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Research review

# Interorgan, intraorgan and interplant communication mediated by nitric oxide and related species

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## Summary

Plant survival to a potential plethora of diverse environmental insults is underpinned by coordinated communication amongst organs to help shape effective responses to these environmental challenges at the whole plant level. This interorgan communication is supported by a complex signal network that regulates growth, development and environmental responses. Nitric oxide (NO) has emerged as a key signalling molecule in plants. However, its potential role in interorgan communication has only recently started to come into view. Direct and indirect evidence has emerged supporting that NO and related species (*S*-nitrosoglutathione, nitro-linolenic acid) are mobile interorgan signals transmitting responses to stresses such as hypoxia and heat. Beyond their role as mobile signals, NO and related species are involved in mediating xylem development, thus contributing to efficient root–shoot communication. Moreover, NO and related species are regulators in intraorgan systemic defence responses aiming an effective, coordinated defence against pathogens. Beyond its *in planta* signalling role, NO and related species may act as *ex planta* signals coordinating external leaf-to-leaf, root-to-leaf but also plant-to-plant communication. Here, we discuss these exciting developments and emphasise how their manipulation may provide novel strategies for crop improvement.

## Introduction

The body of higher plants is composed of organs such as roots, leaves and stems, which receive various signals from the surrounding abiotic (e.g. soil, air) and biotic (e.g. microbes, herbivores) environment. In order to effectively respond to these environmental factors and enhance their survival, land plants have developed unique, complex, bidirectional mechanisms connecting various organs. Interorgan signalling is achieved by the vasculature-associated, long-distance movements of chemical messengers including hormones, peptides, proteins, RNA molecules,

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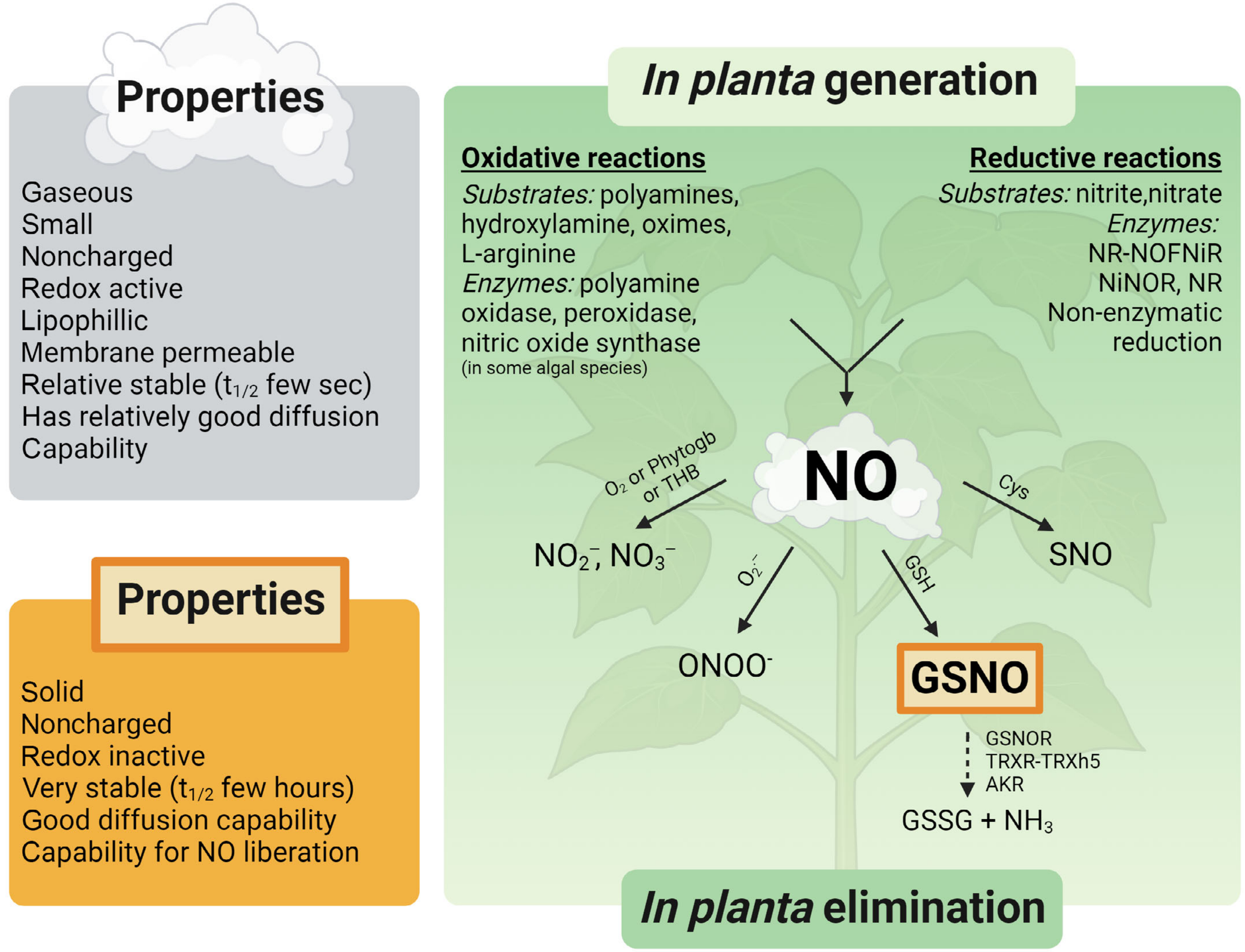

**Fig. 1** Summary of the physico-chemical properties, *in planta* generation and *in planta* elimination reactions of NO and GSNO. See details in the text. Dashed arrow indicate reactions with multiple steps and enzymes involved. AKR, aldo-keto reductase; Cys, cysteine; GSH, glutathione; GSNO, *S*-nitrosoglutathione; GSNOR, *S*-nitrosoglutathione reductase; GSSG, glutathione disulphide; $NH_3$, ammonia; NiNOR, nitrite:nitric oxide reductase; $NO_2^-$, nitrite; $NO_3^-$, nitrate; NR, nitrate reductase; NR-NOFNiR, nitrate reductase-nitric oxide forming nitrite reductase; $O_2$, molecular oxygen; $O_2^{\bullet -}$, superoxide radical; $ONOO^-$, peroxynitrite; Phytogb, phytoglobin; SNO, *S*-nitrosothiol; $t_{1/2}$, half-life; THB, truncated hemoglobin; TRXR-TRXh5, thioredoxin reductase-thioredoxin h5.

metabolites, ions and reactive oxygen species (ROS, Li *et al.*, 2021). Interestingly, ROS waves have been suggested as long-distance signal transmitting leaf-to-leaf communication (Miller *et al.*, 2009) and mediate acclimation responses under high light and elevated temperature (Fichman *et al.*, 2022; Kuromori *et al.*, 2022). Molecules closely cooperating with ROS are reactive nitrogen species (RNS), which is a group of radical and nonradical molecules derived from the nitric oxide (NO) signal molecule.

Nitric oxide is one of the smallest diatomic gaseous molecules. An unpaired electron in its $\pi$ orbital ensures its radical and redox active characteristics. Loss of the unpaired electron yields nitrosonium cation ($NO^+$), while gaining an electron leads to the formation of nitroxyl anion ($NO^-$) (Stamler *et al.*, 1992). Their origin, fate and biological role in plants have been only recently uncovered (Arasimowicz-Jelonek *et al.*, 2023). It is worth emphasising that NO shows reactivity only towards compounds with unpaired electrons, such as free radicals, transition metals such as heme iron and molecular oxygen, thus has a surprisingly low reactivity (Beckman & Koppenol, 1996; Thomas, 2015). Consequently, NO has relatively long half-life (in order of seconds), which is influenced by its own concentration (Wink & Mitchell, 1998) or due to the presence of other radical molecules such as superoxide ($O_2^{\bullet -}$), particularly under stress conditions, with which it reacts quickly to generate the formation of peroxynitrite ($ONOO^-$). Beyond its relative stability, the relatively good diffusion capability (diffusion distance of NO is *c.* 100–200 μm; Lancaster, 1997) due to its lipophilic character enables NO to be a powerful intra- and intercellular signal molecule (Fig. 1).

Among the multiple forms of nitrogen (N) in plants, NO is in the middle in terms of oxidation state. Therefore, its formation

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within the plant body is possible through the oxidation of reduced nitrogen compounds (e.g. amines) and through the reduction of higher oxides (e.g. nitrate, nitrite). These pathways of NO formation are mediated by enzymes or occur without the involvement of enzymatic activity. Regarding its physiological roles, the spatiotemporal regulation of NO levels is of great importance. Due to the fact that the root system is the site of the absorption and assimilation of reduced and oxidised N forms, the pathways for the NO formation in the root system are better explored than those of the shoot. One of the most characterised possibility of NO formation in the root is the reduction in nitrite to NO with the participation of the nitrate reductase (NR) enzyme (Rockel *et al.*, 2002; Mohn *et al.*, 2019), which, in the light of the latest results in Chlamydomonas, indirectly contributes to NO formation, through mediating the electron transfer to the NO-forming nitrite reductase enzyme (Chamizo-Ampudia *et al.*, 2016). A related mechanism may operate in the roots and shoots of higher plants. However, recent work of Maiber *et al.* (2022) showed that either ARC1 (NOFNiR1) or ARC2 (NOFNiR2) from Arabidopsis are not involved in physiologically relevant nitrite-dependent NO formation. A similar cooperation of enzymes has been previously described in tobacco roots, where plasma membrane-bound NR synthetises the substrate, nitrite, for the nitrite:NO reductase enzyme localised in the plasma membrane as well (Stöhr *et al.*, 2001). Mitochondrial electron transport chain has the capability to reduce nitrite to NO (Kumari *et al.*, 2023). The reduction of nitrite in the presence of ascorbate at acidic pH can also spontaneously lead to the formation of NO (Wang & Hargrove, 2013). The indirect participation of the polyamine catabolic enzymes, copper amine oxidases (CuAOs) has been supposed in the formation of NO in Arabidopsis root (Wimalasekera *et al.*, 2011; Groß *et al.*, 2017), and the synthesis of NO from hydroxylamine or salicylhydroxamate has also been described in plant cells (Rümer *et al.*, 2009). Carotenoids of photosynthesising tissues have been proven to form NO *in vitro* by the reduction of nitrite in a light-dependent manner (Cooney *et al.*, 1994), which is also an exciting but still unknown possibility for the formation of NO in the plant body. According to the latest findings, plants are able to synthetise NO from oximes and flavins in peroxidase-catalysed reactions suggesting the operation of an oxidative pathway of NO production in higher plants (López-Gómez *et al.*, 2024) (Fig. 1).

In the spatiotemporal regulation of NO levels, the operation of elimination processes has major relevance (Fig. 1). Scavenging mechanisms include simple chemical reactions between NO and molecular oxygen present in the microenvironment of NO, which leads to the formation of nitrate and nitrite (Thomas, 2015). Moreover, NO elimination can be realised with the participation of proteins. It has been known for a long time that NO interacts with animal globins (Gow & Stamler, 1998), with the NO being shown to interact with the haem iron. Plants have globin homologues too (Becana *et al.*, 2020), with NO-leghemoglobin complexes being reported (Mathieu *et al.*, 1998). It has been suggested that such interactions may scavenge NO (creating nitrate) and peroxynitrite (Meilhoc *et al.*, 2011). Others too have shown that phytoglobins (Phytogb) may act as NO dioxygenases and catalytically metabolise NO to nitrate (Seregélyes *et al.*, 2004). Furthermore, inert atoms, such as xenon (Xe), and small molecules, such as NO, can also interact with globins by a physical interaction in hydrophobic pockets (Daigle *et al.*, 2009). Such interactions may stabilise proteins, or alter their function, but may also buffer NO out of solution, so altering its bioactivity. If proteins in the phloem (De Schepper *et al.*, 2013) or xylem (Buhtz *et al.*, 2004) were to partake in such hydrophobic pocket interactions with NO it would allow systemic movement of NO through the plant.

In order for a molecule to be capable of performing long-distance signal transduction, one of the crucial factors is its relatively long half-life, which is defined as the time required for its concentration to be reduced by half in the event of complete termination of its synthesis. The half-life of known long-distance signals, including mobile mRNAs, peptides and proteins, and hormones, has been observed to range from a few dozen minutes to 24 h or even several days (Narsai *et al.*, 2007; Kramer & Ackelsberg, 2015). Accordingly, in order for the NO signal to spread over a longer distance within the multicellular plant organism, more stable mobile forms with prolonged half-lives must be developed. *S*-nitrosocysteine formed in the reaction of RNS with free cysteine has a half-life of < 2 min (Singh *et al.*, 1996) which is not enough to carry out long-distance signal transmission. However, the oxides of nitrogen *S*-nitrosate the cysteine thiol of glutathione (GSH) yielding *S*-nitrosoglutathione (GSNO). It is noteworthy that the removal of glutathione, a pivotal redox molecule, by NO represents one of the indirect mechanisms through which NO exerts a substantial influence on the redox state of the cell (for a more comprehensive discussion, see Hancock, 2019). GSNO has a half-life of the order of hours and its homolytic cleavage liberates NO (Dent & DeMartino, 2023) and such properties contribute to GSNO being a good candidate for orchestrating the long-distance (e.g. root-shoot) translocation of the NO signal. The level of GSNO, and thus the transfer of NO bioactivity, is controlled by the function of NADH-dependent GSNO reductase (Sakamoto *et al.*, 2002), NADPH-dependent thioredoxin reductase-thioredoxin h5 system (Kneeshaw *et al.*, 2014) and NADPH-dependent aldo-keto reductase (Treffon *et al.*, 2021) (Fig. 1). The cooperation of the biosynthetic and eliminating mechanisms ensures local and transient NO level increases contributing to the formation of NO 'hot spots' in plant cells, which may be key mechanism in order for this small molecule to perform such a diverse physiological functions (Neill *et al.*, 2008; Freschi, 2013).

Coordinated communication between organs is an important element of plants' responses to environmental factors. The complex network of interorgan signal compounds seems to involve NO and its stable derivatives. Additionally, NO and its derivatives may participate in intraorgan as well as in interplant communication. This review discusses the known roles of NO/RNS/RSS in the above *in planta* and *ex planta* signalling in higher plants and assigns future research directions in the field.

## Indirect evidences for NO/RNS as interorgan signals

The anoxia/hypoxia-triggered NO production of plant roots has been widely documented (reviewed by Gupta *et al.*, 2020) and

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proved to be dependent on the availability of nitrate and nitrite (Liu *et al*., 2015). Interestingly, hypoxia leads to increased NO emissions also from the leaves and stems and there is a tight correlation between leaf and stem NO emission of hypoxia-treated plants (Liu *et al*., 2015). The authors suggest that NR-associated NO, either itself or in the form of a derivative, is transported in the xylem from the roots to the shoot, thereby mediating NO emission from the aboveground plant parts (Liu *et al*., 2015). In another study, NO and other volatile stress marker metabolites (e.g. lipoxygenase products) have been revealed to be emitted from the shoot of tree seedlings exposed to root zone waterlogging (Copolovici & Niinemets, 2010). Additionally, stomatal conductance negatively correlates with NO concentration and NO flux within the seedlings (Copolovici & Niinemets, 2010). Overall, the results of these studies suggest that NO is a root-to-shoot mobile signal molecule in plants exposed to root-site hypoxic stress (Fig. 2).

To further support the hypothesis regarding the interorgan mobility of NO and related species, NO/RNS have been detected in vascular tissues of different plant species during different conditions (Fig. 2). There is clear evidence for the endogenous production and mobility of NO and *S*-nitrosothiols (SNO) in vascular bundles in both the phloem and xylem, and independently of the cell differentiation state (Gabaldón *et al*., 2005). Indeed, apart from both the phloem and xylem acting as primary sites of NO production (Gabaldón *et al*., 2005), they may harbour NO/RNS-mediated long-distance signalling pathways (Besson-Bard *et al*., 2008; Dempsey & Klessig, 2012; Gaupels & Corina Vlot, 2012; Lucas *et al*., 2013; Gaupels *et al*., 2017). Thus, NO and RNS have been detected in vascular bundles of different plant species (Gabaldón *et al*., 2005) and under a range of stress conditions (Valderrama *et al*., 2007; Corpas *et al*., 2008; Tanou *et al*., 2009) with the phloem being particularly well-equipped with NO-generating sources (Gaupels *et al*., 2008). It is worth mentioning that Phytogbs with putative NO metabolizing role have been detected in vascular bundles and cells associated with the plant vascular system in several species (Bogusz *et al*., 1990; Jacobsen-Lyon *et al*., 1995; Arechaga-Ocampo *et al*., 2001; Lira-Ruan *et al*., 2001; Ross *et al*., 2001; Parent *et al*., 2008). Additionally, the expression and localization of globins have been recently described in Medicago, and globins were observed in the cytosol of meristem and vascular bundle cells and suggested to regulate NO levels in response to oxygen concentrations (Villar *et al*., 2020). GSNO has been localised in vascular tissues, collenchyma cells and epidermal cells (Barroso *et al*., 2006; Chaki *et al*., 2011a,b), which implies this molecule being considered a long-distance mobile NO signal in plants (Espunya *et al*., 2012). Indeed, the presence of endogenous GSNO in vascular tissues under basal conditions and its regulation in response to stress (Barroso *et al*., 2006; Valderrama *et al*., 2007; Chaki *et al*., 2011a,b) suggest a function as a signal molecule because it would be ready to travel throughout the plant in response to external signals (Espunya *et al*., 2012). Hence, it is worth mentioning that the phloem is able to propagate redox messengers, such as ROS and RNS, during plant defence (Gaupels *et al*., 2017), and GSNO is involved as a key player in the systemic response, such as mechanical damage stress. In this case, mechanical wound damage increases GSNO content in injured and systemic leaves, first in vascular tissue and then in parenchyma cells (Espunya *et al*., 2012). In the same vein, studies

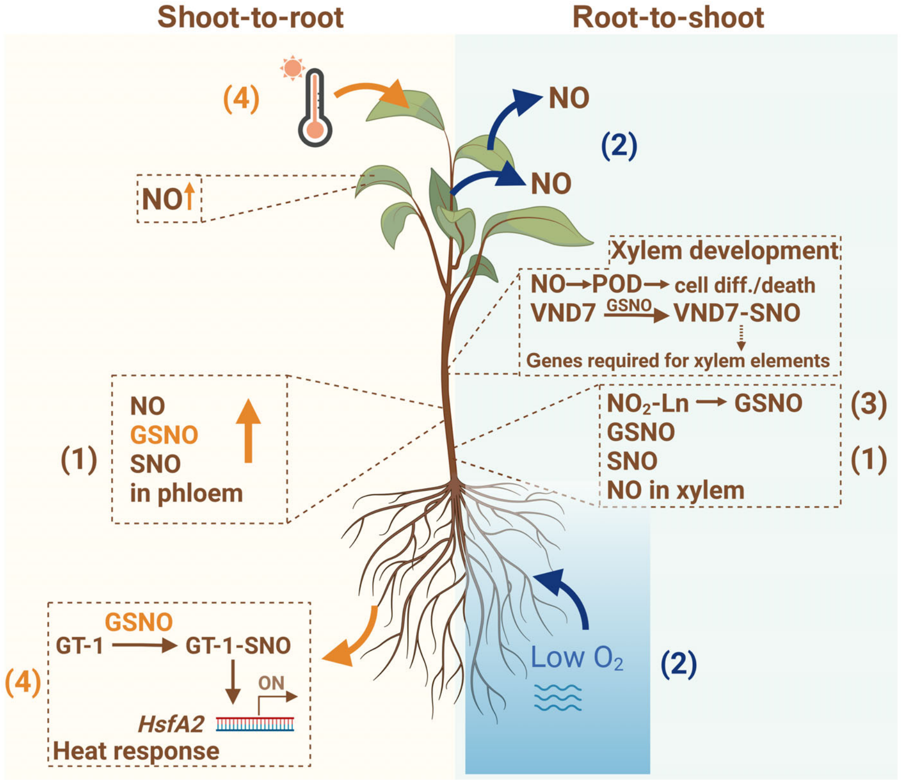

**Fig. 2** Summary of the present knowledge about the *in planta* long-distance signalling mediated by NO and related reactive nitrogen species. (1) The presence of RNS (e.g. NO, GSNO, SNO) in the vascular system, (2) Low oxygen supplementation of the root system results in NO emission from the shoot, (3) $NO_2$-Ln translocates from root to shoot and forms GSNO, (4) Heat stress induces GSNO formation in the phloem which is accompanied by *S*-nitrosation events and heat responses in the root. Additionally, NO/GSNO is involved in xylem development. GSNO, *S*-nitrosoglutathione; NO, nitric oxide; $NO_2$-Ln, nitro-linolenic acid; POD, catalase-insensitive basic peroxidase; SNO, *S*-nitrosothiols; VND7, VASCULAR-RELATED NAC-DOMAIN7.

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conducted by applying wound stress and high-temperature stress in sunflower hypocotyls have also shown a redistribution pattern insofar as the endogenous GSNO located mainly in vascular tissues is redistributed after establishing both stress situations to the cortex and epidermal cells (Chaki *et al*., 2011a,b). This behaviour clearly indicates the involvement of GSNO/SNO in signal transmission from injured tissues to the rest of the plant via vascular tissue during the adaptive response of plants to stress conditions (Espunya *et al*., 2012; Houmani *et al*., 2018). In this context, GSNO can be considered to play a central role in NO-dependent signal transduction by acting as a fundamental modulator of NO/SNO metabolism in the plant stress response.

## Direct evidences for NO/RNS as interorgan signals

Although studies on the functional role of NO in plants have focussed mainly on post-translational modifications (PTMs) of NO, research on nitrated fatty acids ($NO_2$-FA), generated from the interaction between unsaturated fatty acids and species derived from NO, is growing. Their specific role as key signalling molecules has been established during plant development (Aranda-Caño *et al*., 2022), defence response against abiotic stress conditions (Mata-Pérez *et al*., 2016, 2017), and recently on the profile of lipid accumulation during embryonic development in Arabidopsis through $NO_2$-FA-dependent *S*-nitrosation of the transcription factor bZIP67, a master regulator during seed maturation programs (Sánchez-Vicente *et al*., 2024). Lately, endogenous $NO_2$-FAs storage biomolecules, such as nitro-linolenic acid ($NO_2$-Ln), nitro-oleic acid ($NO_2$-OA) and nitro-linoleic acid ($NO_2$-LA), have been identified in *Arabidopsis thaliana* (Aranda-Caño *et al*., 2022). In relation to its ability to act as a NO donor (Begara-Morales *et al*., 2021; Di Fino *et al*., 2021), the relevance of $NO_2$-Ln in NO signalling also has been recently established because this lipid molecule is able to move through the plant and also has the ability to generate GSNO both *in vitro* and *in vivo* in *A. thaliana* (Mata-Pérez *et al*., 2020). The incubation of Arabidopsis roots with $^{15}NO_2$-Ln has allowed the detection of labelled $^{15}NO_2$-Ln and $GS^{15}NO$ in leaves, which confirms that $NO_2$-Ln is able to travel through the plant and contribute directly to GSNO generation *in vivo* (Mata-Pérez *et al*., 2020) (Fig. 2).

Recently, GSNO as a phloem-mobile signal has been shown to participate in the perception of heat at the whole plant level. He *et al*. (2022) revealed that heat stress induces the transcriptional activation of *HsfA2* at the shoot apex and in the whole plant. Heat treatment induces NO burst in the shoot apex and inflorescence apex and strong NO-related fluorescence was detected also in the phloem of stems. Moreover, the level of GSNO in the phloem sap is notably increased by heat treatment and NO mediates transcriptional activation of *HsfA2* in response to heat stress. Regarding the molecular mechanism of NO action, He *et al*. (2022) revealed that *S*-nitrosation of the trihelix transcription factor GT-1 by GSNO promotes its binding to the promoter of *HsfA2* in response to heat stress. These data elegantly support the role of GSNO as a long-distance signal moving through the vascular system and transmitting whole-plant responses to heat (Fig. 2).

## NO contributes to interorgan signalling by mediating xylem development

Developmental plasticity of the vasculature in response to stresses is of key importance for long-distance transport of signals to help plant stress endurance (Li *et al*., 2021). In addition to the fact that NO itself is a mobile signal, it plays a further role in the effective interorgan communication of the plant. Early pharmacological data indicate the necessity of NO for tracheary element differentiation and programmed cell death in *Zinnia elegans* model systems (Gabaldón *et al*., 2005; Neill, 2005). Furthermore, the NO regulation of catalase-insensitive activity of basic peroxidases may be a programmed event during xylem differentiation and cell death (Barceló *et al*., 2002*)*. Recently, the involvement of protein *S*-nitrosation in the regulation of xylem vessel cell differentiation in Arabidopsis has been highlighted (Kawabe *et al*., 2018). This indicates that GSNO/GSNOR is crucial in regulating xylem differentiation through *S*-nitrosation of VASCULAR-RELATED NAC-DOMAIN7 (VND7), a NAC-domain transcription factor that modulates the expression of the genes required for the formation of xylem vascular elements. Accordingly, VND7 nitrosation could be responsible for the defective formation of the ectopic and endogenous xylem vessels observed in GSNOR-defective mutant plants (*Atgsnor1-3*). This organ-specific regulation of xylem vessel formation could be a consequence of GSNO and total SNO accumulation in GSNOR-defective mutants, given that GSNO is able to mediate the organ-specific regulation of its target genes (Begara-Morales *et al*., 2014b). These findings implicate the interplay between GSNOR-mediated denitrosation, transcription factors and hormones in the complex network that regulates vascular tissue formation and, ultimately, plant growth.

## Inter- and intraorgan signalling by the interaction between NO and hydrogen sulphide ($H_2S$)

$H_2S$ has emerged as a new signalling molecule reminiscent of how the study of NO in plants began. Thus, in the nineties, it was proved that $H_2S$, which was considered to be toxic thus far, was generated by animal cells where it displayed signalling potentialities in the neuronal system (Abe & Kimura, 1996). Then, it was reported that plant cells also had the capacity of generating $H_2S$, where this molecule can exert diverse functions in seed germination, root formation, plant growth and development, leaf senescence, flowering, and fruit ripening (Ziogas *et al*., 2018; Corpas *et al*., 2019a,b; González-Gordo *et al*., 2020; Mishra *et al*., 2021).

NO and $H_2S$ are lipophilic so they can diffuse across cell membranes. Furthermore, NO can react with $H_2S$ and generate nitrous acid (HSNO) (Fig. 3a), which is the smallest nitrosothiol that diffuses through cell membranes, thus extending its effect to other organs. HSNO can also be generated through transnitrosation with GSNO (Fig. 3a) (Marcolongo *et al*., 2019). The information on HSNO in plants is inexistent due to its detection difficulty, but this is a promising area in plant research to explore.

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**(a)** **Chemical reactions**

$^{\bullet}NO + H_2S \rightarrow HSNO$ (thionitrous acid)

$H_2S + GSNO \rightarrow HSNO + GSH$ (transnitrosation)

**(b)** **oxiPTMs**

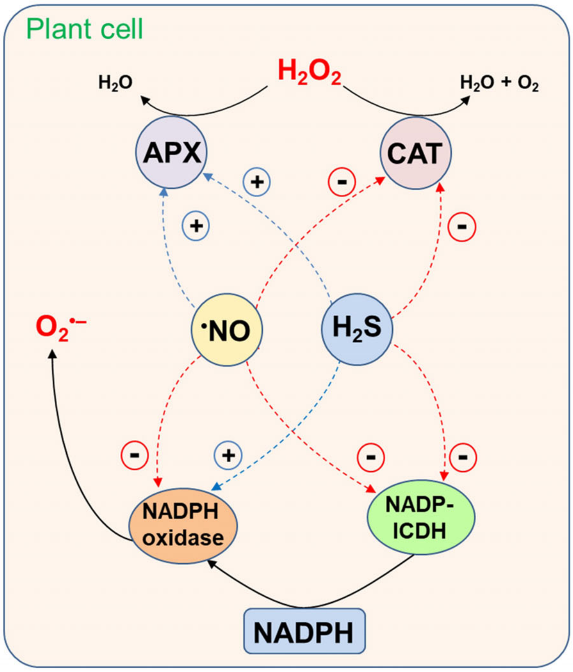

**Fig. 3** Crosstalk between $^{\bullet}NO$ and hydrogen sulphide ($H_2S$). (a) Direct chemical reactions between both gases. (b) Thiol-based oxidative posttranslational modifications (oxiPTMs) mediated by NO and $H_2S$ and some target proteins involved in ROS and redox metabolism in plant cells. Blue and red dashed arrows indicate positive or negative modulation of a given enzymatic activity, respectively. Black arrows depict enzymatic reactions where ROS and NADPH are involved. APX, ascorbate peroxidase; CAT, catalase; $H_2O_2$, hydrogen peroxide; NADP-ICDH, NADP-isocitrate dehydrogenase; $O_2^{\bullet-}$, superoxide radical; RBOHD, NADPH oxidase.

Likewise, NO and $H_2S$ may have common targets and regulate the production of each other. Thus, $H_2S$ modulates NO function during stomatal closure (Scuffi *et al.*, 2014), but NO can also affect the activity of $H_2S$-generating enzymes, suggesting that NO functions as an upstream signal for $H_2S$ generation (Muñoz-Vargas *et al.*, 2023). Besides, RNS and reactive sulfur species (RSS) derived from NO and $H_2S$, respectively, can compete and react with cysteine residues affecting protein functions through thiol-based oxidative PTMs (oxiPTMs) (Corpas *et al.*, 2022), either *S*-nitrosation (promoted by RNS) or persulfidation (triggered by RSS). Fig. 3(b) illustrates some examples of common protein targets showing biochemical links among ROS/RNS/RSS.

In the case of the cytosolic ascorbate peroxidase (cAPX), this enzyme is a target of both *S*-nitrosation and persulfidation causing a positive modulation in its activity. Thus, in cAPX from pea leaves, Cys32 was the target residue for *S*-nitrosation (Begara-Morales *et al.*, 2014a), but this residue was also prone to be persulfidated in cAPX from Arabidopsis (Aroca *et al.*, 2015). On the contrary, in the case of catalase, which is a peroxisomal enzyme, an opposite effect has been described since both *S*-nitrosation and persulfidation provoke a negative modulation of the enzyme activity (Palma *et al.*, 2020). Studies on blind docking of GSNO to *Arabidopsis thaliana* catalases suggested that Cys420 was the putative target of *S*-nitrosation; however, in the case of persulfidation, the susceptible residue has not been yet identified. Recent findings have also indicated that pepper catalase is also a target of tyrosine nitration leading to its inhibition, particularly at residues Tyr348 and Tyr360 (González-Gordo *et al.*, 2024).

In the case of the Arabidopsis, the $O_2^{\bullet-}$-generating NADPH oxidase (AtRBOHD), which is involved in different processes such as plant immunity or stomatal closure, *S*-nitrosation at Cys 890 was demonstrated to abolish its enzymatic activity (Yun *et al.*, 2011), whereas persulfidation on Cys825 and Cys890 of AtRBOHD enhanced its activity (Shen *et al.*, 2020) and, consequently, its capacity to increase the $O_2^{\bullet-}$ content.

The NADPH-generating enzymatic systems include a diversified group of enzymes such as the ferredoxin-NADP reductase, NADP-glyceraldehyde-3-phosphate dehydrogenase, NADP-dependent malic enzyme, NADP-dependent isocitrate dehydrogenase (NADP-ICDH), and two enzymes of the oxidative pentose phosphate pathway designated as glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase. Many of them are targets of NO and $H_2S$ (for a wider review, see Corpas *et al.*, 2021) and, accordingly, both gases can regulate the redox cellular state through the NADPH metabolism. Among the indicated systems, one of the most studied is the NADP-isocitrate dehydrogenase (NADP-ICDH) from different plant species which is a target of tyrosine nitration, *S*-nitrosation and persulfidation, triggering in all cases its inhibition (Begara-Morales *et al.*, 2013; Muñoz-Vargas *et al.*, 2018).

## NO/RNS participation in intraorgan systemic responses

Systemic acquired resistance (SAR) is a long-lasting systemic defence induced after a hypersensitive response (HR) to avirulent pathogens. SAR is effective against a broad spectrum of pathogens including viruses, bacteria, fungi and oomycetes (Durrant & Dong, 2004). Key signalling actors contributing to SAR have been identified, amongst them salicylic acid (SA) and methyl salicylate, the positive regulator protein Non-Expresser of PR genes 1 (NPR1), the lipid transfer protein Defective in Induced Resistance 1 (DIR1), glycerol-3-phosphate (G3P), azelaic acid (AzA), pipecolic acid (Pip) and N-hydroxy-pipecolic acid (Shah *et al.*, 2014; Wendehenne *et al.*, 2014; Gao *et al.*, 2021). Importantly, SAR is thought to involve the synthesis of mobile signals during the primary infection and their subsequent transport from the infected tissue to systemic noninfected parts of the plant (also called distal parts), thus allowing efficient resistance against future aggression. Recent studies provided arguments that SA, AzA, G3P and Pip act as such mobile signals during SAR. Experimental findings indicate that SA moves preferentially through the apoplast while AzA and

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G3P move through the plasmodesmata (Kachroo & Kachroo, 2020). In addition, SA, AzA, G3P and Pip were detected in the petiole exudates collected from leaves inoculated with avirulent pathogens (Wang *et al.*, 2018).

Several studies reported the contribution of NO and GSNO to SAR. For instance, Espunya *et al.* (2012) provided evidence that in *A. thaliana* SA-induced SAR requires GSNO spreading from vascular tissue in distal leaves. In addition, the expression of the defence gene *PR1* was impaired in plants overexpressing GSNOR while it was amplified in GSNOR-antisense plants. Accordingly, local application of NO donors to *A. thaliana* leaves was shown to reduce the growth of the virulent pathogen *Pseudomonas syringae* pv tomato (Pst) DC3000 in distal leaves (Wang *et al.*, 2014). Furthermore, SAR was abolished by NO scavengers (Song & Goodman, 2001; Wang *et al.*, 2014). In resistant tomato genotypes, an increase in NO production in distal uninoculated leaves was observed after local infection with a biotrophic pathogen, tomato powdery mildew (Piterková *et al.*, 2009). The increased NO and also hydrogen peroxide levels coincided with the development of HR symptoms on resistant plant leaves. In the same tomato pathosystem, up- and downregulation of GSNOR activity were found on the systemic level (Jahnová *et al.*, 2020). GSNOR activity in susceptible and moderately resistant tomatoes strongly decreased while remaining unchanged in the resistant genotype in the 1st leaf above the inoculation site. By contrast, GSNOR activities in the susceptible and resistant genotypes increased in 1st leaf below the infection site. Increased levels of *S*-nitrosothiols in vascular bundles of both proximal and distal leaves to the site infected with *Phythophtora infestans* confirms their important signalling role in tomato systemic responses also to hemibiotrophic pathogens (Jedelská *et al.*, 2021).

The link between NO and the induction of SAR has been further established by the finding that NO modulates the activity of NPR-1 by *S*-nitrosation (Tada *et al.*, 2008) and other immune-related proteins such as the transcription factors TGA1 (Lindermayr *et al.*, 2010) and the chloroplast carbonic anhydrase enzyme Salicylic Acid-Binding Protein 3 (SABP3; Wang *et al.*, 2009). The investigations of Wang *et al.* (2014, 2018) were also particularly relevant. First, the authors demonstrated that the avirulent pathogen *Pseudomonas syringae* pv *tomato* (Pst) avrRpt2 triggers a transient NO production both in the infected and in the distal leaves, although to a lesser extent. Second, they found that once produced downstream of the SAR regulator Pip, NO is part of a SA-independent pathway in which it promotes the production of ROS. In turn, ROS catalyse the oxidation of free C18 unsaturated fatty acids, thus leading to AzA generation. Next, this latter favours the production of G3P through the upregulation of G3P biosynthesis-related genes. This pathway occurs in the infected leaves and is also initiated in the distal ones in response to mobile signals including G3P and SA (Kachroo & Kachroo, 2020; Fig. 4).

## Interplant NO signalling

It has recently been demonstrated that ROS waves play a significant role in plant-to-plant signalling, enabling systemic acquired acclimation between a plant subjected to local wounding or light stress and its neighbour in physical contact through their touching leaves (Szechyńska-Hebda *et al.*, 2022) or through a parasite plant (Fichman *et al.*, 2024). Besides ROS, also NO might act as an *ex planta* signalling molecule, enabling external leaf-to-leaf, root-to-leaf but also plant-to-plant communication.

The amount of NO released from plants can vary depending on various factors such as plant species, environmental conditions and physiological state. Generally, plants release small amounts of NO compared with other signalling molecules such as ethylene or auxins. However, even small amounts of NO can have significant effects on plant growth and development (Fig. 4).

NO emission from plant species exhibited large variations, ranging from 0 to 41.7 nmol $m^{-2}$ $h^{-1}$, and depends on leaf N content, net photosynthetic rate and estimated photosynthetic N use efficiency (Chen *et al.*, 2015). Especially, the amount of available nitrate and nitrite seems to affect NO production. For example, sunflowers adapted to constant nitrate nutrition, usually emit no significant amounts of NO in the dark. However, in light up to 2 nmol NO $g^{-1}$ FW $h^{-1}$ are released (Rockel *et al.*, 2002). High concentrations of nitrate have an inhibitory effect on NO production, whereas nitrite seems to be a substrate for xanthine oxidase, which was shown to catalyse the reduction of nitrite to NO under anaerobic conditions (Godber *et al.*, 2000).

However, because several stressors induce NO formation in plants, the release is often higher during environmental changes. In Arabidopsis, transient exposure to high light led to a substantial increase in the emission of NO (approximately five-fold) in comparison with low light conditions (Ageeva-Kieferle *et al.*, 2021). In barley, NO emission from detached leaves/roots and whole plants treated with 60 mM nitrate was relatively higher under anaerobic condition (Chen *et al.*, 2010). Interestingly, under darkness and anaerobic conditions NO emission from detached barley leaves is remarkably induced. On the contrary, NO emission from detached roots and whole plants was relatively higher in light (Chen *et al.*, 2010). Welle *et al.* (2024) demonstrated that tomato, tobacco and barley roots exhibit NO emissions in a highly oxygen-dependent manner. All investigated plant species reached a constant rate of NO release after 3–5 h exposure to low-oxygen conditions (Welle *et al.*, 2024). It is likely that, at least partially, the decreased production and levels of superoxide, a highly efficient NO scavenger, may contribute to higher NO emmisions from plant tissues under low oxygen conditions (Karpinska & Foyer, 2024). Besides high light and low-oxygen conditions, also treatment with pathogens results in enhanced NO emission. Tobacco leaves infiltrated with suspensions of HR-inducing *P. syringae* pv *phaseolicola* results in release of 3 nmol NO $g^{-1}$ FW $h^{-1}$ within 2 h (Mur *et al.*, 2012).

Although the emission of NO by plants has been demonstrated, it is not clear whether this released NO functions as an external leaf-to-leaf, root-to-leaf and/or plant-to-plant signal. There is a limited number of studies that analysed the effects of external gaseous NO on plant transcriptome (Palmieri *et al.*, 2008; Kuruthukulangarakoola *et al.*, 2017), plant growth (Leshem & Haramaty, 1996; Jin *et al.*, 2009; Takahashi *et al.*, 2014; Kuruthukulangarakoola *et al.*, 2017), fruit ripening (González-Gordo *et al.*, 2019; Zuccarelli *et al.*, 2021) and postharvest life of fresh horticultural

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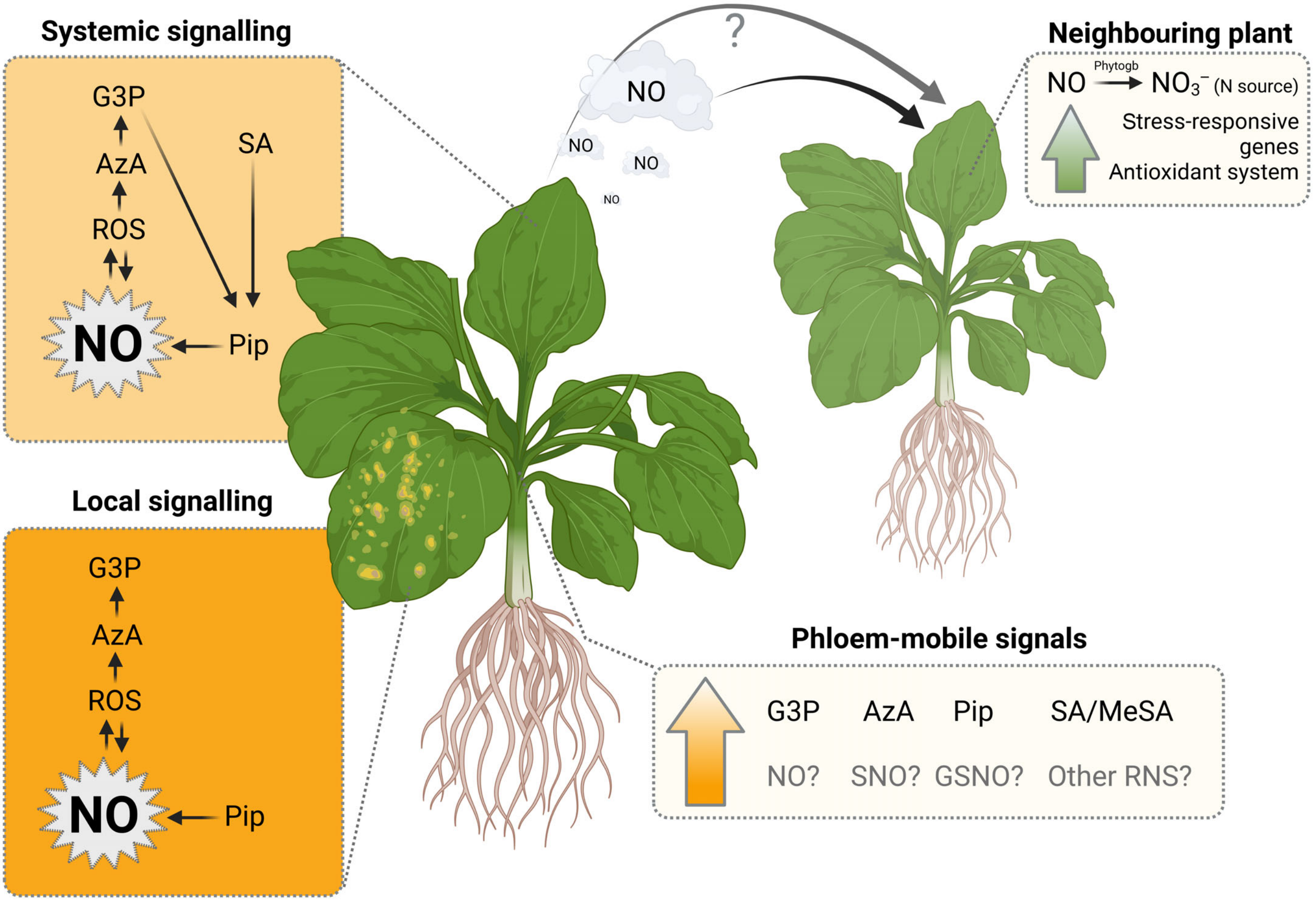

**Fig. 4** Summary of the present knowledge about the involvement of NO in local and systemic defence signalling and interplant signalling. Question marks indicate experimentally not yet verified possibilities. See explanations in the text. AzA, azelaic acid; G3P, glycerol-3-phosphate; GSNO, *S*-nitrosoglutathione; MeSA, methyl salicylate; N, nitrogen; NO, nitric oxide; $NO_3^-$, nitrate; Phytogb, phytoglobin; Pip, pipecolic acid; RNS, reactive nitrogen species; ROS, reactive oxygen species; SA, salicylic acid; SNO, *S*-nitrosothiols.

products (Leshem & Haramaty, 1996). However, in all of these studies, much higher concentrations of gaseous NO (in the low ppm range) have been used for the treatment than are released by plants under natural conditions (in the low ppb range). Interestingly, besides a putative signalling function, up-taken gaseous NO can also be used as a N source via the activity of Phytogb enzymes, which oxidise NO to nitrate (Kuruthukulangarakoola *et al*., 2017; Zhang *et al*., 2019). On the transcript level, gaseous NO treatment results in significantly enhanced expression of genes involved in primary metabolic processes, such as photosynthesis and protein biosynthesis (Kuruthukulangarakoola *et al*., 2017). Moreover, stress-responsive genes as well as genes of the anti-oxidative system are induced (Palmieri *et al*., 2008; Kuruthukulangarakoola *et al*., 2017, Fig. 4). Too high concentrations of exogenous gaseous NO can also have negative effects on plant development. In barley, for example, treatment with >800 ppb of NO results in reduced dry matter weight, spikes and kernel number per plants (Zhang *et al*., 2019). Most likely, this is not only a direct effect of high NO, but also the effect of NO-related oxidation products, such as $NO_2$ (Kasten *et al*., 2016).

In summary, the signalling function of released NO on a neighbouring plant still needs to be investigated. Systems are established for analysing the effect of released volatile organic compounds from a ‘sender plant’ on a neighboring ‘receiver plant’ (Rosenkranz *et al*., 2021). Since plants emit a huge number of compounds, it is also not easy to analyse the function of a single compound in a plant-to-plant signalling system. The use of chemical traps, similar to those developed for methyl salicylate (MeSA, Shulaev *et al*., 1997), may prove an appealing avenue for elucidating the function of NO in plant-to-plant signalling. A chemical trap based on subsequent nitrite detection by Griess reagent has been described by Vitecek *et al*. (2008). However, it should be noted that NO in the air phase is much less stable compared to compounds such as MeSA. Of course, first of all the effect of low physiological exogenous concentrations of NO on plants needs to be investigated. Only these results will give hints to a plant-to-plants signalling function of NO. If low gaseous concentrations (in the low ppb range) have an effect on plant physiology, also anthropogenic and other environmental sources of NO, such as microbial nitrification and

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denitrification in soils (Pilegaard, 2013), burning of forests and fossil fuels or lightning, have to be considered, since this atmospheric NO could then also act as signalling molecule and affect plant physiology. Moreover, it has to be highlighted that the stability of NO in the atmosphere strongly depends on the concentration of other reactive compounds, for example ozone or volatile organic compounds, which oxidises NO to $NO_2$ (Kasten *et al.*, 2017).

## Conclusion and recommendations for future directions

For sessile organisms such as plants, coordinated communication between above-ground and below-ground organs is essential to survive in a stressful environment. How shoot- and root-related signals are synchronised using mobile chemical compounds is an emerging field of research. Indirect and direct evidence supports that NO and its more stable derivatives (GSNO, $NO_2$-Ln) are mobile in vascular tissue. The participation of NO/RNS in interorgan signalling is implied by their presence in phloem and xylem tissues and by the NO generation in the shoot of plant affected by root zone stresses. Direct evidence regarding interorgan NO/RNS signalling has been provided by studies in which $NO_2$-Ln was traced with isotopic labelling within the plant and GSNO level increase due to heat stress has been detected in the phloem sap (Fig. 2). Further studies should support and confirm that NO and its derivatives mediate whole-plant signalling during diverse environmental conditions. NO has a beneficial effect on the development of the vascular system enabling interorgan signal transmission, which may support practice-oriented research towards promising novel strategies for crop improvement. Evidence supports the functional crosstalk among NO and $H_2S$ and their respective metabolites (Fig. 3), as they can exert their regulatory function in places far from their production, and point towards new avenues of focusing on the involvement of NO and $H_2S$ in the plant inter- and intraorgan communication. Studies highlight a signalling function of NO during SAR, both at the site of infection and in distal parts of plants under the control of SAR mobile signals (Fig. 4). Although suggested in several studies (Gaupels *et al.*, 2017), whether NO and GSNO might also constitute a SAR mobile signal remains to be demonstrated. Furthermore, the perspective should be broadened and plant NO should be considered as a plant-to-plant signal (Fig. 4), which, similar to volatile organic compounds, may also mediate communication between plants and between plants and beneficial/pathogenic microorganisms (Ma *et al.*, 2020). Overall, the available data establish the multifaceted role of NO and related species in interorgan, intraorgan and interplant signalling and open up new perspectives in plant stress physiology research. An efficient inter-organ signal could be a selection marker for the identification of crops with a higher capacity for adaptation to environmental perturbations. In the future, we can imagine targeting this NO-dependent communication between organs by adding biostimulants to plants to improve their resilience to biotic stresses and abiotic stress situations generated by extreme climate change.

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## Competing interests

None declared.

## Author contributions

ZK conceptualised and wrote the original draft, revised the manuscript and designed the figures. JBB, AB, FJC, JGK, JTH, CL, JMP, MP, DW and GJL contributed to the text of the manuscript. All authors have read and approved the manuscript.

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## References

**Abe K, Kimura H. 1996.** The possible role of hydrogen sulfide as an endogenous neuromodulator. *The Journal of Neuroscience* **16**: 1066–1071.

**Ageeva-Kieferle A, Georgii E, Winkler B, Ghirardo A, Albert A, Hüther P, Mengel A, Becker C, Schnitzler JP, Durner J *et al.* 2021.** Nitric oxide coordinates growth, development, and stress response via histone modification and gene expression. *Plant Physiology* **187**: 336–360.

**Aranda-Caño L, Valderrama R, Chaki M, Begara-Morales JC, Melguizo M, Barroso JB. 2022.** Nitrated fatty-acids distribution in storage biomolecules during *Arabidopsis thaliana* development. *Antioxidants* **11**: 1869.

**Arasimowicz-Jelonek M, Floryszak-Wieczorek J, Suarez S, Doctorovich F, Sobieszczuk-Nowicka E, Bruce King S, Milczarek G, Rębiś T, Gajewska J, Jagodzik P *et al.* 2023.** Discovery of endogenous nitroxyl as a new redox player in *Arabidopsis thaliana*. *Nature Plants* **9**: 36–44.

**Arechaga-Ocampo E, Saenz-Rivera J, Sarath G, Klucas RV, Arredondo-Peter R. 2001.** Cloning and expression analysis of hemoglobin genes from maize (*Zea mays* ssp. mays) and teosinte (*Zea mays* ssp. parviglumis). *Biochimica et Biophysica Acta* **1522**: 1–8.

**Aroca A, Serna A, Gotor C, Romero LC. 2015.** *S*-sulfhydration: a cysteine posttranslational modification in plant systems. *Plant Physiology* **168**: 334–342.

**Barceló AR, Pomar F, Ferrer MA, Martínez P, Ballesta MC, Pedreño MA. 2002.** *In situ* characterisation of a NO-sensitive peroxidase in the lignifying xylem of *Zinnia elegans*. *Physiologia Plantarum* **114**: 33–40.

**Barroso JB, Corpas FJ, Carreras A, Rodríguez-Serrano M, Esteban FJ, Fernández-Ocaña A, Chaki M, Romero-Puertas MC, Valderrama R, Sandalio LM *et al.***

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**2006.** Localization of *S*-nitrosoglutathione and expression of *S*-nitrosoglutathione reductase in pea plants under cadmium stress. *Journal of Experimental Botany* **57**: 1785–1793.

**Becana M, Yruela I, Sarath G, Catalan P, Hargrove MS. 2020.** Plant hemoglobins: a journey from unicellular green algae to vascular plants. *New Phytologist* **227**: 1618–1635.

**Beckman JS, Koppenol WH. 1996.** Nitric oxide, superoxide, and peroxynitrite: the good, the bad, and ugly. *The American Journal of Physiology* **271**: C1424–C1437.

**Begara-Morales JC, Chaki M, Sánchez-Calvo B, Mata-Pérez C, Leterrier M, Palma JM, Barroso JB, Corpas FJ. 2013.** Protein tyrosine nitration in pea roots during development and senescence. *Journal of Experimental Botany* **64**: 1121–1134.

**Begara-Morales JC, Mata-Pérez C, Padilla MN, Chaki M, Valderrama R, Aranda-Caño L, Barroso JB. 2021.** Role of electrophilic nitrated fatty acids during development and response to abiotic stress processes in plants. *Journal of Experimental Botany* **72**: 917–927.

**Begara-Morales JC, Sánchez-Calvo B, Chaki M, Valderrama R, Mata-Pérez C, López-Jaramillo J, Padilla MN, Carreras A, Corpas FJ, Barroso JB. 2014a.** Dual regulation of cytosolic ascorbate peroxidase (APX) by tyrosine nitration and S-nitrosylation. *Journal of Experimental Botany* **65**: 527–538.

**Begara-Morales JC, Sánchez-Calvo B, Luque F, Leyva-Pérez MO, Leterrier M, Corpas FJ, Barroso JB. 2014b.** Differential transcriptomic analysis by RNA-Seq of GSNO-responsive genes between Arabidopsis roots and leaves. *Plant & Cell Physiology* **55**: 1080–1095.

**Besson-Bard A, Pugin A, Wendehenne D. 2008.** New insights into nitric oxide signalling in plants. *Annual Review of Plant Biology* **59**: 21–39.

**Bogusz D, Llewellyn DJ, Craig S, Dennis ES, Appleby CA, Peacock WJ. 1990.** Nonlegume hemoglobin genes retain organ-specific expression in heterologous transgenic plants. *Plant Cell* **2**: 633–641.

**Buhtz A, Kolasa A, Arlt K, Walz C, Kehr J. 2004.** Xylem sap protein composition is conserved among different plant species. *Planta* **219**: 610–618.

**Chaki M, Valderrama R, Fernández-Ocaña AM, Carreras A, Gómez-Rodríguez MV, López-Jaramillo J, Begara-Morales JC, Sánchez-Calvo B, Luque F, Leterrier M *et al.* 2011a.** High temperature triggers the metabolism of *S*-nitrosothiols in sunflower mediating a process of nitrosative stress which provokes the inhibition of ferredoxin–NADP reductase by tyrosine nitration. *Plant, Cell & Environment* **34**: 1803–1818.

**Chaki M, Valderrama R, Fernández-Ocaña AM, Carreras A, Gómez-Rodríguez MV, Pedrajas JR, Begara-Morales JC, Sánchez-Calvo B, Luque F, Leterrier M *et al.* 2011b.** Mechanical wounding induces a nitrosative stress by down-regulation of GSNO reductase and an increase in *S*-nitrosothiols in sunflower (*Helianthus annuus*) seedlings. *Journal of Experimental Botany* **62**: 1803–1813.

**Chamizo-Ampudia A, Sanz-Luque E, Llamas Á, Ocaña-Calahorro F, Mariscal V, Carreras A, Barroso JB, Galván A, Fernández E. 2016.** A dual system formed by the ARC and NR molybdoenzymes mediates nitrite-dependent NO production in Chlamydomonas. *Plant, Cell & Environment* **39**: 2097–2107.

**Chen J, Wang C, Wu F-H. 2015.** Variation of nitric oxide emission potential in plants. *Journal of Plant Ecology* **8**: 313–320.

**Chen J, Xiao Q, Wu FH, Pei ZM, Wang J, Wu YG, Zheng HL. 2010.** Nitric oxide emission from barley seedlings and detached leaves and roots treated with nitrate and nitrite. *Plant, Soil and Environment* **56**: 201–208.

**Cooney RV, Harwood PJ, Custer LJ, Franke AA. 1994.** Light-mediated conversion of nitrogen dioxide to nitric oxide by carotenoids. *Environmental Health Perspectives* **102**: 460–462.

**Copolovici L, Niinemets Ü. 2010.** Flooding induced emissions of volatile signalling compounds in three tree species with differing waterlogging tolerance. *Plant, Cell & Environment* **33**: 1582–1594.

**Corpas FJ, Barroso JB, González-Gordo S, Muñoz-Vargas MA, Palma JM. 2019a.** Hydrogen sulfide: a novel component in Arabidopsis peroxisomes which triggers catalase inhibition. *Journal of Integrative Plant Biology* **61**: 871–883.

**Corpas FJ, Chaki M, Fernández-Ocaña A, Valderrama R, Palma JM, Carreras A, Begara-Morales JC, Airaki M, del Río LA, Barroso JB. 2008.** Metabolism of reactive nitrogen species in pea plants under abiotic stress conditions. *Plant & Cell Physiology* **49**: 1711–1722.

**Corpas FJ, González-Gordo S, Cañas A, Palma JM. 2019b.** Nitric oxide and hydrogen sulfide in plants: which comes first? *Journal of Experimental Botany* **70**: 4391–4404.

**Corpas FJ, González-Gordo S, Palma JM. 2021.** Nitric oxide and hydrogen sulfide modulate the NADPH-generating enzymatic system in higher plants. *Journal of Experimental Botany* **72**: 830–847.

**Corpas FJ, González-Gordo S, Rodríguez-Ruiz M, Muñoz-Vargas MA, Palma JM. 2022.** Thiol-based oxidative posttranslational modifications (OxiPTMs) of plant proteins. *Plant & Cell Physiology* **63**: 889–900.

**Daigle R, Rousseau JA, Guertin M, Lagüe P. 2009.** Theoretical investigations of nitric oxide channeling in *Mycobacterium tuberculosis* truncated hemoglobin. *Biophysics Journal* **97**: 2967–2977.

**De Schepper V, De Swaef T, Bauweraerts I, Steppe K. 2013.** Phloem transport: a review of mechanisms and controls. *Journal of Experimental Botany* **64**: 4839–4850.

**Dempsey DMA, Klessig DF. 2012.** SOS – too many signals for systemic acquired resistance? *Trends in Plant Science* **17**: 538–545.

**Dent MR, DeMartino AW. 2023.** Nitric oxide and thiols: chemical biology, signalling paradigms and vascular therapeutic potential. *British Journal of Pharmacology*. doi: 10.1111/bph.16274.

**Di Fino L, Di Palma AA, Perk EA, García-Mata C, Schopfer FJ, Laxalt AM. 2021.** Nitro-fatty acids: electrophilic signalling molecules in plant physiology. *Planta* **254**: 120.

**Durrant WE, Dong X. 2004.** Systemic acquired resistance. *Annual Review of Phytopathology* **42**: 185–209.

**Espunya MC, De Michele M, Gomez-Cadenas A, Martınez C. 2012.** *S*-nitrosoglutathione is a component of wound- and salicylic acid-induced systemic responses in *Arabidopsis thaliana*. *Journal of Experimental Botany* **63**: 3219–3227.

**Fichman Y, Peláez-Vico MÁ, Mudalige AK, Lee HO, Mittler R, Park SY. 2024.** Rapid plant-to-plant systemic signaling via a Cuscuta bridge. *Plant Physiology* **18**: kiae339.

**Fichman Y, Zandalinas SI, Peck S, Luan S, Mittler R. 2022.** HPCA1 is required for systemic reactive oxygen species and calcium cell-to-cell signalling and plant acclimation to stress. *Plant Cell* **34**: 4453–4471.

**Freschi L. 2013.** Nitric oxide and phytohormone interactions: current status and perspectives. *Frontiers in Plant Science* **4**: 398.

**Gabaldón C, Gómez Ros LV, Pedreño MA, Barceló AR. 2005.** Nitric oxide production by the differentiating xylem of *Zinnia elegans*. *New Phytologist* **165**: 121–130.

**Gao H, Guo M, Song J, Ma Y, Xu Z. 2021.** Signals in systemic acquired resistance of plants against microbial pathogens. *Molecular Biology Reports* **48**: 3747–3759.

**Gaupels F, Corina Vlot A. 2012.** Plant defense and long-distance signalling in the phloem. In: Thompson GA, van Bel AJE, eds. *Phloem: molecular cell biology, systemic communication, biotic interactions*. Wiley-Blackwell: Chichester, UK, 227–247.

**Gaupels F, Durner J, Kogel KH. 2017.** Production, amplification and systemic propagation of redox messengers in plants? The phloem can do it all! *New Phytologist* **214**: 554–560.

**Gaupels F, Furch ACU, Will T, Mur LAJ, Kogel KH, Van Bel AJE. 2008.** Nitric oxide generation in *Vicia faba* phloem cells reveals them to be sensitive detectors as well as possible systemic transducers of stress signals. *New Phytologist* **178**: 634–646.

**Godber BL, Doel JJ, Sapkota GP, Blake DR, Stevens CR, Eisenthal R, Harrison R. 2000.** Reduction of nitrite to nitric oxide catalyzed by xanthine oxidoreductase. *The Journal of Biological Chemistry* **275**: 7757–7763.

**González-Gordo S, Bautista R, Gonzalo Claros M, Cañas A, Palma JM, Corpas FJ. 2019.** Nitric oxide-dependent regulation of sweet pepper fruit ripening. *Journal of Experimental Botany* **70**: 4557–4570.

**González-Gordo S, López-Jaramillo J, Rodríguez-Ruiz M, Taboada J, Palma JM, Corpas FJ. 2024.** Pepper catalase: a broad analysis of its modulation during fruit ripening and by nitric oxide. *The Biochemical Journal* **481**: 883–901.

**González-Gordo S, Palma JM, Corpas FJ. 2020.** Appraisal of H2S metabolism in Arabidopsis thaliana: in silico analysis at the subcellular level. *Plant Physiology and Biochemistry* **155**: 579–658.

**Gow AJ, Stamler JS. 1998.** Reactions between nitric oxide and haemoglobin under physiological conditions. *Nature* **391**: 169–173.

**Groß F, Rudolf EE, Thiele B, Durner J, Astier J. 2017.** Copper amine oxidase 8 regulates arginine-dependent nitric oxide production in *Arabidopsis thaliana*. *Journal of Experimental Botany* **68**: 2149–2162.

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**Gupta KJ, Mur LAJ, Wany A, Kumari A, Fernie AR, Ratcliffe RG. 2020.** The role of nitrite and nitric oxide under low oxygen conditions in plants. *New Phytologist* **225**: 1143–1151.

**Hancock JT. 2019.** Considerations of the importance of redox state for reactive nitrogen species action. *Journal of Experimental Botany* **70**: 4323–4331.

**He NY, Chen LS, Sun AZ, Zhao Y, Yin SN, Guo FQ. 2022.** A nitric oxide burst at the shoot apex triggers a heat-responsive pathway in Arabidopsis. *Nature Plants* **8**: 434–450.

**Houmani H, Rodríguez-Ruiz M, Palma JM, Corpas FJ. 2018.** Mechanical wounding promotes local and long distance response in the halophyte *Cakile maritima* through the involvement of the ROS and RNS metabolism. *Nitric Oxide* **74**: 93–101.

**Jacobsen-Lyon K, Jensen EOJ, Ørgensen JE, Marcker KA, Peacock WJ, Dennis ES. 1995.** Symbiotic and nonsymbiotic hemoglobin genes of *Casuarina glauca*. *Plant Cell* **7**: 213–223.

**Jahnová J, Činčalová L, Sedlářová M, Jedelská T, Sekaninová J, Mieslerová B, Luhová L, Barroso JB, Petřivalský M. 2020.** Differential modulation of *S*-nitrosoglutathione reductase and reactive nitrogen species in wild and cultivated tomato genotypes during development and powdery mildew infection. *Plant Physiology and Biochemistry* **155**: 297–310.

**Jedelská T, Sedlářová M, Lochman J, Činčalová L, Luhová L, Petřivalský M. 2021.** Protein *S*-nitrosation differentially modulates tomato responses to infection by hemi-biotrophic oomycetes of *Phytophthora* spp. *Horticulture Research* **8**: 34.

**Jin CW, Du ST, Zhang YS, Tang C, Lin XY. 2009.** Atmospheric nitric oxide stimulates plant growth and improves the quality of spinach (*Spinacia oleracea*). *Annals of Botany* **104**: 9–17.

**Kachroo A, Kachroo P. 2020.** Mobile signals in systemic acquired resistance. *Current Opinion in Plant Biology* **58**: 41–47.

**Karpinska B, Foyer CH. 2024.** Superoxide signalling and antioxidant processing in the plant nucleus. *Journal of Experimental Botany* **9**: erae090.

**Kasten D, Durner J, Gaupels F. 2017.** Gas alert: the $NO_2$ pitfall during NO fumigation of plants. *Frontiers in Plant Science* **8**: 85.

**Kasten D, Mithöfer A, Georgii E, Lang H, Durner J, Gaupels F. 2016.** Nitrite is the driver, phytohormones are modulators while NO and $H_2O_2$ act as promoters of $NO_2$-induced cell death. *Journal of Experimental Botany* **67**: 6337–6349.

**Kawabe H, Ohtani M, Kurata T, Sakamoto T, Demura T. 2018.** Protein *S*-nitrosylation regulates xylem vessel cell differentiation in Arabidopsis. *Plant & Cell Physiology* **59**: 17–29.

**Kneeshaw S, Gelineau S, Tada Y, Loake GJ, Spoel SH. 2014.** Selective protein denitrosylation activity of Thioredoxin-h5 modulates plant Immunity. *Molecular Cell* **56**: 153–162.

**Kramer M, Ackelsberg EM. 2015.** Auxin metabolism rates and implications for plant development. *Frontiers in Plant Science* **6**: 150.

**Kumari A, Kaladhar VC, Yadav N, Singh P, Reddy K, Gupta KJ. 2023.** Nitric oxide regulates mitochondrial biogenesis in plants. *Plant, Cell & Environment* **46**: 2492–2506.

**Kuromori T, Fujita M, Takahashi F, Yamaguchi-Shinozaki K, Shinozaki K. 2022.** Inter-tissue and inter-organ signalling in drought stress response and phenotyping of drought tolerance. *The Plant Journal* **109**: 342–358.

**Kuruthukulangarakoola GT, Zhang J, Albert A, Winkler B, Lang H, Buegger F, Gaupels F, Heller W, Michalke B, Sarioglu H *et al.* 2017.** Nitric oxide-fixation by non-symbiotic haemoglobin proteins in *Arabidopsis thaliana* under N-limited conditions. *Plant, Cell & Environment* **40**: 36–50.

**Lancaster JR. 1997.** A tutorial on the diffusibility and reactivity of free nitric oxide. *Nitric Oxide* **1**: 18–30.

**Leshem YY, Haramaty E. 1996.** The characterisation and contrasting effects of the nitric oxide free radical in vegetative stress and senescence of *Pisum sativum* Linn. foliage. *Journal of Plant Physiology* **148**: 258–263.

**Li H, Testerink C, Zhang Y. 2021.** How roots and shoots communicate through stressful times. *Trends in Plant Science* **26**: 940–952.

**Lindermayr C, Sell S, Muller B, Leister D, Durner J. 2010.** Redox regulation of the NPR1-TGA1 system of *Arabidopsis thaliana* by nitric oxide. *Plant Cell* **22**: 2894–2907.

**Lira-Ruan V, Sarath G, Klucas H, Arredondo-Peter R. 2001.** Synthesis of hemoglobins in rice (*Oryza sativa* var. Jackson) plants growing in normal and stress conditions. *Plant Science* **161**: 279–287.

**Liu B, Rennenberg H, Kreuzwieser J. 2015.** Hypoxia induces stem and leaf nitric oxide (NO) emission from poplar seedlings. *Planta* **241**: 579–589.

**López-Gómez P, Buezo J, Urra M, Cornejo A, Esteban R, Fernández de Los Reyes J, Urarte E, Rodríguez-Dobreva E, Chamizo-Ampudia A, Eguaras A *et al.* 2024.** A new oxidative pathway of nitric oxide production from oximes in plants. *Molecular Plant* **17**: P178–P198.

**Lucas WJ, Groover A, Lichtenberger R, Furuta K, Yadav SR, Helariutta Y, He XQ, Fukuda H, Kang J, Brady SM *et al.* 2013.** The plant vascular system: evolution, development and functions. *Journal of Integrative Plant Biology* **55**: 294–388.

**Ma M, Wendehenne D, Philippot L, Hänsch R, Flemetakis E, Hu B, Rennenberg H. 2020.** Physiological significance of pedospheric nitric oxide for root growth, development and organismic interactions. *Plant, Cell & Environment* **43**: 2336–2354.

**Maiber L, Koprivova A, Bender D, Kopriva S, Fischer-Schrader K. 2022.** Characterization of the amidoxime reducing components ARC1 and ARC2 from *Arabidopsis thaliana*. *The FEBS Journal* **289**: 5656–5669.

**Marcolongo JP, Venâncio MF, Rocha WR, Doctorovich F, Olabe JA. 2019.** NO/$H_2S$ "crosstalk" reactions. The role of thionitrites (SNO–) and perthionitrites (SSNO–). *Inorganic Chemistry* **58**: 14981–14997.

**Mata-Pérez C, Sánchez-Calvo B, Padilla MN. 2016.** Nitro-fatty acids in plant signalling: nitro-linolenic acid induces the molecular chaperone network in Arabidopsis. *Plant Physiology* **170**: 686–701.

**Mata-Pérez C, Sánchez-Calvo B, Padilla MN, Begara-Morales JC, Valderrama R, Corpas FJ, Barroso JB. 2017.** Nitro-fatty acids in plant signalling: new key mediators of nitric oxide metabolism. *Redox Biology* **11**: 554–561.

**Mata-Pérez C, Padilla María N, Sánchez-Calvo B, Begara-Morales JC, Valderrama R, Chaki M, Aranda-Caño L, Moreno-González D, Molina-Díaz A, Barroso JB. 2020.** Endogenous biosynthesis of *S*-nitrosoglutathione from nitro-fatty acids in plants. *Frontiers in Plant Science* **11**: 962.

**Mathieu C, Moreau S, Frendo P, Puppo A, Davies MJ. 1998.** Direct detection of radicals in intact soybean nodules: presence of nitric oxide-leghemoglobin complexes. *Free Radical Biology and Medicine* **24**: 1242–1249.

**Meilhoc E, Boscari A, Bruand C, Puppo A, Brouquisse R. 2011.** Nitric oxide in legume–rhizobium symbiosis. *Plant Science* **181**: 573–581.

**Miller G, Schlauch K, Tam R, Cortes D, Torres MA, Shulaev V, Dangl JL, Mittler R. 2009.** The plant NADPH oxidase RBOHD mediates rapid systemic signaling in response to diverse stimuli. *Science Signaling* **2**: ra45.

**Mishra V, Singh P, Tripathi DK, Corpas FJ, Singh VP. 2021.** Nitric oxide and hydrogen sulfide: an indispensable combination for plant functioning. *Trends in Plant Science* **26**: 1270–1285.

**Mohn MA, Thaqi B, Fischer-Schrader K. 2019.** Isoform-specific NO synthesis by *Arabidopsis thaliana* nitrate reductase. *Plants* **8**: 67.

**Muñoz-Vargas MA, González-Gordo S, Cañas A, López-Jaramillo J, Palma JM, Corpas FJ. 2018.** Endogenous hydrogen sulfide (H2S) is up-regulated during sweet pepper (*Capsicum annuum* L.) fruit ripening. *In vitro* analysis shows that NADP-dependent isocitrate dehydrogenase (ICDH) activity is inhibited by $H_2S$ and NO. *Nitric Oxide* **81**: 36–45.

**Muñoz-Vargas MA, López-Jaramillo J, González-Gordo S, Paradela A, Palma JM, Corpas FJ. 2023.** $H_2S$-generating cytosolic L-cysteine desulfhydrase and mitochondrial D-cysteine desulfhydrase from sweet pepper (*Capsicum annuum* L.) are regulated during fruit ripening and by nitric oxide. *Antioxidants & Redox Signaling* **39**: 2–18.

**Mur LAJ, Mandon J, Persijn S, Cristescu SM, Moshkov IE, Novikova GV, Hall MA, Harren FJM, Hebelstrup KH, Gupta KJ. 2012.** Nitric oxide in plants: an assessment of the current state of knowledge. *AoB Plants* **5**: pls052.

**Narsai R, Howell KA, Millar AH, O'toole N, Small I, Whelan J. 2007.** Genome-wide analysis of mRNA decay rates and their determinants in *Arabidopsis thaliana*. *Plant Cell* **19**: 3418–3436.

**Neill S. 2005.** NO way to die – nitric oxide, programmed cell death and xylogenesis. *New Phytologist* **165**: 5–8.

**Neill S, Bright J, Desikan R, Hancock J, Harrison J, Wilson I. 2008.** Nitric oxide evolution and perception. *Journal of Experimental Botany* **59**: 25–35.

**Palma JM, Mateos RM, López-Jaramillo J, Rodríguez-Ruiz M, González-Gordo S, Lechuga-Sancho AM, Corpas FJ. 2020.** Plant catalases as NO and $H_2S$ targets. *Redox Biology* **34**: 101525.

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14698137, 2024, 3, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20085 by Helmholtz Zentrum Muenchen Deutsches Forschungszentrum, Wiley Online Library on [14/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

**Palmieri CM, Sell S, Huang X, Scherf M, Werner T, Durner J, Lindermayr C. 2008.** Nitric oxide-responsive genes and promoters in *Arabidopsis thaliana*: a bioinformatics approach. *Journal of Experimental Botany* **59**: 177–186.

**Parent C, Berger A, Folzer H, Dat J, Crevècoeur M, Badot P-M, Capelli N. 2008.** A novel nonsymbiotic hemoglobin from oak: cellular and tissue specificity of gene expression. *New Phytologist* **177**: 142–154.

**Pilegaard K. 2013.** Processes regulating nitric oxide emissions from soils. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **368**: 20130126.

**Piterková J, Petrivalský M, Luhová L, Mieslerová B, Sedlárová M, Lebeda A. 2009.** Local and systemic production of nitric oxide in tomato responses to powdery mildew infection. *Molecular Plant Pathology* **10**: 501–513.

**Rockel P, Strube F, Rockel A, Wildt J, Kaiser WM. 2002.** Regulation of nitric oxide (NO) production by plant nitrate reductase *in vivo* and *in vitro*. *Journal of Experimental Botany* **53**: 103–110.

**Rosenkranz M, Chen Y, Zhu P, Vlot AC. 2021.** Volatile terpenes – mediators of plant-to-plant communication. *The Plant Journal* **108**: 617–631.

**Ross EJH, Shearman L, Mathiesen M, Zhou YJ, Arredondo-Peter R, Sarath G, Klucas RV. 2001.** Nonsymbiotic hemoglobins in rice are synthesized during germination and in differentiating cell types. *Protoplasma* **218**: 125–133.

**Rümer S, Gupta KJ, Kaiser WM. 2009.** Plant cells oxidise hydroxylamines to NO. *Journal of Experimental Botany* **60**: 2065–2072.

**Sakamoto A, Ueda M, Morikawa H. 2002.** Arabidopsis glutathione-dependent formaldehyde dehydrogenase is an *S*-nitrosoglutathione reductase. *FEBS Letters* **515**: 20–24.

**Sánchez-Vicente I, Albertos P, Sanz C, Wybouw B, De Rybel B, Begara-Morales JC, Chaki M, Mata-Pérez C, Barroso JB, Lorenzo O. 2024.** Reversible *S*-nitrosylation of bZIP67 by peroxiredoxin IIE activity and nitro-fatty acids regulates the plant lipid profile. *Cell Reports* **43**: 114091.

**Scuffi D, Álvarez C, Laspina N, Gotor C, Lamattina L, García-Mata C. 2014.** Hydrogen sulfide generated by L-cysteine desulfhydrase acts upstream of nitric oxide to modulate abscisic acid-dependent stomatal closure. *Plant Physiology* **166**: 2065–2076.

**Seregélyes C, Igamberdiev AU, Maassen A, Hennig J, Dudits D, Hill RD. 2004.** NO-degradation by alfalfa class 1 hemoglobin (Mhb1): a possible link to PR-1a gene expression in Mhb1-overproducing tobacco plants. *FEBS Letters* **571**: 61–66.

**Shah J, Chaturvedi R, Chowdhury Z, Venables B, Petros RA. 2014.** Signalling by small metabolites in systemic acquired resistance. *The Plant Journal* **79**: 645–658.

**Shen J, Zhang J, Zhou M, Zhou H, Cui B, Gotor C, Romero LC, Fu L, Yang J, Foyer CH *et al.* 2020.** Persulfidation-based modification of cysteine desulfhydrase and the NADPH oxidase RBOHD controls guard cell abscisic acid signaling. *Plant Cell* **32**: 1000–1017.

**Shulaev V, Silverman P, Raskin I. 1997.** Airborne signalling by methyl salicylate in plant pathogen resistance. *Nature* **385**: 718–721.

**Singh SP, Wishnok JS, Keshive M, Deen WM, Tannenbaum SR. 1996.** The chemistry of the *S*-nitrosoglutathione/glutathione system. *Proceedings of the National Academy of Sciences, USA* **93**: 14428–14433.

**Song F, Goodman RM. 2001.** Activity of nitric oxide is dependent on, but is partially required for function of salicylic acid in the signalling pathway in tobacco systemic acquired resistance. *Molecular Plant–Microbe Interactions* **14**: 1458–1462.

**Stamler JS, Singel DJ, Loscalzo J. 1992.** Biochemistry of nitric oxide and its redox-activated forms. *Science* **258**: 1898–1902.

**Stöhr C, Strube F, Marx G, Ullrich WR, Rockel P. 2001.** A plasma membrane-bound enzyme of tobacco roots catalyses the formation of nitric oxide from nitrite. *Planta* **212**: 835–841.

**Szechyńska-Hebda M, Lewandowska M, Witoń D, Fichman Y, Mittler R, Karpiński SM. 2022.** Aboveground plant-to-plant electrical signaling mediates network acquired acclimation. *Plant Cell* **34**: 3047–3065.

**Tada T, Spoel SH, Pajerowska-Mukhtar K, Mou Z, Song J, Wang C, Zuo J, Dong X. 2008.** Plant immunity requires conformational changes of NPR1 via *S*-nitrosylation and thioredoxins. *Science* **321**: 952–956.

**Takahashi M, Furuhashi T, Ishikawa N, Horiguchi G, Sakamoto A, Tsukaya H, Morikawa H. 2014.** Nitrogen dioxide regulates organ growth by controlling cell proliferation and enlargement in Arabidopsis. *New Phytologist* **201**: 1304–1315.

**Tanou G, Job C, Rajjou L, Arc E, Belghazi M, Diamantidis G, Molassiotis A, Job D. 2009.** Proteomics reveals the overlapping roles of hydrogen peroxide and nitric oxide in the acclimation of citrus plants to salinity. *The Plant Journal* **60**: 795–804.

**Thomas DD. 2015.** Breathing new life into nitric oxide signalling: a brief overview of the interplay between oxygen and nitric oxide. *Redox Biology* **5**: 225–233.

**Treffon P, Rossi J, Gabellini G, Trost P, Zaffagnini M, Vierling E. 2021.** Proteome profiling of a *S*-Nitrosoglutathione reductase (GSNOR) null mutant reveals that aldo-keto reductases form a new class of enzymes involved in nitric oxide homeostasis. *Frontiers in Plant Science* **12**: 787435.

**Valderrama R, Corpas FJ, Carreras A, Fernández-Ocaña A, Chaki M, Luque F, Gómez-Rodríguez MV, Colmenero-Varea P, Del Río LA, Barroso JB. 2007.** Nitrosative stress in plants. *FEBS Letters* **581**: 453–461.

**Villar I, Larrainzar E, Milazzo L, Pérez-Rontomé C, Rubio MC, Smulevich G, Martínez JI, Wilson MT, Reeder B, Huertas R *et al.* 2020.** A plant gene encoding one-heme and two-heme hemoglobins with extreme reactivities toward diatomic gases and nitrite. *Frontiers in Plant Science* **11**: 600336.

**Vitecek J, Reinohl V, Jones RL. 2008.** Measuring NO production by plant tissues and suspension cultured cells. *Molecular Plant* **1**: 270–284.

**Wang C, El-Shetehy M, Shine MB, Yu K, Navarre D, Wendehenne D, Kachroo A, Kachroo P. 2014.** Free radicals mediate systemic acquired resistance. *Cell Reports* **7**: 348–355.

**Wang C, Liu R, Lim GH, de Lorenzo L, Yu K, Zhang K, Hunt AG, Kachroo A, Kachroo P. 2018.** Pipecolic acid confers systemic immunity by regulating free radicals. *Science Advances* **4**: eaar4509.

**Wang X, Hargrove MS. 2013.** Nitric oxide in plants: the roles of ascorbate and hemoglobin. *PLoS ONE* **8**: e82611.

**Wang YQ, Feechan A, Yun BW, Shafiei R, Hofmann A, Taylor P, Xue P, Yang FQ, Xie ZS, Pallas JA *et al.* 2009.** *S*-nitrosylation of AtSABP3 antagonises the expression of plant immunity. *The Journal of Biological Chemistry* **284**: 2131–2137.

**Welle M, Niether W, Stöhr C. 2024.** The underestimated role of plant root nitric oxide emission under low-oxygen stress. *Frontiers in Plant Science* **15**: 1290700.

**Wendehenne D, Gao Q-M, Kachroo A, Kachroo P. 2014.** Free radical-mediated systemic immunity in plants. *Current Opinion in Plant Biology* **20**: 127–134.

**Wimalasekera R, Villar C, Begum T, Scherer GFE. 2011.** COPPER AMINE OXIDASE1 (CuAO1) of *Arabidopsis thaliana* contributes to abscisic acid- and polyamine-induced nitric oxide biosynthesis and abscisic acid signal transduction. *Molecular Plant* **4**: 663–678.

**Wink DA, Mitchell JB. 1998.** Chemical biology of nitric oxide: Insights into regulatory, cytotoxic, and cytoprotective mechanisms of nitric oxide. *Free Radical Biology & Medicine* **25**: 434–456.

**Yun BW, Feechan A, Yin M, Saidi NB, Le Bihan T, Yu M, Moore JW, Kang JG, Kwon E, Spoel SH *et al.* 2011.** *S*-nitrosylation of NADPH oxidase regulates cell death in plant immunity. *Nature* **478**: 264–268.

**Zhang J, Buegger F, Albert A, Ghirardo A, Winkler B, Schnitzler JP, Hebelstrup KH, Durner J, Lindermayr C. 2019.** Phytoglobin overexpression promotes barley growth in the presence of enhanced level of atmospheric nitric oxide. *Journal of Experimental Botany* **70**: 4521–4537.

**Ziogas V, Molassiotis A, Fotopoulos V, Tanou G. 2018.** Hydrogen sulfide: a potent tool in postharvest fruit biology and possible mechanism of action. *Frontiers in Plant Science* **9**: 1375.

**Zuccarelli R, Rodríguez-Ruiz M, Lopes-Oliveira PJ, Pascoal GB, Andrade SCS, Furlan CM, Purgatto E, Palma JM, Corpas FJ, Rossi M *et al.* 2021.** Multifaceted roles of nitric oxide in tomato fruit ripening: NO-induced metabolic rewiring and consequences for fruit quality traits. *Journal of Experimental Botany* **72**: 941–958.

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