

H2S-Mediated Mechanism

Subjects: **Plant Sciences**

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Hydrogen sulfide (H2S) is predominantly considered as a gaseous transmitter or signaling molecule in plants.

abiotic stress

hydrogen sulfide

1. Introduction

Hydrogen sulfide has been known as a crucial player during various plant cellular and physiological processes and has been gaining unprecedented attention from researchers since decades. They regulate growth and plethora of plant developmental processes such as germination, senescence, defense, and maturation in plants. Owing to its gaseous state, they are effectively diffused towards different parts of the cell to counterbalance the antioxidant pools as well as providing sulfur to cells. H2S participates actively during abiotic stresses and enhances plant tolerance towards adverse conditions by regulation of the antioxidative defense system, oxidative stress signaling, metal transport, Na^+/K^+ homeostasis, etc. They also maintain H2S-Cys-cycle during abiotic stressed conditions followed by post-translational modifications of cysteine residues. Besides their role during abiotic stresses, crosstalk of H2S with other biomolecules such as NO and phytohormones (abscisic acid, salicylic acid, melatonin, ethylene, etc.) have also been explored in plant signaling.

2. H₂S-Mediated Mechanism of Action in Plants

It has been reported that hydrogen sulfide is generated for performing various important physiological functions, usually by post-translational oxidation of cysteine moiety to per sulfide form ^[1]. The persulfidation mechanism of various proteins have been well documented in case of mammals ^{[2][3]}. Hydrogen sulfide mediated persulfidation of proteins in case of plants for the proper functioning of biological processes has been discussed as follows.

2.1. Role of H₂S in Post-Translational Modification of Cysteine Residues and Protein Sulfidation

Since, H₂S is a type of gasotransmitter in plants as well as in animal cells, it is known to be equally important as other signaling molecules such as carbon monoxide (CO), nitric oxide (NO), and hydrogen peroxide (H₂O₂), etc. ^[4] ^{[5][6]}. Moreover, H₂S has been reported to have a significant role in plant growth and also in plant protection against various types of stresses such as drought, heat, heavy metal toxicity, etc. Despite of all this, the main function of H₂S is its potential of acting as a signaling molecule ^{[7][8]}. Its role as a signaling molecule can be explained through a post-translational modification of protein, which is frequently known as 'persulfidation', which is characterized by

upgradation of thiol group of cysteine residues (-SH group) of protein into persulfide (-SSH) group. Previously, this modification was termed as 'S-sulphydratation', but in actual practice, there is no hydration reaction that occurs to complete the process, so the process was renamed as persulfidation. Moreover, it has also been documented that modified cysteine has greater reactivity when compared to the unmodified thiol form [3].

2.1.1. Protein Persulfidation

As discussed earlier, H₂S perform its function by promoting the persulfidation of active cysteine moiety of protein into persulfide form via covalent conversion of thiol group into persulfide group [9][10]. However, the studies suggests that there is no direct reactivity between the thiol group of protein and H₂S group. The reason behind this non-reactivity is due to the oxidation of both hydrogen and sulfur atoms in the reaction, the electrons thus produced end up as protons that are not able to form hydrogen gas [1]. Despite this, when the thiol group of protein reacts with hydrogen peroxide, the oxidized product formed is Sulfenic acid (R-SOH), which further reacts with H₂S to form persulfidated (R-SSH) product. Furthermore, the resultant component thus formed reacts with reactive oxygen species (ROS) and generate the product, perthiosulfenic acid (R-SSO_nH), which has low stability. Further, it has been documented by Filipovic [1] that if the excess number of oxidants are present, R-SSO_nH may get further converted to two products via oxidation namely, perthiosulfinic (R-SSO₂H) and perthiosulfonic acid (R-SSO₃H). It has been reported that within the cell the level of persulfidation is regulated by thioredoxin, i.e., thioredoxin is involved in catalyzing the reverse reaction of persulfidation (Figure 1) [11][12]. This reversion reaction of protein persulfidation evades the chances of irreversible oxidative damage that normally occurs at the thiol group of the protein [13][12][10].

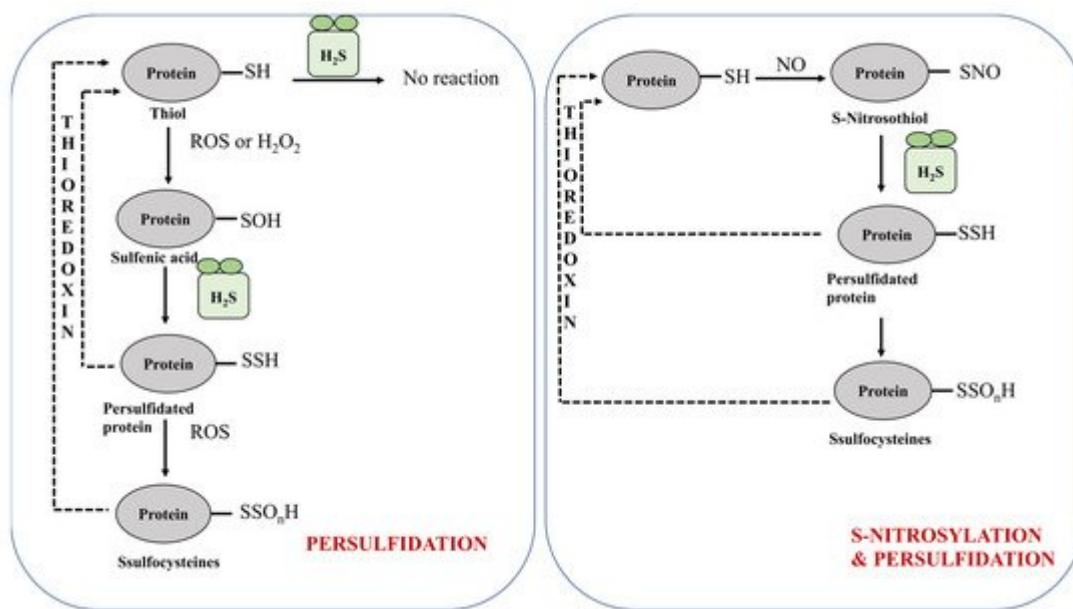


Figure 1. A brief model explaining persulfidation and S-nitrosylation in plants. The thiol group of protein undergo oxidation in presence of ROS and form sulfenic acid, which then undergo persulfidation in the presence of hydrogen sulfide to form persulfidated protein. If the persulfidated protein is exposed to ROS, S-sulfocysteines are formed. Both S-sulfocysteines and persulfidated proteins can revert back to thiol form by thioredoxin. In S-

nitrosylation, nitric oxide (NO) combines with thiol group of protein to form S-nitrosothiol, which can further react with hydrogen sulfide to form persulfidated protein, which can then revert back to thiol form in presence of thioredoxin.

In addition to this, other signaling molecules such as NO are also capable of manipulating proteins by a process called S-nitrosylation (R-SNO). This reaction involves the covalent attachment of thiol group of cysteine moiety in protein to the NO [14]. The products formed as a result of this reaction are known as S-nitrosothiols [15][16]. These S-nitrosothiols are capable of reacting with H₂S, thus ultimately resulting in protein persulfidation (R-SSG).

Furthermore, it has been well documented that the modified or persulfidated proteins have high reactivity in comparison to normal unmodified form. The valid reason for this reactivity is the enhanced nucleophilicity of -SSH group that can undergo easy chemical reaction with the electrophiles [17]. The main electrophilic agents include S-4bromobenzyl methanethiosulfonate (BMMTS), methanethiosulfonate (MMTS), and methylsulfonylbenzothiazole (MSBT) (Figure 1).

2.1.2. Protein Persulfidation in Plants

The first report of persulfidation in plants was reported in *Arabidopsis* with about 106 protein that are modified at cysteine residues by Aroca et al. [8]. Furthermore, 2015 persulfidated proteins were reported from wild type and des1 mutant *Arabidopsis* plants with the help of an assay in which an electrophile MSBT was used as blocking agent. All the reported proteins were found mainly involved in amino acid metabolism, protein biosynthesis, glycolysis, and in response to various stress conditions [18].

Similarly, as per the reports of Li et al. [19], H₂S has a role in the regulation of actin and thus ultimately has effect on root hair growth. Basically, the genome of *Arabidopsis* consists of 8 ACTIN genes, which are further categorized into two major groups on the basis of their functioning in reproductive and vegetative organs [20]. However, whenever there is an overaccumulation of H₂S, persulfidation at cys 287 residue of one of the vegetative gene, i.e., ACTIN2 occurs. This persulfidation leads to depolymerization of actin cytoskeleton and thus ultimately resulting in root hair growth inhibition [19]. These findings were further proved by introduction of *actin* 2-1 mutant with Cys-287 mutated ACTIN2; the outcome of the study is the partial suppression of root hair inhibition, which is H₂S dependent [19]. Moreover, according to the literature, H₂S suppresses the activity of aminocyclopropane carboxylate oxidase (ACC oxidase) enzyme (rate limiting enzyme in ethylene biosynthesis), thus ultimately inhibiting the elongation of root hairs [21].

Moreover, H₂S has also reported to have role in the persulfidation of various enzymes that are involved in signaling of abscisic acid (ABA), which make H₂S, a contributor in stomatal closure [8][22]. This whole cascade of interactions has been studied in *Arabidopsis*, a model plant, and it has been reported that when the level of ABA increases in the cell, it binds to the receptor PYR/PYL/RCAR (PYRABACTIN RESISTANCE/PYR-LIKE/REGULATORY COMPONENT OF ABA RECEPTOR) and suppresses the activity of PP2C (clade A protein phosphatases) [22]. Further, the *SnRK2.6* (SNF1-RELATED PROTEIN KINASE2.6) or *OST1* (OPEN STOMATA 1) is stimulated to initiate multiple downstream signaling pathways. This is the stage from where H₂S regulates the ABA signaling by

persulfidation of Cys-131 and Cys-137 residues of *SnRK2.6*, present in guard cell [23]. The persulfidation of cysteine residues enhances the kinase potential of *SnRK2.6* and also promotes its interaction with *ABF2* (ABA RESPONSE ELEMENT-BINDING FACTOR 2), thus resulting in the phosphorylated *ABF2*, which further stimulates the downstream genes that control the closure of stomata [23]. In addition to this, H₂S is also found involved in persulfidation of Cys-44 and Cys-205 of *DES1* in the presence of ABA, resulting in the enhanced level of H₂S in the guard cell. This increment further promotes overproduction of ROS through persulfidation at Cys-825 and Cys-890 residues of *RBOHD* (NADPH oxidase RESPIRATORY BURST OXIDASE HOMOLOG D). The excessive production of ROS resulted in suppressing the activity of ABA signaling. Conclusively, all these potencies of H₂S have a role in the regulation of ABA signaling in plant tissue (Figure 1).

3. H₂S-Signaling during Abiotic Stresses

Under stressed conditions, various signaling molecules such as ABA, Ca²⁺, various phytohormones, H₂O₂, etc., come into action. Likewise, H₂S levels are also triggered in plants in response to various stressors. This H₂S- is triggered in response to many stresses and forms a signaling cascade. Following sections describe the role of H₂S-signaling pathway under diverse stress conditions.

3.1. H₂S-Signaling during Heavy Metal Stresses

It has been observed that there is an accumulation of H₂S in plants subjected to heavy metal stresses due to their extreme toxic nature. H₂S enhances the number of mitochondria, endoplasmic reticulum, and golgi bodies in plants [24]. Moreover, it also stimulates metal ion fixation, co-related to cell wall functioning, transporter regulation, and closed association of chelators with specific signals. The cell wall acts as a barrier to external metals, and H₂S in turn induces pectin and pectin methylesterases for strengthening the cell wall [25]. A study affirmed by Zhu et al. [26], revealed that Al-stressed rice plants showed stability in the cell wall towards metals by H₂S-mediated reduction of negative charges in cell wall along with plummeting pectin methylesterases, pectins and hemicelluloses within roots and shoots, respectively. Plants also possess specific mechanism to mitigate metal toxicity via transporting metals into vacuoles through H⁺-ATPases and citrate transporters localized onto vacuolar membrane. This is further amplified by H₂S with upregulation of H⁺-ATPases expression in tonoplast followed by reducing cytoplasmic metal accumulation [27]. Alongside, induced expression of *MATE13*, *MATE47*, and *FRPL4* genes in soybean and rice by H₂S not only alleviates Cd and Al toxicity but also enhanced citrate exudation [25]. Another study reported that rice exposed to Al-stress showed upregulation in *NRT1* and *ALS1* genes after H₂S treatment along with controlling Al level in cytoplasm by transporting it to vacuoles [27].

Nevertheless, one of the most efficacious mechanism possessed by plants to counteract metal toxicity is to momentarily pause the metals through PCs and MTs, having a close connection to sulfur metabolism (H₂S-cysteine-core). Cysteine is crucial for GSH-biosynthesis through different enzymes, therefore, H₂S-induces the expression profile of genes encoding MTs and PCs through transcriptional regulation [28]. A certain co-related factor of H₂S that works during heavy metal stresses is NO, which is considered a principal partner of H₂S [29]. Sodium nitroprusside show similar action to NaHS in mitigating metal toxicity, depicting the closed relation among NO and

H_2S , respectively [30]. In addition, H_2S also works along with Ca^{2+} ions for metal stress amelioration. This is most likely due to blocking of Ca -channels by metal ions followed by their detoxification through Ca^{2+} -pathway [31]. Strikingly, NaHS modulated CDPK-transcripts in zucchini exposed to Ni-stress [28]. Apart from this, H_2S -mediated metal stress alleviation is also accompanied by phytohormones such as salicylic acid, jasmonic acid, gaseous molecules, and different mineral elements [32]. All these components trigger H_2S -pathway or H_2S -producing enzymes or endogenous H_2S [32]. The regulatory action of transcripts in promoter sites of vital genes encoding H_2S -biosynthesis have been observed. Certain transcripts such as *WRKY18*, *WRKY13*, *WRKY60*, etc., are enhanced, which further induces H_2S -levels under metal stressed conditions [32]. Likewise, ZIP-transcript *TGA* also increase the production of H_2S during metal toxicity [33].

3.2. H_2S -Signaling during Salinity Stress

Salinity has caused many adversities towards agricultural crops by reducing plant growth and productivities. Climatic disturbances have altered the agricultural practices, specifically at coastal sites. H_2S has been known to play a pivotal role in ongoing cellular responses in plants against salinity, therefore considered a powerful agricultural intervention. It has been observed that exogenously applied H_2S enhanced salinity resistance through regulating Na^+/K^+ -homeostasis along with endogenous H_2S levels with boosted antioxidant activities in cucumber [34]. Another study reported by Kaya et al. [35], showed that melatonin mediated salinity tolerance in pepper through triggering H_2S and antioxidant levels. In addition, NaHS induced salinity in cabbage via enhancing antioxidants and enzymes involved in ascorbate/glutathione cycle [36]. Further, it has also been observed that NaHS stimulated salt tolerance and osmotic stress in strawberry through antioxidants and ascorbate/glutathione redox states, thereby minimizing oxidative/nitrosative stress [37]. Interestingly, it has been revealed that H_2S play key role in regulating antioxidants and various transcription factors namely, dehydration responsive element binding factor, ascorbate/glutathione biosynthesis along with salt overly sensitive genes [37]. H_2S on combination with NO also mitigate salt toxicity as H_2S acts downstream of NO in the signaling pathway. Henceforth, accrual of H_2S has a direct impact on the stress-mediated signaling pathway under salt conditions with the motive to alleviate the toxicity.

3.3. H_2S -Signaling during Drought/Osmotic Stress

As climatic conditions are altering on global scale and precipitation is therefore altering due to such weather conditions. Few areas experience high rain, while others perceive lower or very minimal rainfall depending on where there is disaster in the form of either drought or flooding. Overall agriculture faces a huge impact and treatments to such conditions are required. Strategies such as NO -based molecules, H_2S compounds, etc., act as impactful adjuncts. Drought stress has seriously impacted horticultural crops and impediment towards achieving productivity targets [38]. Additionally, limited rainfall and higher evaporation due to enhanced temperature also induces the impact of drought. Therefore, plants possess adaptive measures to survive during such unfavorable situations through regulating stomatal activities by reducing the transpiration rate so as to retain the water within for regulating physiological activities. H_2S also acts up/down stream in NO -signaling pathways, based on activities such as stomatal movement, closure, etc., during stressed conditions [39]. The role of H_2S in stomatal activities has

been observed and studies are further conducted to understand its exact mechanism. To elucidate, H₂S causes stomatal opening and closing under varied conditions in response to adverse conditions. Another study reported that short H₂S-exposure in plants led to induce stomatal closure whereas long exposure led to stimulate stomatal activities and H₂S was also mediated by 8-mercaptop-cGMP, respectively [40]. cGMP also acts as a downstream mediator of NO in plants and therefore both of them work in corroboration with one another. H₂S treatment in plants regulates the relative water content of plants subjected to drought, however, the H₂S acts as a donor during such conditions followed by inducing the metabolic profiles of plants in the form of polyamines, glycine betaine, osmolytes, proline and H₂S-biosynthesis [41]. Additionally, genes encoding soluble sugars, aquaporins, polyamines, choline monooxygenases, and betaine aldehyde dehydrogenases, etc., are also upregulated after H₂S application in drought stressed plants [41]. In addition to this, plants with H₂S treatment also reduced oxidative stress markers such as MDA and H₂O₂ [41]. NaHS treatment in Bermuda grass also stimulated tolerance against salt, osmotic, and chilling stress and this is mainly due to increased activities of antioxidants and osmolytes [32]. Further, proteomic approaches were used in H₂S-mediated drought resistance. They reported the imperative role of proteins namely, S-nitrosated proteins, photosynthetic proteins, etc., induced by H₂S. Henceforth, the plant-water relations, plant movements, stomatal opening/closing, etc., act as suitable target sites for H₂S for modulating different physiological activities in plants. H₂S-formulations act as the most suitable molecules for stress resistance in plants.

3.4. H₂S-Signaling during Temperature Stress

Global warming has been observed to be the most adverse effect of climate change, basically due to the enhanced average temperature of the Earth. However, there are various regions where temperature extremity is observed both in the form of warming as well as freezing, therefore affecting the normal agricultural patterns. Certainly, there are H₂S based compounds that participate in counteracting temperature extremities. Plants being sessile have to tolerate the varying temperatures of environment. H₂S has been observed to cope up in mediating tolerance towards high/low temperature conditions. To illustrate, Tang, et al. [42], reported that exogenous H₂S and hypotaurine, H₂S-scavenger mediated cooling stress tolerance in blueberry plants. This improvement is mainly due to enhanced tolerance after NaHS treatment owing to regulated activities of leaf gaseous exchange parameters, declined photoinhibition of PSI/PSII and higher proline levels. Concomitantly, the oxidative stress markers such as H₂O₂, MDA, etc., were also declined after H₂S treatment. Meanwhile, hypotaurine enhanced the negative effects of cooling stress. Another study reported exogenously applied NaHS boosted chilling tolerance in cucumber and the most probable reason behind this was crosstalk among H₂S and auxins during stressed conditions along with higher flavin monooxygenases (FMO) and FMO-like proteins. This in turn inclined auxins that further reduced chilling stress-generated electrolyte leakage and ROS-generation with higher expression of photosynthetic enzymes. They concluded that auxins act downstream in H₂S-mediated chilling stress tolerance in plants [43]. Further, H₂S-mediated chilling stress tolerance also revealed stimulation in cucurbitacin C, a secondary metabolite that enhanced tolerance as well as bitter taste in cucumber [44]. Contrastingly, H₂S also determined an ameliorating agent in high temperature stress that could prove lethal towards agricultural crops. A study carried out in strawberry raised under induced temperatures showed declined oxidative damage and higher heat show defense upon H₂S

application. H₂S-mediated heat tolerance was found by antioxidants, aquaporins and heat shock proteins along with upregulation of genes encoding these components along with ascorbate/glutathione pools [37].

3.5. H₂S-Signaling during Nutritional Stress

Agricultural crops are susceptible to nutritional stresses, nutrient deprivation or excessive of nutrients, therefore, plants have to tolerate such conditions when there are either excessive nutrients or there is shortage. Climatic disturbances often alter CO₂ but may also affect the nutritional availability by interfering micro-biotic associations among plants. Exogenously applied NaHS lowers oxidative stresses in plants raised under nitrate stress conditions [44]. The ROS was observed to decline with aggravated activities of antioxidants via mitogen-activated protein kinases and NO-signaling. Sidewise, the expression levels of *CsNMAPK* transcripts were also found to upregulate in cucumber after H₂S treatment [44]. Moreover, H₂S application also improved the seed germination rate of tomato during nitrate stress through improvement in the levels of antioxidants [45]. Furthermore, Kaya and Ashraf [46] depicted that Fe-deprivation caused chlorosis, which was ameliorated by NaHS. Subsequently, oxidative stress markers were also reduced with promoted plant growth and metabolism. Hence, the inter-relationship among plants, microbiotic environment, and nutrient availability mediated by H₂S is an interesting art of work that should be further explored.

References

1. Filipovic, M.R. Persulfidation (S-sulfhydration) and H₂S. *Handb. Exp. Pharmacol.* 2015, 230, 29–59.
2. Krishnan, N.; Fu, C.; Pappin, D.J.; Tonks, N.K. H₂S—Induced sulfhydration of the phosphatase PTP1B and its role in the endoplasmic reticulum stress response. *Sci. Sign.* 2011, 4, ra86.
3. Paul, B.D.; Snyder, S.H. H₂S: A novel gasotransmitter that signals by sulfhydration. *Trends Biochem. Sci.* 2015, 40, 687–700.
4. Vandiver, M.; Snyder, S. Hydrogen sulfide: A gasotransmitter of clinical relevance. *J. Mol. Med.* 2012, 90, 255–263.
5. Garcia-Mata, C.; Lamattina, L. Hydrogen sulphide, a novel gasotransmitter involved in guard cell signalling. *New Phytol.* 2010, 188, 977–984.
6. Kimura, H. The physiological role of hydrogen sulfide and beyond. *Nitric Oxide* 2014, 41, 4–10.
7. Mustafa, A.K.; Gadalla, M.M.; Sen, N.; Kim, S.; Mu, W.; Gazi, S.K.; Barrow, R.K.; Yang, G.; Wang, R.; Synder, S.H. H₂S signals through protein S-sulfhydration. *Sci. Signal.* 2009, 2, ra72.
8. Aroca, A.; Serna, A.; Gotor, C.; Romero, L.C. S-sulfhydration: A cysteine posttranslational modification in plant systems. *Plant Physiol.* 2015, 168, 334–342.

9. Aroca, A.; Gotor, C.; Romero, L.C. Hydrogen sulfide signaling in plants: Emerging roles of protein persulfidation. *Front. Plant Sci.* 2018, 9, 1369.
10. Shen, J.; Zhang, J.; Zhou, M.; Zhou, H.; Cui, B.; Gotor, C.; Romero, L.C.; Fu, L.; Yang, J.; Foyer, C.H.; et al. Persulfidation-based modification of cysteine desulfhydrase and the NADPH Oxidase RBOHD controls guard cell abscisic acid signaling. *Plant Cell* 2020, 32, 1000–1017.
11. Ren, X.; Zou, L.; Zhang, X.; Branco, V.; Wang, J.; Carvalho, C.; Holmgren, A.; Lu, J. Redox signaling mediated by thioredoxin and glutathione systems in the central nervous system. *Antioxidants Redox Signal.* 2017, 27, 989–1010.
12. Wedmann, R.; Onderka, C.; Wei, S.; Szijártó, I.A.; Milkovic, J.L.; Mitrovic, A.; Lange, M.; Savitsky, S.; Yadav, P.K.; Torregrossa, R.; et al. Improved tag-switch method reveals that thioredoxin acts as depersulfidase and controls the intracellular levels of protein persulfidation. *Chem. Sci.* 2016, 7, 3414–3426.
13. Filipovic, M.R.; Zivanovic, J.; Alvarez, B.; Banerjee, R. Chemical biology of H2S signaling through persulfidation. *Chem. Rev.* 2018, 118, 1253–1337.
14. Feng, J.; Chen, L.; Zuo, J. Protein S-nitrosylation in plants: Current progresses and challenges. *J. Integr. Plant Biol.* 2019, 61, 1206–1223.
15. Stamler, J.S.; Simon, D.I.; Jaraki, O.; Osborne, J.A.; Francis, S.; Mullins, M.; Singel, D.; Loscalzo, J. S-nitrosylation of tissue-type plasminogen activator confers vasodilatory and antiplatelet properties on the enzyme. *Proc. Natl. Acad. Sci. USA* 1992, 89, 8087–8091.
16. Hess, D.T.; Matsumoto, A.; Kim, S.O.; Marshall, H.E.; Stamler, J.S. Protein S-nitrosylation: Purview and parameters. *Nat. Rev. Mol. Cell Biol.* 2005, 6, 150–166.
17. Zhao, D.D.; Zhang, J.; Zhou, M.J.; Zhou, H.; Gotor, C.; Romero, L.C.; Shen, J.; Yuan, X.X.; Xie, Y.J. Current approaches for detection of hydrogen sulfide and persulfidation in biological systems. *Plant Physiol. Biochem.* 2020, 155, 367–373.
18. Aroca, A.; Benito, J.M.; Gotor, C.; Romero, L.C. Persulfidation proteome reveals the regulation of protein function by hydrogen sulfide in diverse biological processes in *Arabidopsis*. *J. Exp. Bot.* 2017, 68, 4915–4927.
19. Li, J.; Chen, S.; Wang, X.; Shi, C.; Liu, H.; Yang, J.; Shi, W.; Guo, J.; Jia, H. Hydrogen sulfide disturbs actin polymerization via S-sulfhydration resulting in stunted root hair growth. *Plant Physiol.* 2018, 178, 936–949.
20. McDowell, J.M.; Huang, S.; McKinney, E.C.; An, Y.; Meagher, R.B. Structure and evolution of the actin gene family in *Arabidopsis thaliana*. *Genetics* 1996, 142, 587–602.
21. Jia, H.; Chen, S.; Liu, D.; Liesche, J.; Shi, C.; Wang, J.; Ren, M.; Wang, X.; Yang, J.; Shi, W.; 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.
22. Gong, Z.; Xiong, L.; Shi, H.; Yang, S.; Herrera-Estrella, L.R.; Xu, G.; Chao, D.Y.; Li, J.; Wang, P.Y.; Qin, F.; et al. Plant abiotic stress response and nutrient use efficiency. *Sci. China Life Sci.* 2020, 63, 635–674.
23. Chen, L.; Wu, R.; Feng, J.; Feng, T.; Wang, C.; Hu, J.; Zhan, N.; Li, Y.; Ma, X.; Ren, B.; et al. Transnitrosylation mediated by the non-canonical catalase ROG1 regulates nitric oxide signaling in plants. *Dev. Cell* 2020, 53, 444–457.
24. Ali, B.; Gill, R.A.; Yang, S.; Gill, M.B.; Ali, S.; Rafiq, M.T.; Zhou, W. Hydrogen sulfide alleviates cadmium-induced morpho-physiological and ultrastructural changes in *Brassica napus*. *Ecotoxicol. Environ. Saf.* 2014, 110, 197–207.
25. Yu, Y.; Zhou, X.; Zhu, Z.; Zhou, K. Sodium hydrosulfide mitigates cadmium toxicity by promoting cadmium retention and inhibiting its translocation from roots to shoots in *Brassica napus*. *J. Agric. Food Chem.* 2018, 67, 433–440.
26. Zhu, C.Q.; Zhang, J.H.; Sun, L.M.; Zhu, L.F.; Abliz, B.; Hu, W.J.; Zhong, C.; Bai, Z.G.; Sajid, H.; Cao, X.C.; et al. Hydrogen sulfide alleviates aluminum toxicity via decreasing apoplast and symplast Al contents in rice. *Front. Plant Sci.* 2018, 9, 294.
27. Wang, H.; Ji, F.; Zhang, Y.; Hou, J.; Liu, W.; Huang, J.; Liang, W. Interactions between hydrogen sulphide and nitric oxide regulate two soybean citrate transporters during the alleviation of aluminium toxicity. *Plant Cell Environ.* 2019, 42, 2340–2356.
28. Valivand, M.; Amooaghaie, R.; Ahadi, A. Interplay between hydrogen sulfide and calcium/calmodulin enhances systemic acquired acclimation and antioxidative defense against nickel toxicity in zucchini. *Environ. Exp. Bot.* 2019, 158, 40–50.
29. Shi, H.; Ye, T.; Chan, Z. Nitric oxide-activated hydrogen sulfide is essential for cadmium stress response in bermudagrass (*Cynodondactylon* (L). Pers.). *Plant Physiol. Biochem.* 2014, 74, 99–107.
30. Shivaraj, S.M.; Vats, S.; Bhat, J.A.; Dhakte, P.; Goyal, V.; Khatri, P.; Kumawat, S.; Singh, A.; Prasad, M.; Sonah, H.; et al. Nitric oxide and hydrogen sulfide crosstalk during heavy metal stress in plants. *Physiol. Plant.* 2020, 168, 437–455.
31. Fang, H.; Liu, Z.; Long, Y.; Liang, Y.; Jin, Z.; Zhang, L.; Liu, D.; Li, H.; Zhai, J.; Pei, Y. The Ca²⁺/calmodulin2-binding transcription factor TGA3 elevates LCD expression and H2S production to bolster Cr⁶⁺ tolerance in *Arabidopsis*. *Plant J.* 2017, 91, 1038–1050.
32. Kaya, C.; Ashraf, M.; Alyemeni, M.N.; 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, 345–360.

33. Liu, Z.; Fang, H.; Pei, Y.; Jin, Z.; Zhang, L.; Liu, D. WRKY transcription factors down-regulate the expression of H₂S-generating genes, LCD and DES in *Arabidopsis thaliana*. *Sci. Bull.* 2015, 60, 995–1001.
34. Jiang, J.L.; Tian, Y.; Li, L.; Yu, M.; Hou, R.P.; Ren, X.M. H₂S alleviates salinity stress in cucumber by maintaining the Na⁺/K⁺ balance and regulating H₂S metabolism and oxidative stress response. *Front. Plant Sci.* 2019, 10, 678.
35. Kaya, C.; Higgs, D.; Ashraf, M.; Alyemeni, M.N.; Ahmad, P. Integrative roles of nitric oxide and hydrogen sulfide in melatonin-induced tolerance of pepper (*Capsicum annuum* L.) plants to iron deficiency and salt stress alone or in combination. *Physiol. Plant.* 2020, 168, 256–277.
36. Zulfiqar, F.; Hancock, J.T. Hydrogen sulfide in horticulture: Emerging roles in the era of climate change. *Plant Physiol. Biochem.* 2020, 155, 667–675.
37. Christou, A.; Manganaris, G.A.; Papadopoulos, I.; Fotopoulos, V. Hydrogen sulfide induces systemic tolerance to salinity and non-ionic osmotic stress in strawberry plants through modification of reactive species biosynthesis and transcriptional regulation of multiple defence pathways. *J. Exp. Bot.* 2013, 64, 1953–1966.
38. Kopta, T.; Sekara, A.; Pokluda, R.; Ferby, V.; Caruso, G. Screening of chilli pepper genotypes as a source of capsaicinoids and antioxidants under conditions of simulated drought stress. *Plants* 2020, 9, 364.
39. Corpas, F.J. Hydrogen sulfide: A new warrior against abiotic stress. *Trends Plant Sci.* 2019, 11, 983–988.
40. Honda, K.; Yamada, N.; Yoshida, R.; Ihara, H.; Sawa, T.; Akaike, T.; Iwai, S. 8-Mercapto-cyclic GMP mediates hydrogen sulfide-induced stomatal closure in *Arabidopsis*. *Plant Cell Physiol.* 2015, 56, 1481–1489.
41. Chen, J.; Shang, Y.T.; Wang, W.H.; Chen, X.Y.; He, E.M.; Zheng, H.L.; Shangguan, Z. Hydrogen sulfide-mediated polyamines and sugar changes are involved in hydrogen sulfide-induced drought tolerance in *Spinacia oleracea* seedlings. *Front. Plant Sci.* 2016, 7, 1173.
42. Tang, X.; An, B.; Cao, D.; Xu, R.; Wang, S.; Zhang, Z.; Liu, X.; Sun, X. 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.
43. Zhang, W.; Cao, J.; Fan, X.; Jiang, W. Applications of nitric oxide and melatonin in improving postharvest fruit quality and the separate and crosstalk biochemical mechanisms. *Trends Food Sci. Technol.* 2020, 99, 531–541.
44. Liu, Z.; Li, Y.; Cao, C.; Liang, S.; Ma, Y.; Liu, X.; Pei, Y. The role of H₂S in low temperature-induced cucurbitacin C increases in cucumber. *Plant Mol. Biol.* 2019, 99, 535–544.

45. Li, S.; Yan, J.P.; Yang, E.; Bai, X.G.; Long, J.; Li, K.Z.; Xu, H.N. Effects of exogenous H₂S on the germination of tomato seeds under nitrate stress. *J. Hortic. Sci. Biotechnol.* 2015, 90, 39–46.
46. Kaya, C.; Ashraf, M. The mechanism of hydrogen sulfide mitigation of iron deficiency-induced chlorosis in strawberry (*Fragaria × ananassa*) plants. *Protoplasma* 2019, 256, 371–382.

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