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Ascorbic acid as a master redox regulator of fruit ripening

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ABSTRACT

Ascorbic acid plays an essential role in human health and its deficiency severely impacts physical well-being. Fruits are a good dietary source of ascorbic acid and thereby, its composition and strategies to increase total vitamin C contents in fruits have been reviewed previously. Nevertheless, ascorbic acid is also a fundamental antioxidant that regulates fruit ripening by its efficiency to eliminate reactive oxygen species and modulate the cellular redox state. The present review summarizes current knowledge on ascorbic acid from a plant physiological perspective both during preharvest and postharvest to dissect key regulatory points and offers an updated discussion on its capacity to regulate fruit ripening. At the same time, ascorbic acid capacity to modulate ethylene and abscisic acid signaling is discussed, together with its relevance to control the cellular redox state thereby fine-tuning fruit ripening onset and postharvest shelf-life. Finally, we emphasize the relevance of ascorbic acid to regulate fruit physiological disorders during postharvest and its relationship with current technologies of postharvest management.

1. Introduction

Ascorbic acid (AsA) is a water-soluble antioxidant molecule that is essential for all living organisms. In humans, the role of AsA (also known as ascorbate or vitamin C) has been widely studied, especially since its discovery to prevent scurvy, and its role as a free radical scavenger is nowadays regarded as a key component for the prevention of cancer, cardiovascular diseases and cataracts (Baron, 2009; Carr and Rowe, 2020; Smirnoff, 2018), among other physiological disorders. AsA is involved in many physiological processes not only due to its antioxidant properties, but also to its function as a cofactor of multiple enzymes required for the proper functioning of the body (Blaschke et al., 2013; Young et al., 2015; Myllyharju, 2008). AsA biosynthesis pathways have been identified and well-characterized in animals, plants, green algae and photosynthetic protists, being the occurrence of a sugar precursor the main divergence between them (Wheeler et al., 2015). AsA cannot be synthesized in certain groups of animals, including primates, because some organisms lack the L-gulono-1,4-lactone oxidase gene, coding for the last enzyme in the AsA biosynthesis pathway. In this case, fresh fruits and vegetables are the main source of vitamin C for humans, who need to consume this vitamin on a daily basis to prevent scurvy and other diseases associated to AsA deficiency (Davey et al., 2000). Several fruits accumulate high amounts of vitamin C at their optimal ripening, especially citrus fruits (30–50 mg/100 g), grapefruits (40 mg/100 g), strawberries (60 mg/100 g) and kiwis (60 mg/100 g) , but other fruits accumulate significantly less AsA as for example in apples (2–10 mg/100 g), pears (3 mg/100g), cherries (8 mg/100 g) or tomatoes (20 mg/ 100 g) (Davey, 2000). Furthermore, there is a considerable variability in the intrinsic amount of AsA not only within fruit species but also due to the fruit ripening stage (Badejo et al., 2012; Cruz-Rus et al., 2011; Zhang et al., 2018).

The biological function of AsA in aerobic organisms lies in its capacity to control redox chain reactions. AsA is present in its ionized form (AsA^-) at pH 7.0, and it can easily react with free radicals (superoxide anion, and hydroxyl and peroxyl radicals), Fe^{3+}, Cu^{2+}, hydrogen peroxide (H_2O_2) and nitric oxide (NO) (Gęgotek and Skrzydlewska, 2023). AsA oxidation leads to the production of monodehydroascorbate (MDHA), a resonance stabilized radical that does not react easily with oxygen. MDHA can be spontaneously oxidized to dehydroascorbate (DHA), which is extremely unstable and reactive, and it is predominantly found as a hydrated hemiacetal (Deutsch, 1998). Both MDHA and DHA can be regenerated to ascorbate by NAD(P)H and glutathione-dependent enzymes, respectively (Foyer, 2018). Therefore, the oxidation chain of AsA-MDHA-DHA is critical for the reduction of

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reactive species and the protection of cellular compounds. Paradoxically, because AsA cause the production of radicals, it can also act as a pro-oxidant when present at high concentrations (Castro et al. 2018) and hence, a balance in its metabolism is very important.

AsA is involved in a plethora of processes in plant cells, in particular as a direct scavenger of reactive oxygen species (ROS). Due to its antioxidant properties, AsA plays an essential role in ROS elimination, which are produced in different organelles, including the chloroplasts, peroxisomes, the apoplast or the mitochondria, the latter being one of the most important sources of ROS at the end of fruit ripening and during postharvest (Maruta et al., 2016; Wheeler et al., 2015). Moreover, AsA can also recover the antioxidant function of other cellular antioxidants such as glutathione or α-tocopherol, the later by interacting with tocopheroxyl radicals (Foyer and Shigeoka, 2011), altogether controlling the cellular redox state. At the same time, AsA facilitates iron uptake by reduction of Fe^{3+} (Grillet et al., 2014) and acts as a cofactor of essential enzymes such as violaxanthin de-epoxidase, needed for photoprotection, or phytohormones biosynthesis-related enzymes (Brisson et al., 2012; Saga et al., 2010). Besides, other functions such as control of cell division, elongation and differentiation as well as modulation of programmed cell death have also been reported (De Pinto et al., 1999; Li et al., 2017; Pavet et al., 2005). Taken together, AsA is involved in several physiological processes, especially those where important redox modifications take place such as seed germination, plant growth, flowering, senescence and fruit ripening. Here, we will discuss the physiological role of AsA during fruit ripening and its interaction with different key ripening regulators. Besides, both the physiological role of AsA during postharvest over-ripening and its involvement in the prevention of fruit physiological disorders will be discussed. This knowledge is essential for future technological agri-food applications to modulate fruit ripening and enhance postharvest shelf-life.

2. Physiological roles of ascorbic acid in fleshy fruit ripening

During ripening of fleshy fruits, several physiological, biochemical and morphological modifications take place to achieve the final fruit quality. Fruit softening is one of the chief changes that fruits undergo to become edible. This textural change is caused by the dismantling of fruit cell wall and has a direct impact on turgor and fruit shape (Brummell, 2006; Harker et al., 1997; Paniagua et al., 2020). The cell wall is composed of a network of polysaccharides, mainly cellulose, hemicellulose and pectins, as well as glycoproteins. At first, fruit softening is characterized by a dissolution of the middle lamellae, which is a pectin-rich layer entailing connections between cells (Chylińska et al., 2017; Brummell, 2006). Then, a breakdown and solubilization of cell wall polymers, alteration of linkages between polysaccharides and a reduction of intercellular cell wall adhesion occur, causing both fruit softening and tissue disruption (Goulao and Oliveira, 2008). AsA shares a tight relationship with cell wall biosynthesis since some of its precursors, such as GDP-D-mannose or GDP-L-galactose, are also known to be used for pectins and hemicelluloses synthesis. Likewise, myoinositol can be converted to D-glucuronic acid, which is the precursor of both AsA and cell wall polysaccharides (Cronje et al., 2012). This interconnection has been well characterized, for example studies of RNAi silencing of *GDP-D-MANNOSE 3,5-EPIMERASE* (*GME)* in tomato induced the reduction of both AsA content and cell-wall components, which promoted a decrease on fruit firmness and an increase of ROS accumulation (Gilbert et al., 2009; Mounet-Gilbert et al., 2016). Likewise, it has been described that overexpression of the tomato *MYOINOSITOL MONOPHOSPHATASE 3* (*SlIMP3*) improved AsA and myoinositol content followed by increased cell wall thickness and delayed softening (Zheng et al., 2022). Nevertheless, when the increase of AsA is resulting from the overexpression of tomato *DEHYDROASCORBATE REDUCTASE* (*SlDHAR*) in fruits, no effects in firmness, cell wall loss, thickness and softening were observed, suggesting that the increase of myoinositol but not AsA contents were accountable for slowed tomato fruit softening (Zheng et al., 2022). Additionally, it has been reported that tomato *GDP-L-GALACTOSE PHOSPHORYLASE* (*SlGGP)* mutants with 65% lower AsA content in fruits showed delayed ripening as well as higher firmness. However, this firmness increase could not be reverted after AsA treatment, indicating that these changes were not associated to AsA contents but most probably to an accumulation of precursors involved in cell wall formation (Steelheart et al., 2020). Taken together, results suggest that AsA has a crucial role in the control of cell wall softening during ripening beyond sharing precursors.

AsA may be involved in the solubilization of arabinogalactan-pectin complexes which leads to cell wall dismantling (Leszczuk et al., 2019). In tomato, the number of pectins decrease as ripening progresses, which is related to pectin solubilization and depolymerization due to enzymatic degradation. Arabinogalactans are highly glycosylated proteins of the family of hydroxyproline-rich glycoproteins. They are present in the cell wall attached to pectins and hemicelluloses forming the ARABINOXYLAN PECTIN ARABINOGALACTAN PROTEIN1 (APAP1) complex which acts as an anchor between the cell wall and plasma membrane (Tan et al., 2018). The involvement of AsA in the arabinogalactan-pectin complex leading to cell wall-loosening has been related to a high expression of genes encoding pectin-degrading enzymes. Rigano et al. (2018) reported an increase on the expression of *PECTIN METHYLESTERASE* (*PME*) and *POLYGALACTURONASE* (*PG*), while AsA content increased during tomato ripening. The role of AsA in pectin solubilization is a consequence of its pro-oxidant action generating hydroxyl radicals by the Fenton reaction where AsA can reduce Fe^{3+} to Fe^{2+} and in turn, Fe^{2+} can react with H_2O_2 forming $OH^{\bullet}$, causing pectin solubilization and oxidative scission of polysaccharide chains (Fry, 1998). The role of AsA in pectin solubilization has also been proven in vitro. Dumville and Fry (2003) reported that AsA, either in the presence of H_2O_2 or metal ions such as Cu^{2+}, can solubilize up to 40% of total pectin in vitro due to the action of AsA-generated hydroxyl radicals. However, AsA can also act as a cofactor of several enzymes, including proline hydroxylases that catalyze the hydroxylation from proline to hydroxyproline, a required reaction to synthesize hydroxyproline-rich glycoproteins that confere higher cell wall assembly and rigidity (De Tullio, 2020). For all this, AsA has a very essential function in the regulation of cell wall integrity both because of its biosynthetic relationship and enzyme cofactor capacity as well as its role in cell wall degradation and fruit softening during ripening related to its pro-oxidant action (Fig. 1). This functional duality in cell wall assembly and disassembly reflects its important role linked to a tight regulation of complex physiological processes during the different stages of fruit ripening. Hence, at early stages of fruit development when there is high availability of cell wall precursors, AsA may contribute to cell wall assembly as an enzyme cofactor; but once hydroxyl radicals are prominent due to the oxidative burst associated to the ripening process, AsA may promote pectin solubilization and contribute to fruit softening, a process that is also tightly regulated by other key components modulating the redox balance in fruit cells.

The ripening process is indeed fine-tuned by AsA through the modulation of the cellular redox state, not only in the mitochondria, but also during the transition of chloroplasts to chromoplasts, that lead to changes in fruit color (Ghifari et al., 2023; Morelli et al., 2023; Muñoz and Munné-Bosch, 2018). Mitochondria are ubiquitous organelles in eukaryotic cells and a central regulatory hub of energy and redox metabolism. Mitochondria synthesize ATP via the oxidation of organic acids during the tricarboxylic acid (TCA) cycle and the transfer of electrons to oxygen in the mitochondrial electron transport chain. However, the production of ROS occurring during the respiratory process may negatively impact the proper functioning of fruit cells due to a redox imbalance (Huang et al., 2016). In this sense, fruit ripening is generally considered an oxidative phenomenon where respiration rate increases in mitochondria leading to enhanced ROS production and carbonylation of proteins (Tian et al., 2013), so that the tight regulation of ROS production and their removal by antioxidants is a determining

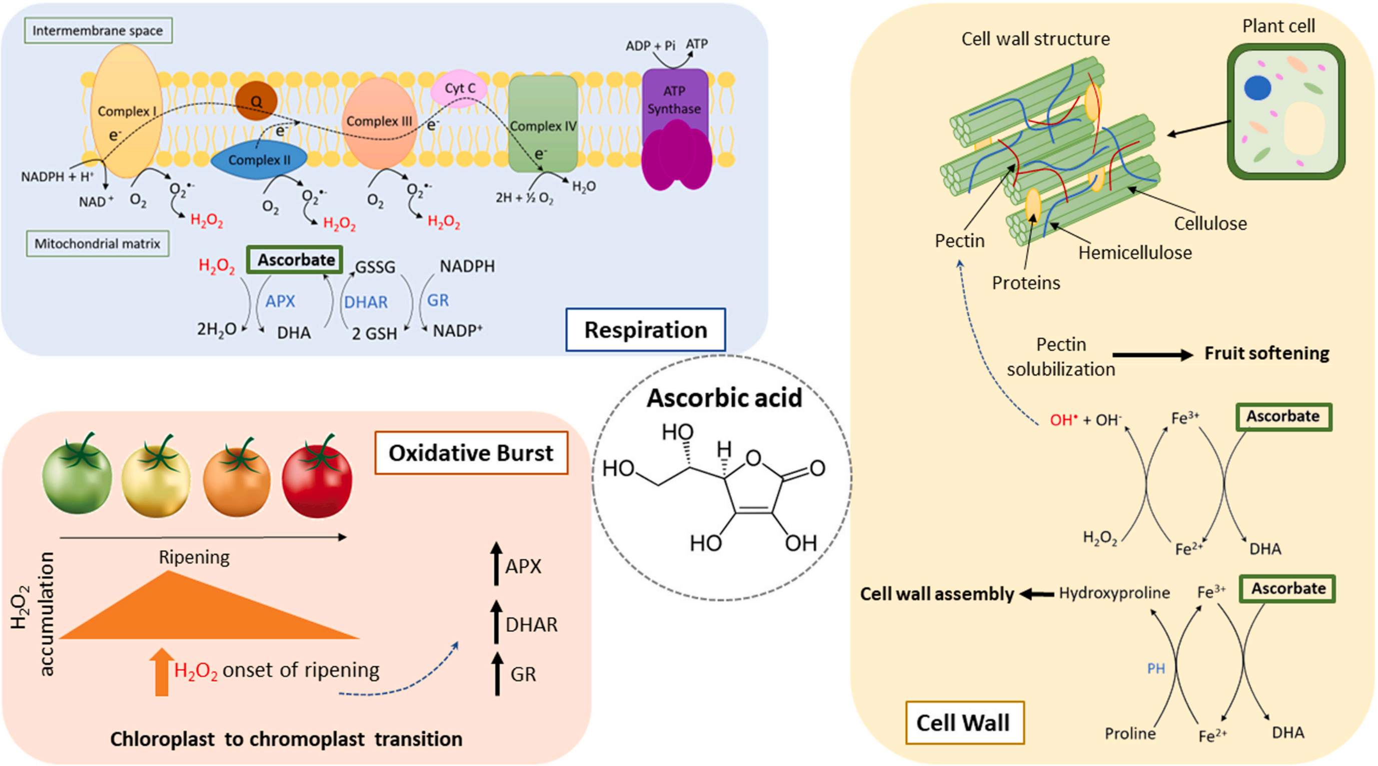

Fig. 1. Role of ascorbic acid during fruit ripening. Ascorbic acid is mainly involved in maintaining ROS homeostasis in the different physiological processes of ripening avoiding ROS over-production during mitochondrial respiration and controlling the oxidative burst linked to the onset of ripening and the chloroplasts-chromoplast transition. Ascorbic acid entails a role in fruit softening, contributing to pectin solubilization because of hydroxyl radical formation but also participates in proline hydroxylation which will confer cell wall assembly. Abbreviations: $O_2^{\bullet-}$: superoxide anion; H_2O_2: peroxide hydrogen; APX: ascorbate peroxidase; DHA: dehydroascorbate; DHAR; dehydroascorbate reductase; GSSG: glutathione disulfide; GSH: glutathione; GR: glutathione reductase.

factor for fruit quality (Jiménez et al., 2002). AsA is crucial for the control of mitochondrial ROS removal and redox balance. It reacts with H_2O_2 through ascorbate peroxidase (APX) to form MDHA and DHA, which are recycled back to AsA by GSH (Van Aken, 2021). Indeed, quantification of the mitochondrial proteome in pepper fruit revealed that the final part of the mitochondrial electron transport chain is crucial in the electron transfer from cytochrome *c* to complex IV through L-galactono-1,4-lactone dehydrogenase (González-Gordo et al., 2022). Moreover, López-Vidal et al. (2016) evaluated the ascorbate-glutathione cycle in the mitochondria of tomato fruits during ripening and reported that the activity of monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) enzymes increased with ripening, being responsible for the regeneration of AsA. Mondal et al. (2004) also reported that tomato fruits responded to the increment of oxidative stress during fruit development by increasing AsA content, coinciding with the respiratory burst. Nevertheless, Jiménez et al. (2002) isolated mitochondria from green and red peppers and observed an up-regulation of ascorbate-glutathione enzyme activity in green peppers but not in red peppers, where APX and superoxide dismutase (Mn-SOD) were preferentially activated. This probably indicates a species-specific regulation and/or a particular behavior between different types of ripening (climacteric vs. non-climacteric).

Additionally, it has been studied that a dysfunctional status of mitochondria, where a failure in the mitochondrial electron partition and ROS over-production occurred, is the result of high L-galactone-1,4-lactone (L-GalL) production. L-GalL is the precursor of AsA and its oxidation to form AsA is catalyzed by L-GalL dehydrogenase (L-GalLDH). Using RNAi-plant lines silencing *L-GalLDH* transcription, it was demonstrated that this mitochondrial dysfunction is dependent on L-GalLDH activity, and that alternative oxidase (AOX) helps to maintain AsA synthesis in the event of mitochondrial failure (Morales et al., 2022). Indeed, it is also known that GalLDH is located at the mitochondrial inner membrane associated to the complex I (NADH dehydrogenase complex). Its oxidative reaction is not coupled to any coenzyme pair resulting in a direct transfer of the electrons to the cytochrome *c* (Hervás et al., 2013; Bartoli et al., 2000). Morales et al. (2022) also demonstrated that AOX is likely the key regulatory factor of the electron flux during AsA biosynthesis, so that if AOX capacity fails, the excess of ROS and the deficiency of AsA may compromise maintenance of the electron transport capacity in mitochondria. At least, GalLDH seems to be an important regulatory point of the AsA accumulation that could affect the good functioning of mitochondria and highlights a complex relationship between GaLDH, AsA and electron transport chain. Thus, AsA has a predominant function in the mitochondria, being an indispensable antioxidant to ensure the maintenance of an adequate redox state.

Several studies have revealed that a rise of H_2O_2 is produced at the onset of ripening when there is a transition of different plastid types and is associated with crucial biochemical modifications such as color change (Fig. 1). AsA, as a powerful antioxidant, can also play a role in this oxidative burst participating in the control of H_2O_2 signaling. Jiménez et al. (2002) reported that an increase in the cellular redox state in tomato correlated with the onset of ripening at the breaker stage, coincident with an increase in the redox state of the AsA pool. An enhanced capacity for AsA regeneration at this crucial ripening stage was associated with increases in the activities of MDHAR and DHAR. In this regard, Palma et al. (2015) showed that higher APX activity, leading to the oxidation of AsA and reducing the H_2O_2 content, prevented the accumulation of ROS during pepper fruit ripening. Likewise, Camejo et al. (2010) also observed an increase in APX, MDHAR and GR activities in mature peaches in comparison to immature ones. In contrast, a decrease in DHAR enzyme activity was observed. In papaya fruit, ripening was also associated with a high activity of APX and increase of H_2O_2 (Pandey et al., 2013). Moreover, Steelheart et al. (2020) demonstrated that *GGP* tomato mutants with low AsA content avoided the peak of H_2O_2 but not after AsA treatment. Overall, results obtained thus far indicate that AsA is important for an adequate ROS balance during plastid transformation from chloroplasts at early stages of fruit development to chromoplast accumulation at later stages of fruit ripening, although spatiotemporal changes in ROS levels vary between species and cannot be fully attributed to the action of a particular antioxidant only, but to a balance between the action of non-enzymatic and enzymatic antioxidants. In this sense, Martí et al. (2009) reported that AsA contents were enhanced during the differentiation of chloroplasts into chromoplasts in red and yellow pepper fruits. Besides, the activity of different enzymes involved in the AsA metabolism such as APX, MDHAR, DHAR and GR were up-regulated. Moreover, a quantitative proteomic analysis of purified plastids from the sweet orange flesh during chromoplast differentiation also described an increase in the abundance of the proteins involved in stress responses such as the Asc-GSH cycle (Zeng et al., 2015). Similarly, a comparative proteomic approach in tomato identified that chloroplast to chromoplast transition could be associated with an increase in stress-response proteins such as enzymes of the AsA-GSH cycle (Barsan et al., 2012). Interestingly, it has been described that a spontaneous sweet orange mutant with high lycopene accumulation in the pulp, presented an enhanced level of oxidative stress as well as high levels of antioxidative enzymes such as APX and GR. This study may provide evidence of the involvement of AsA metabolism and its regulatory role in oxidative stress during carotenoid production (Pan et al., 2009). Hence, these findings suggest that AsA and its metabolism-related compounds contribute to the protection of plastids controlling the redox homeostasis during fruit ripening.

Taken together, the AsA pool has been demonstrated to have a fundamental role in different but essential processes of fruit ripening, such as promoting fruit softening, controlling ROS production in mitochondrial respiration, modulating the oxidative burst linked to the onset of fruit ripening and, in addition, regulating ROS homeostasis in the chloroplast to chromoplast transition (Fig. 1).

3. Evidence of ascorbic acid involvement in redox signaling during fruit ripening

Increased ROS production is mainly predominant in fruits during chloroplast-to-chromoplast transitions, at the latest stages of fruit ripening and massively produced during overripening (Muñoz and Munné-Bosch, 2018; Decros et al., 2019). However, balancing ROS production during these phases has an important role for redox signaling in fruits because it determines the spatiotemporal dynamics of ROS signaling by generating specific cellular fingerprints in lipids, carbohydrates and proteins that constitute the components of retrograde signaling.

Because AsA modulates the oxidative cellular homeostasis and is produced at higher rates at the ripening onset, it has been proposed as one important redox regulator of fruit development. Hydrogen peroxide (H_2O_2) is the main ROS species produced during fruit ripening and overripening, and it has a pivotal relevance determining fruit shelf-life (Lin et al., 2017; Liu et al., 2021b) and pathogen infection (Sapers and Simmons, 1998). In fruits, H_2O_2 is produced from an oxidative burst in mitochondria and is necessary for the correct progression of fruit ripening since it is involved in fruit softening (Cheng et al., 2008), free sugar production (Ozaki et al., 2009) and increased antioxidant accumulation (Yun et al., 2021). Indeed, AsA production is promoted in parallel to H_2O_2 increases since AsA efficiently scavenges H_2O_2 thereby controlling cellular redox homeostasis (Pavet et al., 2005). With this view, the general conception is that AsA accumulation should be promoted to prevent overproduction of H_2O_2 in a spatiotemporal manner to control fruit ripening and overripening, while reductions in AsA contents may accelerate these processes. When artificial ripening is induced in fruits by direct application of ROS species like H_2O_2 (Guo et al., 2019) or the application of chemical compounds mimicking stress responses elevating ROS production such as methyl jasmonate (Zhu et al., 2022) or salicylic acid analogues (Li et al., 2020), all promote the production of AsA. Surprisingly, AsA reductions in tomato through downregulation of *GGP* expression showed that tomato mutants with a 30% deficiency in AsA showed a delay in fruit ripening and reduced H_2O_2 accumulation, contrary to what was expected (Steelheart et al., 2020), but may indicate that AsA is an important component triggering the ripening onset together with a network of hormonal regulators (Fig. 2). A more recent study by Steelheart et al. (2022) analyzed two different Micro-Tom tomato lines deficient in GGP activity by splice junctions and nonsense mutations of *Slggp1* and showed that a reduction of 50% in AsA contents under normal conditions did not enhance H_2O_2 production at turning color conditions but enhanced its accumulation in full red stages. Moreover, AsA deficiencies by *Slggp1* mutations partially repressed *JUB1* expression, a gene known for being redox activated and that it negatively regulates leaf senescence. In fact, *Slggp1* tomato mutant lines showed increased accumulation of glutathione and overexpression of *DREB1* during orange stages but this expression was heavily repressed at full red stages (Steelheart et al., 2022). Since *DREB* genes are activated through signaling by JUB1 and positively regulate antioxidant activity, deficiencies in AsA indicate that this antioxidant is playing an important role in the whole regulation of the fruit subcellular redox state and redox signaling, being especially relevant at the latest stages of fruit development when there is an increment in H_2O_2 production. However, the same study highlights that when H_2O_2 production is exacerbated by high light conditions, the effects of AsA deficiency are surpassed and only counteracted by other signaling events such as those involving ethylene signaling (Steelheart et al., 2022). Hence, a differential signaling behavior could be explained for the involvement on ascorbic acid redox signaling in fruits where a ROS threshold could be important for its action, which only indicates the intricate network of redox signaling. A good example is the work performed in RNAi tomato lines for ascorbate oxidase (AO), MDHAR and L-GalLDH, where the transcriptome, proteome and metabolites were analyzed in the orange exocarp of the fruit transgenic lines (Stevens et al., 2018). The study indicated that the transcriptome was completely inversed in RNAi AO lines compared to MDHAR and L-GalLDH, and this transcriptome did not correlate with the proteome and metabolome. In fact, both the proteome and metabolome were highly correlated with the redox state of enzymes related to AsA biosynthesis and recycling. Therefore, AO and hence AsA steady state might be highly involved in the transcriptional response of AsA, while the ascorbate pool might be accountable for attenuating the intensity of redox imbalances and control the redox cellular state.

An exceptional novel work by (Decros et al., 2023) evaluating dynamics and associated regulations of AsA and the AsA-glutathione cycle with ROS metabolism proposed a redox kinetic model for tomato development. The experiment evaluated both metabolite concentrations and enzymatic capacities of redox metabolites and enzymes related to the AsA-glutathione cycle in control and AsA-enriched MicroTom plants generated by CRISPR-Cas9, which allowed the establishment of an enzyme-based kinetic model of the AsA-glutathione cycle. The results of this model showed that during the early phases of tomato fruit development, there is a strong oxidative environment regulated by the oxidative pool of AsA, since there is a predominant presence of oxidized AsA and increased APX activity. A shift in MDHAR activity during growing phases increases the reduced form of AsA in green tomatoes accompanied by higher reducing power (NAD(P)H), thereby decreasing the H_2O_2 accumulation at the expense of metabolite accumulation. Hence, during ripening, the starch remobilization and the oxidative respiratory burst shift the NAD(P) metabolism and reprogram the enzyme related antioxidants which strongly influences the AsA content and redox state. Altogether, this study indicates that there is a clear pattern of AsA redox transitions during ripening that is accompanied by energy related metabolism and reprograming of the core antioxidant

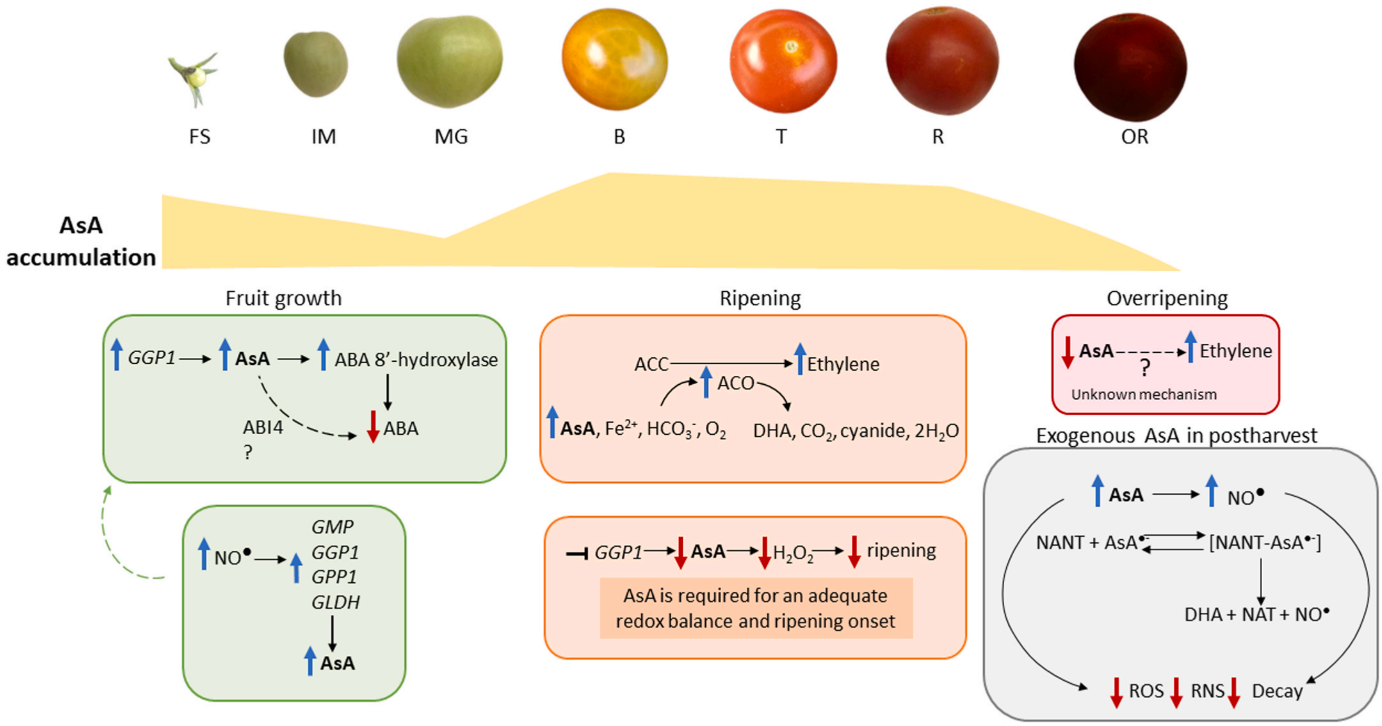

Fig. 2. Ascorbic acid (AsA) mechanisms to control fruit growth, ripening and postharvest shelf-life. AsA can interact with important ripening players such as ethylene, abscisic acid (ABA), hydrogen peroxide (H_2O_2) and nitric oxide ($NO^\bullet$). Dashed lines indicate unknown mechanisms. 1-Aminocyclopropane-1-carboxylic acid oxidase, ACO; 1-aminocyclopropane-1-carboxylic acid, ACC; ABSCISIC ACID-INSENSITIVE-4, ABI4; Breaker, B; Dehydroascorbic acid, DHA; Fruit set, FS; GDP-D-mannose pyrophosphorylase, GMP; GDP-L-galactose phosphorylase, GGP1; Immature green, IM; L-galactose 1–phosphate phosphatase, GPP1; L-galactose dehydrogenase, GLDH; Mature green, MG; N-acetyl-N-nitrosotryptophan, NANT; N-acetyltryptophan, NAT; Overripen, OR; Reactive nitrogen species, RNS; Reactive nitrogen species, ROS; Ripen, R; Turning, T.

enzymes. Linking these AsA state transitions with components of the redox signaling is still a pending issue that would be essential to elucidate to understand the mechanism of AsA in regulating fruit development and ripening.

4. Interaction between ascorbic acid and other key players of fruit development

Final fruit quality is determined by multiple organoleptic attributes and health-related compounds as a result of the correct progression of fruit development and ripening. These physiological events are tightly controlled by regulatory molecules, being phytohormones one of the most important players that allow optimal fruit growth and ripening, together with an adequate metabolite profiling and accumulation. Phytohormones establish an intricate signaling network between them but also interacting with other regulatory compounds that can modulate their action. Although much effort has been put to depict mechanisms by which phytohormones regulate AsA accumulation at different points of fruit development (Adaskaveg and Blanco-Ulate, 2023; Zheng et al., 2022), the reverse interaction has been explored to a lesser extent in fruit ripening and overripening. Mutants deficient in AsA biosynthesis have shown phenotypes of flowering delay and repressed growth related to increased biosynthesis of growth repressors such as abscisic acid (ABA) and ethylene (Caviglia et al., 2018; Kerchev et al., 2011; Plumb et al., 2018). In this sense, it has been established that AsA can function as the cofactor of several enzymes related to phytohormone biosynthesis involved in fruit development as well as in redox-dependent reaction in phytohormone biosynthesis pathways. For instance, ethylene is indeed an essential phytohormone for fruit ripening, in particular for climacteric fruits where a peak in the accumulation of this molecule elicits a regulatory signal to initiate fruit ripening and the associated physiological changes (Paul et al., 2012). For the biosynthesis of ethylene, the ring of its precursor, 1-aminocyclopropane-1-carboxylate (ACC) needs to be open, a biosynthesis step catalyzed by ACC oxidase (ACO) that requires AsA as a cofactor (Murphy et al., 2014; Zhang et al., 2004). In fact, ACO is a unique member of the plant 2-oxoglutarate-dependent dioxygenase (2OGD) superfamily because it uses AsA as a catalyst instead of 2-oxoglutarate (Kawai et al., 2014). Indeed, melon fruits with increased AsA contents, as a result of silencing of *CoAO*, showed increased ethylene production by elevated ACO activity and gene expression (Chatzopoulou et al., 2020). Even though ripening dynamics were not evaluated in this study, there was evidence of arrested cell expansion in melon fruits by repressed AsA oxidation and altered redox state in the apoplast. This probably explains reduced fruit growth by increased hyperpolarization of the cell membrane because of a lack of MDHA taking electrons to regenerate AsA that in turn, putatively induced the apoplast acidification and changed the osmotic pressure reducing cell expansion (Chatzopoulou et al., 2020). Other studies in tomato fruits (Koukounaras et al., 2022) also showed that increased AsA contents by overexpression of tomato *GDP-L-galactose phosphorylase* (*SlGGP1*) or *L-galactose 1–phosphate phosphatase* (*SlGPP)* elicited an overexpression of *SlACO* and genes encoding transcription factors related to ethylene signal transduction such as *SlERF1*, *SlERF3*-like, *ERF025*, *ERF027*, *ERF038*, *1B*, *ABR1*, the AP2-like ethylene-responsive transcription factor *AIL1* and the ethylene insensitive 5/7 (*SlXRN4*), together with a downregulation of *SlACS* genes. However, there was not any reference to ethylene quantification in transformed fruits or ripening dynamics. These results contrast with other studies in tomato fruits where AsA contents were reduced by mutagenesis, but the resulting fruit phenotype also had higher ethylene production. For instance, silencing of *SlGalLDH* in tomato plants (Alhagdow et al., 2007) resulted in pleiotropic alterations of the plant phenotype, including dwarf plants with no fruit production or plants producing tomato fruits but with a strong reduction in their size and showing an increased activation of differentially expressed genes related to abiotic stresses, including *ETR2* and *ERF1* (although ripening patterns were not altered from reductions in AsA contents). At the same time, Alegre et al. (2020) showed that tomato mutants deficient in expression of the *GGP1* gene with 30% lower AsA contents also had higher ethylene production in tomato fruits at the breaker stage and showed higher firmness and total soluble sugars contents. Indeed, AsA-deficient tomato plants showed a reduced number of fruits even though the number of flowers was the same, which reflects lower fruit setting probably due to enhanced ethylene production and reduced gibberellin contents. These studies highlight the tight relationship between AsA and ethylene production (Fig. 2).

Another important ripening regulator is ABA, particularly relevant for non-climacteric fruits where this phytohormone progressively accumulates during ripening to induce quality changes associated to ripe fruits, but also in climacteric fruits, where ABA is thought to promote ethylene production (Fenn and Giovannoni, 2021). As it was initially the case for ethylene, the relationship between AsA and ABA has been mostly unidirectional and focused to depict regulatory events to increase total vitamin C in the fruit (Liu et al., 2022; Miret and Munné-Bosch, 2016). However, some evidence already accumulates in the other regulatory direction. In plant development, it is known that growth is constrained in *vtc-1* mutants of *Arabidopsis*, by the modulation of ABA signaling because ABA contents are significantly higher in *vtc-1* than in the wild type (Pastori et al., 2003). The same results were found in another study of *vtc-1* plants where leaves accumulated higher contents of ABA than those of the wild type under controlled conditions (López-Carbonell et al., 2006). However, when *vtc-1* mutants were submitted to abiotic stress, these plants showed an altered pattern of ABA accumulation and were unable to counteract the abiotic stress conditions (López-Carbonell et al., 2006). When performing exogenous applications of AsA in plants, it was found that AsA significantly increased the level of gibberellins and auxin but decreased the level of ABA (Hassanein et al., 2009; Niu et al., 2019; Terzi et al., 2015). Likewise, supplementation of exogenous AsA at 3 mM revealed that the application further reduced ABA and increased JA, enhancing water evaporation rates to increase water-stress tolerance (Ullah et al., 2017). In fact, genetic and genome-wide transcriptomic analyses in tomato plants support the contention that AsA content co-regulates genes involved in hormone signaling and they are dependent on the oxidative state of the fruit (Lima-Silva et al., 2012). *Arabidopsis* plants deficient in AsA showing delayed growth accumulate more ABA and jasmonic acid that together inhibit growth through activation of the gene encoding for the ABSCISIC ACID-INSENSITIVE-4 (ABI4) transcription factor (Kerchev et al., 2011). Data from direct mutagenesis in fruits shows that overexpression of *Slggp1* or *Slgpp* with higher contents of AsA leads to an upregulation of ABA 8′-hydroxylase (*SlCYP707A1*), coding for a key enzyme in ABA degradation (Koukounaras et al., 2022). The upregulation of this enzyme that is mainly expressed in ovules and placenta could indicate that AsA can modulate ABA contents by reducing them (Koukounaras et al., 2022), which is vital because several studies have demonstrated the inhibitory role of ABA in fruit set (Fenn and Giovannoni, 2021). This role of AsA in fruit set is further evidenced in studies of induced parthenocarpy, where auxin treated plants had a significant influence in AsA metabolism compared to seeded tomato fruits (Tsaniklidis et al., 2014). Induced parthenocarpy by auxin treatment lowered AsA contents in immature green fruits immediately after fruit set and reduced APX expression and activity, together with AsA recycling enzymes (Tsaniklidis et al., 2014). This experiment further evidenced that AsA levels need to be high at early stages of fruit development for complete organ formation (Fig. 2). In red stages of tomato fruit development, high AsA contents have been associated to an upregulation of *ABI* genes, which encode protein phosphatases 2 C (PP2C) that are negative regulators of ABA responses through the interaction with ABA receptors (Lima-Silva et al., 2012).

The cellular redox state is a chief component of fruit ripening and molecules derived from oxidative stress such as ROS and reactive nitrogen species (RNS) have been demonstrated to act as important elements of the signaling network that determines the timing and progress of fruit ripening and overripening (Muñoz and Munné-Bosch, 2018). One of the main redox regulators related to RNS is nitric oxide ($NO^•$), a gaseous signal produced at early stages of fruit development (Palma et al., 2019) that has received much attention in diverse postharvest application studies (Corpas et al., 2020; Zhang et al., 2020). Sources of $NO^•$ include oxygen- and NADPH-dependent oxidation of L-arginine by enzymes with nitric oxide synthase-like activity, from the conversion of nitrite (NO_2^-) by nitrate reductase or from non-enzymatic conversion of NO_2^- under low pH or highly reductive environments (Pols et al., 2022). $NO^•$ was first related to fruit ripening because its capacity to negatively regulate endogenous levels of ethylene in fruits (Leshem and Haramaty, 1996). Since then, tremendous research has been performed on preharvest and postharvest applications of $NO^•$ and has postulated this gaseous molecule as a ripening retardant with important implications for postharvest management and fruit shelf-life (see Pols et al., 2022) for a thorough description of $NO^•$ mechanisms and applications). However, there is a lack of positive legislation for the use of $NO^•$ for postharvest technology, partially because the European Food Safety Authority (EFSA) recognizes that $NO^•$ can have important physiological roles such as vasoregulation and neurotransmission with relevant health-related implications (European Food Safety Agency, 2008). Therefore, manipulating accurately the spatiotemporal production of $NO^•$ in fruit tissues might be an alternative strategy to safely obtain the same beneficial effects of this molecule. In this regard, it has already been described that AsA and DHA can positively regulate $NO^•$ production through their reaction with nitrosated derivatives from tryptophan and thiol residues (Kytzia et al., 2006; Kirsch et al., 2009). Although the relationship between these molecules has been determined after exogenous applications of $NO^•$ for the general concept that increased antioxidant production contributes to greater fruit shelf-life (Gergoff-Grozeff et al., 2017; Zuccarelli et al., 2021), overproduction or repression of AsA biosynthesis in transgenic fruit lines should be studied to further examine AsA -dependent $NO^•$ production. These studies will undoubtedly offer a new paradigm to better understand and manipulate redox processes associated with fruit ripening (Fig. 2).

Once the fruit is harvested, and therefore, it has been separated from its main source of nutrients, the postharvest period starts until the fruit is consumed. During this period, overripening takes place and several physiological changes are triggered such as the degradation of free sugars, darkening, softening and increased lipid peroxidation, dehydration, respiration, pathogen susceptibility, among others, which contribute to a general loss of organoleptic properties, consumer rejection and important economic losses (Pott et al., 2020). In general, AsA levels decrease during postharvest influenced by storage period, temperature, light and humidity (Lee and Kader, 2000; Zhang et al., 2021). Strong oxidation takes place during the postharvest period by higher respiration rates and increased lipid peroxidation that exacerbate lipid peroxyl radicals production from peroxidation processes (Hodges, 2003). AsA is the least chemically inert nutrient, susceptible to postharvest loss, being subject to oxidative and enzymatic degradation to DHA and latter a permanent oxidation to diketogulonic acid (DKG) with no vitamin C activity (Johnston et al., 2007; Odriozola-Serrano et al., 2007). Related to the oxidative state of AsA, the ratio between AsA and DHA may constitute an important redox marker for postharvest management as evidenced by studies in sweet cherries (Wang et al., 2019), kiwis (Ali et al., 2019) or pitaya (Xu et al., 2021), where strong reductions of the AsA/DHA ratio occurred immediately after harvest and different treatments trying to control postharvest shelf-life also attenuated increases of DHA over AsA. Such knowledge could be important to further develop innovative solutions with smart packaging where detection of reduced AsA/DHA could be an efficient strategy to ameliorate postharvest losses. Nevertheless, more research is needed to understand the differential behaviour of changes in the AsA/DHA ratio in different fruits and how this could be monitored.

5. Ascorbic acid prevents fruit physiological disorders

Different fruit physiological disorders tend to appear during preharvest and postharvest life, hindering their acceptance and in turn, contributing to food waste (Oldoni et al., 2022). Abiotic factors during fruit development on tree such as excess of light and high temperature can cause sunburn in many fruits. This physiological disorder appears when fruit surface temperature exceeds a determined threshold and consequently, oxidative damage occurs by an increase in ROS production (Munné-Bosch and Vincent, 2019). Zhang et al. (2015) described that both AsA and DHA contents decreased as H_2O_2 and sunburn severity increased in apples. Besides, the activity of GalDH and GalLDH was lower in sunburned fruits, which indicates a decrease in AsA synthesis and a close association between photo-oxidative sunburn and AsA levels. Nonetheless, Chen et al. (2008) reported that no significant changes in AsA content but in total AsA pool (AsA + DHA) were observed in sunburned apple peel. These results could be related to higher oxidation of AsA to protect against oxidative stress. Moreover, cold storage of sun-exposed sections of the fruits can induce postharvest sunscald or delayed sunburn (Lurie et al., 1991). In this regard, Hernandez et al. (2014) showed that during apple cold storage, fruits with sunburn symptoms experimented worst phenotypes and lower AsA contents compared to fruits without sunburn symptoms. These low levels of AsA and enzyme activities (APX, DHAR, MDHAR) make it difficult to cope with postharvest oxidative stress. Moreover, even fruits with no sunburn symptoms can develop sunscald during storage, which can be related to the degradation of AsA throughout postharvest days (Hernandez et al., 2014). Hence, the aforementioned studies and those reported in Table 1 indicate that low contents of vitamin C, including both AsA and DHA, could closely contribute to a more susceptible physiological state of the fruit by reducing its defense mechanisms against stress and enhancing the appearance of fruit diseases.

During postharvest, optimal storage conditions are important to delay senescence and maintain fruit quality to extend shelf-life (Buccheri et al., 2021; Chen et al., 2022b; Ghafouri et al., 2022; Guillén et al., 2022; Kan et al., 2021; Mujtaba et al., 2023), and inadequate or suboptimal conditions may result in severe fruit physiological disorders. In this regard, storage at low temperatures is one of the most efficient methods implemented for preserving fruits and prolonging their postharvest life. Nonetheless, over long periods it can also constitute a factor of abiotic stress for fruits and induce some physiological disorders such as chilling injury (CI). CI occurs in certain susceptible fruits, and it is mainly characterized by pitting, pulp browning (discoloration), mealy texture and juice reduction, altogether resulting in a loss of flavor and texture (Liu et al., 2023; Ali et al., 2022). An imbalance in ROS metabolic homeostasis inducing high oxidative stress is considered one of the main causes (Hou et al., 2021). Several studies, which have been compiled in Table 1, have reported that CI increases during cold storage and the appearance of symptoms has been associated with a decrease in AsA content in different fruits such as peach, banana, guava, pear and nectarine (Ali et al., 2022; Chen et al., 2022a; Varela et al., 2005; Wang et al., 2022b; Zhang et al., 2020; Zhou et al., 2022a). The decline of *GDP-D-mannose pyrophorylase* (*GMP*) and *GDP-D-mannose-3',5'-hetero-isomerase* (*GME*) transcripts during cold storage has also been described (Zhou et al., 2022a). AsA, as an excellent antioxidant, contributes to the defense against oxidative stress and cell protection scavenging the excess of ROS and reducing oxidative damage (Veltman et al., 1999). Hence, the gradual decrease of AsA concentration with storage represents a decline in the antioxidant system which enhances fruit susceptibility and results in a reduction of stress resistance during postharvest. Indeed, exogenous applications of AsA during postharvest storability of logan fruits enhanced the accumulation of antioxidants such as carotenoids, anthocyanins, flavonoids and total phenolic compounds (Liu et al., 2021c). This was also the case for banana fruits where applications

Table 1
The most common physiological disorders appeared in fruits during postharvest storage and the pattern of endogenous ascorbate accumulation during disease progression. AsA: Ascorbic acid, DHA: Dehydroascorbic acid, APX: Ascorbate peroxidase.

Physiological disorder	Fruit	AsA accumulation pattern	References
Chilling injury	Kiwifruit	No significant change in the AsA content during storage	Liu et al., 2023
	Peach	AsA content decreased over storage time as chilling injury increased	Wang et al., 2022a; Zhou et al., 2022a;
	Pepper fruit	AsA, DHA and AsA/DHA levels decreased during storage and chilling injury rate and index increased	Wang et al., 2022c; Yao et al., 2021;
	Banana	AsA content decreased and DHA increased during days as chilling injury progressed	Ali et al., 2022
	Guava fruit	Decreased AsA content during 42 cold storage days	Chen et al., 2022a; Xiao et al., 2022
	Persimmon fruit	Increased AsA content the first days of storage but then decreased concomitantly with chilling injury symptoms	Jiao et al., 2022
	Pear	Declined AsA content during storage	Wang et al., 2022b
	Nectarine	Decreased AsA content during storage as chilling injury proceeded	Zhang et al., 2020
	Mandarin	Decreased AsA levels with the progress in the storage period	Ali et al., 2021a
Core breakdown	Pear	Declined AsA content in browning-induced conditions	Franck et al., 2003
Pulp breakdown	Longan fruit	Decreased AsA content and APX activity during storage time and increased breakdown process	Lin et al., 2021
Internal browning	Pineapple	AsA levels decreased during storage and browning increased	Hou et al., 2022; Sangsoy et al., 2022;Song et al., 2022
	Papaya	Decreased AsA levels as browning index increased	Zhou et al., 2022b;
	Plum	Increased tendency at first and decreased gradually from mid-term period to the end of storage	Shao et al., 2011
	Pear	AsA content generally declined after harvest	Cascia et al., 2013
Pericarp browning	Pomegranate	Increased firstly, then declined when browning index reached its maximum degree	Qi et al., 2022
	Rambutan	AsA content and AsA/DHA ratio decreased over time as browning index increased	Wei et al., 2022
	Litchi	Reduced AsA accumulation over days in storage while browning was promoted	Ali et al., 2021b; Siddiqui et al., 2021;Yun et al., 2021

(*continued on next page*)

Table 1 (*continued*)

Physiological disorder	Fruit	AsA accumulation pattern	References
Brown heart	Pear	Brown heart appeared when AsA decreased in storage	Eccher Zerbini et al., 2002
Senescence scald and internal breakdown	Pear	Total ascorbate and AsA decreased during storage and physiological disorders increased	Flaherty et al., 2018
Superficial scald	Pear	Ascorbate levels sharply decreased during the first 15 days of storage and then decreased gradually as fruit damage increased	Larrigaudière et al., 2016
Sun scald	Apple	AsA decreased through cold storage days, but AsA was lower on fruit with sunburn symptoms compared to fruits with no sunburn symptoms	Hernandez et al., 2014
Sunburn	Apple	AsA and DHA decreased as sunburn severity increased. Activity of GalDH and GalLDH decreased in severe sunburn.	Zhang et al., 2015
	Apple	No significant changes in AsA content in sunburned peel but decreased AsA/total AsA ratio	Chen et al., 2008
	Pomegranate	Higher increase of sunburn in non-shading pomegranate trees with low AsA levels	Moradi et al., 2022

of AsA during long-term cold storage promoted the activity of important antioxidant enzymes like APX, catalase (CAT) and superoxide dismutase (SOD), while also enhanced the accumulation of total phenols and flavonoids (Lo'Ay and El-Khateeb, 2018). Unfortunately, the direct implications of AsA in maintaining the antioxidant system during postharvest storage is largely misunderstood since fruits deficient in AsA accumulation have not been tested for postharvest storability and evidence is only gathered from indirect experiments where different treatments reduced AsA contents in fruits. For instance, an analysis on the effects of pear fruit bagging showed that the process induced a decline in AsA accumulation where the activity of glutathione oxidoreductase and APX was also reduced (Wang et al., 2021). Likewise, γ-radiation treatments for phytosanitary purposes in mandarins negatively affected vitamin C accumulation, together with those of carotenoids and α-tocopherol (Ornelas-Paz et al., 2017). Since AsA is known to positively regulate antioxidant production and tocopherol recycling (Asada, 1999; Thomas et al., 1992), it is likely that a similar process can occur during postharvest of fleshy fruits but there is an important gap of direct evidence of such regulatory role.

Suboptimal storage conditions may also result in the development of other physiological disorders such as core breakdown. In pears, this physiological disorder can occur during storage under high CO_2 conditions and is characterized by softening and browning of the tissue near the core and subsequent cavities formation (Lammertyn et al., 2000). Franck et al. (2003) showed that the core breakdown in pears was linked to a loss of AsA content during controlled atmosphere storage. Besides, Pintó et al. (2001) reported an association between AsA and core breakdown because of an impairment of the mitochondrial function leading to a high increase in ROS levels and APX activity and consequently, an imbalance between AsA consumption and regeneration. Likewise, low AsA content inactivates APX and an increase in oxidative damage occurs (Franck et al., 2003). Similarly, pulp breakdown in longan fruit, which is manifested as juice extravasation and erosion in pulp during postharvest, is also associated with AsA levels (Table 1). Lin et al. (2021) have reported that a reduction of AsA content together with an increase in pulp breakdown occurred during longan postharvest. A deregulation of ROS production and scavenging systems, such as AsA, enhanced ROS accumulation triggering pulp cell membrane disruption, which led to pulp breakdown. Another common and serious physiological disorder that occurs during storage is internal browning (IB), which is characterized by a localized browning of the flesh (Franck et al., 2007). Although browning may involve non-enzymatic reactions, such as Maillard reaction, caramelization or chemical oxidation of phenolic compounds (Hong and Betti, 2016), enzymatic reactions are the principal causes. The enzymatic browning is mainly a consequence of the oxidation of phenolic compounds to *o*-quinones by polyphenol oxidase (PPO) and peroxidase. These quinones are very reactive and their polymerization leads to brown pigments (Tomás-Barberán and Espín, 2001). In addition, IB can be a result of CI. When fruits are exposed to low temperatures, ROS bursts cause membrane damage producing a loss of organellar structure, which in turn allows the PPO to oxidize the polyphenols (Zhou et al., 2003). Previous studies (see Table 1) have shown that a decrease in AsA is related to an increase in browning index during the storage of pineapple, papaya, litchi, plum and pomegranate (Hou et al., 2022; Qi et al., 2022; Shao et al., 2011; Yun et al., 2021; Zhou et al., 2022b). AsA plays a key role in controlling the levels of ROS and restraining PPO activity, and hence, a reduction of AsA content over postharvest days could result in an acceleration of browning and fruit deterioration. In addition, it has been reported that AsA also plays a key role in the differences in superficial scald susceptibility between pears (Larrigaudière et al., 2016). Superficial scald is also a consequence of cold storage causing brown–dark patches on the fruit skin due to an enhanced PPO activity, and a higher resistance of pears to scald was positively associated with higher AsA levels (Larrigaudière et al., 2016). Therefore, AsA may act as an inhibitor of PPO and a scavenger of generated ROS inside the cell during superficial scald of pear.

Physiological disorders are closely related to ROS accumulation promoting lipid peroxidation and resulting in membrane dysfunction, which declines the storability of fruits. Concerning that AsA, as a powerful antioxidant, is an interesting option to be used as postharvest technology, some studies have explored the application of exogenous AsA during fruit postharvest to reduce the incidence of different physiological disorders (Table 2). For instance, in preharvest physiological disorders such as sunburn in apple, exogenous AsA reduced the occurrence of high-light-induced photo-oxidative sunburn by removing H_2O_2 and altering anthocyanin accumulation (Xue et al., 2021). In this study, it was also evidenced the relevance of AsA as a substrate in the xanthophyll cycle converting violaxanthin to antheraxanthin and zeaxanthin, involved in thermal dissipation to prevent oxidative stress. Lo'Ay and El-Khateeb (2018) also demonstrated that AsA treatment was effective to reduce chilling injury in bananas during postharvest, decreasing lipid peroxidation and increasing the activity of enzymatic antioxidants like APX. In other fruits such as apricot, avocado or plum, AsA has also been shown to be an effective option for reducing internal browning. In these cases, the exogenous treatment was associated with an increase of the endogenous AsA content which led to an increase in APX, CAT and SOD activity coupled with a decrease in PPO activity and MDA content (Derardja et al., 2019; Shao et al., 2011). Ali et al. (2021b) also demonstrated that exogenous AsA in postharvest litchi, which triggered an increase in endogenous AsA, reduced the peel browning index because of an increase in anthocyanins and APX, SOD and CAT activities, followed by a decrease in MDA, H_2O_2 and $O_2^{\bullet-}$ contents and PPO activity. Moreover, Lin et al. (2007) showed that AsA treatment reduced by 40% core browning in pear by preventing endogenous AsA and glutathione degradation and decreasing MDA and H_2O_2 accumulation. These studies highlight the positive effects of exogenous AsA to restrain the incidence of physiological disorders by boosting fruit

Table 2
Effects of exogenous applications of ascorbic acid in fleshy fruits and its impact to alleviate different physiological disorders appearing in fruits during postharvest storage. AsA: Ascorbic acid, APX: Ascorbate peroxidase; POD: Peroxidase, CAT: Catalase, SOD: Superoxide dismutase, MDA: Malondialdehyde, LOX: Lipoxygenase, PPO: Polyphenol oxidase, H_2O_2; Hydrogen peroxide, $O_2^{\bullet-}$: Superoxide anion radical.

Physiological disorder	Fruit	Ascorbic acid treatment	Effect	References
Chilling injury	Banana	9 mM, dipping	Reduced chilling injury incidence in fruit peel decreasing membrane dysfunction, lipid peroxidation and protein oxidation. Increased antioxidant enzyme activities (APX, POD, CAT, SOD)	(Lo'Ay and El-Khateeb, 2018)
Peel browning	Litchi	40mM	Increased AsA content and reduced browning index and degree. Reduced soluble quinones, MDA, H_2O_2 and $O_2^{\bullet-}$ content, PPO activity and increased anthocyanins and APX, SOD and CAT activity	Ali et al., 2021b
Internal browning	Apricot	2 mM, in vitro preparations	Prevented browning reactions and inhibited PPO	Derardja, et al., 2019
	Avocado	10 mM, dipping	Increased AsA content and reduced enzymatic browning in fresh-cut avocado. Increased total polyphenols content and antioxidant activity, APX, SOD and CAT activity, and decreased MDA and LOX	Magri et al., 2022
	Plum	0,5%, vacuum infiltration	Increased AsA accumulation during cold storage and reduced by 50% the browning rate. Inhibited PPO activity	Shao et al., 2011
Pericarp browning	Longan	4 g/L, dipping	Increased the AsA content, kept a lower browning index during storage and reduced weight loss	Liu et al., 2021c
Core browning	Pear	10 mM	Reduced core browning by 40% decreasing MDA and H_2O_2 accumulation and maintained AsA and glutathione levels and APX, CAT, SOD activities.	Lin et al., 2007
Sunburn	Apple	150 mM, dipping	Reduced the occurrence of high light–induced photooxidative sunburn	Xue et al., 2021

antioxidant defences due to a higher endogenous AsA content that in turn also enhances mechanisms to improve fruit stress tolerance.

Beyond applications of exogenous AsA, there are multiple postharvest technologies that have been implemented to prevent and counteract fruit disorders during the storage period and that partially owed their benefits because of AsA increases (Table 3). The effect of several exogenous applications of regulatory molecules such as ethylene, melatonin, methyl jasmonate, glutathione, γ-aminobutyric acid or hydrogen sulfide to reduce chilling injury or browning have been evaluated in association with AsA metabolism (Chen et al., 2022a; Liu et al., 2023; Shu et al., 2022; Wang et al., 2022a; Wei et al., 2022; Zhou et al., 2022a; Ali et al., 2022). As a result of these treatments, an increase in AsA content and a higher expression of its biosynthesis-related genes as well as a higher activity of enzymes related to its oxidation and/or regeneration were observed (Table 3). Moreover, treatments with 1-MCP, a competitor of ethylene receptors, have been assessed to combat chilling injury in nectarines and kiwifruits or superficial scald and browning in pears (Liu et al., 2021a; Xu et al., 2020; Zhang et al., 2020; Giné-Bordonaba et al., 2020). 1-MCP is reported to be one of the most effective strategies to prevent scald due to its efficacy in reducing α-farnesene production downregulating the expression of α-farnesene synthase gene as well as decreasing the expression of PPO (Busatto et al., 2018; Lurie and Watkins, 2012). However, Giné-Bordonaba et al. (2020) observed that 1-MCP inhibited the appearance of scald not only by regulating ethylene metabolism but also up-regulating the AsA-GSH cycle such as APX, DHAR and MDHAR activity. Moreover, 1-MCP was also effective to alleviate chilling injury symptoms stimulating the antioxidant system both the enzymatic antioxidants such as APX and the non-enzymatic ones such as AsA, causing a decrease in MDA content maintaining cellular integrity (Liu et al., 2021a; Zhang et al., 2021). In addition, other postharvest technologies including edible coatings, calcium chloride or near-freezing temperatures are effective alternatives to reduce chilling injury through an increase in AsA metabolism (Ali et al., 2021a; Hou et al., 2021; Xiao et al., 2022). Likewise, postharvest techniques during fruit conservation such as hot air, UV-C irradiation or modified atmosphere, which are mainly involved in the reduction of browning, are also associated with an increase in the AsA concentration (Ali et al., 2019a; Song et al., 2022; Yuan et al., 2022). Previous works have revealed that a combination of more than one technique provides satisfactory results in browning reduction. For instance, Ali et al. (2021b) showed that a combination of AsA with oxalic acid under a controlled atmosphere (5% CO_2 + 1% O_2) in litchi maintained higher endogenous contents of AsA and phenolic compounds, improved membrane integrity, increased APX, CAT and SOD activities and decreased MDA and ROS levels. The combination of these three treatments was much more effective than each application individually. At the same time, the combination of AsA and chitosan in papaya to reduce browning also provided better results than individual applications, since the combination increased antioxidant enzymes activity and total phenol content, together with a reduction of weight loss, MDA, H_2O_2 and cell-wall-degrading enzymes (Zhou et al., 2022b). Nonetheless, a decrease in AsA content during storage was reported after the application of AsA and chitosan in papaya fruits, probably explained because during browning, a high amount of free radicals are produced inducing a higher AsA consumption.

Overall, low endogenous AsA content is involved in the emergence of common fruit disorders during postharvest shelf-life, which causes both quality and economic losses, especially in those cases where it cannot be

Table 3
Different postharvest technologies used to reduce fruit physiological disorders during storage. The main effect of these treatments and their specific effect on endogenous ascorbate metabolism are shown. AsA: Ascorbic acid, DHA: Dehydroascorbic acid, DHAR: Dehydroascorbate reductase, MDHAR: Monodehydroascorbate reductase, APX: Ascorbate peroxidase.

Treatment	Physiological disorder	Fruit	Treatment effect	Effect on AsA content	References
AsA + oxalic acid + controlled atmosphere	Peel browning	Litchi	Decreased browning degree and index	2-fold increased AsA content	Ali et al., 2021b
AsA+ chitosan	Browning	Papaya	Reduced browning index	Decreased AsA content	Zhou et al., 2022b
γ-aminobutyric acid	Chilling injury	Peach	Inhibited chilling injury	Increased AsA content and the expression of its biosynthesis-related genes	Zhou et al., 2022a
	Chilling injury	Kiwifruit	Reduced 50% the chilling index	Increased the levels of AsA and expression of AsA metabolism genes	Liu et al., 2023
Hydrogen sulfide	Chilling injury	Peach	Mitigated chilling injury of refrigerated peaches	Induced the accumulation of AsA and APX activity	Wang et al., 2022a
	Chilling injury and browning	Banana	Reduced chilling injury index and lowered browning degree	Induced higher APX, DHAR and MDHAR activity and increased AsA content	Ali et al., 2022
	Pericarp browning	Litchi	Minimized pericarp browning during storage	Prevented loss of AsA content	Siddiqui et al., 2021
Nitric Oxide	Chilling injury	Peach	Alleviated redox damage during refrigeration	NO up-regulated key genes in the AsA-GSH cycle	Liu et al., 2022
Sodium nitroprusside (exogenous NO donor)	Chilling injury	Peach	Enhanced chilling tolerance and defense response	Upregulated the activity and expression of APX	Jiao et al., 2019
Glutathione	Chilling injury	Pepper fruit	Minimized chilling injury	Enhanced AsA content and the activities of enzymes involved in its regeneration	Yao et al., 2021
Methyl jasmonate	Chilling injury	Pear	Decreased chilling injury	Inhibited the decline of AsA during storage	Wang et al., 2022b
Melatonin	Chilling injury	Pepper fruit	Minimized chilling injury	Enhanced AsA content and the activities of enzymes involved in its regeneration	Wang et al., 2022c;
	Chilling injury	Guava fruit	Lowered chilling injury index	Exhibited higher vitamin C amount	Chen et al., 2022a
	Pericarp browning	Rambutan	Ameliorated the browning and senescence of rambutan	Increased AsA accumulation and AsA/DHA ratio	Wei et al., 2022
Melatonin + 1-MCP	Chilling injury	Persimmon fruit	Reduced by 70% chilling injury	2-fold increased AsA content	Jiao et al., 2022
1-MCP + ethylene	Chilling injury	kiwifruit	Alleviated chilling injury	Increased APX activity	Liu et al., 2021a
1-MCP + low temperatures	Browning	Pear	Suppressed browning index	Increased APX activity	Xu et al., 2020
1-MCP	Core breakdown and superficial scald	Pear	Reduced the incidence of core breakdown and superficial scald	Preserved APX activity	Li et al., 2021;Gao et al., 2015
	Superficial scald	Pear	Inhibited superficial scald during 4 months of cold storage	Redgulated genes involved in the AsA/glutathione pathway (APX, DHAR, MDHAR)	(Giné-Bordonaba et al., 2020)
Multiple 1-MCP applications	Chilling injury	Nectarine	Alleviated chilling injury	Increased the content of AsA	Zhang et al., 2020
Etephon	Chilling injury	Tomato	Decreased chilling injury index and incidence	Increased APX activity	Shu et al., 2022
Carboxymethyl cellulose coating	Chilling injury	Mandarin	Reduced chilling injury	Suppressed AsA degradation	Ali et al., 2021a
Aloe vera gel coating	Surface browning	Litchi	Reduced browning index	Increased AsA concentration during storage	Ali et al., 2019b
Calcium carbonate nanoparticles	Sunburn	Pineapple	Remediated effects of sunburn	Increased in AsA content in the pulp	Teixeira et al., 2022
Kaolin-based particle film	Bitter pit, brown core and water core	Apple	Reduced the incidence of storage disorders of apples such as bitter pit, brown core and water core.	Increased AsA content	Sharma et al., 2020
Calcium chloride ($CaCl_2$)	Chilling injury	Loquat	Repressed the increase in browning index and firmness and the decrease in extractable juice rate	Maintained higher contents of AsA and APX, DHAR and MDHAR levels of activity	Hou et al., 2021
Near freezing temperature	Chilling injury	Guava fruit	Inhibited chilling injury effects	Increased AsA, DHA content and APX and DHAR activity.	Xiao et al., 2022
Hot air	Internal browning	Pineapple	Reduced internal browning index	Accumulated higher AsA contents and decreased APX activity	Song et al., 2022
	Browning	Fresh-cut pitaya	Alleviated browning	Increased AsA content and the activity of APX, DHAR and MDHAR	Li et al., 2022
Hot water	Pericarp browning	Litchi	Delayed pericarp browning	Increased MDHAR expression and higher levels of APX at the later stage. Decreased AsA content	Yun et al., 2021
UV-C irradiation	Internal browning	Fresh-cut apple	Delayed browning of apple slices	Increased APX activity	Yuan et al., 2022
Net shading + Salicylic acid	Chilling injury	Pomegranate	Reduced chilling injury symptoms	Maintained higher levels of AsA during storage.	Moradi et al., 2022
Polyols	Chilling injury	Mango	Alleviated chilling injury	Induced higher activity of APX	Sanches et al., 2021
Light-yellow bags	Bitter pit, brown core	Apple	Lowered incidence of storage disorders	Increased AsA concentration	Sharma et al., 2014

(*continued on next page*)

Table 3 (*continued*)

Treatment	Physiological disorder	Fruit	Treatment effect	Effect on AsA content	References
Black polyethylene bag	Chilling injury	Mandarin	Reduced chilling injury index during storage	Decreased vitamin C (AsA+ DHA) content	Rey et al., 2020
Modified atmosphere packaging	Browning	Litchi	Delayed browning under cold storage.	Increased AsA contents and APX activity	Ali et al., 2019a

distinguished externally. Moreover, the decrease of AsA, being one of the most operative antioxidants, correlates with oxidative stress protection and is considered a symptom of tissue senescence and lower quality. Therefore, due to the relevance of AsA on fruit preservation and its consumer-friendly properties, exogenous AsA applications have been contemplated as a method of disease reduction, which stimulates the fruit antioxidant system. Furthermore, other innovative postharvest technologies with promising results alleviating fruit disorders have a direct effect on the AsA metabolism, which lead to an even stronger association between AsA function and disease occurrence. Because AsA is rapidly degraded during postharvest by oxidative reactions, the combination of exogenous AsA with other techniques that together stimulate endogenous AsA and other protective physiological processes are of particular interest. Hence, a combination of AsA with other postharvest technologies such as edible coatings could be a successful alternative not only to achieve a higher antioxidant defense but also to enhance other protective mechanisms such as maintenance of fruit firmness. Therefore, combinations of different approaches, if economically feasible, appears to be more effective than each technique applied individually to achieve an optimal reduction of physiological disorders during fruit storage. Nonetheless, there is still a lack of direct evidence on the potential role of increased AsA for postharvest preservation and associated endogenous mechanisms since studies overexpressing enzymes related to AsA biosynthesis and giving rise to fruits with higher contents of this antioxidant have not tested postharvest preservation. Likewise, because of the high lability of AsA in oxidative environments such as postharvest preservation and transport processes, exogenous treatments and coatings with AsA precursors with higher stability could open a new frame to enhance endogenous AsA accumulation in fruits and prevent postharvest diseases.

6. Conclusions and future prospects

AsA is an important antioxidant controlling the cellular redox state. Current knowledge highlights its implication in fruit growth and development, involved in the dynamics of fruit cell wall assembly and pectin solubilization during fruit softening, together with its relevant role to control ROS production from mitochondrial respiration and the transition from chloroplast to chromoplast biogenesis, which is characteristic of the ripening process for several fruits. At the same time, it is clear that AsA can interact with ripening regulators such as ethylene, ABA, H_2O_2 and $NO^{\bullet}$, influencing the timing of ripening during preharvest and the intensity of overripening during postharvest. Moreover, AsA has also been implicated in the control of several fruit physiological disorders such as fruit sunburn, chilling injury, internal browning or superficial scald, among others. For this reason, both exogenous applications of AsA and postharvest techniques that aim to increase endogenous contents of this antioxidant, may provide an efficient solution to increase fruit quality and postharvest shelf-life.

Despite recent advances in the field, more information is still needed to get deeper insights into the physiological role of AsA during ripening or overripening because there is still a lack of detailed molecular mechanisms on how AsA modulates phytohormone accumulation in fruits and its involvement in redox signaling through $NO^{\bullet}$ or thiol residues. A throughout analysis of AsA-deficient fruits in mutants, both in model and non-model species, would be required to better understand the mechanisms underlying the interaction between AsA and other key ripening regulators. Likewise, understanding the spatiotemporal dynamics of AsA in different fruit tissues and its capacity to interact with transcription factors related to fruit ripening would be important points to disclosure in the upcoming years. Finally, development of new postharvest techniques considering AsA redox state not only from its antioxidant properties but also with its ability to modulate other fruit ripening regulators, would be essential to provide innovative solutions for postharvest preservation.

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.

Data Availability

Data will be made available on request.

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