Nitric Oxide as an Inhibitor of Postharvest Senescence

Subjects: Horticulture

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Horticultural products display fast senescence after harvest at ambient temperatures, resulting in decreased quality and shorter shelf life. As a gaseous signal molecule, nitric oxide (NO) has an important physiological effect on plants. Specifically, in the area of NO and its regulation of postharvest senescence, tremendous progress has been made. The following summarizes NO synthesis; the effect of NO in alleviating postharvest senescence; the mechanism of NO-alleviated senescence; and its interactions with other signaling molecules, such as ethylene (ETH), abscisic acid (ABA), melatonin (MT), hydrogen sulfide (H_2S), hydrogen gas (H_2), hydrogen peroxide (H_2O_2), and calcium ions (Ca^{2+}). The aim of this text is to provide theoretical references for the application of NO in postharvest senescence in horticultural products.

nitric oxide postharvest senescence molecular interaction

1. Introduction

Nitric oxide (NO) is a redox-active gaseous compound that regulates diverse physiological processes in plants. Numerous studies have demonstrated a regulatory role of NO in seed germination [1], adventitious root formation [2], fruit ripening [3], abiotic stress [4][5][6][7], and biotic stress [8][9].

Horticultural products undergo rapid senescence after harvest at ambient temperatures. Postharvest senescence is an important biological process for fresh horticultural products, accompanied by a series of materials and energy metabolism, including cell wall softening [10], chlorophyll degradation [11], new pigment (carotenoid, lutein, and flavonoid) synthesis [10][11][12], volatile accumulation [13], and the change in soluble substance content [12][13][14]. Senescent products are susceptible to fungal pathogens, which lead to decay and a decline in quality. According to statistics from 2017, the average postharvest loss rate is about 15% to 20% due to postharvest senescence, resulting in a large amount of postharvest loss of fresh horticultural products, which seriously affects the commodity value and economic income.

Currently, the role of NO in postharvest senescence has been widely reported in cut flowers [15][16], vegetables [17], and fruits [18][19]. Studies have shown that NO plays an essential role in preventing postharvest senescence.

2. NO Delays Postharvest Senescence

Horticultural plants are prone to rapid senescence after postharvest storage at ambient temperature. Postharvest senescence is affected by several factors, such as temperature [20], light [21][22], and some plant growth regulators [23][24][25]. Multiple studies have shown that NO is an effective way to delay postharvest senescence.

2.1. Exogenous NO Delays Postharvest Senescence

The effect of NO on alleviation of postharvest senescence can be demonstrated by the exogenous application of NO on postharvest plants. In exogenous NO treatment, three methods are available: fumigation, immersion, and spraying. Fumigation with direct NO gas delayed the senescence in postharvest mangoes and peaches [26][27]. The immersion of NO gas solution and NO donor sodium nitroprusside (SNP) or *S*-nitrosoglutathione (GSNO) solution also delays the postharvest senescence in some fruits by inhibiting ethylene production and reducing respiration rates [28][29]. Additionally, spraying NO donor GSNO solution is commonly used to extend the postharvest life of blueberries by improving their concentrations of ascorbic acid and glutathione [30]. The effects of exogenous NO on delaying postharvest senescence in horticultural products are listed in **Table 1**.

Table 1. Effects of NO on postharvest senescence in horticultural products.

Species	Treatment	NO-Mediated Effect	References
Pear	100 μM L^{-1} SNP	Decreased the transcript levels of cell wall- and ethylene synthetase-related genes; reduced respiration rate and ethylene production	[31]
Apple	100 μM L^{-1} GSNO	Activated nucleocytoplasmic MdERF5 and suppressed ethylene biosynthesis	[18]
Strawberry	5 μM L^{-1} SNP	Inhibited ethylene production, respiration rate, and activity of ACC synthase; reduced the content of ACC	[32]
Peach	10 μL L^{-1} NO	Maintained higher sucrose content but decreased glucose and fructose to lower levels during late storage	[27]
Carnation	0.1 mM L^{-1} SNP	Maintained water metabolism and antioxidative enzyme activity and mass-eliminated ROS as well as cell membrane stability	[33]
Rose	200 μM L^{-1} SNP	Decreased ethylene output by inhibiting ACO activity in cut rose flowers	[16]
Lily	100 μM L^{-1} SNAP	Increased Ca^{2+}/CaM contents, enhanced Ca^{2+}-ATPase activity, and up-regulated gene expression of *CaM*, *CBL1*, and *CBL3*	[15]
Consolida ajacis L.	40 μM L^{-1} SNP	Alleviated deteriorative postharvest changes by modulating physiological and biochemical mechanisms underlying senescence	[34]

Species	Treatment	NO-Mediated Effect	References
Calendula officinalis L.	100 μM L^{-1} SNP	Improved flower longevity by delaying neck bending, inhibited bacterial growth, and increased activities of antioxidant enzymes	[35]
Tomato	1 mM L^{-1} SNP	Retarded pericarp reddening of tomato fruit, suppressed ethylene production, and influenced quality parameters during storage	[28]
Water bamboo shoots	30 μL L^{-1} NO	Delayed softness and weight loss and enhanced ATP levels by activating the expression and activity of SDH, MDH, and CCO	[17]
Lettuce	100 and 200 ppm NO	Inhibited the accumulation of H_2O_2, delayed senescence, and prolonged shelf life	[36]

The effect of NO on postharvest senescence can also be revealed by endogenous NO production during postharvest senescence processes delayed by environmental factors and some chemical substances. For example, UV-B treatment can maintain decreased fruit firmness and delay postharvest senescence in mangoes by enhancing endogenous NO levels [37]. Endogenous NO production and NOS activity were induced by 1-methylcyclopropene (1-MCP) in the senescence process in cut roses [16]. Likewise, melatonin (MT) led to an increase in NO content through an increase in NOS activity and upregulation of *PcNOS* transcript levels, which subsequently delayed senescence in peaches [31]. However, in cold-stored peaches, abscisic acid (ABA) can induce endogenous NO synthesis via the NR pathway [38]. Similarly, NO production was also triggered by hydrogen gas (H_2) by enhancing NR activity, which mitigated postharvest senescence in cut rose flowers [39].

3. The Mechanism of NO-Regulated Postharvest Senescence

NO delays postharvest senescence by regulating various metabolism pathways, including ethylene biosynthesis, respiratory metabolism, cell wall metabolism, reactive oxygen species (ROS) metabolism, and energy metabolism (**Figure 1**). Moreover, a set of *senescence-associated genes* (*SAGs*) that drive postharvest senescence are regulated by NO during postharvest senescence processes.

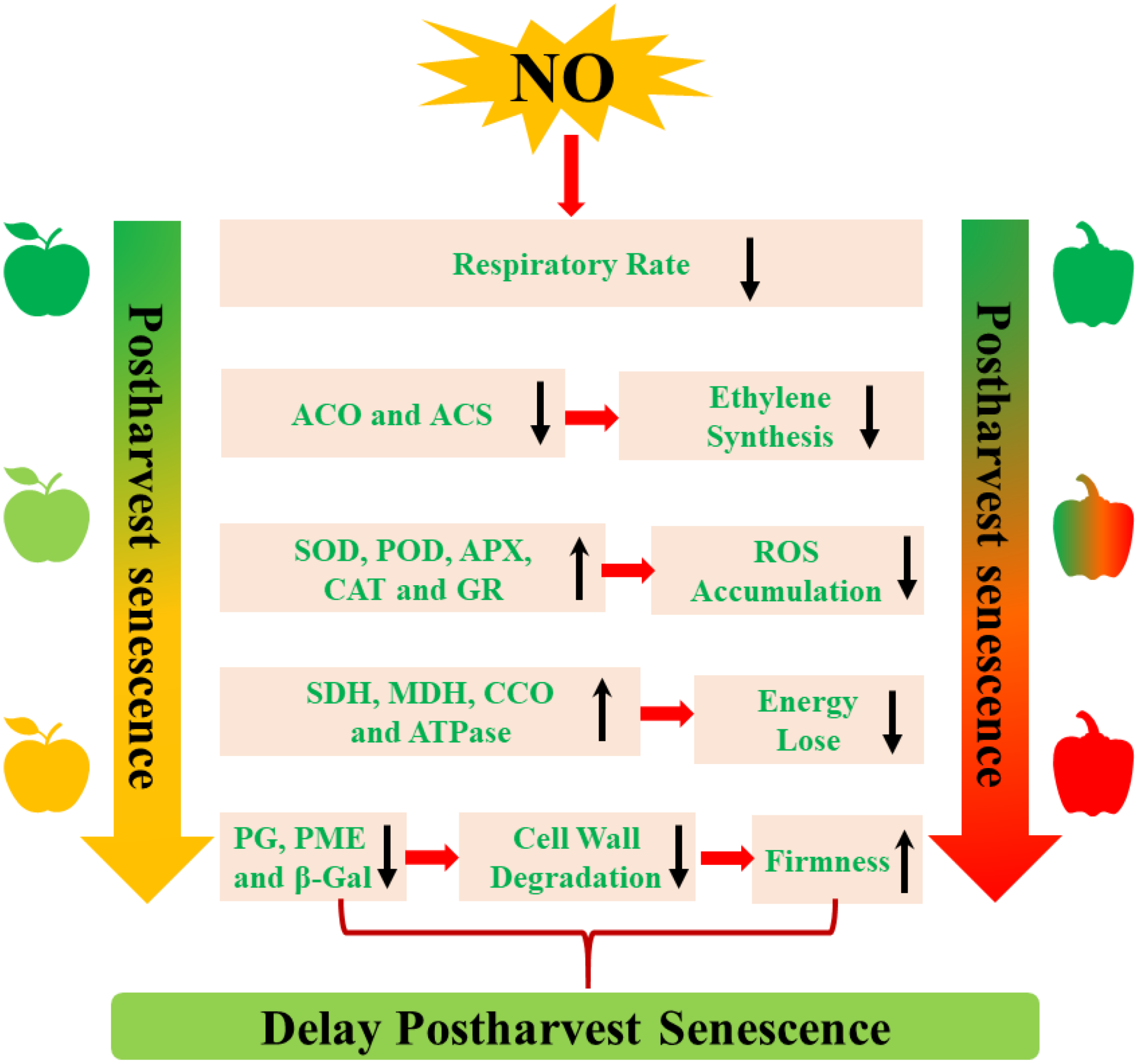

Figure 1. NO-regulated metabolism pathways during postharvest senescence. ACO, 1-aminocyclopropane-1-carboxylic acid oxidase; ACS, 1-aminocyclopropane-1-carboxylic acid synthase; APX, ascorbate peroxidase; CAT, catalase; CCO, cytochrome oxidase; ETH, Ethylene; GR, glutathione reductase; MDH, malic acid dehydrogenase; NO, nitric oxide; PG, polygalacturonase; PME, pectinmethylesterase; POD, peroxidase; ROS, reactive oxygen species; SDH, succinic dehydrogenase; SOD, superoxide dismutase; *β*-Gal, *β*-galactosidase. Upward arrow indicates up-regulation; Downward arrow indicates down-regulation.

3.1. The Inhibition of Ethylene (ETH) Biosynthesis

It is well known that an increase in endogenous ETH is a sign of senescence. Thus, inhibiting endogenous ethylene production is considered a useful method to delay postharvest senescence. Exogenous NO can inhibit ETH production, which delays postharvest senescence of horticultural products, including mangoes [26][27], peaches [27], and cut rose flowers [16]. In addition, the inhibition of ETH biosynthesis-related enzymes 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase (ACO) and ACC synthase (ACS) activity and their expression levels is associated with NO-induced decreases in the endogen ETH during the postharvest senescence process

[26][28]. Therefore, the positive effect of NO on postharvest senescence is largely dependent on the inhibition of the ETH biosynthesis pathway.

3.2. The Decrease of Respiratory Metabolism

Climacteric transition is generally regarded as an important signal of the initiation of senescence in climacteric plants, which affects the storage life of postharvest plants. Reducing the respiratory rate can effectively delay postharvest senescence and prolong the shelf life of horticultural crops. A previous study showed that NO treatment restrained the increase in the respiration rate and extended the postharvest life of water bamboo shoots [17]. The application of 10 μL of NO gas fumigation significantly inhibited the respiratory rate of climacteric plums and peaches, thereby extending their shelf life [27][40]. Rather than suppressing the respiratory rate of climacteric fruits, NO was also shown to depress the respiratory rate of non-climacteric fruit. For example, the respiratory rate was significantly inhibited by NO treatment throughout the entire storage period of winter jujube fruit [41].

3.3. The Activation of Cell Wall Metabolism

Generally, senescent fruits exhibit the symptom of softening as a result of cell wall degradation. Several degrading enzymes, including polygalacturonase (PG) and pectin methylesterase (PME), are involved in the degradation of the cell wall [42]. Changes in cell wall metabolism-related enzyme activity are responsible for the decrease in firmness affected by a set of abiotic factors. The application of exogenous NO maintains the decrease in firmness and extends the postharvest life of blueberries [30]. Similarly, cornelian cherries treated with 500 μM of NO donor SNP exhibited higher firmness, possibly resulting from the lower activity of PE and PME, which degrade cell walls [43]. A decrease in the NO-induced activities of PG, PME, and *β*-galactosidase (*β*-Gal) delayed postharvest winter jujube fruit softening as well [44]. At the transcript level, NO treatment suppressed the softening of postharvest tomatoes by downregulating the gene expression levels of *LePG*, *LePhy1*, and *LePME* [28]. In summary, NO can inhibit cell wall metabolism-related enzyme activities, which maintains the decrease in firmness of horticultural products during the NO-delayed postharvest senescence process.

3.4. The Regulation of ROS Metabolism

Postharvest senescence is often accompanied by increased ROS, followed by the induction of some *SAGs*. The increase in ROS level occurs in parallel with increases in lipid peroxidation in senescent cells. In addition to endogenous ROS, ROS-related antioxidant enzymes are also related to postharvest senescence. Extensive research has shown that NO can delay postharvest senescence by decreasing ROS levels and enhancing antioxidant activities. Exogenous NO fumigation reduces ROS, $O_2^{\bullet -}$, and hydrogen peroxide (H_2O_2) contents but increases superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR), and catalase (CAT) gene expression and enzymes activity, which prolongs the shelf life of table grape and appears to be strongly linked to the lipid peroxidation of membranes [45]. Likewise, NO enhances ROS scavenging capacity through the increased activity of SOD, CAT, APX, and GR, which are capable of diminishing the accumulation of $O_2^{\bullet -}$ and H_2O_2, thereby delaying the senescence of winter jujube [41]. Therefore, NO can decrease the accumulation of ROS and enhance the antioxidant system, which leads to delayed senescence in postharvest horticultural crops.

3.5. The Promotion of Energy Metabolism

The lack of energy caused by the impaired respiratory chain and reduced ATP synthesis leads to cellular breakdown and dysfunction during the postharvest senescence stage [46]. The maintenance of cellular ATP and energy levels can thus maintain the normal physiological activities of the tissues, thereby postponing postharvest senescence and prolonging the shelf life of horticultural products. Several studies have established that NO-delayed postharvest senescence is ascribed to the optimization of energy metabolism. NO treatment, for example, delayed the softness and weight loss of water bamboo by maintaining the integrity of the mitochondrial ultrastructure and enhancing ATP levels [17]. Furthermore, NO donor SNP treatment enhanced ATP synthase activity, ATP synthase CF1 alpha subunit (AtpA) content, and *AtpA* expression levels in the postharvest freshness of cut lilies [47].

3.6. The Induction of SAGs

Various external and internal signals are likely to activate a set of *SAGs* that drive postharvest senescence. During postharvest senescence, *SAGs* can be induced by NO to delay senescence. These NO-induced *SAGs* include various transcription factors (*ERFs*) and some structural genes encoding enzymes related to cell wall metabolism, ethylene biosynthesis, and antioxidants. The *SAGs* regulated by NO during the postharvest senescence process are listed in **Table 2**.

Table 2. NO-regulated *SAGs* during postharvest senescence process.

Horticultural Products	Species	*SAGs*	References
Fruits	Pear	*PcPG*, *PcCel*, *PcACO1*, *PcACO2*, *PcACS1*, *PcNOS*, *PcNR1*, and *PcNR2*	[31]
	Apple	*MdACS1*, *MdACO1*, *MdERF5*, and *MdPP2C57*	[18]
	Mango	*MiACO*, *MiACS*, *MiETR1*, *MiERS1*, *MiEIN2*, and *MiERF*	[48]
	Table grape	*VvSOD*, *VvCAT*, *VvPOD2*, and *VvGR*	[45]
	Kiwifruit	*PG*, *PL*, *β-Gal*, *PE*, *ACO*, *ERS1*, *ETR2*, *ERF016*, *ERF7*, *ERF010*, *ERF062*, *ERF110*, *ERF037*, *ERF008*, *ERF113*, *ERF12*, *ERF095*, *CNGC1*, *CPK1*, *CIPK2*, *CML31*, *CML48*, and *ZIFL1*	[49]
	Wax apple	*PAL*, *POD*, *GLU*, *C3H*, *CA*, *F5H*, *4CL*, *CCoAOMT*, and *C4H*	[50]
	Peach	*PpaSOD*, *PpaCAT*, *PpaPOD*, *PpaPOD-1*, *PpaAPX*, and *PpaPAL*	[51]

Horticultural Products	Species	*SAGs*	References
Cut flowers	Gladiolus	*GgCyP1* and *GgDAD1*	[52]
	Lily	*CaM*, *CBL1, CBL3*, and *LlatpA*	[15][47]
Vegetables	Tomato	*LeACS2*, *LeACS4*, *LeACO1*, *LePME*, *LePG*, *LePhy1*, and *LeGAPDH*	[28]
	Water bamboo shoots	*ZlH$^+$-ATPase*, *ZlNa$^+$-K$^+$-ATPase*, *ZlCa^{2+}-ATPase*, *ZlMDH*, *ZlSDH*, and *ZlCCO*	[17]

4CL, 4-coumarate−CoA ligase; ACO, 1-aminocyclopropane-1-carboxylic acid oxidase; ACS, 1-aminocyclopropane-1-carboxylic acid synthase; APX, ascorbate peroxidase; AtpA, ATP synthase CF1 alpha subunit; C3H, *p*-coumarate 3-hydroxylase; C4H, *trans*-cinnamate 4-monooxygenase; CA, coniferyl-aldehyde dehydrogenase; CaM, calmodulin; CAT, catalase; CBL, calcineurin B-like protein; CCO, cytochrome oxidase; CCoAOMT, caffeoyl-CoA O-methyltransferase; Cel, cellulase; CIPK, calcineurin B-like protein-interacting protein kinase; CML, calmodulin-like protein; CNGC, cyclic nucleotide-gated channel; CPK; calcium-dependent protein kinase; CyP, cysteine protease; DAD, defender against death; EIN, ethylene insensitive; ERF, ethylene response factor; ERS, ethylene response sensor; ERT, ethylene receptor; F5H, ferulate-5-hydroxylase; GAPDH, glyceraldehyde 3-phosphate dehydrogenase; GLU, *β*-glucosidase; GR, glutathione reductase; MDH, malic acid dehydrogenase; NOS, nitric oxide synthase; NR, nitrate reductase; PAL, phenylalanine ammonia-lyase; PE, pectin esterase; PG, polygalacturonase; Phy, phytoene synthase; PL, pectate lyase; PME, pectin methylesterase; POD, peroxidase; SAGs, senescence associated genes; SDH, succinic dehydrogenase; SOD, superoxide dismutase; ZIFL, calmodulin-binding heat-shock protein; *β*-Gal, *β*-galactosidase.

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