



Review

Nitric Oxide Is Essential to Keep the Postharvest Quality of Fruits and Vegetables

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Abstract: Nitric oxide (NO) is a gaseous free radical that has become a potential tool to maintain the quality of postharvest horticultural produce. It plays important roles in delaying ripening, alleviating chilling injury, preventing browning, and enhancing disease resistance. The regulatory function of NO is achieved through the post-transcriptional modification of proteins, such as tyrosine nitration, S-nitrosylation, and nitroalkylation. Secondly, NO can also induce the expression of stress-related genes by synergistically interacting with other signaling substances, such as Ca²⁺, ethylene (ETH), salicylic acid (SA), and jasmonic acid (JA). Here, research progress on the role of NO and its donors in regulating the quality of postharvest fruits and vegetables under storage is reviewed. The function of NO crosstalk with other phytohormones is summarized. Future research directions for NO commercial application and the endogenous NO regulatory mechanism are also discussed.

Keywords: nitric oxide; fruits and vegetables; ripening; chilling injury; browning; crosstalk



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1. Introduction

Fruits and vegetables are becoming increasingly important sources of nutrients for humans [1]. However, it is a great challenge to maintain the postharvest quality of fruits and vegetables, including the prevention of pests and diseases, browning after fresh-cutting, softening, and decay, etc. Senescence and environmental stress are the main causes of declines in the postharvest quality of fruits and vegetables [2]. As a natural gas molecule that can freely pass through lipid membranes to regulate plant development and mediate the stress response of plants [3], NO has been widely used to control the postharvest quality of fruits and vegetables. Finally, research directions on the effects of NO on postharvest fruits and vegetables meriting future attention are discussed.

The homeostasis of NO in fruits and vegetables is maintained through regulation of its synthesis and degradation (Figure 1). NO can be synthesized via the reductive pathway and oxidative pathway [4,5]. Nitrite (NO₂⁻) reduction is the major source of NO in plants, which occurs by both enzymatic and non-enzymatic mechanisms [6]. Nitrate reductase (NR) in the cytosol, nitrite–NO reductase (Ni–NOR) in the plasma membrane, nitrate reductase (NiR) in plastids, and xanthine oxidoreductase (XOR) are involved in reductive NO synthesis [7,8]. Non-enzymatic nitrite reduction occurs spontaneously in the apoplast owing to the acidic conditions or the presence of ascorbic acid or phenols [9,10]. Several oxidative pathways of NO synthesis have been studied. L-arginine can be oxidized to produce NO by NO synthase-like (NOS-like) enzyme [11], while N-omega hydroxyl-L-arginine is also converted to NO by peroxidase (POD) and hemoglobin. Alternatively, NO can be produced from polyamine (PA) through PA oxidase [7]. Cytochrome oxidase is also involved in the NO production.

NO production has been shown to be associated with the electron transport chain in chloroplasts and mitochondria [12–14]. Under O₂ deficiency, reductive NO synthesis is achieved via NO₂⁻ reduction mediated by cytochrome-c oxidase (complex IV) of the

electron transport chain in mitochondria [13]. In addition, the transport of electrons to O_2 is inhibited at complex IV, and the consumption of O_2 is reduced. In isolated chloroplasts, NO generation has been documented and NOS-like protein appears to be involved in this process; in return, the chlorophyll biosynthesis and chloroplast differentiation can be stimulated by the increase in iron availability mediated by NO [14,15].

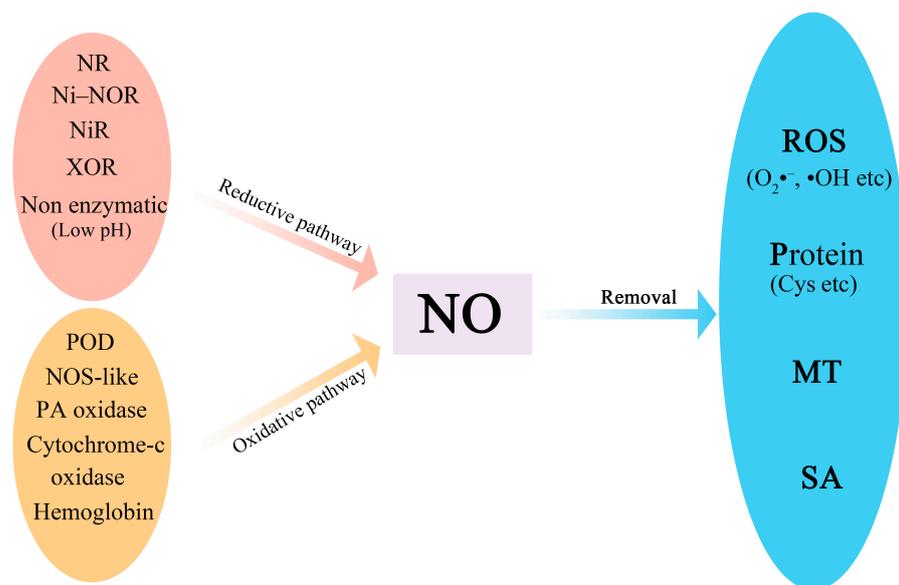


Figure 1. A schematic model of NO synthesis and removal. NO is synthesized via the reductive pathway and the oxidative pathway. The enzymes for the reductive pathway include NR, Ni-NOR, NiR, and XOR. Non-enzymatic nitrite reduction occurs spontaneously under low pH. POD, NOS-like, PA oxidase, cytochrome-c oxidase, and hemoglobin are involved in the oxidative pathway. NO can be removed by reaction with ROS, proteins, MT, and SA. NR: nitrate reductase; Ni-NOR: nitrite-NO reductase; NiR: nitrate reductase; XOR: xanthine oxidoreductase; POD: peroxidase; PA: polyamine; MT: melatonin; SA: salicylic acid.

NO is removed when it interacts with superoxide anion ($O_2\bullet^-$), hydrogen peroxide (H_2O_2), hydroxyl radical ($\bullet OH$), proteins (e.g., cysteine and tyrosine), or small signaling molecules (e.g., melatonin (MT) and salicylic acid (SA)) by oxidation reactions or S-nitrosylation. Many NO derivatives (peroxynitrite ($ONOO^-$), S-nitrosothiols (SNO), S-nitrosoglutathione (GSNO), N-nitrosomelatonin (NOMela), dinitrogen tri-oxides, dinitrogen tetra-oxides, nitroxyl (NO^-), and nitrosonium ions) are produced and involved in the regulation of plant development and stress responses [6,16]. Among these donors, SNO, GSNO, and NOMela are the main long-distance transport molecules in the NO signaling pathway.

2. Effects of NO on Fruit Ripening

The commodity value and shelf life of fruits and vegetables are greatly affected by their degree of ripeness. Short-term exposure to low concentrations of NO or its donor compounds has been shown to extend the postharvest life of various fresh fruits and vegetables. The reason might be through inhibiting ETH synthesis through the formation of the ternary stable complex ACO-NO-ACC or directly reducing the activity of ACS and ACO (1); inhibiting the expression of genes involved in the ETH signaling pathway (2); and affecting lignin accumulation (3). However, the inhibition of the maturation and senescence by NO depends on its concentration and specific species of fruits and vegetables (Table 1). In some species, co-treatment with other substances (e.g., 1-MCP or H_2S) is more effective than treatment with NO alone (Table 1).

Table 1. The effects of NO treatment on postharvest fruit ripening.

Fruits	Best Treatment	Effects	References
Blueberry (Blue Cuinex, Blue Chip and Misty)	Blue Cuinex: 1 $\mu\text{L L}^{-1}$ 1-MCP + 1 mM GSNO Misty: 1 $\mu\text{L L}^{-1}$ 1-MCP Blue Chip: Not affected by treatment.	Maintained higher firmness, malic acid, citric acid, ascorbic acid, and glutathione contents for 14 d at 4 °C.	[17]
Tomato (Elpida)	1 mM GSNO + 0.5 $\mu\text{L L}^{-1}$ 1-MCP	Delayed fruit softening, reduced the ETH synthesis significantly.	[18]
Red raspberry (<i>Rubus idaeus</i> L.)	15 μM NO solution for 2 min (immersed in)	Reduced ETH production, respiratory intensity, ROS contents and increased the contents of flavonoids, anthocyanin, rutin, influenced metabolism of sugars.	[19]
Sweet pepper	160 μM (5 ppm) NO gas for 1 h	Delayed the ripening of fruit, decreased lipid peroxidation, and increased antioxidant capacity, ascorbate content.	[20–22]
Banana (Brazil)	5 mM SNP solution	Reduced ETH production, inhibited degreening of the peel, and delayed softening of the pulp. Inhibited the activity of ACO.	[23]
Papaya (Sui you 2)	60 mL L^{-1} NO fumigated for 3 h	Suppressed ETH formation and respiratory rate (CO_2 levels), reduced weight loss, maintained firmness, and delayed changes in peel color and soluble solid contents during 20 d of storage.	[24]
Wax apple (<i>Syzygium samarangense</i>)	10 $\mu\text{L L}^{-1}$ NO fumigated for 2 h	Lower rate of weight loss, a softening index, and loss of firmness during storage. Decreased total lignin content.	[25]
Tomato (Lichun)	0.1 mM L-NAME solutions for 0.5 min	Decreased endogenous ETH release and delayed the breaker stage of fruits.	[26]
Peach (Dahong)	15 $\mu\text{L L}^{-1}$ NO + 20 $\mu\text{L L}^{-1}$ H_2S fumigated for 20 min	Inhibited ripening of peach fruits, reduced softening related enzymes activities, ETH production, ACC content, ACC synthase, and oxidase activities.	[27]
Water bamboo shoots (<i>Zizania latifolia</i>)	30 $\mu\text{L L}^{-1}$ NO fumigated for 4 h	Suppressed the softening and lignification effectively.	[28]

NO can inhibit ETH synthesis during the postharvest storage of several fruits, such as mango [29], apple [30], tomato [18,26], peach [27], banana [23], strawberry [31], Chinese bayberry [32], and red raspberry [19]. The precursor of ETH is S-adenosyl methionine (SAM), which is catalyzed into amino cyclopropane carboxylic acid (ACC) by ACC synthase (ACS) and further oxidized into ETH by ACC oxygenase (ACO) [33]. NO inhibits the activity of ACS and ACO and the expression of the genes encoding these enzymes, which further affects the production of ETH and the accumulation of ACC [34,35]. Moreover, NO and ACO can be chelated by ACC to produce the ternary stable complex ACO-NO-ACC, which inhibits the ETH signaling [34,36]. NO also regulates the ETH signaling pathway by inhibiting the expression of ETH perception genes (*ETH3* and *ETR4*) and ETH signaling pathway-related genes (EIN3-binding F-box, constitutive triple response 1, and sub-class E ethylene response factors) during the breaker stage in tomato [35]. These results indicate that NO negatively affects ETH synthesis and signaling (Figure 2).

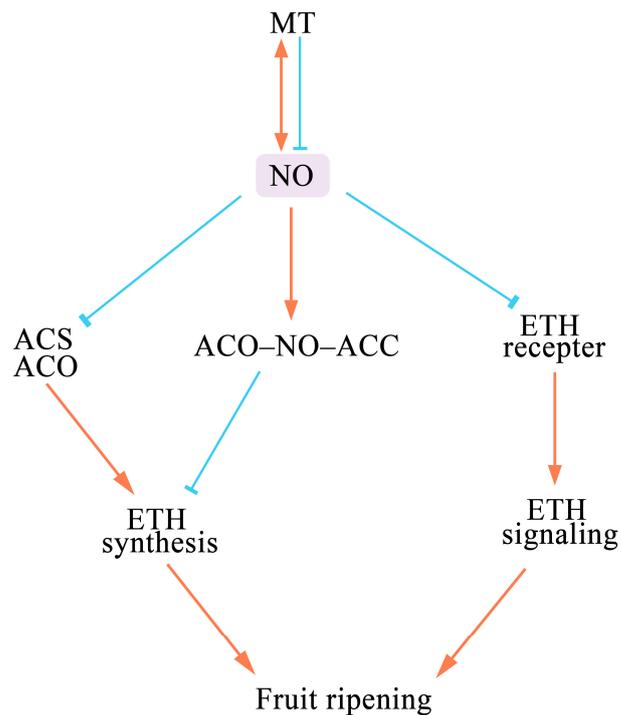


Figure 2. A schematic model of how NO affects the senescence of fruits. (“↓” indicates promote, and “⊥” indicates inhibit). NO affects fruit ripening and senescence by altering ETH synthesis and signaling. It can down-regulate the activities of the ETH synthesis-related enzymes ACS and ACO to reduce ETH production. NO can also form a stable ternary ACO–NO–ACC complex to antagonize ETH formation. NO inhibits the ETH signaling pathway by down-regulating the expression of ETH perception genes. MT acts upstream of NO and can induce or inhibit NO production to regulate the senescence of fruits and vegetables. NO also induces the synthesis of MT in plants.

Interestingly, NO inhibitor treatment has also been shown to delay the ripening of tomato fruit, which is consistent with the effect of NO treatment. Thus, the mechanism by which NO inhibitor regulates ETH through its effect on NO in green mature tomato fruit differs. Treatment with the NO synthase inhibitor L-nitro-arginine methyl ester (L-NAME) in green mature tomato fruit inhibits ETH biosynthesis, which might be explained by the delay or reduction in the expression of the calcium-dependent protein kinase (CDPK) and mitogen-activated protein kinase (MAPK) genes *SICDPK1/2* and *SIMAPK1/2/3* [26]. It remains unclear whether other synthetic inhibitors have the same effect.

The accumulation of lignin also affects the quality of fruits and vegetables during storage [28,37]. NO can regulate lignin synthesis by affecting the expression of genes encoding enzymes involved in lignin production, such as cinnamyl alcohol dehydrogenases and caffeoyl-CoA O-methyltransferase [37,38]. The rapid loss of tenderness in bamboo shoots (*Phyllostachys violascens*) mostly stems from lignification, treated with SNP could decrease the activities of phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), and POD and lignin accumulation were also significantly reduced [39]. Moreover, NO treatment could also delay the cellulose formation and maintain the content of ascorbic acid, soluble protein, and chlorophyll in green asparagus [40]. For wax apple, after treatment with NO, the weight loss, loss of flesh firmness, and total lignin content were significantly reduced [25]. In contrast, SNP treatment may improve disease resistance by inducing lignin accumulation and enhancing the activity of PAL or POD during the storage of postharvest “Tainong” mango, kiwifruit, and wounded muskmelon [38,41,42]. In context, these results indicate that NO could increase or decrease lignin accumulation which may depend on the fruit and vegetable species and the biological process (ripening, senescence, or biotic stress).

3. NO Can Enhance the Defense of Fruits and Vegetables against Chilling Injury

Chilling injury seriously affects the quality and commercial value of fruit and vegetable products. Several studies have been reported that NO treatment could alleviate chilling injury and oxidative damage of fruits and vegetables by consuming excess ROS and alleviating oxidative damage in plants (1); improving antioxidant enzyme activity and inducing the expression of chilling injury-related genes (*CBFs*) (2); and maintaining a high energy state and inducing the activity of enzymes involved in energy metabolism (3). We list some results in Table 2.

Table 2. The effect of NO treatment on alleviating chilling injury.

Fruits	Best Treatment	Effects	References
Mango (Kensington Pride)	10, 20, 40 $\mu\text{L L}^{-1}$ NO fumigated for 2 h	Reduced the chilling injury index, retarded color development, softening, and delayed fruit ripening and maintained quality during storage at 5 °C for 2 and 4 weeks.	[29]
Banana (Brazil)	0.05 mM SNP solution for 5 min (10 kPa)	Inhibited the development of chilling injury during storage at 7 °C for 20 d. The contents of ATP and energy charge were higher. The activities of enzymes involved in energy metabolism were markedly enhanced. Reduced chilling injury during storage at 7 °C for 15 d.	[43]
Banana (Brazil)	60 $\mu\text{L L}^{-1}$ NO gas for 3 h	Reduced increases in electrolyte leakage and malondialdehyde content. Postponed the degradation of chlorophyll. Decreased the chilling injury index and chilling injury incidence during storage at 1 °C.	[43,44]
Hami melon (86-1)	60 mL L^{-1} NO for 3 h	Reduced the increases in membrane permeability and malondialdehyde (MDA), H_2O_2 content. Inhibited $\text{O}_2\bullet^-$ production rates. Sustained higher activity of SOD, POD, CAT, and APX in the rind. Delayed the decrease of mitochondrial	[45]
Peach (Feicheng)	15 μM NO solutions for 0.5 h	permeability transition, promoted a more stable internal medium in mitochondria.	[46]
Longkong (Griff)	30 mM SNP solution for 20 min	Controlled the chilling injury index, electrolytic leakage and regulated the production of MDA, $\text{O}_2\bullet^-$, and H_2O_2 .	[47]
Sweet orange (Midknight Valencia and Lane Late)	10 $\mu\text{L L}^{-1}$ NO fumigated for 2 h	Reduced chilling injury, weight loss, total sugars, and vitamin C in both Midknight Valencia and Lane Late during storage for 90 d at 4 °C and 7 °C. Weight losses 7 °C were higher than 4 °C.	[48]
Table grape (Munage)	300 $\mu\text{L L}^{-1}$ NO fumigated for 2 h	Increased the activities of antioxidant enzymes; alleviated ROS accumulation and membrane lipid peroxidation during storage at 0 °C for 60 d.	[49]

Under low temperature, an oxidative burst (including $\text{O}_2\bullet^-$, H_2O_2 , and $\bullet\text{OH}$) has been reported in many fruits [50,51]. The excessive ROS promotes lipid peroxidation, alters the function of the membrane system, leads to the production of abnormal cells, induces cell dysfunctions, and finally results in a decrease in product quality [52]. Mitochondria is the main subcellular organelle of ROS production. As the ROS content increases, the mitochondrial permeability transition (MPT) decreases. NO treatment might delay the decrease in MPT and mediate the decomposition of the excess ROS, maintain ROS homeostasis, and alleviate oxidative damage in fruits and vegetables (Figure 3).

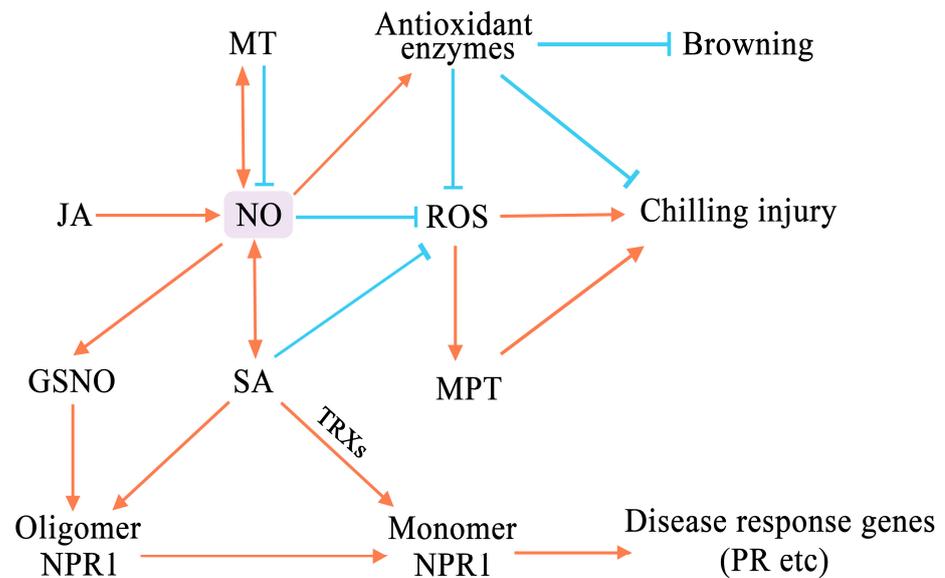


Figure 3. A model for the regulation of NO on browning, chilling injury, and disease resistance of postharvest fruits and vegetables. JA, MT, and SA can interact with NO to resist these stresses. NO promotes the activity of antioxidant enzymes to inhibit browning and alleviate chilling injury. ROS is a key regulator of chilling injury that can directly induce chilling injury or indirectly increase the MPT. NO, SA, and antioxidant enzymes can remove excess ROS. The NO donor GSNO can trigger the oligomerization of NPR1, and SA can maintain protein homeostasis. TRXs can catalyze SA-induced NPR1 oligomer-to-monomer reactions, and then the monomer NPR1 enters the nucleus to induce the expression of disease response genes. JA: jasmonic acid; MT: melatonin; SA: salicylic acid; GSNO: S-nitrosoglutathione.

Studies in loquat fruit have shown that low temperature can induce the generation of endogenous NO, and this cold-induced endogenous NO generation plays a critical role in alleviating the symptoms of chilling injury by affecting antioxidative defense systems [53]. The protective effect of NO against oxidative stress in plants is achieved via reaction with $O_2\bullet^-$, which leads to the generation of $ONOO^-$ and reduces ROS levels [54,55].

Reduced cell energy levels can induce hypothermia damage [56,57]. Cell energy can directly affect the biosynthesis of membrane lipids and the repair of cell membranes, which mediates the cold resistance of fruits under cold stress [58]. After treatment with NO, higher levels of ATP and energy charges and less severe symptoms of chilling injury are observed during the storage of fruits and vegetables.

4. Effects of NO on Disease Resistance and Pest Control after Harvest

Infection of pathogenic microorganisms, such as *Monilinia fructicola*, *Colletotrichum gloeosporioides*, *Alternaria alternate*, etc., substantially affect the quality of postharvest fruits and vegetables [59,60]. It was reported that treatment with NO could enhance disease resistance of fruits and vegetables, such as tomato, peach (Figure 4), pitaya, muskmelon, etc., (Table 3) by mediating activation of defense-related enzymes (1); accumulation of antifungal compounds (e.g., phenylpropanoic acids, flavonoids, phenolics, and lignin) (2); and induction of H_2O_2 accumulation in the early stage of storage (3).

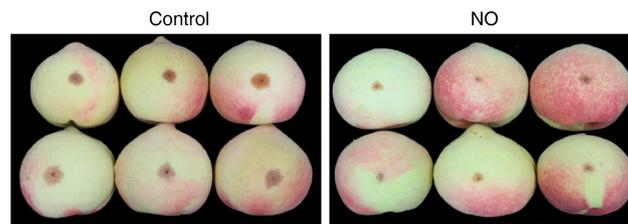


Figure 4. NO treatment enhanced peach fruit resistance to *Monilinia fructicola* [61]. © 2023 Yu, Cao, Zhu, Zhang, Peng and Shi.

Table 3. The effects of NO on disease and disorder resistance.

Fruits	Disease	Best Treatment	Effects	References
Tomato (Target NF1)	Boron toxicity (B)	0.1 mM NO as a foliar spray	Overcame the deleterious effects of B toxicity on tomato fruit yield and whole plant biomass by reducing the concentrations of B, MDA, EL (electrolyte leakage), and H ₂ O ₂ in the leaves.	[62]
Peach (Feicheng)	<i>Monilinia fructicola</i>	15 µmol L ⁻¹ NO solution for 10 min	Inhibited postharvest peach brown rot caused by <i>M. fructicola</i> . Had a positive effect on enhancing resistance against postharvest anthracnose and delayed the ripening and senescence during storage at 20 °C.	[63]
Citrus (Valencia)	<i>Colletotrichum gloeosporioides</i>	50 µmol L ⁻¹ SNP for 10 min	Inhibited the lesion expansion on pathogen-inoculated pitaya fruit during storage and reduced the natural disease incidence and index of pitaya fruit stored at 25 °C.	[64]
Pitaya (Baiyulong)	<i>Colletotrichum gloeosporioides</i>	0.1 mM SNP for 8 min	Suppressed lesion development on mango fruit inoculated with <i>C. gloeosporioides</i> and reduced natural anthracnose incidence during stored at 25 °C.	[65]
Mango (Guifei)	<i>Colletotrichum gloeosporioides</i>	0.1 mM SNP for 5 min	Reduced diseases incidence; delayed the increase in soluble solid content; increased the activities phenylalanine PAL, POD; elevated the level of total phenolics, flavonoids, and lignin.	[66]
Kiwifruit (Bruno)		0.2 mM SNP for 10 min	The lesion diameters and lesion depths were decreased.	[42]
Muskmelon (Xizhoumi 25)	<i>Alternaria alternata</i>	60 µL L ⁻¹ NO fumigated for 3 h		[67]

The phenylpropanoid metabolic pathway was involved in the regulation of disease resistance in fruits and vegetables. Exogenous NO treatment could be involved in regulating the accumulation of phenylpropanoic acids, flavonoids, phenolics, and lignin by inducing these enzymes' (PAL, 4-coumarate–CoA ligase, and cinnamic acid 4-hydroxylase) activities and increase the disease resistance of peach and muskmelon [67,68]. The accumulation of phenolic and flavonoid compounds in mushroom enhanced the antioxidase activities and the defense responses against pathogens [69]. The phosphorylation of MAPKs is one of the earliest events occurring after pathogen attack, which transduce extracellular stimuli into intracellular responses in plants [70]. In plants, the MAPK signaling cascades are involved in various processes, including defense signaling [71]. It has been reported that MAPKs were also involved in the NO-dependent response of tomato fruit against *Botrytis cinerea* [72].

Disease resistance is also improved by a rapid increase in ROS. During the ripening of papaya at 20 °C, disease incidence was significantly reduced in 60 $\mu\text{L L}^{-1}$ NO-fumigated fruits, which might stem from the increase in endogenous H_2O_2 levels associated with the application of NO [24]. NO treatment can increase the resistance of melon fruit to *A. alternata* infection by inhibiting the activity of CAT and promoting the rapid accumulation of H_2O_2 in the early stage of storage [73]. However, the excess accumulation of H_2O_2 induces oxidative damage in fruits and vegetables and promotes their decomposition. NO mediates the decomposition of the excess H_2O_2 during later storage, which maintains ROS levels in equilibrium [24].

In recent years, it has been found that NO can be used to control pests during the storage of postharvest fruits and vegetables. The use of NO fumigation can slow down the insect pests during the storage of fruits and vegetables, such as western flower thrips, pepper, strawberry, tomato, apple, etc. [73,74]. Compared with methyl bromide (a traditional fumigant commonly used higher than 4.4 °C), NO fumigation can be used at 2 °C, which is more suitable for low temperature storage [73]. Moreover, NO is effective for a variety of pests (*Frankliniella occidentalis*, *Nasonovia ribisnigri*, *Epiphyas postvittana*, *Drosophila suzukii*, etc.) at different life stages [73]. However, this fumigation process must be conducted under ultralow oxygen conditions and flushed with nitrogen to dilute NO. However, results on insecticidal efficacy of NO and underlying mechanisms are still scarce, which deserves further investigation.

5. Effects of NO on Browning

Fresh-cut fruits and vegetables easily become brown, while surfaces of some intact fruits are also prone to browning during storage, which significantly affects the sensory quality of fruits and vegetables. In recent years, NO has been reported as one of the browning inhibitors which can inhibit the browning of apple slices [75,76], fresh-cut lettuce slices [77], peach slices [78], and fresh-cut chestnut kernels [79] (Table 4). The main mechanism to inhibit browning might be reducing the activity of browning-related enzymes (1) and affecting the accumulation of phenolic substances (2).

NO donors (solutions of DETANO and SNP) and NO gas all inhibit the cut-surface browning of fresh-cut lettuce [80,81]. However, the effectiveness of treatment with NO or its donors varies depending on the ways and stages of postharvest processing. For example, DETANO and SNP are more effective during the washing process, whereas NO gas is more effective when used in modified atmosphere packaging. The combination of NO treatment and controlled atmosphere (CA) storage significantly inhibited the internal browning of 'Laetitia' plums [82].

Fumigation with NO gas could reduce yellowing or browning of broccoli (*Brassica oleracea*), green bean (*Phaseolus vulgaris*), and bok choy (*Brassica chinensis*), and the postharvest life of all these vegetables was extended [85]. Mechanistically, the postharvest browning of fruits and vegetables is primarily attributed to the oxidation of phenolic compounds by PPO or POD [86]. Phenolic compounds, as well as the activity of PAL and PPO, are likely involved in the development of browning after harvest. NO is generally thought to inhibit the browning of fresh-cut fruits and vegetables by inhibiting the activity of PAL, PPO, and POD [39,75,79]. Treatment with NO can also reduce the total phenol content in fresh-cut apple slices [75] and postharvest table grape rachis [87].

Table 4. The effects of NO on browning.

Fruits	Best Treatment	Effects	References
Chestnut kernel (fresh-cut)	5 μM NO solutions for 10 min	Delayed browning; increased the content of catechin, chlorogenic acid, syringic acid, phloretic acid, and ferulic acid but inhibited that of tannic acid during storage at 20 °C.	[79]
Cut lettuce slices (Green Oak, Green Coral, Baby Cos, and Butter)	500 mg L ⁻¹ DETANO or SNP for 5 min	Inhibited cut-face browning during storage at 0 °C.	[80,81]
Fresh-cut apple slices (Granny Smith)	10 mg L ⁻¹ DETANO solution for 5 min	Delayed development of surface browning during storage at 5 °C; resulted in a lower level of total phenols; inhibited PPO activity, reduced ion leakage, rate of respiration.	[75]
Litchi	2.0 mM SNP for 5 min	Reduced pericarp browning, weight loss, MDA content; increased total phenolics, antioxidant capacity; extended shelf life up to 8 d storage at ambient condition.	[83]
Peeled bamboo shoots	0.5 mM SNP for 1 h	Inhibited activities of PPO, POD, and PAL and maintained high total phenol contents, thus delaying external browning during storage at 10 °C for 10 d.	[39]
Table grape (Munage)	300 μL L ⁻¹ NO gas fumigation for 2 h	Reduced pericarp browning and disease incidence for 60 d at 0 °C.	[49]
Cornelian cherry (Cornus mas)	0.5 mM SNP for 20 min	Reduced browning index.	[84]

6. The Application Methods of NO

NO gas itself can be directly used for fumigation of fruits and vegetables (sweet pepper [21], papaya [24], water bamboo [28], banana [43,44], and muskmelon [67]) to extend shelf-life. However, NO gas has a short half-life and can be converted into a toxic gas nitrogen dioxide (NO₂) in the presence of oxygen [85]. The NO₂ can reduce the quality of fruits and vegetables, causing patches of dead leaf tissue on lettuce, gray or brownish stains on broccoli, dark spots on apples and pears, and discolorations of orange and peach [74]. Therefore, when using NO gas, it should be placed in airtight containers to reduce contact with oxygen [28,69,88]. At the end of fumigation, it is better to dilute NO with N₂ flushing to avoid damage to fruits and vegetables by NO₂ [88]. However, the N₂ generation equipment will significantly increase the production cost [88]. Due to these defects of NO gas, it is mainly used for low concentration fumigation of fruits and vegetables in the laboratory and has not been widely used in production.

NO donors (such as DETANO, GSNO, and SNP) are often dissolved as liquids for soaking postharvest fruits and vegetables. These donors were stored under different conditions, and the buffer solutions used to dissolve them were also different [80]. DETANO should be stored in an airtight container at -18 °C, GSNO stored at -18 °C with a sealed bottle brown, and SNP should be placed at 20 °C in a dark place [80]. Moreover, DETANO can quantitatively release NO in the presence of citric acid. Therefore, it is often dissolved in acidic buffer solution (pH 6.5) for use [80,89,90]. GSNO and SNP can be dissolved in neutral distilled water. Furthermore, it was found that co-treatment of postharvest fruits and vegetables with these NO donors and other preservatives (such as 1-MCP) was more effective than treatment alone (Table 1). As for further research on the application methods of NO, the discovery of novel low-cost, safe, and reliable NO donors and the co-treatment technology of NO and other preservatives are the focus of research.

7. Crosstalk between NO and Phytohormones in Fruits and Vegetables

Aside from acting as an independent small signaling molecule, NO can also crosstalk with other signaling molecules, such as MT, ETH, JA, SA, and abscisic acid (ABA) to regulate biological processes and stress responses.

MT, which is mainly synthesized in the chloroplast and mitochondria, is widely involved in the growth and stress responses of plants as an antioxidant or structural analog of indole-3-acetic acid [91]. NO and MT levels have often been observed to be correlated. On one hand, the accumulation of MT during the ripening of fruits may act as a free radical scavenger to remove free nitrogen species [7,92]. Additional studies have shown that MT reacts with NO through nitrosation to form NOMela, which further mediates the storage, release, and long-distance transport NO [16]. On the other hand, MT also acts on upstream processes of NO and thus increases the level of endogenous NO by inhibiting the activity of S-nitrosoglutathione reductase (GSNOR), up-regulating NR expression, or triggering arginine-dependent endogenous NO accumulation [7,93]. NO can also increase the MT level by enhancing the activity of enzymes involved in the MT synthesis pathway, such as tryptophan decarboxylase, tryptamine 5-hydroxylase, and N-acetyltransferase [5].

JA is an important endogenous regulator of stress responses, growth, and development in plants [94,95]. Exogenous NO donor treatment can induce the expression of JA synthesis-related genes (*LOX2*, *AOS*, and *OPR3*) in plants, but this does not result in an increase in the concentration of JA [96]. However, JA can induce the accumulation of NO in plants [97]. Both JA and NO are related to stress resistance in fruits and vegetables. For postharvest cucumber, treatment with MeJA and NO can alleviate CI by inhibiting H₂O₂ generation and activate chilling tolerance signaling pathway. JA acts upstream of and depends on NO in reducing the chilling injury [98,99].

Both SA and NO can induce in plant cells during the response to various types of stress, and their interactions have diverse effects. Exogenous NO treatment can induce the accumulation of SA in fruit, while exogenous SA can increase the content of endogenous NO by stimulating oxidative NO synthesis [63,100]. NPR1 is sequestered in the cytoplasm as an oligomer through intermolecular disulfide bonds. After the invasion of the pathogen into the plant, the content of SA and SNO may increase, and SA will induce the conversion of NPR1 from the oligomer into monomer, thereby promoting the translocation of the monomer NPR1 to the nucleus to activate the expression of SA-mediated genes (e.g., *pathogenesis-related proteins family 1*, *PR-1*) [101]. However, GSNO can promote the oligomerization of NPR1 and maintain protein homeostasis when NPR1 is induced by SA [102]. Treatment with SA or NO can increase the content of flavonoids in fruits and vegetables, which improves antioxidant properties, reduces ETH production, and thus inhibits the ripening of fruit [69,103]. In addition, SA accumulation triggered by NO can suppress the production of superoxide free radicals and other ROS, thereby aiding the maintenance of cell membrane integrity.

8. Future Perspectives

Being a natural signaling molecule that regulates many physiological processes in plants and animals, NO has been proved to have the effect of delaying the ripening and maintaining the quality of fruits and vegetables. Compared with some chemical preservatives and pesticides, NO has less safety concerns for the use in postharvest fruits and vegetables. However, the application of NO in agricultural production (including postharvest application on horticultural produces) is still largely at the laboratory level. This is partially caused by its instability in plant tissues and the natural environment. To improve the application efficacy, additional efforts should be made to explore practical NO products and improve application technology. Otherwise, NO is a signal molecule that is unstable in plant tissues. How long does the physiological act of NO last in fruits and vegetables in postharvest? Can repeated treatments strengthen or prolong the physiological effects of NO? Moreover, the practical NO carrier/controlled release system has not been developed well until now. As for the practical carrier, a NO donor with stable and controlled release rate is the key to solve the problem. The release rate should meet the requirements of different postharvest produce under practical use conditions. As NO-releasing chitosan nanoparticles that protected maize plants from salt stress have been successfully synthe-

sized [104], it is a promising strategy to combine NO and nanotechnology for developing new carriers in current agricultural production [105].

As for further study about the mechanism of NO, NO synthesis enzymes in plants have been a major focus of research. NO synthesis in the electron transport chain can greatly affect the energy supply and color of fruits and vegetables during storage. However, the metabolic mechanisms by which NO achieves its effects via the electron transport chain in the mitochondria and chloroplasts remain unclear. The level of endogenous NO in fruits and vegetables adjust spontaneously by biological engineering technology, which may provide a feasible method for breeding new varieties. In addition, NO treatment has a positive effect on fruit and vegetable storage by regulating the activity of related enzymes, but the regulatory mechanism and modification methods (tyrosine nitration, S-nitrosylation, and metal nitrosylation) underlying this positive effect remain unclear. NO crosstalk with a variety of signal molecules is involved in the regulation of various biological processes. Consequently, the relationships of NO with other signal molecules in this network are highly complex. Combined treatments often achieve better results than single treatments. The effectiveness of NO crosstalk with other plant hormones depends on specific species, cell types, tissues or organs, as well as the NO concentrations applied.

9. Conclusions

NO plays an important role in quality changes of postharvest fruits and vegetables by delaying ripening or senescence, alleviating chilling injury, controlling postharvest diseases, and inhibiting browning. These effects are related to the ability of NO to inhibit ETH synthesis, increase antioxidant enzyme activity, activate antimicrobial enzymes, increase the accumulation of antimicrobial substances, and maintain a high energy level and membrane integrity. However, it is still unknown how NO affects these enzymes' activities and the involved modifications. In addition, NO synthase and its action mechanism in plants needs to be further studied. Importantly, the effectiveness of NO treatment on preserving the quality depends on the species of fruits and vegetables, the concentration, and form (e.g., liquid or gaseous) of NO applied. Postharvest researchers should study the differences in NO applications for different types of fruits and vegetables separately, for example, climacteric and non-climacteric types. NO application methods and product tailored for different postharvest environment also need further development.

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