



Nitric Oxide (NO) and Hydrogen Sulfide (H₂S): New Potential Biotechnological Tools for Postharvest Storage of Horticultural Crops

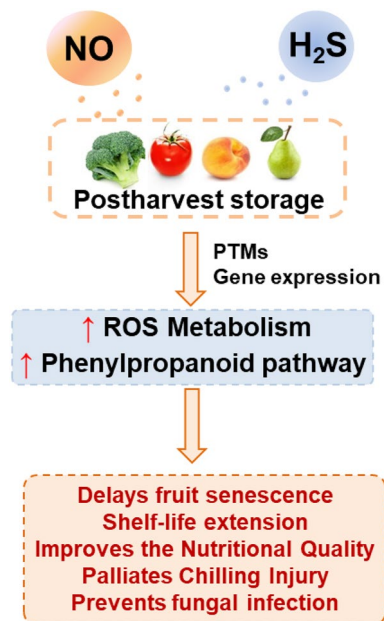
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Abstract

Storage and maintenance of horticultural products in optimal conditions for a reasonable period, once they have been harvested is a technological challenge. Diverse methods are generally used, i.e., low temperature but, in many cases, it may provoke undesirable collateral effects such as softening or promoting pathogens infections, thus causing their deterioration. Nitric oxide (NO) and hydrogen sulfide (H₂S) are compounds generated endogenously by plants with signaling properties that mediate fruit development and ripening. Additionally, when these molecules are applied exogenously, they can provide benefits such as maintaining the quality of horticultural products and even prolonging their shelf-life once they are stored. This review provides a broad perspective of NO and H₂S metabolism in plant cells and, in addition, different plant models are described of how the exogenous application of either NO or H₂S to horticultural products preserves nutritional quality during postharvest storage.

Graphical Abstract



Keywords Climacteric · Non-climacteric · Fruit ripening · Reactive nitrogen species · Vegetable · Transcription factors

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Introduction

In the agricultural sector, from the time the seed sapling is planted until the harvest of the corresponding products, numerous factors can affect the proper development and productivity of crops. The whole process requires great effort and planning to safeguard the quality of the vegetables and fruits against different types of environmental stress (extreme temperature, drought, flooding, pathogens, etc.). Furthermore, after their harvest, preserving the quality of vegetables and fruits is also one of the key stages that connect the agricultural productive sector with the industrial one considering that storage and distribution may be achieved either locally, nationally, or internationally.

From the point of view of consumers, the quality of fruits and vegetables includes external features such as color, firmness, size, and shape but also other sensorial properties including aroma and taste (flavor). All these parameters influence the consumers' decision to purchase specific products. Therefore, all the participants involved in each step should care about how specific horticultural products reach the consumers. Different agents can cause the deterioration of fruits and vegetables such as softening, water loss, or microbial decay triggered by bacteria, fungi, viruses, or yeasts. However, many of these effects are due to an uncontrolled overproduction of reactive oxygen species (ROS) that can cause oxidative stress (Lum et al. 2016; Decros et al. 2019). All these factors will influence the storage conditions. For these reasons, postharvest technology procedures acquire great relevance since they have the goal of providing optimal storage conditions to preserve the properties of horticultural products (Ziv and Fallik 2021). Thus, the products can reach the consumer in optimal nutritional conditions thus avoiding the economic losses that may occur.

At present, there are several strategies for storing fruit and vegetables mostly consisting of keeping them under controlled atmospheres. Thus, the normal air atmosphere is replaced by an atmosphere poor in oxygen (O_2) but rich in carbon dioxide (CO_2). For example, when pears and apples are under 1–3% O_2 and 1–3% CO_2 , their storage is usually extended for three months (Wang et al. 2021). This procedure is usually combined with low temperatures (Majidi et al. 2014; Fang and Wakisaka 2021; Dong et al. 2022). However, the storage conditions must be optimized for each type of horticultural product, and in the case of fruits, another consideration to keep in mind is whether the fruit is climacteric because, in such a case, the levels of ethylene must be reduced (Cocetta and Natalini 2022). Heat treatment of fruits and vegetables has also been used to maintain the quality attributes during postharvest

storage (Yang et al. 2021; Yi et al. 2021; Dai et al. 2021). Currently, other complementary options are being studied consisting of covering horticultural products with edible coatings that protect them from adverse external factors and that allow their shelf-life to be extended (Tavassoli-Kafrani et al. 2020; Rangaraj et al. 2021; Nian et al. 2022; Yadav et al. 2022). There are other strategies to preserve the quality fruit and vegetable during postharvest which include physical treatments (Usall et al. 2016; Palumbo et al. 2022) such as microwave (Martínez-Hernández et al. 2016), pulsed electric-field (López-Gámez et al. 2021), high hydrostatic pressure treatment (Ramos-Parra et al. 2019), and dipping and vacuum impregnation, for example, with calcium salts, pectin methylesterase, or citric acid (Yan et al. 2021).

Nitric oxide (NO) and hydrogen sulfide (H_2S) are two gasotransmitters that are endogenously generated in plant cells exerting multiple functions from seed germination, root formation, growth and development, leaf senescence, flowering, and fruit ripening (Zhang et al., 2014; Ziogas et al., 2018; Corpas et al. 2019; Mishra et al., 2021; Li et al. 2022; He et al. 2023). However, experimental evidence has shown that when NO and H_2S , either individually or in combination, are exogenously applied, they can alleviate or preserve the quality of the horticultural products against negative damage to plants during different types of environmental stress, both biotic and abiotic (Siddiqui et al. 2023; Gupta and Seth 2023; Prajapati et al. 2023). This review aims to provide an outline of NO and H_2S metabolism in higher plants, the main available donors of these molecules, and their use in horticultural products (fruits and vegetables) as an alternative to extending their shelf-life during postharvest storage.

Overview of Endogenous Metabolism of NO and H_2S in Higher Plants

The first reports on the emissions and presence of NO in higher plants in the late 1970s and mid-1980s (Klepper 1979, 1987; Dean and Harper 1986) were received with some skepticism among plant researchers because this molecule was considered toxic as part of atmospheric pollution and the greenhouse effect. However, the significance of this molecule acquired more and more relevance due to its regulatory functions in numerous physiological processes, including seed germination, root formation and development, growth, stomatal closure, senescence, flowering, and fruit ripening, but also in the mechanisms of response against biotic and abiotic stresses (Leshem et al. 1998; Leshem and Pinchasov 2000; Corpas et al. 2011; Xuan et al., 2012; Kolbert et al. 2019).

Nitric oxide has a family of derived molecules designated as reactive nitrogen species (RNS) such as peroxyxynitrite (ONOO^-), *S*-nitrosothiols (SNOs) like *S*-nitrosoglutathione (GSNO), nitrogen dioxide (NO_2), nitroxyl (HNO), nitro- γ -tocopherol, and so on (Kolbert et al. 2019; Arasimowicz-Jelonek et al. 2023). Although the endogenous source responsible for the enzymatic generation of NO is still under debate in plants, there are currently two recognized possible sources of NO , nitrate reductase (NR) and an *L*-arginine-dependent NO synthase-like activity (Mohn et al. 2019; Corpas et al. 2022a). Additionally, another key enzyme involved in NO metabolism is *S*-nitrosoglutathione reductase (GSNOR) which catalyzes the NADH-dependent reduction of GSNO to GSSG and NH_3 (Sakamoto et al. 2002; Letierrier et al. 2011). Thus, this enzyme can modulate the trans-nitrosation equilibrium between GSNO and *S*-nitrosated proteins and consequently participates in the cellular homeostasis of RNS (Lee et al. 2008; García et al. 2018; Treffon et al. 2021) as well as hormone homeostasis (Romera et al. 2023; Zucarelli et al. 2023). However, among the mechanisms that allow the RNS to exert their signaling function are those that imply post-translational modifications (PTMs) of proteins, mainly *S*-nitrosation, tyrosine nitration, and metal nitrosylation (Asgher et al. 2017; Gupta et al. 2020), as well as the regulation of gene expression throughout the transcription factors (TFs), or probably by epigenetic events such as DNA methylation or histone modification.

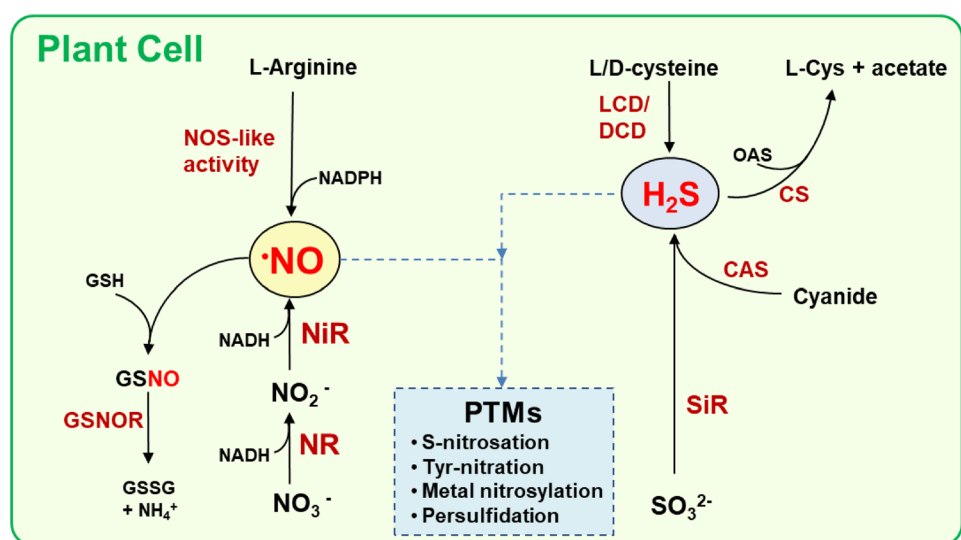
In the mid-90s, it was described that animal cells were available to generate hydrogen sulfide (H_2S), a molecule considered toxic for living organisms, which later showed to have signaling properties in the neuronal system (Abe and Kimura 1996). Afterward, it was observed that plant cells were also capable of generating H_2S as part of the sulfate assimilation pathway and in the cysteine metabolism (Fuentes-Lara et al. 2019; González-Gordo et al. 2020).

Currently, several enzymes with the capacity to generate H_2S located in the different subcellular compartments have been identified. These include the chloroplastic sulfite reductase (SiR), the cytosolic *L*-cysteine desulfhydrase (LCD) and cysteine synthase (OASA 1), and the mitochondrial *D*-cysteine desulfhydrase (DDC) and cyanoalanine synthase (CAS) (Asada 1967; Álvarez et al. 2012; Hu et al. 2021a, b; Muñoz-Vargas et al. 2023a, b).

Like NO , H_2S can also modulate protein function through a PTM called persulfidation in which a thiol ($-\text{SH}$) group of cysteine residues interacts with H_2S and is then converted into the corresponding persulfide ($-\text{SSH}$) (Aroca et al. 2015; Corpas et al. 2021; Vignane and Filipovic 2023). Figure 1 provides a simple working model showing the enzymatic components involved in the generation of NO and H_2S in plant cells.

Remarkably, the cysteine residues of some specific proteins could be targets of both molecules and, in fact, NO and H_2S compete in the modulation of these target proteins and the final effect is the result of the balance of their relative abundance around the target protein and their subcellular location (Corpas et al. 2022b). Some of the most notable examples of this regulation are some antioxidant enzymes that regulate the ROS metabolism such as catalase (Palma et al. 2020) and ascorbate peroxidase (APX) (Begara-Morales et al. 2014a, b; Aroca et al. 2015). Likewise, other enzymes such as the NADPH oxidase also designated as respiratory burst oxidase homologs (RBOHs) directly involved in the generation of superoxide radicals ($\text{O}_2^{\cdot-}$), as well as enzymes involved in $\text{NO}/\text{H}_2\text{S}$ metabolism such as *S*-nitrosoglutathione reductase (GSNOR) or the H_2S -generating *L*-cysteine desulfhydrase are also targets of *S*-nitrosation and persulfidation (Yun et al. 2011; Guerra et al. 2016; Shen et al. 2020), as well as tyrosine nitration (Muñoz-Vargas et al. 2023b). All these data indicate the close relationship

Fig. 1 Main enzymatic components involved in the generation of NO and H_2S generation in plant cells. CAS, cyanoalanine synthase. CS, cysteine synthase. DCD, *D*-cysteine desulfhydrase. GSH, reduced glutathione. GSSG, glutathione disulfide. GSNO, *S*-nitrosoglutathione. GSNOR, GSNO reductase. LCD, *L*-cysteine desulfhydrase. PTMs, post-translational modifications. NiR, nitrite reductase. NOS-like, *L*-arginine-dependent NO synthase-like activity. NR, nitrate reductase. OAS, *O*-acetylserine. SiR, sulfite reductase



between the metabolism of $\cdot\text{NO}$, H_2S , and ROS, since key enzymes involved in the metabolism of all these molecules are regulated among themselves, which creates a complex signaling network that affects numerous biological processes from the germination, development, senescence, and to fruit ripening.

Biochemistry of $\cdot\text{NO}$ and H_2S

Besides the protein PTMs mediated by $\cdot\text{NO}$ and H_2S , another lesser-known aspect is the biochemical reactions resulting from the own chemistry and interactions between both molecules and ROS. Thus, the protonated product of the one-electron reduction of $\cdot\text{NO}$ generates nitroxyl (HNO), also designated as azanone, which has specific biological effects in animal cells (Fukuto and Carrington 2011; Fukuto et al. 2013). This issue has been unexplored in plants until very recently, where it has been involved in the cellular redox balance under senescence and hypoxia conditions (Arasimowicz-Jelonek et al. 2023).

Likewise, peroxynitrite (ONOO^-) is the product of the chemical interaction between $\cdot\text{NO}$ and $\text{O}_2^{\cdot-}$. This reaction is very fast, with a second-order rate constant (k) of approximately $4\text{--}6 \times 10^9 \text{ M}^{-1} \text{ s}^{-1}$ (Goldstein and Czapski 1995) which is even greater than that of many enzymatic reactions. The relevance of this molecule is its great reactivity with macromolecules including proteins, fatty acids, and nucleic acids exerting its immediate oxidizing/nitrating action, thus promoting the formation of nitrated proteins (Bartesaghi and Radi 2018; Corpas et al. 2021; Piacenza et al. 2022), nitrated fatty acids (Mata-Pérez et al. 2016), and nitroguanine in nucleic acids (Niles et al. 2006). Nitric oxide can also interact with reduced glutathione (GSH) to generate

S-nitrosoglutathione (GSNO), a cellular $\cdot\text{NO}$ reservoir with the capacity to mediate the process of trans-nitrosation (Corpas et al. 2013; Broniowska et al. 2013). Figure 2 displays some of the reactions where $\cdot\text{NO}$ is involved.

H_2S is a weak acid and can be dissociated into hydrosulfide (HS^-) and sulfide (S_2^{2-}) anions in an aqueous solution. At physiological conditions, approximately 20% of H_2S exists in the not dissociated form, and the rest is dissociated into HS^- and H^+ , the amount of sulfide anion (S_2^{2-}) being very low at physiological pH (Fig. 2). H_2S can mediate the generation of persulfides (RSSH) through the interaction with either (i) oxidized thiol derivatives such as disulfides (RSSR'), sulfenic acid (RSOH) or (ii) oxidized sulfur derivatives such as polysulfides (HS_nS , $n \geq 1$) (Filipovic et al. 2018; Ogata et al. 2023; Kasamatsu et al. 2023). Thus, H_2S can react with GSH to generate glutathione persulfide (GSSH) (Benchoam et al. 2020). On the other hand, the chemical interaction between H_2S and $\cdot\text{NO}$ can produce thionitrous acid (HSNO) which is the smallest *S*-nitrosothiol (Marcolongo et al. 2019). It should be mentioned that in plants, the information about the function of this molecule is, to the best of our knowledge, inexistent due to the difficulty to detect it. Recently, a novel fluorescent probe (SNP-1) has been described for the detection of HSNO in animal cells in vivo (Zhang et al. 2022), which opens an opportunity to investigate this topic in plants. Figure 2 shows some of these reactions. Despite being molecules with a simple structure, their biochemistry is not straightforward since different intermediary molecules are involved, and due to their reactivity, they are difficult to identify and quantify at the cellular level.

NO and H_2S Donors used in Animal and Plant Research

The battery of compounds capable of releasing $\cdot\text{NO}$ or H_2S is significant and continues to grow, mainly due to their use in the area of medicine for the treatment of numerous pathologies as both molecules mediate relevant functions in multiple systems including the circulatory, nervous, and immune systems (Burgaud et al. 2002; Corvino et al. 2021). The pharmaceutical industry is still working on developing new compounds that might be the most suitable for each type of pathology (Huang et al. 2023; Powell et al. 2018; Iciek et al. 2023) including the development of releasing nanoparticles (Hu et al. 2021a, b; Liu et al. 2023a, b). Table 1 summarizes some of the most representative used donors for $\cdot\text{NO}$ and H_2S . In the case of H_2S , there are natural sources such as garlic or onion and other members of the genus *Allium* (Powell et al. 2018; Muñoz-Vargas et al. 2023a; Wen et al. 2023).

NONOate has the general chemical formula $\text{R}_1\text{R}_2\text{N}-(\text{NO}^-)-\text{N}=\text{O}$, where R_1 and R_2 correspond to

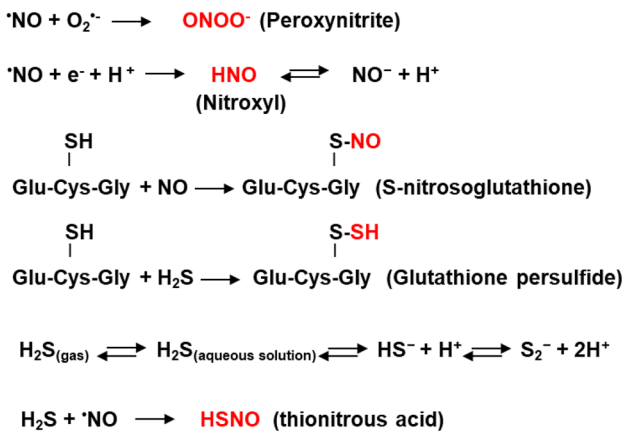


Fig. 2 Some chemical reactions involving nitric oxide (NO) and H_2S that generate different derived molecules such as peroxynitrite, nitroxyl, nitrosoglutathione, glutathione (Glu-Cys-Gly) persulfide, and the thionitrous acid

Table 1 Some of the main NO and H₂S donors used in animal and plant research

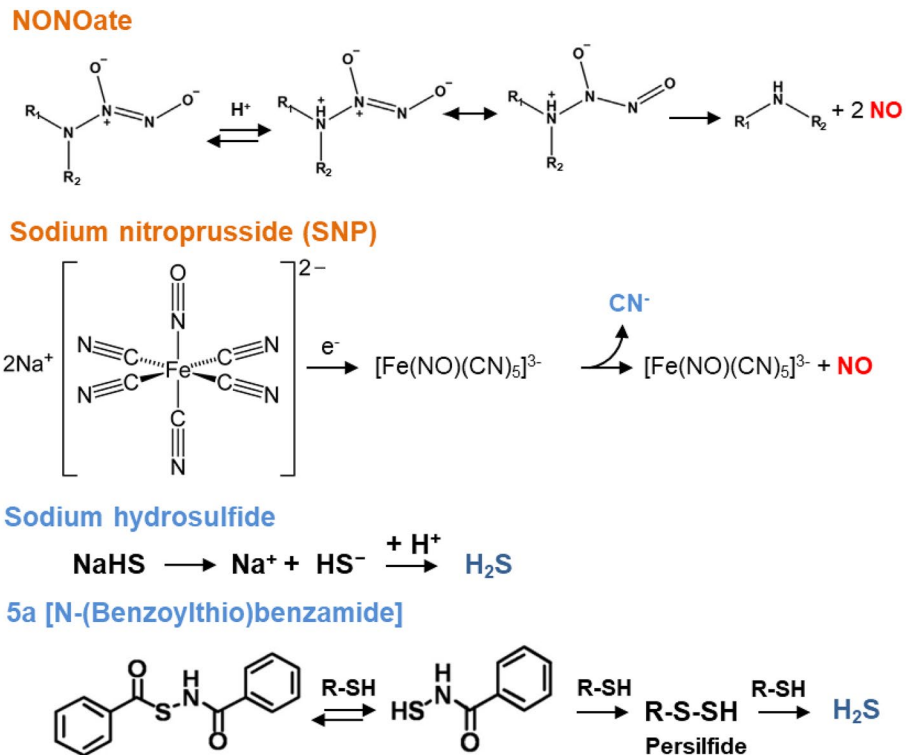
NO donors
NONOate
Diethylamine NONOate
Diethylenetriamine NONOate
Dipropylenetriamine NONOate
Proline NONOate
Spermine NONOate
Diazeniumdiolate (NOC-18)
Nitrosothiols
<i>S</i> -nitroso- <i>N</i> -acetylpenicillamine (SNAP)
<i>S</i> -nitrosoglutathione (GSNO)
<i>S</i> -nitrosocysteine (CysNO)
Thionitrous acid (HSNO)
Other compounds
Sodium nitroprusside (SNP)
NO gas
Nitro-fatty acid (NO ₂ -FA)
NO-releasing nanoparticles (NPs)
SN-MSA-CNPs
GSNO-CNPs
SNAC-CNPs
SNP-CNPs
H ₂ S donors
Inorganic sulfide salts
Sodium sulfide (Na ₂ S) and sodium polysulfides (Na ₂ S _{<i>n</i>} , <i>n</i> = 2–5)
Sodium hydrosulfide (NaHS)
Organic polysulfides
Polysulfides species (R-Sn-R'; <i>n</i> > 2) (R = cysteine, glutathione, polypeptides)
SulfoBiotics-H ₂ S
5a [<i>N</i> -(Benzoylthio)benzamide]
8o [<i>N</i> -Butyl-N2-acetyl- <i>S</i> -pivaloylsulfanyl-DL-penicillamine amide]
8ℓ [<i>N</i> -Butyl-N2-acetyl- <i>S</i> -acetylsulfanyl-DL-penicillamine amide]
GY4137 [(<i>p</i> -methoxyphenyl)morpholino-phosphinodithioic acid]
ADTOH 5-(4-hydroxyphenyl)-3H-1,2-dithiole-3-thione

CNPs, chitosan nanoparticles; GSNO, *S*-nitrosoglutathione; SNAC, *S*-nitroso-*N*-acetylcysteine; SN-MSA; *S*-nitroso-mercaptosuccinic acid; SNP, sodium nitroprusside

alkyl groups, and it can release two molecules of NO (Horton and Schiefer 2019). These compounds are relatively stable in alkaline solution (pH 8.0) and, usually, they will release NO in a controlled way (Fig. 3). On the other hand, *S*-nitrosothiols (SNOs) are compounds that enclose a nitroso group (–NO) attached to the S-atom of a thiol group. SNOs release one molecule of NO and they are more stable under different conditions such as high temperature, metal ions, UV light, or enzymes. GSNO is considered the most physiological SNO that can mediate trans-nitrosation processes (Corpas et al. 2013; Jedelská et al. 2021). More recently, NO-releasing nanomaterials, for example, NO donors linked to chitosan, have been used

in plant research (Murgia et al. 2004; Begara-Morales et al. 2014a, b; Silveira et al. 2019; Muñoz-Vargas et al. 2020; Seabra et al. 2022). However, the most commonly used NO donor has been sodium nitroprusside (SNP) because it is the cheapest and most handling one. Nevertheless, several concerns must be considered when the SNP is applied such as pH, temperature, and light conditions. SNP is a sodium salt consisting of iron complexed with five cyanide anions (Fig. 3). A concentration of 30 μM SNP (at 37 °C) releases NO in a pH-dependent manner. Thus, SNP at pH 5.0 releases the greatest quantity of NO which is significantly decreased at pH 7.2; nevertheless, in the acid solution and under light conditions for a few hours, SNP

Fig. 3 Chemical structures of some representative donors of $\cdot\text{NO}$ (NONOate and SNP) and H_2S (NaHS and 5a [N-(Benzoylthio)benzamide]) and mechanism for their release



is decomposed producing blue smog and a cyanide odor. Moreover, SNP in an aqueous solution is degraded when exposed to white or blue light but not to red light (Grossi and D'Angelo 2005).

Among the H_2S donors, the most used in plant research is sodium hydrosulfide (NaHS). In an aqueous solution, this compound dissociates into Na^+ and HS^- , and then, this latter binds partially to H^+ to form undissociated H_2S . On the other hand, other compounds such as polysulfides (Fukuto et al. 2018; Sawa et al. 2022), GYY4137 (Li et al. 2009), and other chemical donors (Zhao et al. 2011a, b), designated sulfobiotics- H_2S donors 5a, 8 ℓ , and 8o (Table 1; Dojindo Laboratories, Kumamoto, Japan), have been used mainly in medical research, although there are also some reports in plants (Yamasaki et al. 2019). A characteristic of this group of reagents (5a, 8 ℓ , and 8o) is that the release of H_2S is by reaction with molecules containing thiol groups (Fig. 3).

It should be mentioned that nitrite (NO_2^-) and sulfite (SO_3^{2-}) are part of the endogenous metabolism of $\cdot\text{NO}$ and H_2S in plant cells (Corpas et al. 2022a; González-Gordo et al. 2020), but they are not used as direct donors of these gas transmitters. In fact, NaNO_2 and Na_2SO_3 have been used for food preservation (designated E250 and E221, respectively) but, at present, their use is limited or even forbidden due to collateral health problems (Chazelas et al. 2022; Liu et al. 2021). Thus, Na_2SO_3 was used for raw fruits and vegetable preservation but, in the mid-80s, the US Food and Drug Administration forbade its use.

In summary and as has been mentioned previously, in the area of plant physiology, some of these donors are used mainly in research through either experiments in the laboratory or at the field level, seeking a balance between the quantity needed and their cost. Thus, for larger-scale treatment of plants, the most widely used are SNP for $\cdot\text{NO}$, and NaHS for H_2S , since they are the cheapest ones and the easiest to use.

NO, H_2S and Postharvest Storage of Horticultural Products

Once fruits and vegetables are harvested and are not consumed immediately, they must be stored until they reach the consumers. The shelf-life of each product, in which it maintains its good properties, varies significantly among species and, during postharvest storage, a wide of symptoms begins to appear (Aghdam et al., 2020; Brizzolara et al. 2020), either due to the senescence process itself, infections provoked by different pathogens (fungi, bacteria, or viruses), or the storage conditions, for example, at low temperatures.

Accumulating experimental data demonstrates that exogenous treatment with $\cdot\text{NO}$ and H_2S has become a new and complementary tool to delay leaf and fruit senescence and consequently extends the shelf-life of products during postharvest storage (Chen and Zhu et al., 2023; Zhu et al. 2022; Wang et al. 2022a, b, c, d). But also, both gases can improve the nutritional quality of horticultural crops (Huo

et al. 2018; Zhong et al. 2021), palliate chilling injuries, and prevent fungal infection (Zhang et al. 2019). Although the concentration and application way of these molecules must be optimized for each horticultural product, generally these gasotransmitters can exert regulatory functions at different levels including the increase of the ROS metabolism through an enhancement of enzymatic antioxidant systems including catalase, superoxide dismutase isozymes, ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate peroxidase (MDAR), and glutathione reductase (GR), these last four enzymes being components of the ascorbate–glutathione cycle. Furthermore, there is an increase in non-enzymatic antioxidants such as ascorbic acid (AsA), glutathione (GSH), melatonin, phenolic compounds, flavonoids, and other compounds of the phenylpropanoids' group (Rodríguez-Ruiz et al. 2017a; Li et al. 2017; Zhang et al. 2020; Deng et al. 2021; Zuccarelli et al. 2021, 2023). All these antioxidants provide greater protection during storage but also contribute to a higher nutritional value since antioxidants have associated beneficial health effects.

Throughout the fruit ripening of pepper (*Capsicum annuum* L.), a model of non-climacteric fruit, it has been shown the relevance of the ROS metabolism and part of its interaction with NO and H_2S (Corpas et al. 2023). Thus, it was found an increase in lipid peroxidation and $\text{O}_2^{\cdot-}$ -generating RBOH activity (Chu-Puga et al. 2019), which was associated with an increase in the content of nitrated and *S*-nitrosated proteins (Chaki et al. 2015); this latter one connected with a lower GSNOR activity and protein expression (Rodríguez-Ruiz et al. 2017b), where catalase is a key target of these NO -mediated PTMs (Palma et al. 2020). These data support that the ripening of pepper fruit has a very active nitro-oxidative metabolism. Furthermore, the application of exogenous NO gas (5 ppm for 1 h) during the pepper fruit ripening caused a delay in this process that is accompanied by a significant increase (40%) in the AsA content. The analysis of the AsA biosynthesis pathway confirmed an increase in the activity and gene expression of the galactono-1,4-lactone dehydrogenase (GalLDH), a mitochondrial enzyme that catalyzes the final step of AsA production, involving the oxidation of L-galactono-1,4-lactone to AsA (Rodríguez-Ruiz et al. 2017a).

Lipoxygenases (LOXs) and small heat shock proteins (sHSP) play significant functions in plant development and stress response. The LOX analyses during pepper fruit ripening allowed identifying a total of eight LOX genes whose expression was differentially regulated during ripening and by the treatment with NO gas (González-Gordo et al. 2022a, b). Complementarily, the analysis of the sHSP system indicated the presence of 19 sHSP genes in pepper fruits, where the NO treatment triggered the upregulation of 7 sHSP genes and the downregulation of 3 sHSP genes (González-Gordo et al. 2023). Furthermore, the analysis

of the H_2S metabolism showed that it was also modulated. Thus, the H_2S -generating L-cysteine desulphydrase (LCD) and D-cysteine desulphydrase (DCD) activities were down-regulated during pepper ripening, but this effect was reverted after NO treatment of fruits (Muñoz-Vargas et al. 2023b). Similarly, in the climacteric goji berry (*Lycium barbarum* L.) fruit, experimental data support the beneficial effect of the exogenous applications of NO and H_2S . Thus, after NaHS treatment, the senescence of goji berry fruits was delayed, whereas the postharvest quality improved. This was due to a modulation of the ROS metabolism since the content of H_2O_2 , $\text{O}_2^{\cdot-}$, and lipid peroxidation was diminished, whereas the activity and gene expression of catalase, SOD, APX, and GR were increased. At the same time, the gene expression of LOX and RBOH was down-regulated (Wang et al. 2023). Similar observations have been found with the exogenous application of SNP as an NO donor (Elam et al. 2022). All these data support the metabolic relationship among the metabolisms of NO , H_2S , and ROS.









Although the available information is still very limited, the couple $\text{NO}/\text{H}_2\text{S}$ can also modulate the gene expression by affecting either promoters, cis-acting regulatory elements, or epigenetic factors such as DNA methylation, chromatin remodeling, histone methylation/demethylation, and acetylation (Kuang et al. 2012; Mengel et al. 2017; Hao et al. 2020). Thus, the analysis of tomato (*Solanum lycopersicum* cv. Lichun) fruit pretreated with the NO donor SNP and then stored at 2 °C indicates that the NO reduces the content of malondialdehyde (MDA) and ion leakage, representative markers of lipid peroxidation, and stability of the cell membrane, respectively. Furthermore, it was found that the transcription factor C-repeat/dehydration-responsive element (CRT/DRE)-binding factor (CBF), which participates in the mechanism of response against low temperature, had higher expression levels in fruit treated with NO (Zhao et al. 2011a, b). Similarly, in cucumber (*Cucumis sativus* L.), the exogenous application of 200 μM SNP mitigates the damage associated with low temperature (10 °C during the day and 6 °C at night). Among the effects exerted by NO , it has been reported that it reduces the chilling damage index, the MDA content, and alters the expression of genes related to the metabolism of phenylalanine, lignin synthesis, and hormones such as ethylene and salicylic acid. Furthermore, it was found that two transcription factors, HD-ZIP (Homeodomain leucine zipper) and b-ZIP (basic region/leucine zipper motif), responded to exogenous NO under low-temperature stress (Wu et al. 2022).

Recently, the exogenous application of 0.1 mM NaHS in grapes (*Vitis vinifera* L.) berry triggered their color change, particularly by the anthocyanin accumulation. A deeper analysis at the molecular and biochemical level revealed an increase in the expression of the transcription factor WRKY30, which, at the same time, promotes

Table 2 Main effects of the exogenous application of NO on representative horticultural products including vegetables and fruits of herbaceous plants and trees

Plant species	[NO] donor	Effects	References
<i>Vegetables</i>			
Broccoli (<i>Brassica oleracea</i> L.)	0.02 mM NO (SNP)	Alleviates salinity stress, increases the postharvest life, and enhances enzyme antioxidant activities	Akram et al. (2020) Munawar et al. (2019)
Spinach (<i>Spinacia oleracea</i> L.)	0.2 ppm NO	Alleviates salinity stress and enhances the activity of antioxidant enzymes	Du et al. (2015)
Potato (<i>Solanum tuberosum</i> L. cv. Pampeana)	100 µM SNP 200 µM NaNO ₂	Protects from herbicides and protects against fungal infections	Beligni and Lamattina, (1999) Lazalt et al. (1999)
Lettuce (<i>Lactuca sativa</i> L.)	5–1000 ppm NO	Increases the postharvest life of cut leaves	Wills et al. (2008)
Chard (<i>Beta vulgaris</i> L. var. cicla)	0–200 µM NO	Alleviates drought stress and increases the antioxidant enzyme content	Ekinci et al. (2020)
<i>Fruits</i>			
<i>Climacteric fruit (ripening associated with ethylene production)</i>			
Banana (<i>Musa</i> spp.)	1–5 mM SNP	Alleviates salt stress, reduces ethylene production, and increases the postharvest life of fruits	Mohd Amnan et al. (2021) Cheng et al. (2009)
Tomato (<i>Solanum lycopersicum</i> , Micro-Tom cultivar)	10 µM GSNO 0.15 mM SNP 100 ppm NO gas	Alleviates salt toxicity, alleviates biotic damage, regulates endogenous hormonal equilibrium, and enhances photosynthetic capacity Accumulation of ascorbate and flavonoids	Wei et al. (2022) Wang et al. (2022a, b, c, d) Zuccarelli et al. (2021)
Kiwifruit (<i>Actinidia chinensis</i>)	1 µM NO	Increases the postharvest life and vitamin C and E contents	Zhu et al. (2010)
Apple (<i>Malus x domestica</i> Bork cv. Granny Smith)	500 µM NO	Increases the postharvest life of slices	Pristijono et al. (2006)

Table 2 (continued)

Plant species	[NO] donor	Effects	References
Pear (<i>Pyrus communis</i> L. x <i>P. bretschneideri</i> Rehd)	 100 µM SNP	Alleviates damage caused by iron deficiency, reduces ethylene production, and increases the postharvest life of fruits	Liu et al. (2022) Liu et al. (2019)
Mango (<i>Mangifera indica</i> L.)	 0.25 mM SNP	Inhibits the growth of fungal pathogen	Ren et al. (2020)
Goji berry (<i>Lycium barbarum</i> L.)	 0.6 mM SNP	Improves the freshness of fruit by maintaining higher activities of CAT, POD, PPO, and APX, whereas polyphenol oxidase (PPO) and peroxidase (POD) activities were decreased	Elam et al. (2022)
Peach (<i>Prunus persica</i> L. Batsch)	 10 µM SNP 15 µM NO solution 15 µM NO solution	Alleviates chilling injury by regulating the metabolism of lipid and cell wall Mediates DNA methylation enhancing cold resistance in postharvest Resistance against <i>Monilinia fructicola</i> through activating the phenylpropanoid pathway	Zhao et al. (2021) Guo et al. (2023) Li et al. (2017)
<i>Non-climacteric fruit (ripening not-associated with ethylene production)</i>			
Sweet pepper (<i>Capsicum annuum</i> L.)	 5 ppm NO gas	Increases the postharvest life of fruits, increases the enzymatic and non-enzymatic antioxidant (ascorbate) levels, modulates the ROS and RNS content, and increases the gene expression of <i>sHSPs</i>	González-Gordo et al. (2022a, b, 2023) Rodríguez-Ruiz et al. (2017a, b)
Strawberry (<i>Fragaria</i> spp.)	 Infiltration with DETANO	Increases the postharvest life of fruits	Wills et al. (2007)
Cucumber (<i>Cucumis sativus</i> L.)	 200 mM SNP	Decreases chilling damage by regulating four TFs (MYB63, WRKY21, HD-ZIP, and b-ZIP) and their target genes such as <i>LHCA1</i> , <i>CHS</i> , <i>EIN3</i> , and <i>PAL</i>	Wu et al. (2022)
Citrus (<i>Citrus sinensis</i> L. Osbeck cv. Valencia)	 50 µM NO	Reduces fungal diseases and induces enzymatic antioxidants activities (catalase, peroxidase, etc.) and increases postharvest life of fruits	Zhou et al. (2016)

SNP, sodium nitroprusside. sHSP, small heat shock protein. CSH, chalcone synthase. EIN3, ethylene-insensitive protein 3. LHCA1, light-harvesting complex I chlorophyll a/b binding protein 1. PAL, phenylalanine ammonia-lyase. POD, peroxidase. CAT, catalase. GSNO, nitrosoglutathione. PPO, polyphenol oxidase. APX, ascorbate peroxidase. TF, transcription factor

Table 3 Main effects of the exogenous application of H₂S on representative horticultural products including vegetables and fruits of herbaceous plants and trees















Plant species	[H ₂ S] donor	Effects	References
<i>Vegetables</i>			
Spinach (<i>Spinacia oleracea</i>)	 100 µM NaHS	Increases the drought resistance	Chen et al. (2016)
Lettuce (<i>Lactuca sativa</i>)	 0.01–0.5 mM Na ₂ SO ₃ ; (0.01– 0.1 mM H ₂ S)	Increases shoot elongation	Liu and Lal (2015)
Ginger (<i>Zingiber officinale Roscoe</i>)	 0.8 mM NaHS	Alleviates the toxic effects of cadmium and increases the antioxidant enzymes: APX, GR, MDAR, and DHAR	Chen et al. (2022)
<i>Fruits</i>			
<i>Climacteric fruit (ripening associated with ethylene production)</i>			
Banana (<i>Musa</i> spp.)	 0.25–2 mM NaHS 1 mM NaHS	Mitigates chilling injury of postharvest and increases APX, CAT, GR, DHAR, MDAR, and SOD enzyme activities Alleviates postharvest ripening and senescence by antagonizing the effect of ethylene	Ali et al. (2022); Li et al. (2016) Ge et al. (2017)
Tomato (<i>Solanum lycopersicum</i> , cultivar Micro-Tom)	 0.9 mM NaHS	Antagonizes the effect of ethylene, prolongs the postharvest period, inhibits proteases, and maintains higher levels of nutritional-related metabolites	Yao et al. (2020)
Kiwifruit (<i>Actinidia deliciosa</i>)	 1 mM NaHS	Maintains the highest levels of chlorophyll, ascorbate, and increases the enzyme activity of POD, CAT, APX, and GR	Gao et al. (2012) Zhu et al. (2014)
Apple (<i>Malus x pumila</i>)	 0.2–1 mM NaHS	Mitigates postharvest senescence, maintains higher levels of ascorbic acid, mitigates ROS accumulation, and significantly increases the APX, CAT, GR, POD, and SOD activities	Zheng et al. 2016
Apple (<i>Malus domestica</i> Borkh cv. Delicious)	 5 mM NaHS	Promotes the resistance against <i>Penicillium expansum</i> by promoting the synthesis of H ₂ S, H ₂ O ₂ and NO as well as phenolic acids	Deng et al. 2021

Table 3 (continued)

Plant species	[H ₂ S] donor	Effects	References
Pear (<i>Pyrus pyrifolia</i> cv. Dangshan)	 0.5–5 mM NaHS	Prolongs the shelf-life, enhances the antioxidant enzyme activity of APX, CAT, and POD, and inhibits the growth of fungal pathogens	Hu et al. (2014)
Goji berry (<i>Lycium barbarum</i> L.)	 1.4 mM NaHS in aqueous solution	Delays the senescence, improves postharvest quality, increases the bioactive compounds accumulation, and boosts the antioxidant capacity	Wang et al. (2023)
Peach (<i>Prunus persica</i> L. Batsch)	 10–20 µM NaHS	Provides chilling resistance through regulation of ROS and RNS metabolism and maintains cell structure	Zhao et al. (2023) Wang et al. (2022b)
<i>Non-climacteric fruit (ripening not-associated with ethylene production)</i>			
Grape (<i>Vitis vinifera</i> L. x <i>V. labrusca</i> L. cv. Kyoho)	 1–2.2 mM NaHS 0.1 mM NaHS	Inhibits the decreases in firmness and weight loss, maintains the highest levels of ascorbic acid, and enhances the antioxidant enzymes activity of APX and CAT Promotes color changes	Ni et al. (2016) Liu et al. (2023a, b)
Strawberry (<i>Fragaria ananassa</i> L. 'Fengxiang')	 0.2–1.25 mM NaHS	Prolongs the shelf-life and reduces the decay rate of harvested fruits, and increases CAT, APX, and GR enzyme activity	Chang et al. (2014) Hu et al. (2012)
Cucumber (<i>Cucumis sativus</i> L.)	 1 mM NaHS	Reduces chilling injury, lowers the level of ROS, and enhances the enzyme antioxidant levels	Wang et al. (2022a, b, c, d)

APX, ascorbate peroxidase. GR, glutathione reductase. MDAR, monodehydroascorbate reductase. DHAR, dehydroascorbate reductase. CAT, catalase. SOD, superoxide dismutase. POD, peroxidase

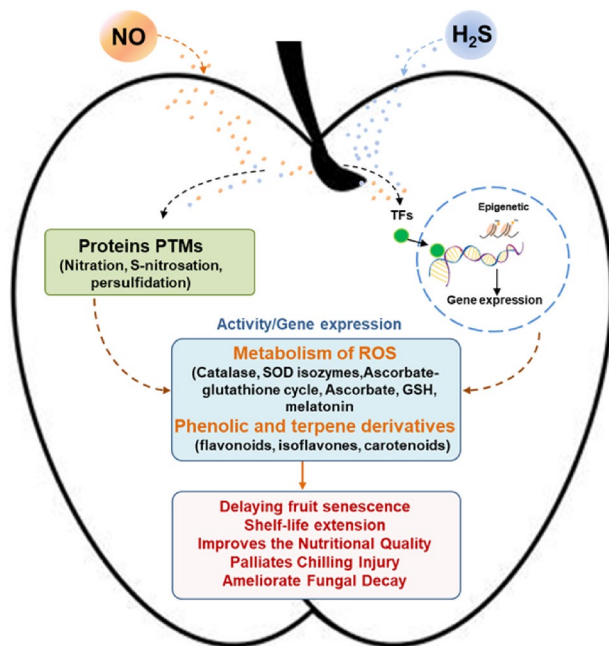


Fig. 4 Model of the cascade of events triggered by the exogenous application of NO and H₂S in horticultural products through the modulation of proteins and genes that modify the metabolism of reactive oxygen species (ROS), thus alleviating the possible damages associated with the postharvest storage. GSH, glutathione. PTMs, post-translational modifications. SOD, superoxide dismutase. TFs, transcription factors

the increase in the expression of SiR (sulfite reductase) that encoded an enzyme involved in the H₂S generation. Furthermore, these genes mediate the upregulation of the expression of genes involved in anthocyanin synthesis (Liu et al. 2023a, b).

Table 2 and Table 3 summarize the main effect of exogenous NO and H₂S, respectively, on some representative examples of horticultural crops including vegetables, and fruits of herbaceous plants and trees, either climacteric or non-climacteric fruits.

Figure 4 illustrates a working model indicating the mechanism of action after the exogenous application of NO or H₂S which would act directly on the activities of specific protein targets through the different PTMs or through the expression of genes that code for target proteins, either by transcription factors (TFs) or by epigenetic processes. In this cascade of signals, ROS metabolism is significantly affected and in general is characterized by an increase in enzymatic and non-enzymatic antioxidant systems, thus allowing to palliate possible oxidative damage to macromolecules. The final beneficial effects depend on the horticultural product and they could include delay of fruit senescence, shelf-life extension, and improvement of the nutritional quality, palliate chilling injury, and/or prevent fungal infection.

Conclusion and Future Perspectives

There are currently different compounds that are being studied because they provide beneficial effects on horticultural products such as melatonin (Zhang et al. 2020; Aghdam et al. 2023; Corpas et al. 2022a, b, c), chitosan (Mahmoudi et al. 2022), silicon (Peris-Felipo et al. 2020; Tripathi et al. 2021, 2023), nanoparticles (Seabra et al. 2022; Zhou et al. 2022), and edible coatings (Tavassoli-Kafrani et al. 2020), among other. NO and H₂S have become good candidates, either alone or in combinations, for exogenous treatments. These signaling gas molecules should be greatly considered, since they can help to preserve the quality of horticultural products as well as to expand the self-life during storage, mainly through the stimulation and the homeostasis of the ROS and the antioxidant metabolisms. To our knowledge, the exogenous application of either NO or H₂S has only been carried out at the research level and, although there are still many aspects that have to be investigated at the biochemical level to determine how they exert their beneficial effects, the reality is that, to the best of our knowledge, there is no application in the horticultural industry that has used these molecules. Therefore, one of the aspects that should be explored at the agro-industrial level is that for a given horticultural crop, the type of donor to be used, concentration, and exposure time must be optimized to corroborate its beneficial effects. Although we must be aware of the difficulties of transferring the information obtained in the laboratories to its possible application at the industry level, we hope that what is mentioned in this review can contribute modestly to cover this gap soon.

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Declarations

Conflict of interest The authors declare no conflict of interest of any kind.

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