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Nitric Oxide as a Key Gasotransmitter in Fruit Postharvest: An Overview

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Abstract

Currently, the field of postharvest technology is a growing research area of particular interest since the increase in world population and the need to satisfy its nutritional requirements. These aspects establish a demand to produce fruits with high market quality while minimizing the losses from production to consumption stages. In the past few years, nitric oxide (NO) has emerged as a novel gasotransmitter to improve fruit postharvest shelf-life, owing to its influence on physiological processes (including fruit ripening) and on acclimation responses to stress conditions. In this review, we summarize some of the research related to the effects of NO exposure on different fruits with the aim to extend postharvest shelf-life and quality. The protection against chilling injury and postharvest diseases are addressed. The mechanisms of NO action and its interactions with other phytohormones are analyzed. Finally, the potential use of NO donors (and other strategies destined to enhance its levels) with a technological scope is also discussed.

Keywords Chilling injury · Fruit quality · Hormone interaction · Postharvest · Reactive nitrogen species · Technological use

Introduction

The increase in global population, the growing interest in consuming fresh fruits and vegetables to provide a healthy diet and the need to achieve nutritional requirements of the global population have raised the research focus on the field of postharvest technology. As it is known, from the cultivation to the consumption stages, there are several steps that should be considered. In this sense, almost half of the harvested fruits and vegetables are lost before reaching the consumer's table, and these losses are higher in underdeveloped countries due to the lack of infrastructure at different stages of the food supply chain (harvest, storage, transportation, processing, and distribution) before reaching the consumer's table (Porat et al. 2018); (Elik et al. 2019). The research in the field of postharvest handling and storage technology, in addition to the coordination and management of other postharvest stages, will contribute to reduce losses and to improve fresh fruit quality (Kader 2005; Elik et al. 2019).

During fruit growth and ripening processes, several traits evolve and determine different biochemical characteristics. Fleshy fruits are mainly water, sugars, dietary fiber (from the cell wall components), organics acids, minerals, pigments, antioxidants, aromatic volatiles, and vitamins, that contribute to human nutrition (Kader 2008). Postharvest physiology studies focus their attention on maintaining these desirable biochemical characteristics using environmentally sustainable technologies and on providing horticultural commodities of good quality for the consumers (Lee and Kader 2000).

Fruit growth and development need the help of plant hormones, among other systems, to coordinate different biochemical pathways that determine fruit attributes and trigger the fruit ripening process. Auxins, gibberellins, cytokinins, brassinosteroids, abscisic acid (ABA), and ethylene

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regulate fruit set, cell division and expansion, and ripening (McAtee et al. 2013). Nowadays, it is considered that the two main hormones that participate at the ripening process are ethylene and ABA (reviewed in (McAtee et al. 2013). The interaction of ethylene and the respiration rate led to a characterization of different fruit ripening physiologies: climacteric and non-climacteric. The climacteric fruit was characterized by a peak in the respiration rate (Kidd and West 1925), and the non-climacteric fruit was negatively defined due to the lack of this symptom. Then, a novel volatile hormone was discovered as the one responsible for this respiration rise: ethylene (Burg and Thimann 1959). Years later, methionine was revealed as the ethylene precursor, leading to the formation of *S*-adenosylmethionine (SAM) through the Yang Cycle. Then, SAM is converted into a four-carbon molecule, 1-aminocyclopropane-1-carboxylic acid (ACC) by the action of the ACC synthase (ACS), and afterward, ACC is oxidized by the ACC oxidase (ACO) to produce a two-carbon molecule, ethylene, together with a molecule of CO_2 and a molecule of hydrocyanic acid (Yang and Hoffman 1984). Afterward, the methionine pool is recycled in the Yang Cycle to maintain high rates of ethylene synthesis even at low concentration of this amino acid (Bürstenbinder et al. 2007). Ethylene synthesis is controlled by an autoinhibitory system, called System 1, present in all plants and during the whole ontogeny. On the other hand, an autocatalytic system of ethylene synthesis, named System 2, is present exclusively in climacteric fruit and is activated during the course of the ripening process (Liu et al. 2015; Cara and Giovannoni 2008). While System 1 delays the ethylene synthesis (autoinhibitory system) during the first stages of fruit growth, at a certain moment ABA concentration raises, allowing System 2 to switch on the autocatalytic synthesis of this hormone, leading to the ripening progress (Klee 2004).

The knowledge of the aspects mentioned above has opened a broad range of strategies during postharvest involving the control of ethylene synthesis and the inhibition of its action at the receptor level. From the first studies of fruit physiology in the 1930s to the new advances and techniques in plant molecular biology, a more complex but wide panorama added new molecules and mechanisms that contributed to understanding the process of fruit growth and ripening. In this sense, nitric oxide (NO) is a small gaseous bioactive molecule with a broad range of functions in many physiological processes in all living organisms (Astier et al. 2018; Jeandroz et al. 2016; Mur et al. 2013). The growing knowledge about the effects of NO on different aspects of plant growth, metabolism, ripening, and responses to biotic and abiotic stress conditions (Simontacchi et al. 2015; Steelheart et al. 2019b) led to an increased interest in the research involving NO treatments as a tool in postharvest technology.

This review summarizes and updates the research related to the effects of NO on postharvest shelf-life of different fruits. The effects of exogenous NO treatments over quality traits, and the amelioration of damage (such as chilling injury and postharvest diseases) are analyzed. This work also focuses on the NO signaling pathways and its interaction with other gaseous signaling molecules and phytohormones that may contribute to the observed effects. Finally, the potential use of NO donors, and other strategies destined to enhance its levels, with a technological scope are discussed.

Nitric Oxide: Sources, Levels, and Effects in Fruit Ripening

NO Synthesis in Plants: Possible Sources Involved in NO Generation in Fruits

The synthesis of NO and its multiple roles in plants have been a subject of intense research during the last forty years, and an interesting revision of the main key research during this journey has been recently published by (Kolbert et al. 2019). NO can be generated through several pathways (Astier et al. 2018) and can operate in different cell compartments such as mitochondria, chloroplasts, and peroxisomes during plant development or under stress conditions. Both pathways NR and L-arginine dependent (NOS_{like}) are considered the most relevant sources of NO generation in plants (Kolbert et al. 2019). However, the understanding of NO generation in plants is still incomplete, even more, related to fruits during their development and after harvest.

The pioneering works of Leshem and coworkers (Leshem et al. 1998; Leshem and Wills 1998; Leshem and Pinchasov 2000), which monitored the NO emissions from a wide spectrum of intact fruits and vegetables, provided evidence of NO generation. Despite this, the NO synthesis pathways involved in these NO emissions are less known. An L-Arg dependent pathway may be operative in apple (Golden Delicious and Fuji) (Zhang et al. 2011), and in tomato fruit (*Solanum lycopersicum*) treated with an elicitor from *Botrytis cinerea* (Zheng et al. 2011). NR may be involved in NO synthesis in loquat fruit under cold storage (Xu et al. 2012), and in a tomato mutant line under blue light + UV-B exposure (anthocyanin fruit -Aft- tomato) (Kim et al. 2020). Both NR and NOS_{like} seem to operate in peach fruits (*Prunus persica* (L.) Batsch, cv Xintaihong) under cold storage (Tian et al. 2020). Thus, depending on the species, treatment and storage conditions, one or more NO sources could work together to maintain or increase endogenous NO levels under favorable or unfavorable conditions. Advances in this field can help to understand NO metabolism in the fruit, and to develop proper strategies for its employment to extend postharvest shelf-life.

NO Affects Ethylene-Induced Fruit Ripening

NO plays important roles in the ripening process and in the inhibition of the senescence process in climacteric and non-climacteric fruits (Leshem et al. 1998; Leshem and Wills 1998). The interaction between NO and ethylene during fruit ripening and postharvest was early suggested by Leshem et al. (1998). In this work, the authors reported that unripe fruits, both climacteric and non-climacteric, presented higher levels of NO than ripe fruits and that its levels decreased as ripening progressed. They also observed that alfalfa sprouts showed a stoichiometric emission of NO and ethylene, and when exposed to heat stress, NO and ethylene emissions responded inversely: the increase in NO emission paralleled the reduction in ethylene emission (Leshem et al. 1998). Later, Sozzi et al. (2003) found that pears exposed to NO showed a delayed and lower ethylene peak and a delay in fruit softening. Similar effects were found in apple (Deng et al. 2013; Rudell and Mattheis 2006), banana (Cheng et al. 2009), tomato (Eum et al. 2008), peach (Flores et al. 2008; Liu et al. 2007; Zhu et al. 2006), papaya (Guo et al. 2014b), kiwi (Zhu et al. 2010a), Japanese plum (Singh et al. 2009), and mango (Zaharah and Singh 2011a, b), among others. The antagonistic effects of NO respect to ethylene during fruit ripening and senescence may be related to an effect on ethylene biosynthesis and/or its action (Leshem and Pinchasov 2000; Liu et al. 2007). Recently, it was found that NO supplementation affected multilevel down-regulation of ripening regulatory genes related to the production and tissue sensitivity to ethylene in tomato (Zuccarelli et al. 2021). Also, NO effects on ethylene-induced fruit ripening are mediated by hydrogen sulfide (H_2S) and melatonin over ROS generation and antioxidant metabolism in both, climacteric and non-climateric fruit (Mukherjee 2019; Corpas et al. 2019). Moreover, it has been described that NO influences the ethylene-induced fruit ripening not only by inhibiting ethylene synthesis, but also through the interaction with other plant hormones such as ABA, auxin, jasmonic acid, salicylic acid, gibberellic acid, cytokinin, brassinosteroids, and polyamines (McAtee et al. 2013; Palma et al. 2019; Steelheart et al. 2019b).

NO and Reactive Oxygen Species (ROS) Metabolism Affect Fruit Ripening

Since a moderate oxidative stress situation, observed as a peak in ROS production and an increase in lipid peroxidation, has been related to fruit ripening process; the effect of NO treatment on ROS metabolism may be extended to other ripening parameters such as color change and firmness (Corpas et al. 2018; Palma et al. 2019; Steelheart et al. 2019b). The connection between NO and H_2O_2 on ripening delay was proved in pepper (*Capsicum annuum* L.), where exogenous application of NO led to an inhibition of catalase (CAT) activity by nitration (Chaki et al. 2015) and an inhibition of chloroplastic peroxiredoxin II E by nitrosation (Rodríguez-Ruiz et al. 2017b), being both enzymes involved in H_2O_2 metabolism. In tomato, exogenous application of NO repressed the H_2O_2-scavenging enzymes, intensifying the nitro-oxidative stress, and S-nitrosation, and nitration events during ripening (Zuccarelli et al. 2021). González-Gordo et al. (2020) observed that NO treatments modulated superoxide anion ($O_2^{\cdot -}$) generation by a NADPH oxidase system-like at breaker stage of sweet pepper fruits, where the levels of ROS in NO-treated fruits were lower than untreated fruits, supporting a role for NO in the regulation of $O_2^{\cdot -}$ generation, during fruit ripening. Moreover, exogenous application of NO appears to have effects on antioxidant metabolism by increasing the activity of enzymes of both ascorbate–glutathione cycle and ROS metabolism (such as superoxide dismutase -SOD- and CAT) in peach (*Prunus persica* L.) (Kang et al. 2016; Li et al. 2017), tomato (Fan et al. 2008; Lai et al. 2011; Steelheart et al. 2019a), and banana (Cheng et al. 2009; Wu et al. 2014). NO effects on antioxidant metabolism in non-climacteric fruit was proved in cucumber (*Cucumis sativus* L. cv. Deltastar) with increases in the activity of SOD, CAT, ascorbate peroxidase (APX), and peroxidases (POD) (Yang et al. 2011).

As it is indicated in Tables 1 and 2, NO treatments led to changes in the activity and/or the expression of several proteins involved in ROS metabolism in different fruits. NO and other reactive nitrogen species (RNS) affect numerous proteins during ripening, favoring or inhibiting their activity through post-translational modifications (PTMs) in irreversible and reversible ways (protein Tyr-nitration and protein S-nitrosation, respectively), that may explain the lower NO content in the ripe fruit; where NO is consumed in the process to promote both PTMs (Jain and Bhatla 2018; Palma et al. 2019). However, despite the advances in the study of NO action in fruits during postharvest, here mentioned, it remains to be clarified the NO role in the signaling pathways of fruit ripening involving ROS and RNS interaction.

Effects of Exogenous NO Treatments Over Fruit Quality Traits

The physiological maturity is achieved when the fruit has completed the growth and development processes and can onset the ripening process independently from the plant; once the fruit is harvested, where it attains acceptable quality parameters. Immature fruits are not able to continue the ripening process when they are harvested prematurely, and therefore they do not achieve suitable attributes for consumption. To reach the optimal harvest moment, fruit needs to achieve consistent physical and chemical parameters that determine its maturity (Crisosto et al. 2005, 2007).

Table 1 Exogenous NO effects on chilling injury in cold stored fruits

Species	Ripening stage	NO donor and treatments	Storage conditions	Physiological and biochemical effects		References
Climacteric fruit						
Tomato	Mature green stage	Immersed in 0.02 mM SNP and vacuum infiltrated at low pressure for 0.5 min	2 °C	↓ Chilling injury ↓ Lipid peroxidation ↓ Ion leakage ↑ Proline content	↑ Protein concentration ↑ LeCBF1 relative expression ↑ SOD, APX, CAT POD activities	Zhao et al. (2011)
		Immersed in 10 uM L-NNA and vacuum infiltrated at low pressure for 0.5 min		↑ Chilling injury ↑ Lipid peroxidation	↓Proline content ↓ LeCBF1 relative expression	
Loquat	Ripe stage	Immersed in 0.5 mM cPTIO in sealed chambers at 20 °C for up to 24 h	1 °C, 95% RH	↑ Chilling injury ↑ Membrane permeability	↑ Lipid peroxidation ↑ O_2^- production rate, H_2O_2 content ↓ SOD, APX, CAT POD activities	Xu et al. (2012)
Banana	Mature green stage	Treated with 60 μL L^{-1} NO for 3 h at 22 °C	7 °C, 90% RH	↓ Chilling injury ↓ Membrane permeability ↓ Lipid peroxidation	↓ O_2^- production rate, H_2O_2 content ↑ SOD, APX, CAT POD activities ↑*MaSOD*, *MaAPX*, *MaCAT*, *MaPOD* relative gene expression	Wu et al. (2014)
’Amber Jewel’ Japanese plum	Commercial maturity	Fumigated with 0, 5, 10, and 20 μL L^{-1} NO gas for 2 h at 20 °C	0 °C, 90% RH	↓ Chilling injury ↓ Respiration rate	↓ Ethylene production rate ↓ Fruit softening restricted skin color changes	Singh et al. (2009)
‘Santa Rosa’ Japanese plum	Mature stage	Dipped in 0.5 mM SNP for 10 min at 20 °C	2 ℃ and 90 ± 5% RH	↓ Chilling injury ↓ Electrolyte leakage, lipid peroxidation ↓ PAL, PME activities	↑ Ascorbic acid content, antioxidant capacity ↓Anthocyanin content	Sharma and Sharma (2015)
Mango	Mature stage	Fumigated with 0, 5, 10, 20, and 40 μL L^{-1} NO in a sealed plastic container (67 L) for 2 h at ambient temperature	5 ± 1 °C, 93.9 ± 2.1% RH	↓ Chilling injury ↓ Ethylene production	↓ Respiration rate ↑ Tartaric and shikimic acid content	Zaharah and Singh (2011b)
Peach	Mature stage	Fumigated with15 μL L^{-1} NO for 2 h at ambient temperature	5 ± 0.5 °C, 85–90% RH	↓ Chilling injury ↑ Fruit firmness	↓PG activities	Zhu et al. (2010b)
Non-climacteric fruit						
Cucumber	Commercial maturity	Treated with 25 μL L^{-1} NO in sealed chambers for 12 h at 20 °C	2 °C	↓ Chilling injury ↑ SOD, APX, CAT POD activities	↓ Membrane permeability ↓ Lipid peroxidation	Yang and Cheng (2011)

Table 1 (continued)

Species	Ripening stage	NO donor and treatments	Storage conditions	Physiological and biochemical effects		References
Pomegranate	Mature stage	Immersed in 0, 30, 100, 300, and 1000 µM SNP for 2 min at ambient temperature	5 ± 1 °C, 85 ± 5% RH	↓ Chilling injury ↓ Membrane permeability	↑ Titratable acidity ↑ Antioxidant capacity ↑ Anthocyanin content	Ranjbari et al. (2017)
Grape	Commercial maturity	Immersed in 0.25, 0.5 mM SNP for 5 min at ambient temperature	Enclosed in polyethylene film bags at 95% RH and stored at -0.5 °C	↓ Chilling injury ↓ Ion leakage, lipid peroxidation	↓ H_2O_2 content ↑ Vitamin C, organic acids, total soluble solids ↑ POD, SOD, CAT activities	Ghorbani et al. (2017)

APX ascorbate peroxidase, *CAT* catalase, *LeCBF1 L.esculentum CRT/DRE*-binding factors, *cPTIO* 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide, *DPPH* 2,2-diphenyl-1-picrylhydrazyl, *L-NNA* N-(omega)-nitro-L-arginine, *NO* nitric oxide, *PAL* phenylalanine ammonia-lyase, *PME* pectinmethyl-esterase, *PG* polygalacturonase, *POD* peroxidase, *RH* relative humidity, *SNP* sodium nitroprusside, *SOD* superoxide dismutase

The respiration rate, one of the most important traits in postharvest physiology, has an inverse correlation with shelf-life: the higher the respiration rate, the shorter the postharvest shelf-life is (Saltveit, 2016). It was demonstrated that exogenous applications of NO reduced ethylene production and led to a lower and delayed peak of respiration rate during ripening in papaya (*Carica papaya* L.) (Li et al. 2012; Guo et al. 2014b), guava (*Psidium guajava* L.) (Sahu et al. 2020), mango (*Mangifera indica* L.) (Hu et al. 2014), and tomato (*Solanum lycopersicum* L.) (Steelheart et al. 2019a). In strawberry (*Fragaria* × *ananassa* Duch.), a non-climacteric fruit with low ethylene production rate after harvest, NO also reduced respiration rate (Zhu and Zhou 2007). Some authors suggest that NO could be a potent inhibitor of the mitochondrial respiratory chain, where it binds to the iron–sulfur proteins and inhibits their biological activities (Caro and Puntarulo 1999; Li et al. 2012).

Another fruit quality trait is flavor. This trait is mostly dominated by the content of sugars (fructose, sucrose, and glucose) and acidity (mainly determined by the contents of citric and malic acids) (Kader 2008). In some cases, cultivars are accepted based on total soluble solids (TSS) content or TSS:TTA (total titratable acidity) ratio in ripe fruit (Crisosto et al. 2005, 2007). In climacteric fruit, a growing number of evidence indicates that exogenous application of NO increases the concentration of sugars in pear (*Pyrus communis* L.) (Liu et al. 2011; Han et al. 2002) and papaya (Li et al. 2012) due to an effect on the sucrose metabolism; decreases the degradation of starch in banana (*Musa spp.*, AAA group cv. “Brazil”) (Cheng et al. 2009); and reduces the loss of TSS and acidity in guava, acting over respiration rate and ethylene production (Sahu et al. 2020). Li et al. (2012) established that glucose and fructose levels in NO-treated papaya fruit was related to the inhibitory effects of NO on respiration, since glucose and fructose are metabolized by the glycolysis-tricarboxylic acid cycle, mitochondrial respiratory chain, and pentose phosphate pathway in plants. However, exogenous NO decreased TSS in tomato (Lai et al. 2011) and pear (Liu et al. 2011), and TSS:TTA ratio in kiwi (*Actinidia chinensis* L. Planch) (Zhu et al. 2010a), mango (Hu et al. 2014), and tomato (Steelheart et al. 2019a). In orange (*Citrus sinensis* L. Osbeck cv. Valencia), a non-climacteric fruit, the exogenous application of NO increased TSS content and decreased TSS:TTA ratio (Mohamed et al. 2016). These results obtained from diverse species and cultivars with different ripening physiologies add complexity to the study of NO effects on the flavor, being difficult to find clear and conclusive patterns regarding this trait.

Firmness is another important quality trait, closely related to fruit ripeness, that can be greatly affected by postharvest treatments (Ruiz-Altisent et al. 1994). Fumigation with NO gas in papaya delayed softening as result of a down-regulation of the activity of cell wall softening

Table 2 Effect of NO treatment on postharvest diseases incidence

Species	Ripening stage	Treatments	Storage conditions	Effects	References
Climacteric fruit					
Peach fruit	Commercial maturity	Immersed in 15 μmol L^{-1} NO solution. After that fruits were inoculated with a suspension of *Monilinia fructicola*	25 °C	↓ Brown rot caused by *M. fructicola* ↑ Total phenolics, flavonoids and lignin content ↑ Ascorbic acid and titratable acidity content ↑ PAL, PC4H, 4CL, CHS and CHI activities	Li et al. (2017)
Mango	Mature green stage	Immersed in 0.1 mM SNP for 5 min at 25 ± 1 °C and 24 h later inoculated with a spore suspension of *Colletotrichum gloeosporioides*	25 ± 1 °C, 85–90% RH	↓ Anthracnose symptoms ↓ Lesion diameter ↑ Total phenolics, flavonoids and lignin content ↓ Respiration rate, ethylene production ↓ Flesh softening, yellowing, and changes in soluble solids content and titratable acidity ↑ Activity of defense-related enzymes (PAL, C4H, 4CL, POD, GLU, CHI)	Hu et al. (2014)
Peach fruit	Maturestage	Inoculation with NO treated spores of *M. fructicola* (1 × 10^5 spores mL^{-1}, immersed in0, 10, 30, 60, 200 μmol L^{-1} NO solutions for 10 min at 25 °C)	Fruit were enclosed in a polyethylene bag and stored at 25°	↓ Disease incidence ↑ CHI, GNS activities ↑ CHI, GNS, PR-1-PR-10 (pathogenesis-related protein 1to 10) relative gene expression	Gu et al. (2014)
Cherry tomato	Mature greenstage	Immersed in 2 mM SNPsolution under a pressure of-35 kPa for 2 min. After 24 h, fruits were inoculated with a suspension of *Botrytis cinerea*	25 ± 1 °C and 90–95% RH	↓ Disease incidence and lesion area ↑ GLU, CHI, PPO, and PAL activities ↑LeMAPK1 and LeMAPK2relative gene expression	Zheng et al. (2014))
Tomato	Mature green stage	Immersed in 1 mM SNP solutions for 10 min. After that, fruit were wounded at the equator and inoculated with a suspension of *B. cinerea*	25 °C and 95% RH	↓ Disease incidence (gray mold) ↓ Ethylene production ↑ Membrane permeability ↑ Firmness ↑ CAT and POD enzymes activities ↑ LeACS2, LeACO1, LePG, LePhy1, 40 for LeACS4 LePME relative gene expression	Lai et al. (2011)
Non-climacteric fruit					
Chinese bayberry	Commercial maturity	Fumigated with 20 μL L^{-1} of NO under a pressure of 1 atm at 20 °C for 2 h	1 ± 0.5 °C and 90% RH	↓ Disease incidence ↓ Ethylene production ↑ Firmness ↓ Electrolyte leakage ↑ Rate of $O_2^{\bullet-}$ production and H_2O_2 contents ↑ SOD, CAT and APX enzymes activities	Wu et al. (2012)
Citrus fruit	Commercial maturity	Immersed in 50 μmol L^{-1} for 10 min. After 4 h, fruits were inoculated with a suspension of *C. gloeosporioides*	Fruit were packed into plastic bags and stored at 20 °C, 85–90% RH	↓ Disease incidence (%) ↓ Lesion diameter ↑ Synthesis of phenolic compounds ↑ Ascorbic acid and titratable acidity content ↑ PAL, PPO, POD and CAT activities	Zhou et al. (2016)

ACO 1-aminocyclopropane-1-carboxylic acid oxidase, *ACS* 1-aminocyclopropane-1-carboxylic acidsynthase, *APX* ascorbateperoxidase, *CAT* catalase, *C4H* cinnamate 4-hydroxylase, *CHI* chalconeisomerase, *CHS* chalconesynthase, *4CL* 4-coumarate:CoA ligase, GLU (alsonamedGNS)β-1,3-glucanase; *NO* nitric oxide, *PAL* phenylalanineammonia-lyase, *PME* pectinmethyl-esterase, *PG* polygalacturonase, *POD* peroxidase, *PPO* polyphenol oxidase, *RH* relativehumidity, *SNP* sodiumnitroprusside, *SOD* superoxidedismutase enzymes (polygalacturonase -PG-, pectin methylesterase -PME-, and pectate lyase) (Guo et al. 2014b). Moreover, treatments with a NO donor, *S*-nitrosoglutathione (GSNO), and the inhibitor of ethylene action, 1-methylcyclopropene (1-MCP), maintained firmness in blueberry (*Vaccinium* spp.) (Gergoff Grozeff et al. 2017) and tomato (Steelheart et al. 2019a), and sodium nitroprusside (SNP) maintained firmness in tomato (Lai et al. 2011), banana (Cheng et al. 2009), mango (Hu et al. 2014), and guava (Sahu et al. 2020). However, in some cases, exogenous NO did not benefit fruit quality due to the loss of flesh firmness in fruits such as apple (*Malus* × *domestica* Borkh) stored under controlled atmosphere (Brackmann et al. 2017). In bayberry (*Myrica rubra* Sieb. & Zucc), a non-climacteric fruit, the effects of exogenous NO were similar to climacteric fruit, leading to a retention of fruit firmness (Wu et al. 2012).

During ripening, chlorophyll breakdown and the accumulation of pigments such as carotenoids and lycopene in the plastids are responsible for the orange and red color in the fruit, being the major contributors to the visual signs of the ripening process and quality (Gray et al. 1992). Application of NO gas delayed changes in peel color in papaya (Li et al. 2012), significantly restricted color changes in Japanese plum (*Prunus salicina* Lindl. cv. "Amber Jewel") (Singh et al. 2009), and delayed pericarp reddening of tomato (Lai et al. 2011) and pepper (Chaki et al. 2015). Besides, SNP treatment led to a delay in chlorophyll loss and an increase of carotenoid pigments in guava (Sahu et al. 2020). Also, Wang et al. (2015) observed that SNP treatment in green banana fruit may postpone the degradation of chlorophyll through the regulation of the activity of the enzymes chlorophyllase and Mg-dechelatase. However, the action pattern of NO on carotenoids biosynthesis during fruit ripening needs to be investigated.

Nutritional studies are now focusing on examining foods for their protective and disease preventing potential (Nicoli et al. 1999). Antioxidants in fruit (e.g., ascorbic acid, glutathione, tocopherols) have attracted attention in preventing human diseases caused by oxidative stress (Kaur and Kapoor 2001). NO increased ascorbate and glutathione contents in kiwifruit (Zhu et al. 2010a), blueberry (Gergoff Grozeff et al. 2017), and tomato (Steelheart et al. 2019a; Zuccarelli et al. 2021). Besides, Rodríguez-Ruiz et al. (2017a) observed that NO gas increased mitochondrial L-galactono-1,4-lactone dehydrogenase activity, which catalyzes the final stage of ascorbate synthesis, and its corresponding gene expression, in pepper. These aspects should be considered in order to improve the nutritional quality of fruits regarding health benefits, including vitamins and antioxidants.

NO Alleviates Fresh Fruit Damage During Postharvest Storage

NO Protects Against Fruit Chilling Injury During Postharvest Cold Storage

Temperature is the main environmental factor that influences the deterioration of fruits and vegetables during postharvest and most of these products decay later when stored at temperatures near 0 °C. However, many physiological disorders such as freezing, chilling injury, and heat injury are caused by temperatures outside the optimal range that can produce rapid deterioration (Kader 2013). Chilling injury is commonly used to describe the physiological damage that occurs in plants and fruits because of exposure to low, but nonfreezing temperatures (Parkin et al. 1989). Regarding susceptibility of fruits to chilling, these are divided into: chilling-sensitive fruit (such as avocado, banana, citrus, mango, melon, and tomato), which are best kept at temperatures in the range from 5 °C to 15 °C, and non-chilling-sensitive fruit (such as apple, grape, cherry, and pear), which are best kept at temperatures above their freezing points (− 2 to − 0.5 °C) and up to 2 °C; depending on the cultivar, ripening stage, and other storage conditions (Kader 2013).

Many reports showed that exogenous NO was able to modulate the development of chilling injury symptoms in several fruits including tomato, cucumber, loquat fruit, banana, pomegranate, mango, peach, and plums (Table 1). These reports evidenced that treatments with different NO donors in both, climacteric and non-climacteric fruits, induced reduction in chilling injury, while treatments with different NO scavengers led to an increase on chilling injury during postharvest storage (Xu et al. 2012; Zhao et al. 2011) (see Table 1). The reduction of fruit injury under cold storage by exogenous NO application is related to a decrease in membrane permeability, MDA content, ion leakage, and lipid peroxidation (Sharma and Sharma 2015; Ranjbari et al. 2017; Wu et al. 2014; Yang et al. 2011; Zhao et al. 2011; Zhu et al. 2010a). These effects may be associated with a reduction in ROS generation, as previously described (González-Gordo et al. 2020) (Table 1) and ROS detoxification, or an increase in the activity or expression of the antioxidant enzymes (Wu et al. 2014; Yang et al. 2011). Some studies showed that treatments with NO donors incremented the antioxidant content in different kinds of fruit. Also, an increment in SOD, APX, CAT, and POD activities in response to exposure to different NO donors was reported in cucumber, banana, and pomegranate fruits (*Punica granatum* L. cv. Malaseaveh) (Babalar et al. 2018; Wu et al. 2014). These responses may contribute to decrease the oxidative stress associated with chilling injury. It would be interesting to check if the antioxidant enzymes are included in the nitrosated proteins group in order to unveil the pathway by which

NO influences their activity. Moreover, as it was previously indicated, NO may also affect the expression of several proteins involved in ROS metabolism (Table 1), so pre- and post-translational mechanisms may be involved.

Role of NO in Defense Against Fruit Postharvest Diseases During Postharvest Storage

During fruit postharvest storage, many pests and diseases are responsible for consistent losses and alternative treatments for these issues are always under research. Pathogenic microorganisms, such as fungi (mainly belonging to the genera *Alternaria*, *Aspergillus*, *Botrytis*, *Fusarium*, *Monilinia*, *Penicillium*, *Rhizopus*), are the principal causal agents of postharvest deterioration (Wills et al. 2015), together with different insects such as flower thrips, aphids, confused flour beetles, and rice weevils (Liu 2013, 2016). However, incidence of postharvest decay in fruit and vegetables depends on the type of commodity, cultivar, maturity and ripening stage at harvest, storage and transport conditions (Sivakumar and Bautista-Baños 2014).

In some cases, NO fumigation was used to test its potential as an alternative product to methyl bromide and other toxic fumigants (Yang and Liu 2017). NO fumigation under ultra-low oxygen (ULO) conditions was used against both, different insects at various life stages, and flower thrips in fresh fruits (such as strawberries) during postharvest storage with the same effects; NO was effective in promoting insect and microorganism's mortality and controlling pest (Liu 2013, 2016). Several reports indicate a lower incidence of diseases in many fruits treated with exogenous NO sources including tomato, bayberry, mango, and peach (Table 2). It is known that NO acts as a signal in plant disease resistance by enhancing the induction of hypersensitive cell death reaction mediated by ROS and the induction of gene expression for the synthesis of protective natural products (Delledonne et al. 1998). In this sense, NO-treated fruits presented a higher defense-related enzyme activity such as phenylalanine ammonia-lyase (PAL), cinnamate 4-hydroxylase (C4H), 4-coumarate:CoA ligase (4CL), chalcone synthase (CHS), and chalcone isomerase (CHI), that are key enzymes of the phenylpropanoid metabolism pathway (Li et al. 2017; Hu et al. 2014; Gu et al. 2014). Also, the effects of NO on enhancing resistance against fungal pathogens seems to be related to the role of NO in reducing the rate of ethylene production and thereby affecting the physiological changes associated with fruit ripening (Lai et al. 2011; Wu et al. 2012). In this line, exogenous NO treatment led to a higher fruit firmness and a decrease in the cell wall degradation enzymes activities, as mentioned above (Lai et al. 2011; Zheng et al. 2014). Moreover, oxidative metabolism is influenced by exogenous NO applications as evidenced by an increase in SOD, CAT, and APX enzymes activities in treated fruits (Wu et al. 2012).

Summarizing, evidence shows that exogenous NO employed during postharvest treatments on climacteric and non-climacteric fresh fruits is able to influence respiration rate, flavor, firmness, color change, ROS metabolism, and enzymatic and non-enzymatic antioxidant content, disease incidence, among other effects that deeply affect postharvest shelf-life and fruit quality (Fig. 1). Its effects might be mediated by the direct and indirect modulation of redox balance and enzyme activities by PTMs and by the interaction with ethylene and other biomolecules (as discussed below). Thus, NO could be a good candidate for future industrial improvement of technologies tending to reduce not only the incidence of chilling injury in susceptible fruits, but also postharvest diseases, as discussed above.

Mode of Action of Exogenous NO: Interaction with Other Signaling Molecules During Ripening

As mentioned, early studies suggested an antagonistic effect of NO on ethylene action during ripening. Further studies confirmed that the modulation of NO on ethylene synthesis occurs at least at transcriptional and post-translational levels of the two main enzymes, ACS and ACO (Fig. 2). In banana slices (*Musa* spp. cv. Brazil), it was evidenced that infiltration with 5 mM SNP led to a reduction in ethylene synthesis due to the inhibition of the expression of ACS and ACO genes (Cheng et al. 2009). Although the treatment with NO gas-induced similar effects on the expression of ACO, it did not affect ACS expression in tomato (harvested either at mature green and breaker stages) (Eum et al. 2008), and mango (Hong et al. 2014). In contrast, in peaches exposed to NO gas, using a proteomic approach, it was found that the abundance of ACO protein was more than twofold higher than in control fruit, meanwhile ACS suffered no change in its abundance (Kang et al. 2016). This observation could be a result of NO action not only on protein expression but also on protein degradation. In this sense it would be interesting to evaluate the changes in ACO and ACS enzymes abundance, their expression, and their activity. Regarding the activity of the two main enzymes involved in ethylene synthesis, treatment with SNP led to a reduced activity of ACO and to an unexpected increase of ACS activity in bananas (Cheng et al. 2009). Fumigation with NO gas also inhibited ACO activity in mango but, in contrast to that evidenced in bananas, it led to a reduced activity of ACS (Zaharah and Singh 2011a). Exposure to gaseous NO resulted in an inhibition of ACO activity while it did not affect ACS activity in peach (Zhu et al. 2006); however, another work reported that an equal NO treatment in the same fruit species and cultivar led to a reduced activity not only of ACO but also of ACS (Liu et al. 2007). The inhibition of ACO activity may be due to PTMs mediated by NO. Tierney et al. (2005) reported that NO is able to bind in vitro to the non-heme iron atom present in the active site of the ACO. This is a plausible mechanism for the observed in vivo ACO inhibition by NO in peach proposed by Zhu et al. (2006) but, specific studies are needed to confirm this hypothesis. Nevertheless, it cannot be ruled out the modulation of ACS activity through nitrosation. Employing protein extracts from seedlings of *Brassica juncea* treated with 250 µM GSNO, it was evidenced that this enzyme is susceptible to nitrosation (Abat and Deswal 2009). Nevertheless, this assay employed a high concentration of GSNO, and a detailed study is required to evaluate the possibility of ACS nitrosation in vivo in NO-treated fruits.

Considering that ethylene synthesis requires the conversion of SAM into ACC, it should be taken into account the influence of NO over SAM accumulation as a possible point of regulation, due to a differential modulation of the enzymes involved in its synthesis and use as a precursor. It has been reported that NO modulates the activity of SAM synthetase (SAMS, also known as methionine adenosyltransferase -MAT-), that catalyzes the synthesis of SAM, a methyl donor with a central role in ethylene and polyamines synthesis (Lindermayr et al. 2006). Specifically, NO strongly inhibits MAT1, one isoform of this enzyme in *Arabidopsis* cultured cells, through nitrosation of a cysteine residue located at the active site (Lindermayr et al. 2006). To add more complexity to this scenario, it has been evidenced that SNP treatment induced the expression of SAMS in leaves of yellow alfalfa (*Medicago sativa* subsp. *falcata* (L.) Arcang.), by a pathway that involves ABA and H_2O_2, but in transgenic lines the overexpression of this enzyme did not affect ethylene synthesis (Guo et al. 2014a). It would be interesting to

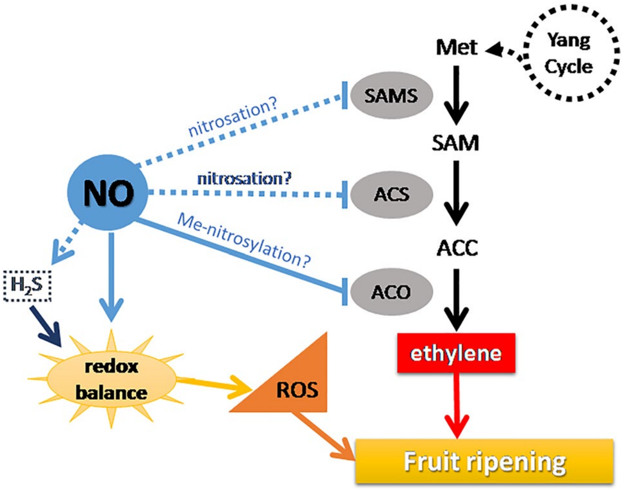

Fig. 2 Proposed NO crosstalk with gasotransmitters in climacteric fruits. NO treatment blocks ethylene increase. This effect is mediated by the inhibition of ACO activity, probably through metal-nitrosylation. Another proposed mechanism is the inhibition of the activity of ACS and SAMS, through nitrosation. NO also acts at the transcriptional level, modifying ACS and ACO gene expression. NO is also capable of impact on redox balance, influencing ROS, that are involved in fruit ripening. Through these actions, NO contributes to the modulation of fruit ripening during postharvest storage. The other proposed mechanism of ripening inhibition mediated by NO is through its interaction with H_2S. Dotted line stands for proposed mechanisms

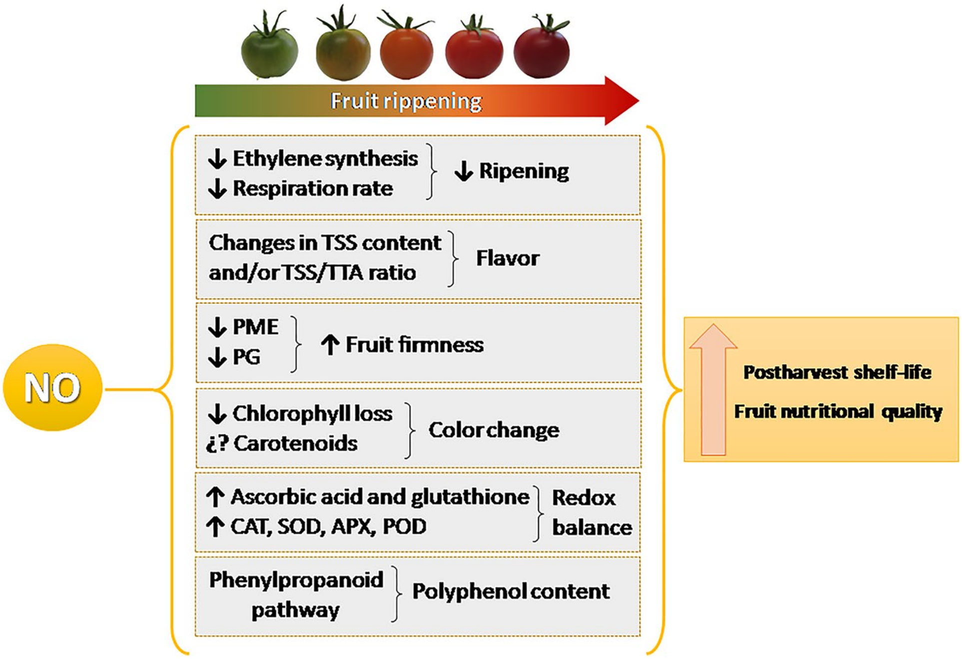

Fig. 1 NO treatment influences ripening and postharvest shelf-life of fruits. Exogenous NO is able to modify different fruit quality traits, such as flavor, firmness, color change, redox balance, and metabolic pathways, through PTMs of key enzymes, the modulation of gene expression and/or the interaction with phytohormones or other signaling biomolecules. These actions modulate the rate of ripening progress and lead to an extension of fruit postharvest shelf-life

analyze the influence of NO over SAMS in fruits regarding not only the modulation of its activity through PTM but also its expression, and its effect on ethylene and polyamines production. Although much of the progress about ethylene and NO effects has been made in climacteric fruits, the precise mechanisms implicated in the interaction between these two gaseous signaling molecules are still under study (Fig. 2).

Unfortunately, less attention has been paid to the action of ethylene and its modulation by exogenous NO in non-climacteric fruits. It has been evidenced that as ripening progresses, NO levels decreased in sweet pepper, a non-climacteric fruit (Chaki et al. 2015; Muñoz-Vargas et al. 2018), and treatment with exogenous NO delayed ripening (Chaki et al. 2015; González-Gordo et al. 2019). Although transcriptomic approaches led to the suggestion that NO modulates the expression of several proteins (González-Gordo et al. 2019) and leads to PTMs of proteins (Chaki et al. 2015), the mechanisms involved in the delay of ripening in non-climacteric fruits by NO are not well understood. The inhibition of ethylene synthesis by NO treatments was evidenced in strawberry. Unlike what was observed in climacteric fruits, where NO mainly affects ACO activity, NO fumigation delayed particularly the increase in ACS activity (Zhu and Zhou 2007). Efforts should be directed to understand the mechanisms by which NO alleviates the deterioration of non-climacteric fruits shelf-life through its crosstalk with ethylene.

As mentioned before, besides ethylene, ABA is an important player in the ripening process (McAtee et al. 2013). It has been evidenced that ABA facilitates the ethylene peak in banana (Jiang et al. 2000), mango (Zaharah et al. 2013), and cherry tomato (Wu et al. 2018). Nevertheless, it was recently reported that the combined treatment with ABA and NO in peach under cold storage led to the retention of fruit firmness, whereas the firmness decreased more quickly in the presence of ABA and the NO scavenger, cPTIO, suggesting that ABA acts upstream of NO (Zhang et al. 2019). Treatment with ABA positively influenced NO synthesis, as it was reported by Tian et al. (2020), maybe through the NR pathway. Overall, these results could be interpreted in the light of the different functions of ABA, as it not only mediates the fruit maturation and ripening processes but also responses to stress conditions (such as chilling tolerance). Unfortunately, only few studies have been conducted in order to reveal the possible crosstalk between ABA and NO and its effect on fruit quality during fruit storage.

Within the last few years, H_2S has emerged as a novel signaling molecule, recognized as a gasotransmitter in plants, acting on physiological processes and responses to stress conditions. A variety of processes influenced by H_2S match with processes regulated by NO, and fruit ripening is not an exception (Corpas et al. 2019). It has been reported that exogenous H_2S was able to extend the postharvest shelf-life of treated fruits, influencing color development, firmness, respiration rate, ethylene production, oxidative metabolism, chilling injury, and disease incidence (Ali et al. 2019; Corpas and Palma 2020). This raises the question whether NO and H_2S can share signaling pathways, triggering the same physiological effects. In fact, it has been reported that treatment with NaHS (a H_2S donor) and SNP on strawberry led to an enhancement of fruit quality (evaluated through firmness, presence of rotten surface and relative conductance) as compared with the treatments with each one separately (Zhang et al. 2014). The results also showed a synergistic effect of these gasotransmitters on partially blocking the rise of the respiration rate (Zhang et al. 2014). Conversely, the pre-treatment of peaches with a NO solution decreased H_2S content, maintained fruit quality, and inhibited ethylene and respiration rate increase during cold storage (Geng et al. 2019). In addition, pre-treatments with known negative modulators of NO levels (sodium tungstate, L-NAME and cPTIO) led to higher H_2S content than in control fruit and showed a negative effect on fruit quality (Geng et al. 2019). It is worth mentioning that the differences in these reports may be due to the differences in fruit physiology, as strawberry corresponds to a non-climacteric fruit and peach is classified as climacteric. This also highlights the relative lack of information, in addition to differences in the treatments, the NO donor, the exposure time, and the NO levels. Beyond the advances in the crosstalk between these two molecules in other areas of plant physiology, the study of this interaction during fruit postharvest will contribute to this incipient area of research.

Another emerging molecule involved in improving fruit postharvest storage is melatonin (Arnao and Hernández-Ruiz 2018; Li et al. 2019). Some reports described that its action on postharvest shelf-life of fruits is mediated by NO. In pears treated with melatonin, ethylene peak was inhibited or delayed, depending on the cultivar (Liu et al. 2019). Besides, the treatment with melatonin and L-NAME did not affect the ethylene evolution as compared to control pears, suggesting that melatonin effect on ethylene synthesis is mediated by NO (Liu et al. 2019). Some recent reviews have proposed an interplay among NO, H_2S, and melatonin during fruit postharvest storage, leading to the retention of fruit quality (Mukherjee 2019; Zhang et al. 2020); however, more research should be undertaken in order to decipher the crosstalk between these molecules and clarify their role during storage of both climacteric and non-climacteric fruits.

Technological Potential of NO Use in Postharvest Storage

The use of NO in postharvest technology requires adequate sources of NO (such as NO gas, or NO donors), and strategies for adequate applications, that need studies of the NO availability and stability, generation of subproducts, that surely will vary with the temperature, atmosphere, packaging, and the fresh produce affected by the treatment (Table 3). Another main aspect of postharvest treatments is the assurance of the healthy characteristics of the final product, where the presence of residues after any treatment must be considered. The possibility to employ NO as a fumigant agent (Table 2) may be an advantage as compared to others such as methyl bromide. Methyl bromide fumigation leaves high levels of residue on some fresh produce, and causes toxic effects on others, in addition to the global phase-out of its production (Yang and Liu 2017).

One disadvantage of the use of NO gas would be the need of a gas-tight fumigation chamber (Table 3), since NO rapidly oxidizes to nitrogen dioxide (NO_2) in the presence of atmospheric O_2 (Snyder 1992). Thus, treatments of horticultural produce with gaseous NO in atmospheres with a low concentration of O_2 may be required, but during short time periods to avoid adverse anaerobic effects (Wills et al. 2015; Soegiarto et al. 2003). Also, if treatments are not flushed with nitrogen (N_2) to low NO levels at the end of fumigation, the reaction of NO with O_2 to produce NO_2 may increase nitrate (NO_3^-) and nitrite (NO_2^-) as residues in fresh fruit and vegetables. It is known that NO_2^- can be converted to carcinogens nitrosamines with a negative impact on human health (Yang and Liu 2017; Wills et al. 2015). Thus, the fumigation procedure may have a significant impact on residue levels. Yang and Liu (2017) analyzed NO_3^- and NO_2^- residue levels on a variety of fruit and vegetables employing NO fumigation treatments under ULO conditions, terminated with N_2 or air flushes. When fumigation was finished with N_2 flushing, no significant amounts of residues (NO_3^- and NO_2^-) were found on fresh products. This finish procedure also reduces the risk of worker exposures to NO_2, improving health security. Nevertheless, the impact of the NO concentration employed for treatments on NO_3^- levels of some products may be negligible as compared to endogenous levels, and also may be encompassed in the maximum permitted limits for each product (Yang and Liu 2017). In addition, Soegiarto et al. (2003) evaluated changes in the concentration of NO in air atmosphere in the presence of a range of fruits, vegetables, and flowers, and showed that the rate of oxidation of NO in air was lower than expected, being the rate of absorption by horticultural products larger than aerial oxidation and subjected to its physical characteristics. Further research related to residue analysis employing different NO donors and treatment strategies should be conducted in order to gain future regulatory approval (such as the possibility of cyanide liberation under SNP treatments).

On the other hand, a key question regarding the employment of NO donors is if they can mimic endogenous NO levels and effects. In this sense, factors as light or the presence of reducing agents should be considered. Floryszak-Wieczorek et al. (2006) showed that the presence of light was essential to mimic effects of endogenous NO in leaf tissue employing SNP as NO donor. PAL, a key enzyme of the phenylpropanoid pathway, was stimulated when leaves were treated in the light with the NO donor. However, other donors such as S-nitroso-N-acetylpenicillamine (SNAP) and GSNO showed some NO release even in the dark. Authors pointed out that NO donor decomposition depends on numerous external and internal factors, as the plant tissue environment, so monitoring or quantifying the amount of NO released by the donor, and NO levels inside the tissues seem an important topic.

When analyzing some contrasting results, another important aspect seems to be the dose of NO (or NO donor) and the time of the exposure during the treatments. In apple disks the treatment either with NO donors (GSNO and SNP) or with NO_2^- led to a reduction in ethylene evolution, while treatment with NO gas did not affect it (Rudell and Mattheis 2006). When pears were exposed to 10 $\mu L\ L^{-1}$ NO gas for 2 h, a delayed and lower ethylene peak was detected and a slower softening was observed, as compared to unexposed fruits (Sozzi et al. 2003). Nevertheless, when pears were exposed to 50 $\mu L\ L^{-1}$ NO gas for 12 h, the ethylene peak was earlier and higher than the one displayed by control pears, but the loss of firmness was not affected. This observation could be due to a stressful action of NO when it is applied in high concentrations, leading to a response of ethylene synthesis not related to the ripening process. A toxic effect of NO treatment was also reported in peach and strawberry fumigated with gaseous NO (Wills et al. 2000; Zhu et al. 2006). A toxic dose of NO led to a rapid appearance of blackening in strawberry (Wills et al. 2000), while a sharp decrease in firmness was detected in peach in response to high exogenous NO levels (Zhu et al. 2006).

The use of NO donors in combination with nanomaterials in crops and even more in fruit postharvest is a relatively new and promising approach where the research is just beginning (Seabra et al. 2014; Corpas and Barroso 2015; Marvasi 2017; Oliveira et al. 2016; Kolbert et al. 2021). However, it must be considered that plants respond to the presence of nanomaterials by synthesizing signal molecules, such as NO. As summarized by Kolbert et al. (2021), the effects of different nanoparticles (NPs) (as chitosan NPs, metal oxide NPs, and carbon nanotubes) on endogenous NO synthesis and signaling in different plant species have been described as involved in innate immunity, antifungal responses, and stress tolerance. So, in some cases, NPs alone (without NO donors) may increase the NO levels in the treated horticultural products, and these aspects should be considered when evaluating the effects of each treatment. The effects of nanomaterials in combinations with NO donors may strongly depend on the fruits and vegetables subjected to the study as

Table 3 Sources for NO delivery: advantages and disadvantages on postharvest technology use

Nitric oxide source	Advantages	Disadvantages
NO gas	Commercial availability	Fast oxidation by atmospheric oxygen Infrastructure: gas chamber Nitrogen atmosphere (risk of anaerobic metabolism)
NO donors	Time dependent NO emission Easy application Stability in adequate media Commercially available and relatively inexpensive (depending on the NO donor)	Toxicity of subproducts The kinetic of NO generation may change according tothe treatment conditions (pH, temperature, light,presence of metals)
NO-releasing nanomaterials	Ability to carry and deliver NO to plants (possibility of light regulation or protection, and ofstoring high NO concentrations depending onthe NO donor and nanomaterial) More controlled NO release Easy application Stability Prolonged effect	Effects of nanoparticles *perse*? Phytotoxicity? Related with the NO donor employed and factors that influence its decomposition
Enhancement of endogenous NO generation		
Safe products or endogenous molecules	Natural occurring compounds (such as arginine) Low or no toxicity	Some sources related to the synthesis of NO have not been clarify yet
Low (or sub lethal) doses of an agent inducing a physical or chemical stress (UV radiation, temperature, controlled atmospheres)	Pest control Hormetic effect Enhance of other metabolic pathways in agreement to NO signaling effects	Infrastructure

Some of these aspects were analyzed by Seabra et al. (2014), Wills et al. (2015), Marvasi (2017) and Kolbert et al. (2021). In all conditions the measurement of NO should be encourage, not only to assess the kinetic of NO generation by the NO donors, but also to determine the NO levels in fruits and vegetables associated to an observed effect

it was described with NO donors alone. Also, the effect may differ from the effects observed with the NO donor alone. Studies should be carefully developed to include adequate controls as NPs alone, NO donor alone, in addition to the complete treatment with the NO-releasing nanomaterial. Oliveira et al. (2016) have described one of the first reports regarding the synthesis and characterization of chitosan nanoparticles (CS-NPs) containing a NO donor, S-nitrosomercaptosuccinic acid (S-nitroso-MSA), and its effects in the mitigation of salt stress in maize plants. In this sense, NO-releasing CS-NPs were more efficient than non-encapsulated NO donor to counteract the effects of salt stress in maize plants. A control treatment employing NPs containing non-nitrosated MSA was performed to evaluate the lack of effect in the absence of the NO donor. Also, S-nitroso-MSA decomposition does not seem to produce toxic subproducts (Oliveira et al. 2016). Another study employing NPs and GSNO in sugarcane plants showed less differences between encapsulated and non-encapsulated NO donor, where both forms reduced plant sensitivity to water deficit (Silveira et al. 2019). Studies employing GSNO-containing CS-NPs have been developed in sweet cherry fruits showing effects on postharvest quality, such as lesser weight loss, ethylene production, respiration rate, and an increase in TSS content (Ma et al. 2019). In all cases, encapsulated NO donors evidenced a reduced rate of NO release as compared to free forms, indicating more stability due to the encapsulation, which would sustain a NO release necessary to apply the NO donor not only in agriculture, but also under postharvest technology processes (Oliveira et al. 2016; Silveira et al. 2019; Ma et al. 2019). However, it should be considered that the kinetic of NO release, half-life, and stability may also differ according to the form of administration in each system (i.e., sprayed, watered, or immersed), and in agreement to Oliveira et al. (2016), further studies are necessary to investigate the uptake, translocation, and accumulation of encapsulated NPs NO donors in plants.

Another interesting aspect of postharvest technology is that multiple treatments with mild stress agents may contribute to improving shelf-life and product quality, as a result of stimulating the defense system of the fruit, where some responses may be mediated by NO. So, strategies conducted to increase endogenous NO generation in fruits during postharvest may be an interesting topic of research. It has been previously described that NO donors improved storage conditions of different fruits and vegetables, but widely used postharvest treatments, as temperature changes and UV light, could induce mild stress situations increasing endogenous

NO levels. Xu et al. (2012) described that low temperature (1 °C) induced endogenous NO generation in loquat fruit during postharvest storage, at least in part, through the NR pathway, suggesting a new strategy to improve chilling tolerance by enhancing a pathway of NO generation. Moreover, irradiation with blue + UV-B light activated the expression and the activity of NR, and promoted the expression of anthocyanin biosynthetic genes and the increase in anthocyanin levels in a mutant tomato line that accumulates anthocyanins in the epidermis (Kim et al. 2020). On the other hand, despite of the lack of knowledge about a NOS_{like} source of NO in plants, L-Arg treatment emerges as a possible strategy to improve postharvest fruit quality, and to avoid the decay due to pathogen attack (Zheng et al. 2011; Shu et al. 2020). In addition, transgenic *Arabidopsis* plants expressing a NOS enzyme from *Ostreococcus tauri* (*OtNOS)* accumulated higher NO concentrations, and were more tolerant to salt, drought, and oxidative stress (Foresi et al. 2015), highlighting the potential of genetic manipulation of endogenous NO levels in other horticultural plants. (Negi et al. 2010) isolated a NO-overproducing mutant of tomato (*Solanum lycopersicum*) associated with a NOS_{like} activity, that conferred increased resistance to the pathogen *Pseudomonas syringae*. The effect of genetic manipulation of NO accumulation on fruits and vegetables during postharvest storage has not been explored yet, being a promising scenario.

Conclusion and Perspectives

Several forms of NO exposure have been employed in postharvest treatments to deal with several problems related to storage, such as chilling injury, water and antioxidant loss, and microbial infection, as described above. The information obtained from diverse experimental designs applied to multiple species of fruits and vegetables makes it difficult to find common treatment protocols, but undoubtedly gives us global knowledge and trends about the influence of NO during the storage of several products. However, it would be of great importance to undertake studies regarding the mechanisms of action of NO in order to improve and take advantage of NO treatments.

The great increase in research in the field of postharvest technology involving NO treatments will allow researchers to collect the results obtained in each fruit, in addition to the information about the required NO levels able to modulate fruit ripening, keeping the equilibrium between adequate nutritional characteristics and commercial quality. In this sense, even though nowadays many works report NO levels in fruits and vegetables, sometimes the techniques employed to measure this molecule may not be properly applied. In some cases, endogenous NO is estimated by indirect quantification of NO_2^-, or employing the hemoglobin assay in homogenates, and in frozen samples instead of fresh tissues. NO_2^- and NO_3^- detection are widely used as an indirect assay of NO levels (Griess reagent assay), but the measurement and the correlation must be carefully assessed, as in plants, NO_2^- and NO_3^- not solely arise from NO metabolism (Zhang et al. 2011; Steelheart et al. 2019b). Several methods for NO detection have been used by plant scientists (Mur et al. 2011) but the correct evaluation of the suitability for a system under investigation, and the possibility of combining more than one technique should be considered.

Overall, the employment of NO donors in fruit postharvest is mainly restricted at experimental level, but the potential use of NO donors and the possibility to elicit endogenous levels by modulating the sources and mechanisms involved in its generation (and the interaction with other gaseous signaling molecules or phytohormones), opened a great field of research. From the experiments developed by Leshem and coworkers (Leshem et al. 1998; Leshem and Wills 1998; Leshem and Pinchasov 2000) to the possibility of genetic manipulation of horticultural products, a broad spectrum of possibilities are now opened to develop new strategies with the aim of improving fruit and vegetable quality and minimizing avoidable losses.

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Declarations

Conflict of interest The authors declare no conflict of interest.

Consent for Publication All the authors approved the publication.

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