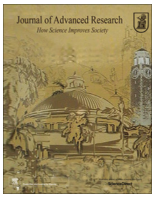
Journal of Advanced Research 24 (2020) 131–137

Contents lists available at ScienceDirect

Journal of Advanced Research

journal homepage: www.elsevier.com/locate/jare



H_2S signaling in plants and applications in agriculture

Francisco J. Corpas *, José M. Palma

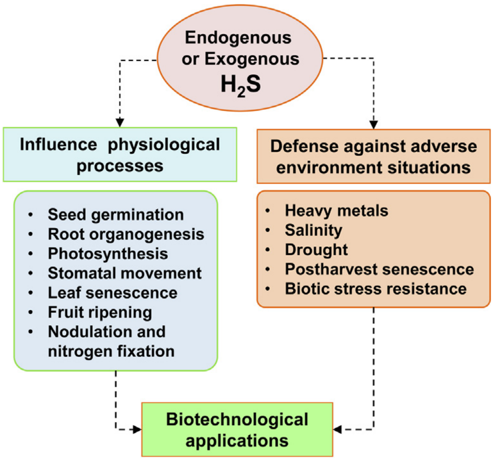
Antioxidant, Free Radical and Nitric Oxide in Biotechnology, Food and Agriculture Group, Department of Biochemistry, Cell and Molecular Biology of Plants, Estación Experimental del Zaidín, Consejo Superior de Investigaciones Científicas (CSIC), C/ Profesor Albareda, 1, E-18008 Granada, Spain

HIGHLIGHTS

- Hydrogen sulfide (H_2S) plays a signaling role in higher plants.
- It mediates persulfidation, a post-translational modification.
- It regulates physiological functions ranging from seed germination to fruit ripening.
- The beneficial effects of exogenous H_2S are mainly caused by the stimulation of antioxidant systems.

GRAPHICAL ABSTRACT

Summary of the main physiological or adverse environmental situations in higher plants where the hydrogen sulfide (H_2S) participates.



ARTICLE INFO

Article history:
Received 10 February 2020
Revised 24 March 2020
Accepted 25 March 2020
Available online 29 March 2020

Keywords:
Hydrogen sulfide
Abiotic stress
Fruit ripening
Nitro-oxidative stress

ABSTRACT

The signaling properties of the gasotransmitter molecule hydrogen sulfide (H_2S), which is endogenously generated in plant cells, are mainly observed during persulfidation, a protein post-translational modification (PTM) that affects redox-sensitive cysteine residues. There is growing experimental evidence that H_2S in higher plants may function as a mechanism of response to environmental stress conditions. In addition, exogenous applications of H_2S to plants appear to provide additional protection against stresses, such as salinity, drought, extreme temperatures and heavy metals, mainly through the induction of antioxidant systems, in order to palliate oxidative cellular damage. H_2S also appears to be involved in regulating physiological functions, such as seed germination, stomatal movement and fruit ripening, as well as molecules that maintain post-harvest quality and rhizobium–legume symbiosis. These properties of H_2S open up new challenges in plant research to better understand its functions as well as new opportunities for biotechnological treatments in agriculture in a changing environment.

Introduction

The description of the gasotransmitter hydrogen sulfide (H_2S), with its toxic impact on the metabolism of animal and plant cells,

---

Peer review under responsibility of Cairo University.

* Corresponding author.
E-mail address: javier.corpas@eez.csic.es (F.J. Corpas).

https://doi.org/10.1016/j.jare.2020.03.011
2090-1232/

changed drastically when this molecule was shown to be endogenously generated in cells. However, its signaling capacity has particularly fascinated researchers in many fields of investigation [1–5]. A number of studies in the field of plants began to show that H_2S is directly or indirectly involved in a wide range of physiological processes including seed germination [6], root organogenesis [7,8], photosynthesis [9], stomatal movement [10–13], fruit ripening [14,15], as well as senescence in leaves, flowers and fruits [16,17]. H_2S has also been shown to be involved in the mechanism of response to adverse biotic and abiotic environmental conditions [18,19]. Research has shown a significant correlation between the functions of H_2S and nitric oxide (NO), another simple molecule, whose metabolisms appear regulate each other [4]. Fig. 1 summarizes the principal functions of H_2S in higher plants. The main aim of this review is to provide a broad overview of the major role played by H_2S in higher plants, with particular attention paid to the beneficial effects of its biotechnological application in crop plants, especially under adverse stressful conditions.

Plant biochemistry of H_2S: An overview

The study of H_2S as a signaling molecule has focused on its capacity to interact with thiol (-SH) groups present in protein cysteine residues through the post-translational modification (PTM) persulfidation [4,20]. It is important to point out the major regulatory role played by protein thiol groups involved in multiple interactions which can activate or inhibit the function of the target proteins [21,22]. H_2S competes with other molecules, such as nitric oxide (NO), glutathione (GSH), cyanide and fatty acids, which generate the PTMs *S*-nitrosation [4,23], *S*-glutathionylation [24,25], *S*-cyanylation [26] and *S*-acylation [27–29], respectively. Fig. 2 shows a simple model of these PTMs involving protein thiol groups. However, fewer studies have explored the potential protein targets of persulfidation, previously known as *S*-sulfhydration, and how this PTM affects up-regulates and down-regulates these proteins.

Information garnered from initial plant proteomic analyses focusing on the model plant *Arabidopsis thaliana* [30,31] and that obtained from animal cells [32,33], as well as complementary studies, have facilitated the evaluation of the *in vitro* effect of H_2S on a specific plant protein using different H_2S donors [15,34,35]. Table 1 shows a list of plant proteins, which have been observed to undergo persulfidation, and how their protein function is modulated [36,37]. In some cases, a specific purified protein can behave differently under *in vitro* conditions depending on whether the H_2S donor is applied to the whole plant, added to the nutrient solution or growth media or sprayed on the aerial part of the plant. This is due to the complex action of H_2S characterized by its functional interaction/competition in whole cells with other molecules including nitric oxide (NO) [4], melatonin [38] and phytohormones such as ethylene, auxin and abscisic acid [39,40].

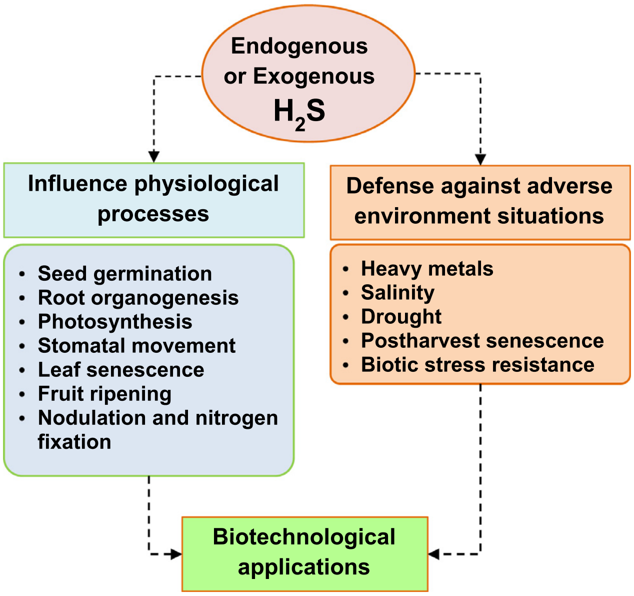


Fig. 1. Summary of the main physiological or adverse environmental situations in higher plants where the endogenous or exogenous H_2S seems to participate which could also have biotechnological applications.

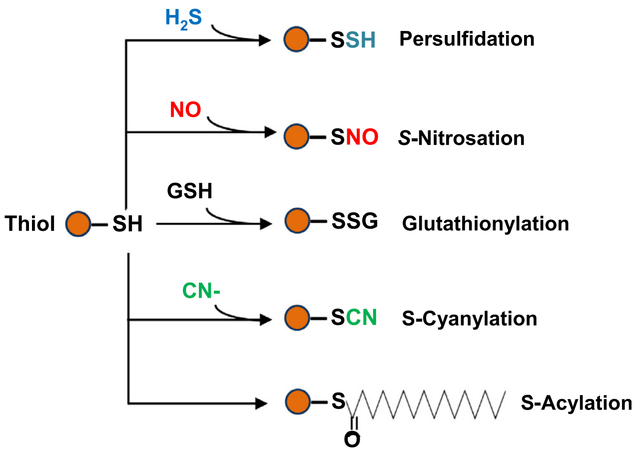


Fig. 2. Protein thiol (-SH) modifications mediated by either the incorporation of H_2S (persulfidation), NO (S-nitrosation), glutathione (GSH) (S-glutathionylation), cyanide (S-cyanylation) or fatty acid (S-acylation).

Although the precise mechanisms involved remain unknown, H_2S has been shown to regulate gene expression [41,42]. Exogenous applications of H_2S to grapevine (*Vitis vinifera* L.) plants trigger gene expression involved in the synthesis of secondary metabolites as well as various defensive compounds which boosts plant development and abiotic resistance [43]. In addition, microarray analysis of differentially expressed genes of tomato plants supplemented with NaHS has shown that 5349 genes were up-regulated, while 5536 were down-regulated [44].

However, any precise biochemistry of endogenous H_2S in plant cells, as well as how and where H_2S is produced and its metabolic interactions with other molecules, is still in its infancy. In higher plant systems, several enzymes involved in cysteine metabolism present in subcellular compartments (the cytosol, chloroplasts, mitochondria and peroxisomes) are available for the production of H_2S [35,45,46]. These enzymes include L-cysteine desulfhydrase (L-DES), L-cysteine desulfhydrase 1 (DES1), previously known as Cys synthase-like (CS-LIKE), and cysteine synthase (CS) in the cytosol; D-cysteine desulfhydrase (D-DES) and cyano alanine synthase (CAS) in mitochondria; and sulfite reductase (SiR) in the chloroplast [3,46–48]. However, given its highly lipophilic nature, the H_2S molecule can spread with ease throughout the lipid bilayer of cell membranes [49]. New promising data also show how activities, such as cysteine desulfhydrases, in some of these enzymes are up-regulated under red light and down-regulated by blue and white light [50].

Potential biotechnological applications of exogenously applied H_2S

Although further basic research on H_2S is required, sufficient experimental data show that the exogenous application of H_2S to different plant species at different stages of development can

Table 1
Examples of plant protein targets which function is affected by H_2S and consequently they undergo persulfidation.

Enzyme	Function	Effect	Ref.
RuBISCO	Photosynthesis	Activity up-regulated	[9]
O-acetylserine(thiol)lyase (OAS-TL)	Sulfur metabolism	Activity up-regulated	[9]
L-cysteine desulphydrase (LCD)	Sulfur metabolism	Activity up-regulated	[9]
Ascorbate peroxidase (APX)	Antioxidant	Activity up-regulated	[30]
Glyceraldehyde 3-phosphate dehydrogenase (GAPDH)	Energy production in the glycolysis	Activity up-regulated	[30]
Glutamine synthetase (GS)	Metabolism of nitrogen	Activity down-regulated	[30]
Actin	Involved in organelle movement, in cell division and expansion	Inhibite actin polymerization	[36]
1-aminocyclopropane-1-carboxylic acid oxidase (ACO)	Ethylene biosynthesis	Activity down-regulated	[37]
NADP-isocitrate dehydrogenase (NADP-ICDH)	Provides NADPH as a reducing agent	Activity down-regulated	[15]
NADP-malic enzyme (NADP-ME)	Provides NADPH as a reducing agent	Activity down-regulated	[34]
Catalase	Antioxidant	Activity down-regulated	[35]
SNF1-RELATED PROTEIN KINASE2.6 (SnRK2.6)	Promote ABA signaling.	Promote ABA-induced stomatal closure	[12]
Respiratory burst oxidase homolog protein D (RBOHD)	Generation of superoxide radical	Activity up-regulated	[13]

palliate damage caused by abiotic stress and enhance physiological features such as seed germination, root development and post-harvest preservation of vegetables [4,51,52]. However, an empirical evaluation of how H_2S is to be applied and appropriate dosages is also required. Up to now, exogenous applications have been carried out using chemicals capable of delivering H_2S. In animal research on biomedical applications, different families of chemicals, with the capacity to slowly release H_2S into cells, have been developed. This has led to the development of water-soluble molecules such as (p-methoxyphenyl)morpholino-phosphinodithioic acid (GYY4137) and a family of cysteine-activated H_2S donors (5a, 8l, and 8o) [53]. Few plant studies have used these chemicals [54] which are comparatively more expensive to produce than standard chemicals such as sodium hydrosulfide (NaHS) and inorganic sodium polysulfides (Na_2S_n) such as Na_2S_2, Na_2S_3, and Na_2S_4. Thus, in aqueous solutions, delivery of H_2S by these polysulfides depends on medium pH and the corresponding pKa [55]. In plant research, the cheaper NaHS is exogenously added to hydroponic solutions and *in vitro* growth media or is sprayed directly on plants. NaHS, which is a short-lived donor and does not mimic the slow continuous process of H_2S generation *in vivo,* is used in a wide range of concentrations. The chemical dialkyldithiophosphate, which is capable of slowly releasing H_2S [56], has recently been demonstrated to increase corn plant weight by up to 39% after 4.5 weeks of treatment. Other compounds, which are capable of releasing NO combined with H_2S, are being used in anti-inflammatory pharmaceutical treatments [57].

H_2S and abiotic stress

Many adverse external conditions are well known to negatively affect plant growth, development and productivity [58]. To palliate these effects, plants have developed various strategies which differ according to the type of stress and plant species involved. In many cases, these stresses are associated with unregulated overproduction of reactivate oxygen and nitrogen species (ROS/RNS) which can trigger nitro-oxidative stress [59] characterized by an increase in key parameters such as lipid peroxidation, protein tyrosine nitration and oxidative damage to proteins and nucleic acids. Table 2 shows different examples of the beneficial effects of the exogenous application of H_2S through the use of different donors on a wide range of agronomically important plants affected by stresses such as heavy metals (cadmium, aluminum, chromium, copper, iron, zinc), metalloids (arsenic), salinity, drought, as well as high and low temperatures [60–84]. Apart from certain specific responses, in most cases, the application of exogenous H_2S appears to cause an increase in the different components of antioxidant systems, such as catalase, superoxide dismutase (SOD) isozymes, as well as enzymatic and non-enzymatic components of the ascorbate-glutathione cycle, which enables H_2O_2 levels and lipid peroxidation content to be reduced.

H_2S in fruit ripening and post-harvest damage to fresh produce

Information available on endogenous H_2S metabolism in fruits and vegetables is highly limited. Recently, endogenous H_2S content in non-climacteric sweet pepper (*Capsicum annumm* L) fruits was reported to increase during the transition from green immature to red ripe [15]. However, the number of studies focusing on the economic impact of biotechnological applications of H_2S on fruit ripening and post-harvest storage, which prevent the loss of fresh produce caused by fungi, bacteria, viruses and low temperatures used to store fruits and vegetables, has increased over the last ten years. Given that all these factors are usually associated with oxidative stress, many studies have shown that the exogenous application of H_2S could have a beneficial effect on the shelf life of a diverse range of fruits, vegetables and flowers [14,16,38,85,86]. Table 3 provides representative examples of the exogenous application of H_2S to fruits and vegetables [87–94] which enables their quality to be maintained. Another common effect observed following exogenous treatment with H_2S is an increase in antioxidant systems which prevent ROS overproduction and consequently oxidative damage.

Implication of H_2S in rhizobium–legume symbiosis

In agriculture and natural ecosystems, a major source of nitrogen-fixation is throughout the nodule formation during the plant-rhizobia interaction [95]. As happened with the NO that was seen to be involved in the interaction rhizobium–legume symbiosis [96–98], H_2S seems to be also involved in different ways in this process. A recent report indicates that exogenous H_2S promotes plant growth, nodulation and nitrogenase activity in the functional symbiosis between rhizobium (*Sinorhizobium fredii*) and soybean (*Glycine max*) plants [99]. Furthermore, the synergy between H_2S and rhizobia allowed the increase of soybean nitrogen contents by the regulation of related enzymes at different levels (activity, protein, and gene expression) as well as senescence-associated genes which were also regulated [100]. Moreover, new data obtained during the *Mesorhizobium–Lotus*

Table 2
Main effects of the exogenous application of H_2S to plants exposed to diverse environmental stresses. ABA, abscisic acid. APX, ascorbate peroxidase. AsA, ascorbate. CAT, catalase. GR, glutathione reductase. GSH, reduced glutathione. GSNOR, *S*-nitrosoglutathione reductase. HT, high temperature. MDA, malondialdehyde. POD, peroxidase. NaHS, sodium hydrosulfide. PIP, plasma membrane intrinsic proteins. PM, plama membrane. SOD, superoxide dismutase.

Environmental stress	H_2S donor(μM)	Plant species	Effects	Ref.
Aluminum	NaHS(2)	Rice (*Oryza sativa* L.)	Increases root elongation and decrease Al contents in rice root tips. Increase antioxidant enzyme activities. Decrease MDA and H_2O_2 content in roots	[60]
	NaHS(50)	Soybean (*Glycine* max L.)	Reduce Al accumulation. H_2S function downstream of NO and induce citrate secretion through the upregulation of PM H^+-ATPase-coupled citrate transporter cotransport systems	[61]
Cadmium (Cd)	NaHS(100)	Alfafa (*Medicago sativa* L.)	Reduces the accumulation of MDA and H_2O_2. Increase the content of GSH and the activity of antioxidant enzymes (SOD, CAT and POD)	[62]
	NaHS(500)	Bermudagrass (*Cynodon dactylon* L)	Alleviates Cd damages by modulating enzymatic and non-enzymatic antioxidants.	[63]
	NaHS(200)	Barley (*Hordeum vulgare* L.)	Reduces the accumulation of H_2O_2 and superoxide ions in roots	[64]
	NaHS(200)	Wheat (*Triticum aestivum*)	Increases the activities of antioxidant enzymes. Inhibits Cd uptake and reduce proline content	[65]
	Endogenous H_2S	Arabidopsis (*Arabidopsis thaliana*)	Overexpression of D-Cysteine desulfhydrase (DCD) decreases Cd and ROS content	[66]
Chromium(Cr)	NaHS(500)	Maize (*Zea mays* L.)	Alleviate chromium toxicity and enhances antioxidant activities (CAT, SOD, APX)	[67]
	NaHS(200)	Caulifower (*Brassica oleracea* L.)	Decreases Cr content, H_2O_2 and MDA concentrations. Increases activity of antioxidant enzymes	[68]
Copper (Cu)	NaHS(1,400)	Wheat (*Triticum aestivum* L.)	Lowers levels of MDA and H_2O_2 in germinating seeds. Increases SOD and CAT activities, and decreases lipoxygenase	[6]
Iron deficiency	NaHS(200)	Strawberry (*Fragaria* × *ananassa*)	Reduces electrolyte leakage, and content of H_2O_2 and MDA. Upregulate activities of antioxidant enzymes. Improved Fe uptake	[69]
Zinc (Zn)	NaHS (200)	Pepper (*Capsicum annuum* L.)	Increases plant growth, fruit yield, water status and proline content. Enhances the activity of antioxidant enzymes	[70]
Arsenic (As)	NaHS(100)	Pea (*Pisum sativum* L.	Increases of AsA and GSH contents and activities of the AsA–GSH cycle enzymes	[71]
Salinity	NaHS(50)	Rice (*Oryza sativa* L.)	Decreases the uptake of Na^+ and the Na^+/K^+ ratio	[72]
	NaHS(50)	Wheat (*Triticum aestivum* L.)	Suppresses ROS accumulation by increasing antioxidant defense	[73]
	NaHS(20)	Cucumber (*Cucumis sativus* L.)	Keeps Na^+ and K^+ homeostasis by the gene expression of plasma membrane Na+/H + antiporter (*SOS1*). Decrease lipid peroxidation content and ROS generation. Increases activity of antioxidant system	[74]
	NaHS(200)	Mangrove plant (*Kandelia obovata*)	Enhances the quantum efficiency of photosystem II (PSII) and the membrane lipid stability	[75]
Drought	NaHS(500)	Wheat (*Triticum aestivum* L.)	Increases antioxidant enzyme activities, reduces MDA and H_2O_2 contents in both leaves and roots. Increases of the transcription levels of genes encoding ABA receptors.	[40]
	NaHS(400)	Wheat (*Triticum aestivum* L.)	Induction of genes that code for antioxidant enzymes	[76]
	NOSH(1) compounds (100)	Alfalfa (*Medicago sativa* L.)	Lowers MDA. Induce *Cu/ZnSOD*, *FeSOD* genes	[77]
Osmotic stress	NaHS(150)	Arabidopsis (*Arabidopsis thaliana*)	Increase phospholipase Dα1 and the antioxidant enzyme system. Reduce ROS and MDA content and reduce electrolyte leakage	[78]
Low temperature	NaHS(50)	Cucumber (*Cucumis sativus* L.)	Increases GSH and cucurbitacin C content	[79]
	NaHS(500)	Lowbush blueberry (*Vaccinium angustifolium*)	Alleviate the degradation of chlorophyll and carotenoids and reduce the photoinhibition of PSII and PSI.	[80]
High temperature	NaHS(100)	Strawberry (*Fragaria* × *ananassa* cv. 'Camarosa')	Induction of gene expression ocoding for antioxidant enzymes (cAPX, CAT, MnSOD, GR), heat shock proteins (HSP70, HSP80, HSP90) and aquaporins (PIP)	[81]
	NaHS(500)	Maize (*Zea mays* L.)	Improves seed germination and increases antioxidant enzymes. Accumulation of proline	[82]
	NaHS (50) or MGYY4137 (10)	Poplar (*Populus trichocarpa*)	Increases GSNOR activity and reduce HT-induced damage to the photosynthetic system	[83]
	NaHS (100) or GYY4137 (10)	*Arabidopsis thaliana*	Enhances seed germination rate under HT.Increases gene expression of *ABI5* (ABA-INSENSITIVE 5).	[84]

[1] Resulted in the Utility Patent Pub. No.: WO/2015/123273.

symbiosis indicate that this interaction is regulated by the cross-talk among H_2S with other signaling molecules including NO and ROS [101].

Conclusions and future perspectives

H_2S, which is part of the plant sulfur metabolism, is a new signal molecule whose regulatory function acts through redox interactions, especially the protein post-translational modification persulfidation. The application of exogenous H_2S, involving a signaling mechanism, causes an increase in different components of the antioxidant system at both the gene and protein level. Nevertheless, the precise biochemical and molecular mechanisms involved in these processes need to be further investigated in future research. However, the exogenous application of H_2S undoubtedly has a beneficial effect on different plant species, especially those of considerable agronomic interest under adverse environmental conditions. Therefore, the use of H_2S alone or combined with other molecules, such as nitric oxide, melatonin, thiourea, silicon, chitosan and calcium, which appear to beneficially affect crop plants, needs to be explored in light of climate change [102–108]. Thus, additional research is necessary in order to decipher the unknowns of H_2S and its interaction with the metabolism of ROS and RNS under physiological and stressful conditions [109], as well as to establish biotechnological strategies to combat these stresses,

Table 3
Representative examples of the main beneficial effects of the exogenous application of H_2S in fruits and vegetables.

Fruit/vegetable	H_2S donor	Effects	Ref.
Strawberry (*Fragaria* × *ananassa* Duch.)	0.8 mM NaHS	Prolongs postharvest shelf life and reduces fruit rot disease	[87]
Broccoli (*Brassica oleracea*)	2.4 mM NaHS	Alleviates senescent symptoms	[88]
Grape (*Vitis vinifera* L. × *V. labrusca* L. cv. Kyoho)	1 mM NaHS	Alleviates postharvest senescence of grape and maintain high fruit quality	[89]
Banana (*Musa acuminata*, AAA group)	1 mM NaHS	Alleviates fruit softening. Antagonizes ethylene effects	[14]
Tomato (*Solanum lycopersicum* L.) 'Micro Tom'	0.9 mM NaHS	Postpones ripening and senescence of postharvest tomato fruits by antagonizing the effects of ethylene	[90]
Hawthorn (*Crataegus oxyacantha*) fruit	1.5 mM NaHS	Confers tolerance to chilling. Triggers H_2S accumulation, increase antioxidant enzyme activities of and promote phenolics accumulation	[91]
Avocado (*Persea americana* Mill, cv. 'Hass')	200 μMNaHS	Protects against frost and day high light	[92]
Kiwifruit (*Actinidia chinensis*)	20 μM H_2S	Delays ripening and senescence. Inhibits ethylene production. Increases antioxidant activities. Regulates the cell wall degrading enzyme gene	[42]
Daylily (*Hemerocallis fulva*)	4 mMNaHS	Delays senescence of postharvest daylily flowers. Increases antioxidant capacity to maintain the redox balance	[93]
Tomato (*Solanum lycopersicum* L.).	1 M NaHS	Inhibits ethylene-induced petiole abscission	[94]

which are responsible for major losses in plant yield and crop productivity.

Compliance with Ethics requirements

This article does not contain any studies with human or animal subjects.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

FJC and JMP research is supported by a European Regional Development Fund cofinanced grant from the Spanish Ministry of Economy and Competitiveness (AGL2015-65104-P and PID2019-103924GB-I00), the Plan Andaluz de Investigación, Desarrollo e Innovación (PAIDI 2020) (P18-FR-1359) and Junta de Andalucía (group BIO192), Spain.

References

[1] Abe K, Kimura H. The possible role of hydrogen sulfide as an endogenous neuromodulator. J Neurosci 1996;16:1066–71.
[2] Lisjak M, Teklic T, Wilson ID, Whiteman M, Hancock JT. Hydrogen sulfide: environmental factor or signalling molecule?. Plant Cell Environ 2013;36(9):1607–16.
[3] Filipovic MR, Jovanovic VM. More than just an intermediate: hydrogen sulfide signalling in plants. J Exp Bot 2017;2017(68):4733–6.
[4] Corpas FJ, González-Gordo S, Cañas A, Palma JM. Nitric oxide and hydrogen sulfide in plants: which comes first?. J Exp Bot 2019;70:4391–404.
[5] Kimura H. Signaling by hydrogen sulfide (H_2S) and polysulfides (H_2S_n) in the central nervous system. Neurochem Int 2019;126:118–25.
[6] Zhang H, Hu LY, Hu KD, He YD, Wang SH, Luo JP. Hydrogen sulfide promotes wheat seed germination and alleviates oxidative damage against copper stress. J Integr Plant Biol 2008;50:1518–29.
[7] Zhang H, Tang J, Liu XP, Wang Y, Yu W, Peng WY, et al. Hydrogen sulfide promotes root organogenesis in Ipomoea batatas, *Salix matsudana* and *Glycine max*. J Integr Plant Biol 2009;51:1084–92.
[8] Mei Y, Zhao Y, Jin X, Wang R, Xu N, Hu J, et al. L-Cysteine desulfhydrase-dependent hydrogen sulfide is required for methane-induced lateral root formation. Plant Mol Biol 2019;99(3):283–98.
[9] Chen J, Wu FH, Wang WH, Zheng CJ, Lin GH, Dong XJ, et al. Hydrogen sulphide enhances photosynthesis through promoting chloroplast biogenesis, photosynthetic enzyme expression, and thiol redox modification in *Spinacia oleracea* seedlings. J Exp Bot 2011;62(13):4481–93.
[10] García-Mata C, Lamattina L. Hydrogen sulphide, a novel gasotransmitter involved in guard cell signaling. New Phytol 2010;188:977–84.
[11] Zhang J, Zhou M, Ge Z, Shen J, Zhou C, Gotor C, et al. ABA-triggered guard cell L-cysteine desulfhydrase function and in situ H_2S production contributes to heme oxygenase-modulated stomatal closure. Plant Cell Environ 2019. doi: https://doi.org/10.1111/pce.13685.
[12] Chen S, Jia H, Wang X, Shi C, Wang X, Ma P, et al. Hydrogen sulfide positively regulates abscisic acid signaling through persulfidation of SnRK2.6 in guard cells. Mol Plant. 2020;S1674–2052(20):30004–6. doi: https://doi.org/10.1016/j.molp.2020.01.004.
[13] Shen J, Zhang J, Zhou M, Zhou H, Cui B, Gotor C, et al. Persulfidation-based modification of cysteine desulfhydrase and the NADPH oxidase RBOHD controls guard cell abscisic acid signaling. Plant Cell 2020. doi: https://doi.org/10.1105/tpc.19.00826.
[14] Ge Y, Hu KD, Wang SS, Hu LY, Chen XY, Li YH, et al. Hydrogen sulfide alleviates postharvest ripening and senescence of banana by antagonizing the effect of ethylene. PLoS One 2017;12(6):e0180113.
[15] Muñoz-Vargas MA, González-Gordo S, Cañas A, López-Jaramillo J, Palma JM, Corpas FJ. Endogenous hydrogen sulfide (H_2S) 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 2018;81:36–45.
[16] Zhang H, Hu SL, Zhang ZJ, Hu LY, Jiang CX, Wei ZJ, et al. Hydrogen sulfide acts as a regulator of flower senescence in plants. Postharvest Biol Technol 2011;60:251–7.
[17] Zheng JL, Hu LY, Hu KD, Wu J, Yang F, Zhang H. Hydrogen sulfide alleviates senescence of fresh-cut apple by regulating antioxidant defense system and senescence-related gene expression. HortScience 2016;51:152–8.
[18] Shi H, Ye T, Han N, Bian H, Liu X, Chan Z. Hydrogen sulfide regulates abiotic stress tolerance and biotic stress resistance in Arabidopsis. J Integr Plant Biol 2015;57(7):628–40.
[19] Banerjee A, Tripathi DK, Roychoudhury A. Hydrogen sulphide trapeze: Environmental stress amelioration and phytohormone crosstalk. Plant Physiol Biochem 2018;132:46–53.
[20] Aroca A, Gotor C, Romero LC. Hydrogen sulfide signaling in plants: emerging roles of protein persulfidation. Front Plant Sci 2018;9:1369.
[21] Duan J, Gaffrey MJ, Qian WJ. Quantitative proteomic characterization of redox-dependent post-translational modifications on protein cysteines. Mol BioSyst 2017;13(5):816–29.
[22] Bhatnagar A, Bandyopadhyay D. Characterization of cysteine thiol modifications based on protein microenvironments and local secondary structures. Proteins. 2018;86(2):192–209.
[23] Astier J, Kulik A, Koen E, Besson-Bard A, Bourque S, Jeandroz S, et al. Protein S-nitrosylation: what's going on in plants?. Free Radic Biol Med 2012;53(5):1101–10.
[24] Zaffagnini M, Bedhomme M, Marchand CH, Morisse S, Trost P, Lemaire SD. Redox regulation in photosynthetic organisms: focus on glutathionylation. Antioxid Redox Signal 2012;16(6):567–86.
[25] Diaz-Vivancos P, de Simone A, Kiddle G, Foyer CH. Glutathione-linking cell proliferation to oxidative stress. Free Radic Biol Med. 2015;89:1154–64.
[26] García I, Arenas-Alfonseca L, Moreno I, Gotor C, Romero LC. HCN Regulates cellular processes through posttranslational modification of proteins by S-cyanylation. Plant Physiol 2019;179(1):107–23.
[27] Hemsley PA. An outlook on protein S-acylation in plants: what are the next steps?. J Exp Bot 2017;68(12):3155–64.
[28] Li Y, Qi B. Progress toward understanding protein S-acylation: prospective in plants. Front Plant Sci 2017;8:346.
[29] Zheng L, Liu P, Liu Q, Wang T, Dong J. Dynamic protein S-acylation in plants. Int J Mol Sci 2019;20(3):E560.
[30] Aroca Á, Serna A, Gotor C, Romero LC. S-sulfhydration: a cysteine posttranslational modification in plant systems. Plant Physiol 2015;168(1):334–42.
[31] Aroca A, Benito JM, Gotor C, Romero LC. Persulfidation proteome reveals the regulation of protein function by hydrogen sulfide in diverse biological processes in Arabidopsis. J Exp Bot 2017;68(17):4915–27.

[32] Mustafa AK, Gadalla MM, Sen N, Kim S, Mu W, Gazi SK, et al. H_2S signals through protein S-sulfhydration. Sci Signal 2009;2:ra72.

[33] Fu L, Liu K, He J, Tian C, Yu X, Yang J. Direct proteomic mapping of cysteine persulfidation. Antioxid Redox Signal 2019. doi: https://doi.org/10.1089/ars.2019.7777.

[34] Muñoz-Vargas MA, González-Gordo S, Palma JM. Corpas FJ. Inhibition of NADP-malic enzyme activity by H_2S and NO in sweet pepper (*Capsicum annuum* L.) fruits. Physiol Plant 2020;168(2):278–88. 10.1111/ppl.13000.

[35] Corpas FJ, Barroso JB, González-Gordo S, Muñoz-Vargas MA, Palma JM. Hydrogen sulfide: a novel component in Arabidopsis peroxisomes which triggers catalase inhibition. J Integr Plant Biol 2019;61(7):871–83.

[36] Li J, Chen S, Wang X, Shi C, Liu H, Yang J, et al. Hydrogen sulfide disturbs actin polymerization via S-Sulfhydration resulting in stunted root hair growth. Plant Physiol 2018;178(2):936–49.

[37] Jia H, Chen S, Liu D, Liesche J, Shi C, Wang J, et al. Ethylene-induced hydrogen sulfide negatively regulates ethylene biosynthesis by persulfidation of ACO in tomato under osmotic stress. Front Plant Sci 2018;9:1517.

[38] Mukherjee S. Recent advancements in the mechanism of nitric oxide signaling associated with hydrogen sulfide and melatonin crosstalk during ethylene-induced fruit ripening in plants. Nitric Oxide 2019;82:25–34.

[39] Jia H, Hu Y, Fan T, Li J. Hydrogen sulfide modulates actin-dependent auxin transport via regulating ABPs results in changing of root development in Arabidopsis. Sci Rep 2015;5:8251.

[40] Ma D, Ding H, Wang C, Qin H, Han Q, Hou J, et al. Alleviation of drought stress by hydrogen sulfide is partially related to the abscisic acid signaling pathway in wheat. PLoS One 2016;11:e0163082.

[41] Pandey AK, Gautam A. Stress responsive gene regulation in relation to hydrogen sulfide in plants under abiotic stress. Physiol Plant 2020. doi: https://doi.org/10.1111/ppl.13064.

[42] Lin X, Yang R, Dou Y, Zhang W, Du H, Zhu L, et al. Transcriptome analysis reveals delaying of the ripening and cell wall degradation of kiwifruit by hydrogen sulfide. J Sci Food Agric 2020. doi: https://doi.org/10.1002/jsfa.10260. [.

[43] Ma Q, Yang J. Transcriptome profiling and identification of functional genes involved in H_2S response in grapevine tissue cultured plantlets. Genes Genomics 2018;40(12):1287–300.

[44] Guo Z, Liang Y, Yan J, Yang E, Li K, Xu H. Physiological response and transcription profiling analysis reveals the role of H_2S in alleviating excess nitrate stress tolerance in tomato roots. Plant Physiol Biochem 2018;124:59–69.

[45] Gotor C, Laureano-Marín AM, Moreno I, Aroca A, García I, Romero LC. Signaling in the plant cytosol: cysteine or sulfide?. Amino Acids 2015;47:2155–64.

[46] Hancock JT, Whiteman M. Hydrogen sulfide signaling: Interactions with nitric oxide and reactive oxygen species. Ann N Y Acad Sci 2016;1365:5–14.

[47] Calderwood A, Kopriva S. Hydrogen sulfide in plants: From dissipation of excess sulfur to signaling molecule. Nitric Oxide 2014;41:72–8.

[48] Liu D, Lu J, Li H, Wang J, Pei Y. Characterization of the O-acetylserine(thiol) lyase gene family in *Solanum lycopersicum* L.. Plant Mol Biol 2019;99(1–2):123–34.

[49] Cuevasanta E, Möller MN, Alvarez B. Biological chemistry of hydrogen sulfide and persulfides. Arch Biochem Biophys 2017;617:9–25.

[50] Liu Z, Cao C, Li Y, Yang G, Pei Y. Light regulates hydrogen sulfide signalling during skoto- and photo-morphogenesis in foxtail millet. Funct Plant Biol 2019. doi: https://doi.org/10.1071/FP19079.

[51] Huo J, Huang D, Zhang J, Fang H, Wang B, Wang C, et al. Hydrogen sulfide: a gaseous molecule in postharvest freshness. Front Plant Sci 2018;9:1172.

[52] Deng Y, Wang C, Wang N, Wei L, Li W, Yao Y, et al. Roles of small-molecule compounds in plant adventitious root development. Biomolecules 2019;9(9).;pii:E420.

[53] Zhao Y, Wang H, Xian M. Cysteine-activated hydrogen sulfide (H_2S) donors. J Am Chem Soc 2011;133(1):15–7.

[54] Yamasaki H, Ogura MP, Kingjoe KA, Cohen MF. D-Cysteine-induced rapid root abscission in the water fern *Azolla pinnata*: implications for the linkage between d-amino acid and reactive sulfur species (rss) in plant environmental responses. Antioxidants (Basel) 2019;8(9):E411.

[55] Gun J, Modestov A, Kamyshny A, Ryzkov D, Gitis V, Goifman A, et al. Electrospray ionization mass spectrometric analysis of aqueous polysulfide solutions. Microchim Acta 2004;46:229.

[56] Carter JM, Brown EM, Irish EE, Bowden NB. Characterization of dialkyldithiophosphates as slow hydrogen sulfide releasing chemicals and their effect on the growth of maize. J Agric Food Chem 2019. doi: https://doi.org/10.1021/acs.jafc.9b04398.

[57] Kashfi K, Chattopadhyay M, Kodela R. NOSH-sulindac (AVT-18A) is a novel nitric oxide- and hydrogen sulfide-releasing hybrid that is gastrointestinal safe and has potent anti-inflammatory, analgesic, antipyretic, anti-platelet, and anti-cancer properties. Redox Biol 2015;6:287–96.

[58] Mantri N, Patade V, Penna S, Ford R, Pang E. Abiotic stress responses in plants: present and future. In: Abiotic stress responses in plants. New York: Springer; 2012. p. 1–19.

[59] Corpas FJ, Barroso JB. Nitro-oxidative stress vs oxidative or nitrosative stress in higher plants. New Phytol 2013;199(3):633–5.

[60] Zhu CQ, Zhang JH, Sun LM, Zhu LF, Abliz B, Hu WJ, et al. Hydrogen sulfide alleviates aluminum toxicity via decreasing apoplast and symplast al contents in rice. Front Plant Sci 2018;9:294.

[61] Wang H, Ji F, Zhang Y, Hou J, Liu W, Huang J, et al. Interactions between hydrogen sulphide and nitric oxide regulate two soybean citrate transporters during the alleviation of aluminium toxicity. Plant Cell Environ 2019;42(8):2340–56.

[62] Li L, Wang Y, Shen W. Roles of hydrogen sulfide and nitric oxide in the alleviation of cadmium-induced oxidative damage in alfalfa seedling roots. Biometals 2012;25(3):617–31.

[63] Shi H, Ye T, Chan Z. Nitric oxide-activated hydrogen sulfide is essential for cadmium stress response in bermudagrass (*Cynodon dactylon* (L). Pers.). Plant Physiol Biochem 2014;74:99–107.

[64] Fu MM, Dawood M, Wang NH, Wu F. Exogenous hydrogen sulfide reduces cadmium uptake and alleviates cadmium toxicity in barley. Plant Growth Regul 2019;89:227–37.

[65] Kaya C, Ashraf M, Alyemeni MN, Ahmad P. Responses of nitric oxide and hydrogen sulfide in regulating oxidative defence system in wheat plants grown under cadmium stress. Physiol Plant 2020;168(2):345–60. doi: https://doi.org/10.1111/ppl.13012.

[66] Zhang Q, Cai W, Ji TT, Ye L, Lu YT, Yuan TT. WRKY13 enhances cadmium tolerance by promoting D-CYSTEINE DESULFHYDRASE and hydrogen sulfide production pp. 01504.2019. Plant Physiol 2020:01504. doi: https://doi.org/10.1104/pp.19.01504.

[67] Kharbech O, Houmani H, Chaoui A, Corpas FJ. Alleviation of Cr(VI)-induced oxidative stress in maize (*Zea mays* L.) seedlings by NO and H_2S donors through differential organ-dependent regulation of ROS and NADPH-recycling metabolisms. J Plant Physiol 2017;219:71–80.

[68] Ahmad R, Ali S, Rizwan M, Dawood M, Farid M, Hussain A, et al. Hydrogen sulfide alleviates chromium stress on cauliflower by restricting its uptake and enhancing antioxidative system. Physiol Plant 2020;168(2):289–300. doi: https://doi.org/10.1111/ppl.13001.

[69] Kaya C, Ashraf M. The mechanism of hydrogen sulfide mitigation of iron deficiency-induced chlorosis in strawberry (*Fragaria* × *ananassa*) plants. Protoplasma 2019;256(2):371–82.

[70] Kaya C, Ashraf M, Akram NA. Hydrogen sulfide regulates the levels of key metabolites and antioxidant defense system to counteract oxidative stress in pepper (*Capsicum annuum* L.) plants exposed to high zinc regime. Environ Sci Pollut Res Int 2018;25(13):12612–8.

[71] Singh VP, Singh S, Kumar J, Prasad SM. Hydrogen sulfide alleviates toxic effects of arsenate in pea seedlings through up-regulation of the ascorbate-glutathione cycle: Possible involvement of nitric oxide. J Plant Physiol 2015;181:20–9.

[72] Mostofa MG, Saegusa D, Fujita M, Tran LS. Hydrogen sulfide regulates salt tolerance in rice by maintaining $Na^{(+)}/K^{(+)}$ balance, mineral homeostasis and oxidative metabolism under excessive salt stress. Front Plant Sci 2015;6:1055.

[73] Deng YQ, Bao J, Yuan F, Liang X, Feng ZT, Wang BS. Exogenous hydrogen sulfide alleviates salt stress in wheat seedlings by decreasing Na^+ content. Plant Growth Regul 2016;79:391–9.

[74] Jiang JL, Tian Y, Li L, Yu M, Hou RP, Ren XM. H_2S alleviates salinity stress in cucumber by maintaining the Na^+/K^+ balance and regulating H_2S metabolism and oxidative stress response. Front Plant Sci 2019;10:678.

[75] Liu YL, Shen ZJ, Simon M, Li H, Ma DN, Zhu XY, et al. Comparative proteomic analysis reveals the regulatory effects of H_2S on salt tolerance of mangrove plant *Kandelia obovata*. Int J Mol Sci 2019;21(1):E118.

[76] Li H, Li M, Wei X, Zhang X, Xue R, Zhao Y, et al. Transcriptome analysis of drought-responsive genes regulated by hydrogen sulfide in wheat (*Triticum aestivum* L.) leaves. Mol Genet Genomics 2017;292(5):1091–110.

[77] Antoniou C, Xenofontos R, Chatzimichail G, Christou A, Kashfi K, Fotopoulos V. Exploring the potential of nitric oxide and hydrogen sulfide (NOSH)-releasing synthetic compounds as novel priming agents against drought stress in Medicago sativa plants. Biomolecules 2020;10(1):E120.

[78] Zhao M, Liu Q, Zhang Y, Yang N, Wu G, Li Q, et al. Alleviation of osmotic stress by H_2S is related to regulated PLDα1 and suppressed ROS in *Arabidopsis thaliana*. J Plant Res 2020. doi: https://doi.org/10.1007/s10265-020-01182-3.

[79] Liu Z, Li Y, Cao C, Liang S, Ma Y, Liu X, et al. The role of H_2S in low temperature-induced cucurbitacin C increases in cucumber. Plant Mol Biol 2019;99(6):535–44.

[80] Tang X, An B, Cao D, Xu R, Wang S, Zhang Z, et al. Improving photosynthetic capacity, alleviating photosynthetic inhibition and oxidative stress under low temperature stress with exogenous hydrogen sulfide in blueberry seedlings. Front Plant Sci 2020;11:108.

[81] Christou A, Filippou P, Manganaris GA, Fotopoulos V. Sodium hydrosulfide induces systemic thermotolerance to strawberry plants through transcriptional regulation of heat shock proteins and aquaporin. BMC Plant Biol 2014;14:42.

[82] Zhou ZH, Wang Y, Ye XY, Li ZG. Signaling molecule hydrogen sulfide improves seed germination and seedling growth of maize (*Zea mays* L.) under high temperature by inducing antioxidant system and osmolyte biosynthesis. Front. Plant Sci 2018;9:1288.

[83] Cheng T, Shi J, Dong Y, Ma Y, Peng Y, Hu X, et al. Hydrogen sulfide enhances poplar tolerance to high-temperature stress by increasing S-nitrosoglutathione reductase (GSNOR) activity and reducing reactive oxygen/nitrogen damage. Plant Growth Regul 2018;84:11–23.

[84] Chen Z, Huang Y, Yang W, Chang G, Li P, Wei J, et al. The hydrogen sulfide signal enhances seed germination tolerance to high temperatures by retaining nuclear COP1 for HY5 degradation. Plant Sci 2019;285:34–43.

[85] Fotopoulos V, Christou A, Antoniou C, Manganaris GA. Hydrogen sulphide: a versatile tool for the regulation of growth and defence responses in horticultural crops. J Hortic Sci Biotechnol 2015;90:227–34.

[86] Ziogas V, Molassiotis A, Fotopoulos V, Tanou G. Hydrogen sulfide: a potent tool in postharvest fruit biology and possible mechanism of action. Front Plant Sci 2018;9:1375.

[87] Hu LY, Hu SL, Wu J, Li YH, Zheng JL, Wei ZJ, et al. Hydrogen sulfide prolongs postharvest shelf life of strawberry and plays an antioxidative role in fruits. J Agric Food Chem 2012;60(35):8684–93.

[88] Li SP, Hu KD, Hu LY, Li YH, Jiang AM, Xiao F, et al. Hydrogen sulfide alleviates postharvest senescence of broccoli by modulating antioxidant defense and senescence-related gene expression. J Agric Food Chem 2014;62(5):1119–29.

[89] Ni ZJ, Hu KD, Song CB, Ma RH, Li ZR, Zheng JL, et al. Hydrogen sulfide alleviates postharvest senescence of grape by modulating the antioxidant defenses. Oxid Med Cell Longev 2016;2016:4715651.

[90] Yao GF, Wei ZZ, Li TT, Tang J, Huang ZQ, Yang F, et al. Modulation of enhanced antioxidant activity by hydrogen sulfide antagonization of ethylene in tomato fruit ripening. J Agric Food Chem 2018;66(40):10380–7.

[91] Aghdam MS, Mahmoudi R, Razavi F, Rabiei V, Soleimani A. Hydrogen sulfide treatment confers chilling tolerance in hawthorn fruit during cold storage by triggering endogenous H_2S accumulation, enhancing antioxidant enzymes activity and promoting phenols accumulation. Sci Hortic 2018;238:264–71.

[92] Joshi NC, Yadav D, Ratner K, Kamara I, Aviv-Sharon E, Irihimovitch V, et al. Sodium hydrosulfide priming improves the response of photosynthesis to overnight frost and day high light in avocado (*Persea americana* Mill, cv. 'Hass'). Physiol Plant 2020;168(2):394–405. doi: https://doi.org/10.1111/ppl.13023.

[93] Liu D, Xu S, Hu H, Pan J, Li P, Shen W. Endogenous hydrogen sulfide homeostasis is responsible for the alleviation of senescence of postharvest daylily flower via increasing antioxidant capacity and maintained energy status. J Agric Food Chem 2017;65(4):718–26.

[94] Liu D, Li J, Li Z, Pei Y. Hydrogen sulfide inhibits ethylene-induced petiole abscission in tomato (*Solanum lycopersicum* L.). Hortic Res 2020;7:14.

[95] Mahmud K, Makaju S, Ibrahim R, Missaoui A. Current progress in nitrogen fixing plants and microbiome research. Plants (Basel). 2020;9(1):97.

[96] Puppo A, Pauly N, Boscari A, Mandon K, Brouquisse R. Hydrogen peroxide and nitric oxide: key regulators of the Legume-Rhizobium and mycorrhizal symbioses. Antioxid Redox Signal 2013;18:2202–19.

[97] Hichri I, Boscari A, Castella C, Rovere M, Puppo A, Brouquisse R. Nitric oxide: a multifaceted regulator of the nitrogen-fixing symbiosis. J Exp Bot 2015;66(10):2877–87.

[98] Berger A, Guinand S, Boscari A, Puppo A, Brouquisse R. *Medicago truncatula* phytoglobin 1.1 controls symbiotic nodulation and nitrogen fixation via the regulation of nitric oxide concentration. New Phytol 2020. doi: https://doi.org/10.1111/nph.16462.

[99] Zou H, Zhang NN, Pan Q, Zhang JH, Chen J, Wei GH. Hydrogen sulfide promotes nodulation and nitrogen fixation in soybean-rhizobia symbiotic system. Mol Plant Microbe Interact 2019;32(8):972–85.

[100] Zhang NN, Zou H, Lin XY, Pan Q, Zhang WQ, Zhang JH, et al. Hydrogen sulfide and rhizobia synergistically regulate nitrogen (N) assimilation and remobilization during N deficiency-induced senescence in soybean. Plant, Cell Environ 2020. doi: https://doi.org/10.1111/pce.13736.

[101] Fukudome M, Shimada H, Uchi N, Osuki KI, Ishizaki H, Murakami EI, et al. Reactive sulfur species interact with other signal molecules in root nodule symbiosis in *Lotus japonicus*. Antioxidants (Basel) 2020;9(2):145.

[102] Fuentes-Lara LO, Medrano-Macías J, Pérez-Labrada F, Rivas-Martínez EN, García-Enciso EL, González-Morales S, et al. From elemental sulfur to hydrogen sulfide in agricultural soils and plants. Molecules 2019;24(12):E2282.

[103] Batista PF, Müller C, Merchant A, Fuentes D, de Oliveira Silva Filho R, da Silva FB, Costa AC. Biochemical and physiological impacts of zinc sulphate, potassium phosphite and hydrogen sulphide in mitigating stress conditions in soybean. Physiol Plant 2019. doi: https://doi.org/10.1111/ppl.13034.

[104] Waqas MA, Kaya C, Riaz A, Farooq M, Nawaz I, Wilkes A, et al. Potential mechanisms of abiotic stress tolerance in crop plants induced by thiourea. Front Plant Sci 2019;10:1336.

[105] Bianchini HC, Marques DJ. Tolerance to hydric stress on cultivars of silicon fertilized corn crops: absorption and water use efficiency. Biosci J 2019;35(2):527–39.

[106] Hidangmayum A, Dwivedi P, Katiyar D, Hemantaranjan A. Application of chitosan on plant responses with special reference to abiotic stress. Physiol Mol Biol Plants 2019;25(2):313–26.

[107] Geng B, Huang D, Zhu S. Regulation of Hydrogen sulfide metabolism by nitric oxide inhibitors and the quality of peaches during cold storage. Antioxidants (Basel) 2019;8:401.

[108] Valivand M, Amooaghaie R, Ahadi A. Seed priming with H_2S and Ca^{2+} trigger signal memory that induces cross-adaptation against nickel stress in zucchini seedlings. Plant Physiol Biochem 2019;143:286–98.

[109] Corpas FJ. Hydrogen Sulfide: a new warrior against abiotic stress. Trends Plant Sci 2019;24(11):983–8.

Francisco J. Corpas is Research Professor of the Spanish National Research Council (CSIC) which has more than 28 years of research experience in the metabolism of Reactive Oxygen, Nitrogen and Sulfur Species (ROS, RNS and RSS, respectively) in higher plants under physiology and environmental stress conditions. Special interests are the implications of these reactive species in fruit ripening and the nitro-oxidative metabolism of plant peroxisome. He was the Head of the Department of Biochemistry, Cell and Molecular Biology of Plants (2014–2018) at Research Institute named "Estación Experimental del Zaidín"-CSIC, Granada Spain. He already published more than 203 refereed research papers/review articles in peer reviewed journals (according with Scopus database with *h*-index: 58) and edited seven books.

José Manuel Palma is Research Professor with expertise on antioxidants and free radicals in plant systems. With more than 120 peer-reviewed research papers published, he has also been editor of five books and several special issues of diverse international journals. At present, he is involved in the investigation of the interaction between nitric oxide and antioxidants during fruit ripening. He leads the research group "Antioxidants, Free Radicals and Nitric Oxide in Biotechnology, Food and Agriculture" at Estación Experimental del Zaidín (EEZ), CSIC, Granada, Spain. He was also Deputy Director and Acting Director of the EEZ (CSIC) in the period 2007–2014.