc application can effectively stymie the proliferation of microorganisms on various fruits, thereby enhancing their postharvest quality and shelf life. Papaya fruits are particularly susceptible to decay after harvest. Zhou et al. (2022) posited that combining Asc with chitosan treatment can effectively enhance the postharvest quality and extend the shelf life of papayas. The combinational coating treatment of Asc and

chitosan prolonged shelf life by mitigating weight loss, reducing malondialdehyde content, and lowering H₂O₂ levels in harvested papaya fruits.

A similar study by Wang et al. (2023b) utilized the ROS scavenging property of Asc, along with chitosan, as a combinational treatment on custard apple (*Annona squamosa*). The results demonstrated a noteworthy slowdown in the deterioration process, attributed to the maintenance of elevated titratable acidity levels, heightened antioxidant enzyme activities, and increased water content. The combined treatment effectively inhibited the activity of cell wall degrading enzymes, including polygalacturonase, pectin methyl esterase, and cellulase, while also reducing their gene expression levels. Consequently, this intervention extended the duration of the fruit ripening process. Table 2 provides a comprehensive overview of studies investigating the role of Asc in fruit development across various horticultural crops.

Apart from preventing ROS accumulation and microbial presence, Asc interacts with ethylene production during fruit ripening. Elevated ethylene and respiration rates in fruits typically result in shorter storage and shelf life, accelerating fruit aging. Studies indicate that regulating ethylene and respiration rates can help maintain Asc levels during post-harvest storage. Ethylene, a crucial regulator of fruit and vegetable ripening, plays a significant role in governing Asc levels during post-harvest storage (Yu et al., 2019).

Table 2 List of studies in different horticultural crops related to Asc and fruit development

Plant species	Ascorbate metabolism	Reference
<i>Olea europaea</i>	Asc content in olives increased by more than two-fold at the mature phase of ripening.	López-Huertas and Palma (2020)
<i>Solanum lycopersicum</i>	The level of ascorbate increased during ripening and these changes are linked to the changes in the redox status. Lower APX activity at the end of ripening allow increased accumulation of Asc.	Jimenez et al. (2002)
<i>Actinidia latifolia</i>	As ripening progresses and the fruits transition to maturation, the Asc content showed an increasing trend from 90 to 170 days after flowering and reached (1 108.76 ± 35.26) mg · 100 g ⁻¹ FW at full maturity.	Deng et al. (2022)
<i>Solanum lycopersicum</i>	Total ascorbate and reduced ascorbate content increased during fruit ripening, while the oxidized form DHA increased.	Gautier et al. (2010)
<i>Vaccinium myrtillus</i>	During the early stages of fruit ripening, the expression of the genes encoding the essential enzymes in the major biosynthetic pathway exhibited consistent patterns with Asc levels as well as with each other. In the course of the ripening process, more pronounced developmental stage-dependent alterations were seen in the expression of genes and the enzyme activities involved in the Asc oxidation and recycling route.	Cocetta et al. (2012)
<i>Malus domestica</i>	Total Asc and Asc levels of the young fruits were much higher than those of the mature fruits.	Li et al. (2008)
<i>Actinidia arguta</i>	Late developmental stages of the 'Yilv' cultivar perform better in terms of Asc, T-Asc and DHA content as well as Asc-related gene expression levels of GGP, GalUR, GalDH, AO and GalLDH, indicating that Asc biosynthesis took place primarily at the late developmental stages and the described genes contributed to the high Asc content.	Lin et al. (2022)
<i>Mangifera indica</i>	On-tree ripening maintains high Asc content and enhance mango fruit quality. Asc level and GalLDH activity were positively correlated, whereas, Asc level and AO/APX were negatively correlated.	Wang et al. (2023a)
<i>Vitis vinifera</i>	Throughout the fruit's growth, the concentration of Asc rises, reaching its peak at the fully ripe stage. VvGalUR, showed strong similarity to a strawberry gene that encodes a D-galacturonate reductase and was up-regulated during fruit ripening concurrently with the rise in Asc concentration.	Cruz-Rus et al. (2010)
<i>Solanum lycopersicum</i>	Upregulation of key Asc biosynthetic genes such as PMM2, GMP1, GMP2, GMP3, GME1, GME2, GGP1, GPP1, GLDH.	Zuccarelli et al. (2021)
<i>Piper nigrum</i>	Nitric oxide (NO)-regulated modulations in GalLDH gene expression at transcriptional and post-transcriptional levels. NO enhanced GalLDH expression and Asc content in pepper fruits.	Rodríguez-Ruiz et al. (2017)
<i>Fragaria</i> sp.	Asc derivatives together with aloe vera gel together prevented browning of strawberries.	Sogvar et al. (2016)
<i>Carica papaya</i>	Asc derivatives with chitosan treatment extended the shelf life of papaya.	Zhou et al. (2022)
<i>Annona squamosa</i>	Asc derivatives with chitosan prevented the deterioration of custard apples.	Wang et al. (2023b)

In addition to ethylene, brassinosteroids also influence the Asc level, particularly in tomato (*Solanum lycopersicum* L.) (Morales et al., 2014). Even though the precise mechanisms underlying the impact of hormones on antioxidant metabolism remain unclear, studies using genetic and chemical approaches suggest that the signaling pathways of brassinosteroids and ethylene interact to regulate Asc content and synthesis in tomatoes (Morales et al., 2014). Brassinosteroid-deficient mutants display lower Asc content, while mutants with elevated brassinosteroid levels exhibit normal Asc levels. Additionally, brassinosteroid-deficient mutants show higher ethylene production with decreased Asc content, indicating that ethylene diminishes Asc content in tomatoes.

Research investigating the impact of Asc application during storage on guavas, known for their climacteric nature and susceptibility to rapid deterioration, aimed to extend their shelf life (Arowora et al., 2013; Sogvar et al., 2016; Azam et al., 2020). Asc application triggered significant improvements in postharvest characteristics of guavas. Notably, the titratable acidity content and ethylene levels in guavas increased upon Asc treatment, regardless of storage temperature. Increased titratable acidity is a crucial indicator of fruit quality preservation, suggesting that Asc application effectively inhibited oxygen uptake during the ripening process, thereby extending the shelf life of guavas.

Browning, a consequence of detrimental enzymatic reactions, can significantly affect the appearance and quality of horticultural crops. Asc, a natural reducing compound, is commonly used as an anti-browning agent due to its ability to convert o-quinones back into phenolic compounds, thereby preventing their involvement in subsequent reactions leading to pigment formation (Perez-Gago et al., 2006; Rojas-Graü et al., 2008; Ali et al., 2015; Zhou et al., 2020). In a study by Lo'Ay and Ameer (2019), mangoes

treated with calcium nanoparticles combined with $9 \text{ mmol} \cdot \text{L}^{-1}$ Asc for 35 days at 6°C and 95% relative humidity exhibited delayed browning compared to untreated fruits. Similarly, Sikora and Świeca (2018) demonstrated that mung bean sprouts washed with $20 \text{ mmol} \cdot \text{L}^{-1}$ Asc for 2 h showed improved quality and reduced enzymatic browning. Additionally, Khan et al. (2020) reported that longan fruits immersed in a 5% Asc solution for 5 min exhibited delayed peel discoloration, effectively inhibiting the browning process.

Asc functions as an antioxidant by inhibiting the enzymatic browning process catalyzed by polyphenol oxidase and by scavenging free radicals generated during fruit ripening and post-harvest storage, as outlined by Altunkaya and Gökmen (2008). In a study conducted by Sun et al. (2010), the treatment of harvested litchi fruits with $40 \text{ mmol} \cdot \text{L}^{-1}$ Asc led to a significant reduction in the activities of key enzymes involved in browning, namely polyphenol oxidase and peroxidase. Additionally, this treatment resulted in increased levels of glutathione, total soluble sugar, and titratable acidity, ultimately contributing to a decreased decay rate in the treated fruit. These findings collectively underscore the efficacy of Asc in preventing browning and preserving the quality of various horticultural crops (Fig. 3).

Treating tomato fruits with nitric oxide has been demonstrated to enhance fruit quality by influencing both the key ethylene biosynthesis pathway and Asc biosynthesis, thereby extending the shelf life of the fruits (Zuccarelli et al., 2021). Furthermore, experiments conducted on pepper fruits revealed that the application of nitric oxide leads to the regulation of GLDH at both transcriptional and post-transcriptional levels (Rodríguez-Ruiz et al., 2017). Interestingly, no post-translational modifications, such as nitration or S-nitrosylation events

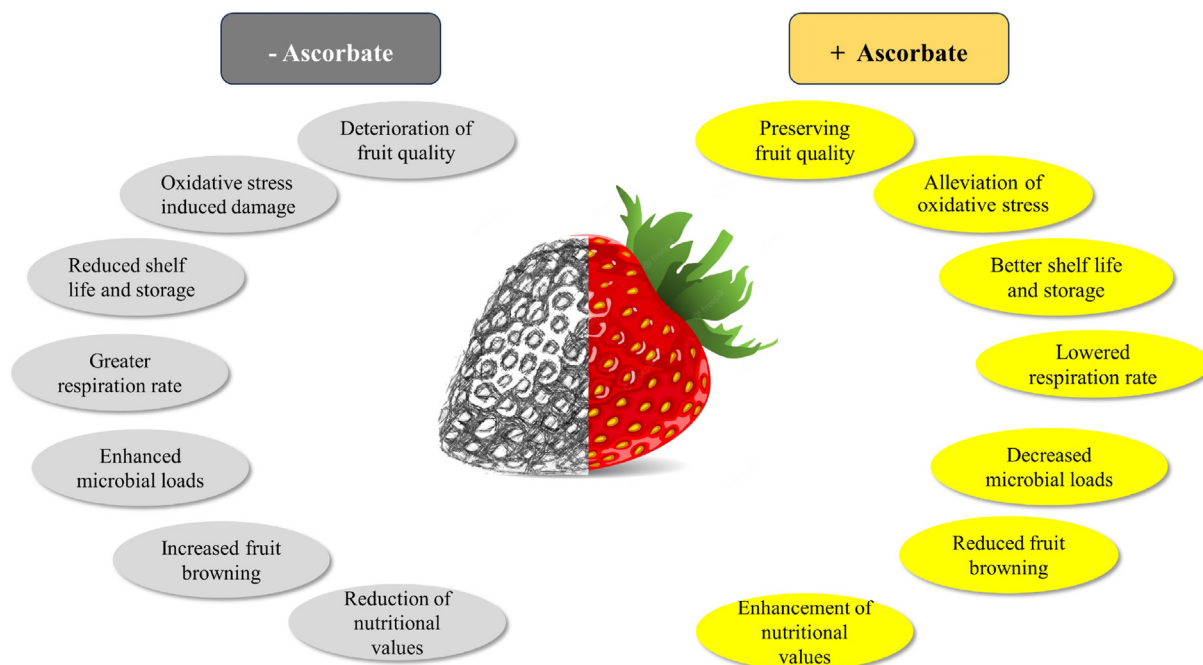


Fig. 3 Asc has various effects on the appearance and quality of fruits

Asc can contribute to enhanced color development, improved texture, and reduced browning of the fruits. Additionally, Asc acts as an antioxidant, protecting the fruit from oxidative damage and prolonging shelf life. This figure highlights the beneficial effects of Asc on the overall visual appeal and preservation of fruit quality. In its absence, reverse effects can be observed.

induced by reactive nitrogen species, were observed. These findings suggest that nitric oxide treatment targeting Asc biosynthesis enzymes may be also a promising approach to enhance Asc levels in fruits.

Fruit softening occurs due to the breakdown of structural polysaccharides in cell walls and decreased cell adhesion (Martin and Rose, 2014). Asc acts as an antioxidant, preventing oxidative damage to cell membranes and cell walls, thus helping to maintain firmness and prevent decay in horticultural crops during the postharvest period. Additionally, it can positively impact postharvest processing, reduce the risk of decay, and minimize physical damage. Managing environmental conditions like temperature and humidity during storage can also preserve Asc content and delay softening and degradation in horticultural crops (Seymour et al., 2013). It's important to acknowledge that Asc degradation can occur due to various factors during post-harvest storage. Therefore, employing appropriate postharvest technology and handling practices is crucial to maintain Asc levels and the quality of horticultural crops.

5. Future prospects and conclusion

Asc, commonly known as vitamin C, is abundant in plants, existing in millimolar concentrations within leaves and storage organs. Its levels are intricately regulated through processes involving synthesis, degradation, regeneration, and transport. The primary pathway for Asc biosynthesis, the L-galactose (Smirnoff-Wheeler) pathway, has been extensively studied. Asc plays pivotal roles in various plant physiological processes, including photosynthesis, root elongation, cell division, expansion, and defense against environmental stresses by combating ROS. Its content significantly influences fruit quality and storage characteristics, making it crucial for horticultural crops. Understanding the regulatory mechanisms of Asc metabolism holds promise for genetic modifications aimed at enhancing fruit Asc levels. Identifying regulatory factors operating at transcriptional and post-translational levels is key to comprehending Asc biosynthesis mechanisms fully. Several plant hormones, such as gibberellin, ethylene, salicylic acid, and abscisic acid, have been shown to impact Asc levels in fruits. However, further research is needed to fully elucidate the precise mechanisms governing Asc biosynthesis, particularly during post-harvest stages.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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