H₂S signaling in plants and applications in agriculture

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HIGHLIGHTS

- Hydrogen sulfide (H₂S) 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 H₂S 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 (H₂S) participates.

INTRODUCTION

The description of the gasotransmitter hydrogen sulfide (H₂S), with its toxic impact on the metabolism of animal and plant cells,
Plant biochemistry of H2S: An overview

The study of H2S 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]. H2S 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 H2S on a specific plant protein using different H2S 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 H2S 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 H2S 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].

Although the precise mechanisms involved remain unknown, H2S has been shown to regulate gene expression [41,42]. Exogenous applications of H2S 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 H2S in plant cells, as well as how and where H2S 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 H2S [35,45,46]. These enzymes include L-cysteine desulphydrase (L-DES), L-cysteine desulphydrase 1 (DES1), previously known as Cys synthase-like (CS-LIKE), and cysteine synthase (CS) in the cytosol; D-cysteine desulphydrase (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 H2S molecule can spread with ease throughout the lipid bilayer of cell membranes [49]. New promising data also show how activities, such as cysteine desulphydrases, 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 H2S

Although further basic research on H2S is required, sufficient experimental data show that the exogenous application of H2S to different plant species at different stages of development can...
Table 2 shows different examples of the beneficial effects of the nitration and oxidative damage to proteins and nucleic acids.

| Enzyme                                      | Function                       | Effect                        | Ref.  |
|---------------------------------------------|--------------------------------|-------------------------------|-------|
| RuBISCO                                    | Photosynthesis                 | Activity up-regulated         | [9]   |
| O-acetylsersine(thiol)lyase (OAS-TL)        | Sulfur metabolism              | Activity up-regulated         | [9]   |
| L-cysteine desulphhydrase (LCD)            | Sulfur metabolism              | Activity up-regulated         | [9]   |
| Ascorbate peroxidase (APX)                 | Antioxidant                    | Activity up-regulated         | [30]  |
| Glyceraldehyde 3-phosphate dehydrogenase   | Energy production in the glycolysis | Activity up-regulated      | [30]  |
| (GAPDH)                                     |                                |                               |       |
| Glutamine synthetase (GS)                  | Metabolism of nitrogen         | Activity down-regulated       | [30]  |
| Actin                                       | Involved in organelle movement, in cell division and expansion | Inhibit 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.         |                               | [12]  |
| Respiratory burst oxidase homolog protein D (RBODH) | Generation of superoxide radical | Activity up-regulated         | [13]  |

Table 3 provides representative examples of the oxidative and nitrosative effects of H₂S on fruit ripening and post-harvest damage to fresh produce.

| Enzyme                                      | Function                       | Effect                        | Ref.  |
|---------------------------------------------|--------------------------------|-------------------------------|-------|
| RuBISCO                                    | Photosynthesis                 | Activity up-regulated         | [9]   |
| O-acetylsersine(thiol)lyase (OAS-TL)        | Sulfur metabolism              | Activity up-regulated         | [9]   |
| L-cysteine desulphhydrase (LCD)            | Sulfur metabolism              | Activity up-regulated         | [9]   |
| Ascorbate peroxidase (APX)                 | Antioxidant                    | Activity up-regulated         | [30]  |
| Glyceraldehyde 3-phosphate dehydrogenase   | Energy production in the glycolysis | Activity up-regulated      | [30]  |
| (GAPDH)                                     |                                |                               |       |
| Glutamine synthetase (GS)                  | Metabolism of nitrogen         | Activity down-regulated       | [30]  |
| Actin                                       | Involved in organelle movement, in cell division and expansion | Inhibit 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.         |                               | [12]  |
| Respiratory burst oxidase homolog protein D (RBODH) | Generation of superoxide radical | Activity up-regulated         | [13]  |

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 reactive 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 H₂S 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 H₂S 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 H₂O₂ levels and lipid peroxidation content to be reduced.

**H₂S in fruit ripening and post–harvest damage to fresh produce**

Information available on endogenous H₂S metabolism in fruits and vegetables is highly limited. Recently, endogenous H₂S content in non-climacteric sweet pepper (Capsicum annum 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 H₂S 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 H₂S 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 H₂S to fruits and vegetables [87–94] which enables their quality to be maintained. Another common effect observed following exogenous treatment with H₂S is an increase in antioxidant systems which prevent ROS overproduction and consequently oxidative damage.

**Implication of H₂S 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], H₂S seems to be also involved in different ways in this process. A recent report indicates that exogenous H₂S 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 H₂S 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$_2$S 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, plasma membrane. SOD, superoxide dismutase.

| Environmental stress | H$_2$S 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$_2$O$_2$ content in roots | [60] |
| Sodium (Na)          | NaHS(50)        | Soybean (Glycine max L.) | Reduce Al accumulation. H$_2$S 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)       | Alfalfa (Medicago sativa L.) | Reduces the accumulation of MDA and H$_2$O$_2$. Increase the content of GSH and the activity of antioxidant enzymes (SOD, CAT and POD) | [62] |
| Sodium (Na)          | NaHS(500)       | Bermudagrass (Cynodon dactylon L.) | Alleviates Cd damages by modulating enzymatic and non-enzymatic antioxidants. | [63] |
| Sodium (Na)          | NaHS(200)       | Barley (Hordeum vulgare L.) | Reduces the accumulation of H$_2$O$_2$ and superoxide ions in roots | [64] |
| Endogenous H$_2$S    | NaHS(200)       | Wheat (Triticum aestivum) | Increases the activities of antioxidant enzymes. Inhibits Cd uptake and reduce proline content | [65] |
| Chromium(Cr)         | NaHS(500)       | Maize (Zea mays L.) | Alleviates chromium toxicity and enhances antioxidant activities (CAT, SOD, APX) | [66] |
| Sodium (Na)          | NaHS(200)       | Cauliflower (Brassica oleracea L.) | Decreases Cr content, H$_2$O$_2$ and MDA concentrations. Increases activity of antioxidant enzymes | [67] |
| Copper (Cu)          | NaHS(1,400)     | Wheat (Triticum aestivum L.) | Lowers levels of MDA and H$_2$O$_2$ in germinating seeds. Increases SOD and CAT activities, and decreases lipoygenase | [68] |
| Iron deficiency      | NaHS(200)       | Strawberry (Fragaria x ananassa) | Reduces electrolyte leakage, and content of H$_2$O$_2$ and MDA. Upregulate activities of antioxidant enzymes. Improved Fe uptake | [69] |
| Zinc (Zn)            | NaHS(200)       | Pepper (Capsicum annum 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)       | Mango tree (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$_2$O$_2$ contents in both leaves and roots. Increases of the transcription levels of genes encoding ABA receptors. Induction of genes that code for antioxidant enzymes | [76] |
|                      | NaHS(400)       | Wheat (Triticum aestivum L.) | Alleviates Cd damages by modulating enzymatic and non-enzymatic antioxidants. | [77] |
|                      | NaHS(20)        | Alalfa (Medicago sativa L.) | Lowers MDA. Induce Cu/ZnSOD, FeSOD genes | [78] |
| Osmotic stress       | NaHS(100)       | Arabidopsis (Arabidopsis thaliana) | Increase phospholipase D2X and the antioxidant enzyme system. Reduce ROS and MDA content and reduce electrolyte leakage | [79] |
| Low temperature      | NaHS(50)        | Cucumber (Cucumis sativus L.) | Increases GSH and cuscubitan C content | [80] |
|                      | NaHS(500)       | Lowbush blueberry (Vaccinium angustifolium) | Alleviate the degradation of chlorophyll and carotenoids and reduce the photoinhibition of PSII and PSI. | [81] |
| High temperature     | NaHS(100)       | Strawberry (Fragaria x ananassa cv. 'Camaroosa') | Induction of gene expression coding for antioxidant enzymes (cAPX, CAT, MnSOD, GR), heat shock proteins (HSP70, HSP80, HSP90) and aquaporins (PIP) | [82] |
|                      | NaHS(500)       | Maize (Zea mays L.) | Improves seed germination and increases antioxidant enzymes. Accumulation of proline | [83] |
|                      | NaHS(50) or     | Poplar (Populus trichocarpa) | Increases GSNOR activity and reduce HT-induced damage to the photosynthetic system | [84] |
|                      | CGY4137(10)     | Arabidopsis | Enhances seed germination rate under HT. Increases gene expression of ABIS (ABA-INSENSITIVE 5). | [85] |

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symbiosis indicate that this interaction is regulated by the cross-talk among H$_2$S with other signaling molecules including NO and ROS [101].

Conclusions and future perspectives

H$_2$S, 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$_2$S, 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$_2$S undoubtedly has a beneficial effect on different plant species, especially those of considerable agronomic interest under adverse environmental conditions. Therefore, the use of H$_2$S 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$_2$S 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.
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.

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Table 3

| Fruit/vegetable | H₂S 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. labruscica L. cv. Kyoho) | 1 mM NaHS | Alleviates postharvest senescence of grape and maintain high fruit quality | [89] |
| Banana (Musa acuminate, 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 H₂S accumulation, increase antioxidant enzyme activities and promote polyphenol accumulation | [91] |
| Avocado (Persea americana Mill, cv. ’Hass’) | 200 μMNaHS | Protects against frost and day high light | [92] |
| Kiwifruit (Actinidia chinensis) | 20 μM H₂S | Delays ripening and senescence. Inhibits ethylene production. Increases antioxidant activities. Regulates the cell wall degrading enzyme gene | [93] |
| Daylily (Hemerocallis fulva) | 4 mM NaH₅S | Delays senescence of postharvest daylily flowers. Increases antioxidant capacity to maintain the redox balance | [94] |
| Tomato (Solanum lycopersicum L.) | 1 M NaH₅S | Inhibits ethylene-induced petiole abscission | [94] |
Zhou ZH, Wang Y, Ye XY, Li ZG. Signaling molecule hydrogen sulfide improves... 

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